PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

A Study of a Non-Marine Lamellibranch Succession in the Anthraconaia lenisulcata Zone of the Yorkshire Coal Measures

R. M. C. Eagar

Phil. Trans. R. Soc. Lond. B 1947 **233**, 1-54
doi: 10.1098/rstb.1947.0005

A STUDY OF A NON-MARINE LAMELLIBRANCH SUCCESSION IN THE *ANTHRACONAIA LENISULCATA* ZONE OF THE YORKSHIRE COAL MEASURES

By R. M. C. EAGAR, Ph.D.

(*Communicated by A. E. Trueman, F.R.S.—Received* 2 *June* 1945)

[Plate 1]

CONTENTS

PART I. INTRODUCTION

Previous investigation has shown that the non-marine lamellibranchs of the Lenisulcata zone vary to an exceptional degree. In Yorkshire, where the Lenisulcata zone was first defined (Wray & Trueman 1931, 1934), most of the material studied has hitherto been derived from borings so that few shells have been available for study. In Lancashire, however, much material was collected from open sections by W. B. Wright, who first demonstrated some of the variational trends of certain Lenisulcata zone faunas and created several new species (Wright 1934*a*, *b*).

Wright made a special study of the fauna above the Bassy Mine at two localities where he found shells on several horizons. For purposes of describing the variation he mixed all his material together and added to it a few specimens from various levels above the Bassy Mine at other localities. Wright concluded that most of these forms were merely variants of his two species, *Carbonicola fallax* and *C. protea*, which were very abundant and appeared to function as norms.

An important part of Wright's work (1934*b*) was the clear demonstration of a series of transitions between *C. fallax* and forms which, on their outline, and without reference to their associated variants, would be identified as *Anthraconaia**. Dr D. Leitch (1936), in a detailed study, described *Anthraconaia*-like variants of *Carbonicola* from a low horizon in the Ovalis zone of the Midlothian Coalfield. Wright again (1937) described *Carbonicola*-like variants of *Anthraconaia* from the base of the Lancashire Lower Coal Measures.

The Bassy Mine of Lancashire was correlated by Wray (1929) with the Soft Bed of Yorkshire, a conclusion which subsequent more detailed work has confirmed. Shells from the corresponding fossiliferous series above the Soft Bed, from the second of two recent boreholes at Bradford, Yorkshire (Hudson & Dunnington 1938, 1939), were examined by Professor A. E. Trueman. A series of bands above the Soft Bed Coal were recorded in detail by Hudson and Dunnington and the faunas of ten successive selected intervals examined separately. All Wright's species were identified with more or less certainty and many of his illustrated variants strongly represented. While Wright's norms, *Carbonicola fallax* and *C. protea* together with *C. recta* Trueman, were the most abundant forms, *C. fallax* and *C. protea* merged so completely that separation was almost impossible. Although the variation at every level was very large, Professor Trueman noted that 'there seems to be a closer similarity in many of the specimens and a more limited range of variation than is illustrated in Wright's paper'. He pointed to differences in lithology and the fact that the larger shells were mostly found in coarse grey micaceous shale while the smaller specimens were found in the softer and darker shales.

The present paper is the first of a series of detailed studies on the Soft Bed-Bassy Mine succession made by the writer under the supervision of Professor Trueman. Their object is to determine, by the study of thin bands and communities, to what extent and in what

* Professor Trueman and Dr Weir, in *A Monograph of British Carboniferous Non-Marine Lamellibranchia*, Paleont. Soc., Part 1 (1946), p. xv, have pointed out that the genus *Anthracomya*, founded by Salter in 1861, was already preoccupied, the name having been used by Rondani for a genus of Diptera in 1856. They proposed therefore the name *Anthraconaia* for the lamellibranchs previously classed as *Anthracomya*. *Anthraconaia* takes precedence by a few months over *Saltermya*, a name proposed by Miss K. van W. Palmer who made the same observation on Rondani's genus in *J. Paleont.* **20** (1946), no. 5, p. 518.

manner these highly variable shells are related to one another, investigating especially their environmental factors as far as these are reflected in the lithology, and the possible influence these may have on the nature of the variation. No statistical studies have previously been made on a fauna of the Lenisulcata zone nor has the lithological variation been investigated in any detailed study on non-marine lamellibranchs of other zones.

From the section to be described at Honley, Yorkshire, twenty-nine collections have been made on various horizons through both thick and thin shale intervals. About 1500 shells have been examined, of which over 570 have been measured.* Many more shells from above the Soft Bed and Bassy Mine at other localities have also been utilized in making a variation diagram which serves as a basis for the comparison of successive slightly differing faunas at Honley.

It has been found necessary to redescribe certain of W. B. Wright's species and to create a new one. Short notes on species† are added at the end of this paper.

Before proceeding to a description of the succession it is necessary to give an account of the writer's methods in the study of variation, to discuss aspects of shell preservation and its influence on shell shape and measurement, and to define certain selected lithological types.

PART II. GENERAL CONSIDERATIONS AND METHODS USED IN THE STUDY OF SHELL VARIATION

1. The variation diagram

It has long been realized that it is possible, given a number of non-marine lamellibranch shells from one horizon, to place them in lines selected to show a gradual change in shape or in the degree of expression of one or more characters. Such series can easily be made to tie up with one another in various ways, when it is usually found that a certain variant is common to most of the series which can be regarded as derived from it. This shell is then the centre or focus of the variation and is termed the norm;‡ forms near it are usually abundant but not necessarily so.

When a number of characters vary independently of one another, as is usually the case, a number of arrangements are possible. One generally finds in every arrangement of many shells that there are forms which show characters intermediate between two, three, or more of the series chosen, and which cannot satisfactorily be placed with any of them. The best or most natural arrangement is that in which there is a minimum of such forms.

Dr D. Leitch (1936), working on a very large collection of shells, found that a simple arrangement around the norm was impossible owing to complexity of variation. Difficulties

* Nearly all the material utilized in this study has been presented to the Hunterian Museum, Glasgow University.

† The authors of the species to which reference is frequently made in this paper are as follows: *Carbonicola sulcata* (Brown); *C. ovalis* (Martin); *C. acuta* (J. Sowerby); *C. recta*, *C. pseudorobusta* Trueman; *C. elliptica* Tchernychev non W. B. Wright; *C. fallax*, *C. protea*, *C. limax*, *C. obliqua*, *C. haberghamensis*, *C. phrygiana* and *C. acutella* W. B. Wright; *Anthraconaia bellula* (Bolton); *A. lenisulcata* (Trueman). The authorship of any other species mentioned is stated in the text.

‡ 'The norm, however, must not be confused with the mode. The former is chosen as a focus of variable characters and the latter is controlled by the relative number of individuals showing special characters' (Leitch 1936, p. 391).

were removed by the establishment of two norms, or a binary focus of variation, and by including amongst his series triangular and quadrangular arrangements of extreme forms within which intermediates could be placed. Less complex variation diagrams were made by the same worker (1940, 1941) using the same principles.

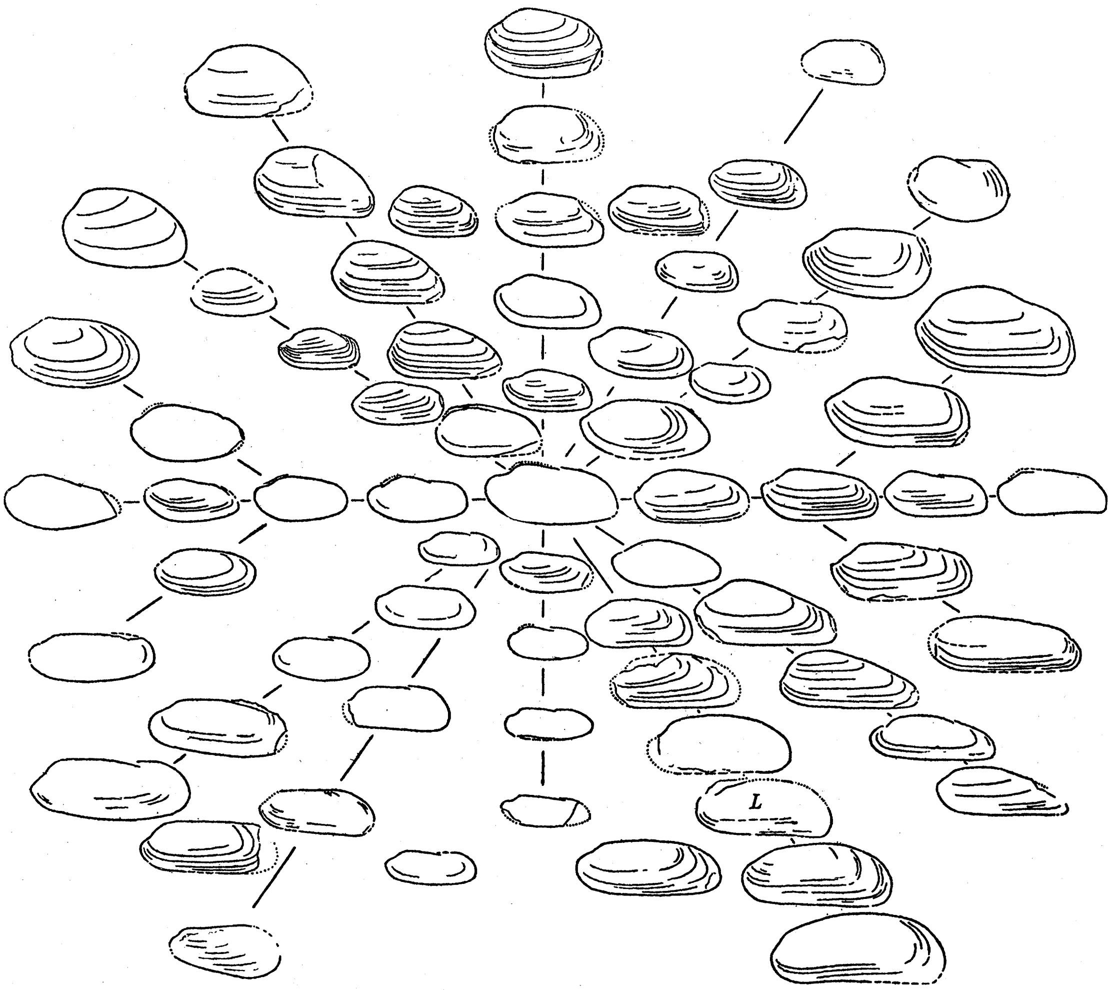


FIGURE 1. The standard diagram, plane I, showing variation around the holotype of *Carbonicola fallax*. All shells, with the exception of *C. limax* (*L*) are from above the Soft Bed or Bassy Mine Coals. Shells three-fifths natural size.

The problem to be solved in the case of the Lenisulcata zone faunas is different from those studied by Dr Leitch since it is necessary to make variation diagrams for the comparison of a number of both successive and contemporaneous faunas which have sometimes a few, but usually many, similar variants. The application of the 'most natural arrangement' (Leitch's method) probably provides the best insight from a pictorial point of view into the true relations existing between the variants of a single community. Yet its application to a number of slightly different communities without some modification makes the direct comparison of successive diagrams difficult and tedious.

Much of the difficulty is removed, however, if variants of similar trend at each level are placed in the same direction with respect to successive fairly similar norms, and if blanks are left in those directions in which a series is absent although present at some other level. Or, in other words, it is possible to compare with ease a number of slightly differing faunas if the variation diagrams can be superimposed on a pre-determined directional skeleton of variational trends which is kept constant throughout. The difficulty of such a method, particularly from the theoretical point of view, is chiefly that in addition to the problems normally met with in the search for the most natural arrangement there is that of the limitation in the choice of a norm and in the directions of the series. In practice, however,

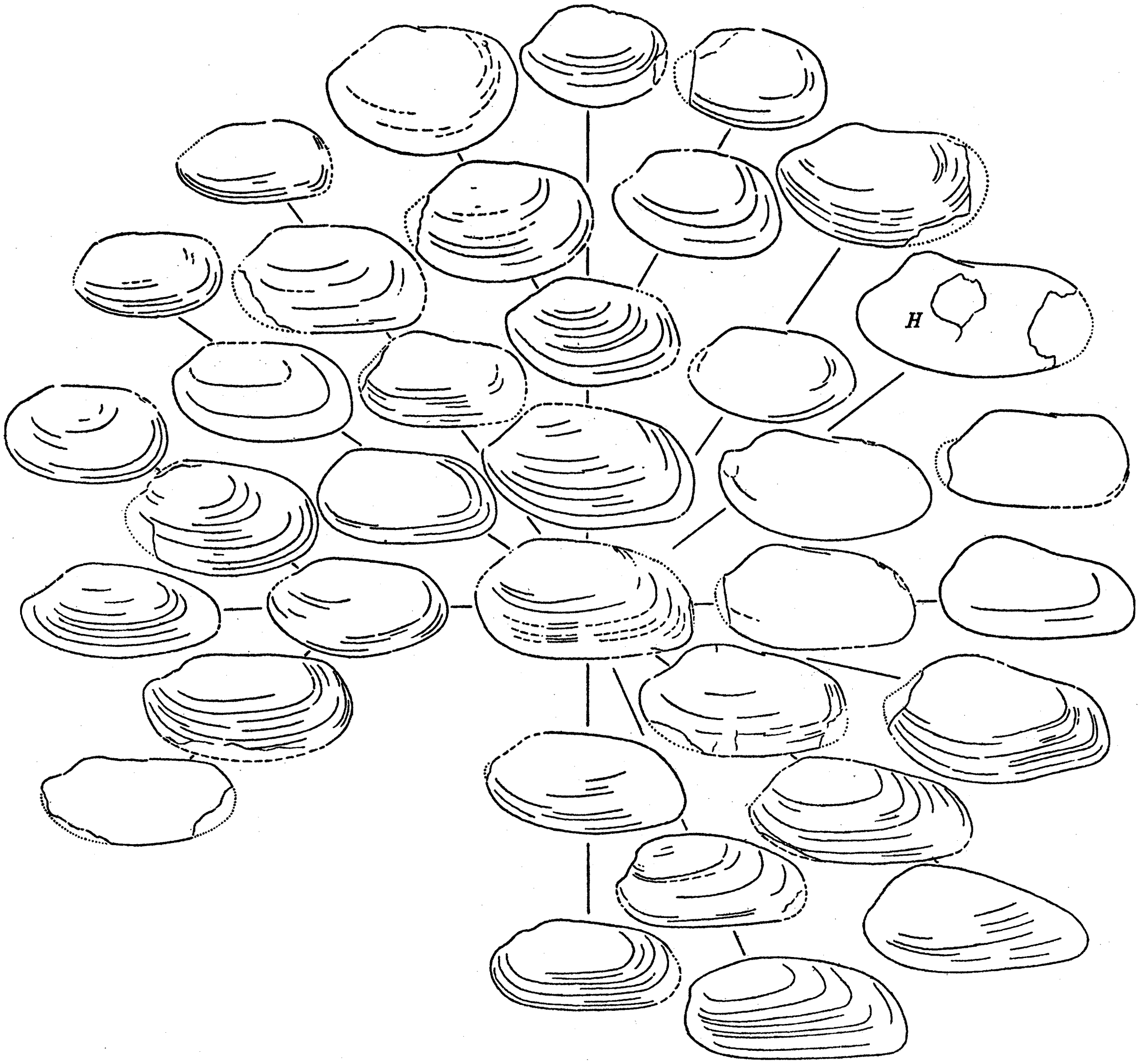


FIGURE 2. The standard diagram, plane II, showing variation of shells around the holotype of *Carbonicola protea*. *H* shows the holotype of *C. haberghamensis*. All shells are from above the Soft Bed or Bassy Mine Coals and are figured three-fifths natural size.

the application of this method to the faunas of the Soft Bed-Bassy Mine succession has, in the writer's opinion, proved satisfactory. This is probably due to certain peculiarities in the type of variation of the *fallax-protea* group, the recurrence of a few forms near Wright's holotypes, either of *C. fallax* or *C. protea* at all horizons, and the unusual degree of correlation of shape characters in certain series.

(i) *The standard diagram and the directional skeleton*

It is first necessary to make a large variation diagram built up with forms from the numerous levels to be later compared, and from this, the *standard diagram* (figures 1 to 3) to derive the directional skeleton (figure 5).

The writer's method of making the standard diagram with forms collected from above the Bassy Mine and Soft Bed is totally different from that of W. B. Wright (1934*b*, figure 1), whose object was merely to demonstrate a number of widely differing forms and their supposed connexions with two generalized, commonly occurring types. His radial variation diagram with binary focus was made with relatively few variants, and its essential purpose was to avoid overmuch description in the text of his paper (Wright 1934*b*, p. 24). Series were taken from it one by one, and the specimens figured 'gauged to show the gradualness of the transition from form to form', which was 'admittedly not so perfect in some cases as in others'. Scarcely any attempt was made to probe the relations between some of the series and little was then known of their relative frequency.

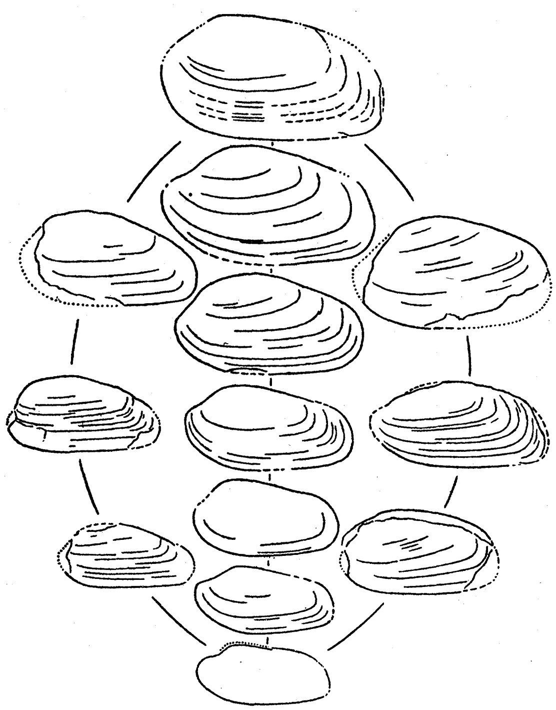


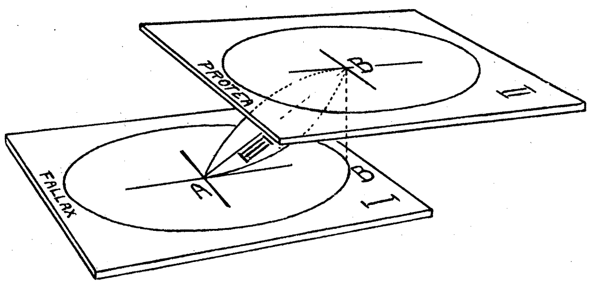
FIGURE 3. The standard diagram, plane III, showing the variation of shells between *Carbonicola fallax* and *C. protea*. All shells are from above the Soft Bed or Bassy Mine Coals and are figured three-fifths natural size.

To build up the standard diagram the writer utilized forms from numerous levels and localities, as Wright did, and adopted the same two norms. Tracings were taken from all Wright's figured variants and from a very much larger number of specimens since collected. After many attempts it was found possible to arrange these in radial manner around *C. fallax* and *C. protea* and at the same time to use Dr Leitch's method of a three-cornered area of extreme forms, in this case a segment of a circle, for the placing of intermediate or interserial specimens. The final scheme (figures 1 to 3) was reached by continual adjustment on two diagrams on which over 260 tracings (160 round the *fallax* norm) were finally pinned. These made it possible to follow very gradual morphological changes.

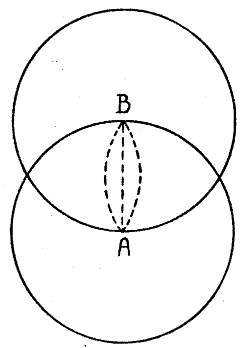
During the planning of the standard diagram it became clear that some supposed series were rare and were best considered as intermediates between more strongly represented series. Those series which were obviously related in communities were placed near together.

Certain of them were found to be characteristic of definite levels or lithological types and these were therefore placed in positions where they would contrast with others characteristic of different levels or sediments. For this reason it was found convenient to make a clear distinction between forms relatively shorter and those longer than the holotype of *C. fallax* and between *Anthraconaia*-like variants of *C. fallax* and those approaching *C.* cf. *sulcata* (Brown). The size of the variants and their manner of growth provided another fairly important consideration in making the arrangement. Thus the whole diagram was built up under the guidance of two principles, which sometimes conflicted with one another: the first to make as *natural* an arrangement as possible, necessitating the least number of unplaceable forms; the second to make the most *useful* arrangement and to preserve simplicity for the directional skeleton.

Figures 1 and 2 show the essential features of the portions of the standard diagram around *C. fallax* and *C. protea* respectively. A number of forms, however, bridge perfectly the interval between these two norms and they are shown in figure 3. The whole diagram may be conceived in three planes (figure 4) in such a way that the holotype of *C. protea*, norm of the *protea* diagram, lies directly over the northern margin of the *fallax* diagram. The third plane (figure 3) can be projected up or down for illustration either with the upper or the lower plane.



(*a*)



(*b*)

Figure 4. (*a*) A sketch showing the arrangement of the three planes of the standard diagram and directional skeleton. (*b*) Their relative positions when viewed directly from above.

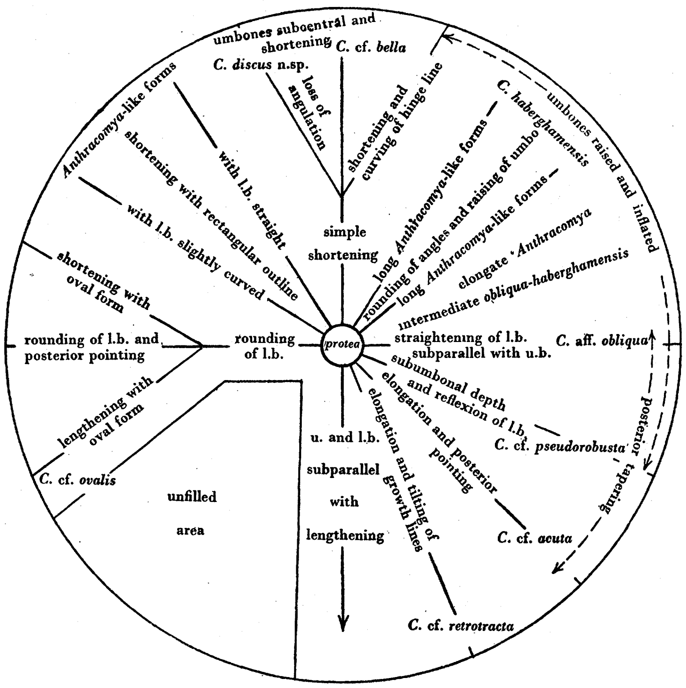
It is not proposed at present to describe the numerous series and segmental arrangements of the standard diagram since they are outlined on the directional skeleton (figure 5) and will be fully treated in later accounts of variation diagrams for thin bands or communities, where many intermediate forms, which cannot here be figured for lack of space,* will then be clearly seen. Of the plan of the standard diagram and directional skeleton, three points only call for emphasis:

(1) Both the *fallax* and *protea* skeletons (figures 1, 2, 5*a*, *b*) have a similar simple fundamental basis: forms shorter than the norm are placed in the northern semicircle and forms longer in the southern: shells with progressive curvature of the lower border lie directly west of the norm and those with progressive straightening and reflexion of it directly east of the norm: *Anthraconaia*-like shells run north-east in both skeletons running also south-west (long forms) in the *fallax* diagram.

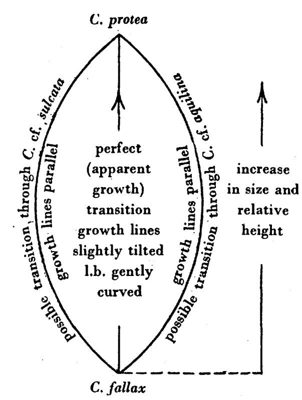
* This is especially the case in the *C. protea* diagram (figure 2).

(2) In the third plane (figures 3, 5*c*) increase in relative height northward is accompanied by increase in size.

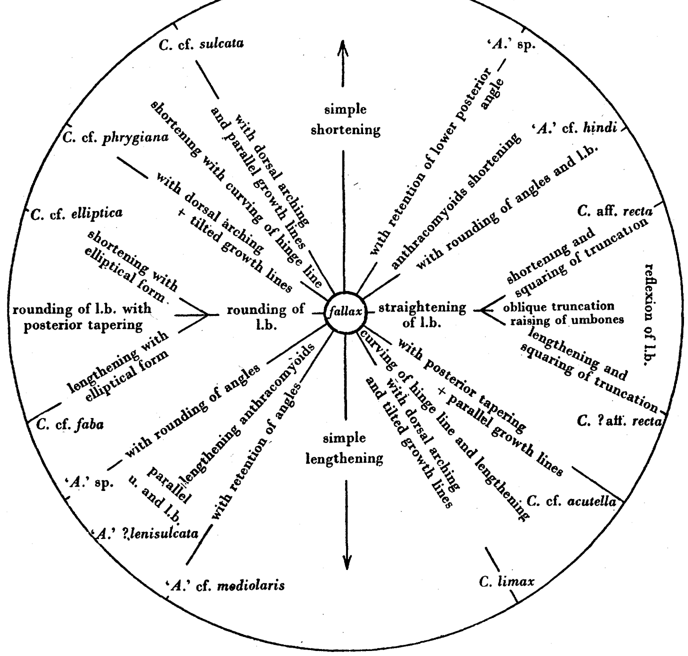
(3) Transitions have been found in the standard diagram in all areas between the series except that marked 'unfilled area'. This is at present empty, but it may be filled as a result of future collecting.



(*b*) plane II



(*c*) plane III



(*a*) plane I

FIGURE 5. The three planes of the directional skeleton, showing the major variational trends of the fauna above the Soft Bed and Bassy Mine Coals and being an explanation of figures 1 to 3. For *Anthracomya* read *Anthraconaia*, and for anthracomyoids read anthraconaioids.

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

(ii) *The community or thin-band variation diagram*

In arranging a variation diagram for a community or a fauna from a thin band a variant is selected which is near, usually as near as possible, to the norm of the standard diagram, either *C. fallax* or *C. protea*. (If both occur, the diagram is made on two or three planes, the third plane being represented by projections on the first or second plane as described for the standard diagram.) Variants are then picked, usually after arrangement of a number of specimens, to show in series from the chosen norm any trends of the directional skeleton. Beyond the modification in the directions of series the diagram is built up as naturally as possible utilizing the maximum number of available specimens. The diagram is illustrated in the manner adopted by Dr Leitch. The figured variants are first drawn in series position while a second diagram shows the positions of all the variants, each represented as a dot or a circle with those figured distinguished by letters or ornament. The latter, the *distribution diagram*, illustrates the numerical strength of the series. After the illustration of a number of faunas by Dr Leitch's method the figures become redundant and the distribution diagram alone is regarded as sufficient in the discussion of the faunas.

A distribution diagram is intended to indicate the relative frequency of the variants in the different series, any concentration or modal effect, and in many cases the degree to which a trend is represented. Certain precautions must therefore be taken in drawing a diagram of this type. It should be emphasized that the arrangement on the directional skeleton is made in accordance with the norm chosen (which may differ slightly from the norm of the standard diagram) while the positions of the variants in the series are modified by continual reference to their position on the standard diagram. Round the norm of the distribution diagram is drawn a large circle which approximates to the circle of extreme variants round the norm of the standard diagram. The position of an extreme variant will therefore be peripheral on both standard and distribution diagrams, but the position of a form in the normal region may be slightly different on the two diagrams when the norms differ appreciably.

As might be expected, variation diagrams of some communities are more naturally arranged on the directional skeleton than others. The *Anthraconaia*-like shells, through their arbitrary division into forms longer and shorter than the norm, provide the most difficulty. With so many variable features it is often difficult to make an intersegmental arrangement. That adopted on the standard diagram is adhered to where possible, but a certain amount of latitude is permissible within the segment.

A few transitions may occur between series spaced too far apart for their placing on the diagram without interference with some other series or distortion of the standard of proportion in arrangement. Such a case occurs in the remarkable series of transitions found at Honley between *Carbonicola limax* W. B. Wright and certain forms which on their outline are indistinguishable from Anthraconaias and which appear to be closely related to *Anthraconaia lenisulcata* (Trueman). In this case the extremes and forms near them in the distribution diagram are placed on the directional skeleton in the normal manner, but they are illustrated, together with unplaceable forms, in another arrangement to bring out the further relationships present in the community.

Figuring. Except in the standard diagram shells are figured natural size. It is thus impossible in the case of the larger shells, and often inconvenient in the case of the smaller, to figure the illustrated variants in their correct relative positions. They are therefore placed in blocks, except in the case of the first described fauna (p. 18), their correct relative positions being shown by letter or ornament reference on the distribution diagram.

2. Modes of preservation and their influence on shell shape and measurement

(i) *Shell thickness*

Most of the specimens collected at Honley are preserved as internal and external moulds, between which, in the case of a small uncrushed shell, there may be an appreciable difference in outline. Immediately in front and over the tip of the umbo the shell is thick, becoming thinner on the post-umbonal slope, while to the posterior it is often very thin. The anterior slope is consequently more re-entrant, the umbo lower and the post-umbonal slope more arched in the internal mould than in the complete shell or external mould. (See figure 14*K*, *M* and *Q*, and compare the holotype of *Carbonicola limax* W. B. Wright, internal mould with external moulds or impressions of similar shells figured on the standard diagram, south-south-east series, figure 1.)

Where a shell is small (under 30 mm. in length) shell thickness over the umbo may make an appreciable difference between the height/length* ratio of its internal and external mould. With a reasonably large number of shells it is possible to calculate the mean difference in height, which can be regarded as constant over a short range in shell size, so that by its addition or subtraction all the specimens of a community may be converted to effective 'externals' or 'internals' for more adequate statistical comparison. Measurements based on good uncrushed material are shown in figure 6, where external and internal height measurements show definite separation, the former having a mean height/length ratio of 42·6 and the latter 39·9. For shells between 18 and 28 mm. in length the mean umbonal shell thickness was calculated by graphical methods† to be 0·7 mm., which is 8 % of the mean height of the internal moulds. With correction (figures 6*b*, *d*) the resultant more limited dimensional range and the clear separation of the specimens from the holotype of *C. fallax* (also an internal mould) is striking. The standard deviation for the ratio (height/length) × 100 is lowered from 2·57 to 1·79 % and the coefficient of variation from 6·3 to 4·49. The change in the calculated mode‡ is, however, small, 40·2–39·2 %.

For large shells the above effect is negligible, and for small ones where crushing has taken place, or where numbers of shells are low and variation considerable, it cannot be calculated. In certain of these cases, however, if considerable precision is required and there is reason to believe that shell thickness over the umbo has some effect on the range and mean value of the height/length ratio, an estimate can be made and correction applied as above.

* Shell length (*L*), height (*H*), thickness or obesity (*T*) and length of anterior end (*A*) have been measured in the manner defined by Davies & Trueman (1927, p. 212).

† The height and length measurements of external and internal moulds were plotted and the distance between their respective cumulative slopes averaged.

‡ In the present paper in all cases where the variation appears continuous and the distribution unimodal the mode is calculated by use of the approximation mode = mean − 3 (mean − median).

(ii) *Crushing*

Crushing of the shell may take place antero-posteriorly, dorso-ventrally or laterally. The first case is rare and is easily recognizable. Dorso-ventral crushing is much less common than lateral crushing; where it has been suspected measurements of height have not been made. Lateral crushing, however, is typical among the larger shells, frequently to the extent of total flattening of the valves, and it is common among the smaller ones in finely laminated shales.

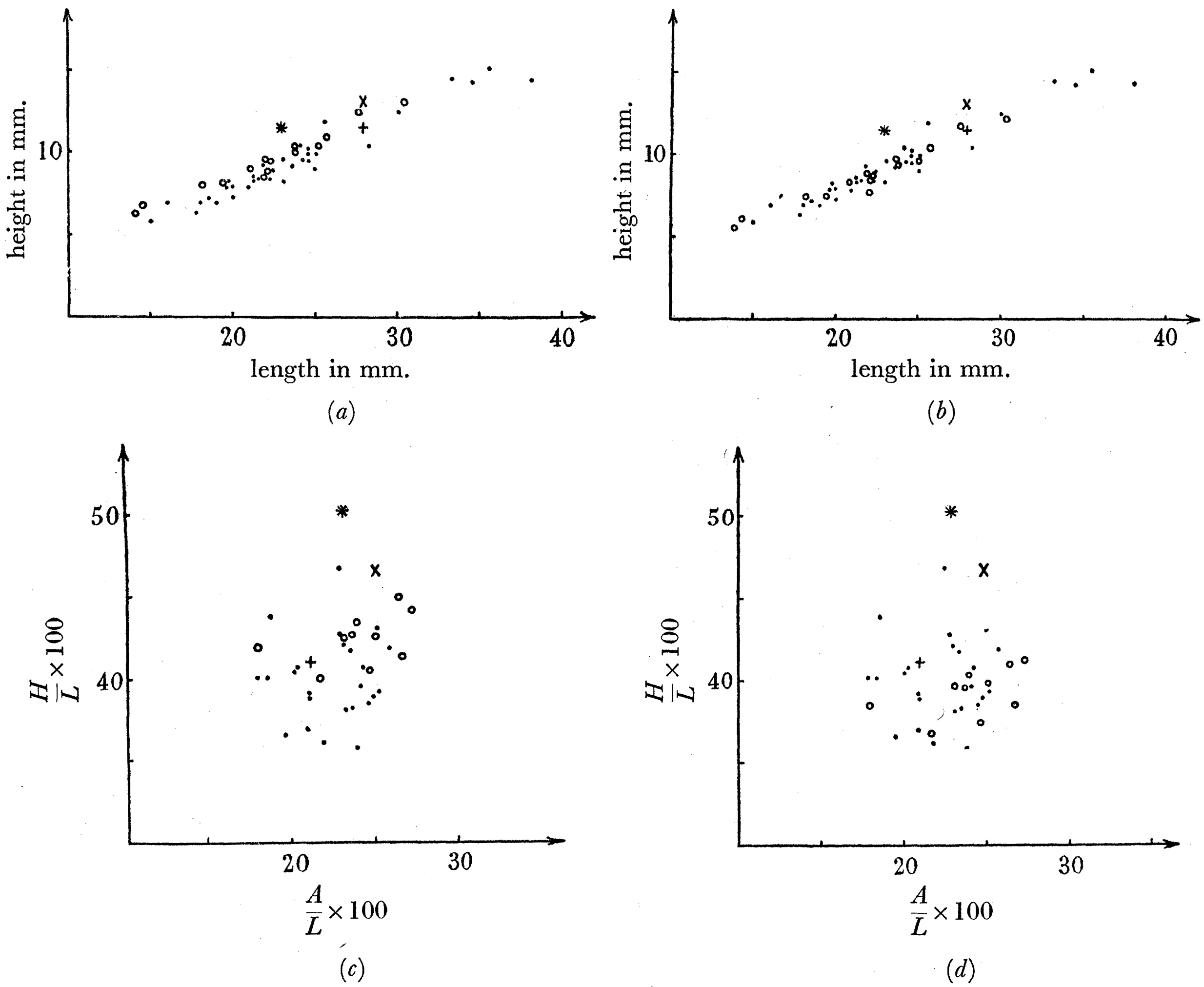


FIGURE 6. Measurements of shells from a community probably about 50 ft. above the Soft Bed Coal, Hazlehead, near Holmfirth. The dots show measurements of internal moulds and the small circles measurements of external moulds. In graphs (*b*) and (*d*) the latter are corrected for umbonal shell thickness, being converted into those of effective internal moulds. Symbols show the positions which would be occupied by the holotype of *Carbonicola fallax* ×, the paratype ∗, and the holotype of *C. limax* +.

Lateral crushing usually affects seriously the precise shape and measurement of the anterior end. Even in an uncrushed shell this standard measurement (A), taken parallel to the hinge line, has always a greater margin of error than those of height, length and thickness (obesity). The proportional error is usually increased with the decreasing size of the shell. In external and internal moulds of small shells, shell thickness over the umbo

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

causes some error. With lateral crushing, distorting or obscuring the umbonal tip (see figures 8*p* or 14*C*) measurement of the anterior end is most unsatisfactory. Little significance is therefore attached to precise umbonal shape where lateral crushing and poor preservation are found in a fauna. In the illustrations attempts are made to indicate the presence and the degree of the crushing.

Apart from the immediate umbonal region lateral crushing appears to alter the outline very little, the greatest effect being found in small tumid shells. For instance, the difference in outline between an uncrushed *Anthraconaia*-like shell and *Carbonicola limax* is very slight, for the distinction depends on the exact mode of curvature of the hinge line (compare the south-west and south-south-east series in the standard diagram, figure 1). With crushing, the more swollen region of the shell may be pushed out of shape with respect to the hinge line, making distinction between the two forms sometimes impossible. In cases where a short shell with a strong posterior carina is flattened the dorsal post-umbonal part may be pushed up to make a higher 'hinge line', giving the shell an anthraconaioid appearance (compare figure 8*c* uncrushed and figure 8*n* a totally crushed shell; the difference may be partly attributable to crushing).

Lateral crushing may slightly increase the relative height of a shell. Data from Honley carrying this suggestion will be referred to in the description of the section.

3. A classification of lithological types found above the Soft Bed and Bassy Mine Coals

In the fifteen complete or partial sections seen by the writer between the Bassy and Lower Foot Mines in Lancashire and between the Soft Bed and Middle Band Coals in Yorkshire, a fairly definite succession has been recognized of a number of characteristic lithological types, between which there is perfect transition. This is repeated three times in rhythmic manner with comparatively little modification. Thus, although the character of a sediment in a general way depends on a number of independent variables, it is possible in this case* to establish a rough linear series of lithological grades which are recognizable in the field. The grades are determined macroscopically by grain size and approximate composition, utilizing also weathering characteristics, degree and nature of lamination and colour. Emphasis is laid on their essentially macroscopic characters, on the fact that several are arbitrarily selected types and that all are chosen with a view to demonstrating graphically a certain type of continuous change or sedimentary rhythm. Nevertheless, in view of the fact that macroscopic characters are largely qualitative, in the case of the shale and mudstone types very short notes on distinctive features and figures roughly defining grain size are added from an examination of thin slices under the microscope.

Grade 1. Black or dark grey fine-grained well-laminated shale, rich in small nodules or blebs of pyrite. The shale weathers sulphurously and is typically soft and papery after exposure, having characteristic flaky lamination surfaces. Gypsum crystals are not uncommon. Variations include a stronger shale with smoother lamination surfaces after

* The writer has seen some of these shale types in the upper part of the Millstone Grit and at other horizons in the Lower Coal Measures. They seem to be much less common in the Middle Coal Measures, where in general the shaly mudstones appear to be distinctly different.

weathering, showing also ochreous colours. The most distinctive feature is the presence of the pyrite or sulphur.

The grain size, excluding occasional large mica flakes, lies well below 0·01 mm. In thin slice bedding planes are slightly uneven, being typically sinuous with small-scale banding or wisps of lighter and darker material.

Grade 2. A black, dark grey or dark blue fine-grained well-laminated shale, with ochreous weathering and with no trace of sulphur. Very little mica is visible in hand specimens. Sharp angular fragments usually result from breakage when slightly weathered.

The grain size is well below 0·01 mm. Thin slices show very even bedding with strongly orientated mica.

Grade 3. Grey or blue shale or shaly mudstone, weathering ochreous and frequently associated with lenticular ironstone into which it may pass imperceptibly. Detrital mica is well seen in hand specimens and contrasts with its poverty in grade 2 shale. Lamination is variable, being in general much less pronounced than in grade 2.

The grain size averages about 0·01 mm. ranging up to 0·03 mm. Mica is more abundant than quartz.

Grade 4. Grey or grey-blue medium-grained mudstone or shaly mudstone, weathering ochreous and not infrequently passing into ironstone; distinguished from grade 3 principally by its rougher appearance and typically lighter colour.

The grain size lies typically between 0·03 and 0·05 mm. Quartz is more abundant than mica.

Grade 5. Blue-grey or grey rather coarse ferruginous mudstone, shaly mudstone or siltstone, often variable in colour and grain size within a small thickness. Typically weathering ochreous and sometimes buff, it breaks in large slabs and is rarely jointed. Where succeeded by grade 1 pyrite is invariably present in its uppermost portion.

The larger quartz grains lie mostly between 0·05 and 0·1 mm. Mica ranging up to 0·08 mm. shows no appreciable orientation. The rock may contain as much as 60 % siderite, usually present in granular aggregates which may occasionally surround centres of pyrite.

Grade 6. A loosely defined grade covering flaggy shale and mudstone coarser than grade 5, flagstone, sandstone, grit ganister and fireclay.

Grade 7. Coal, or occasionally coaly shale.

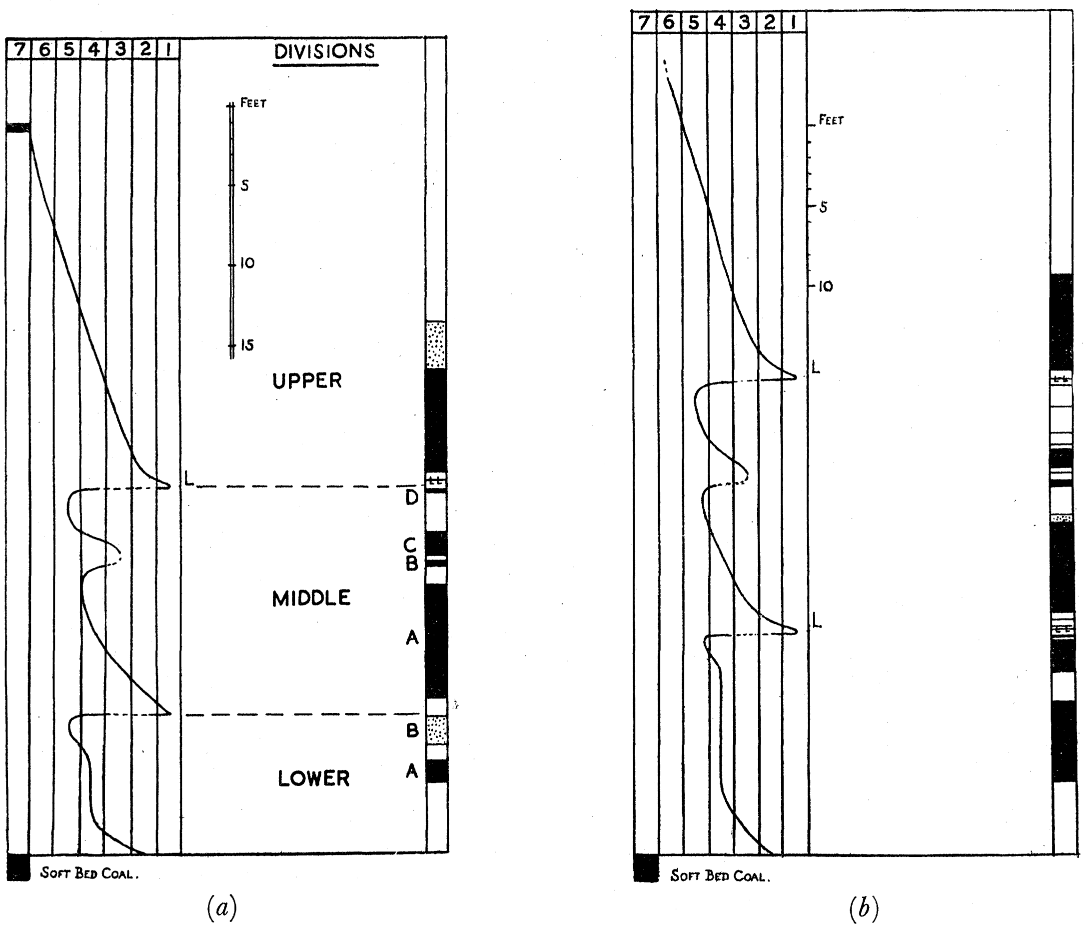
PART III. THE SUCCESSION AT HONLEY

1. Introductory

The section to be described is a good exposure of strata from the Soft Bed to the Middle Band Coal seen at either end of a short tunnel about 150 yd. north of Honley Station, $2\frac{1}{2}$ miles south-south-west of Huddersfield; 1 in. Sheet 86, 6 in. Sheet Yorks 260.

In the *Memoir of the Geological Survey* (Bromehead, Edwards, Wray & Stevens 1933, section on p. 87) only a 6 in. *Carbonicola* band 12 ft. above the Soft Bed Coal is recorded.

The writer found, however, that the section (figure 7*a* and figure 7*c* (facing p. 14)) shows thick shell beds distributed through 30 ft. of measures. In figure 7 fossiliferous bands are marked in the right-hand column, those rich in lamellibranchs in black and those yielding a sparse or very poorly preserved fauna in dots. Bands of fish debris are shown only in the larger scale section (figure 7*c*). A band yielding *Lingula* sp. has been found 24 ft. above the Soft Bed and 22 ft. below the Middle Band Coal (L in figure 7*a*, *b*). In the left-hand grids of figure 7 *a*, *b* the numbers refer to the selected lithological grades described in the preceding section. The lithological type is placed in the appropriate column and a continuous line then drawn in such a way that the approximate lithological grade is given continuously throughout.



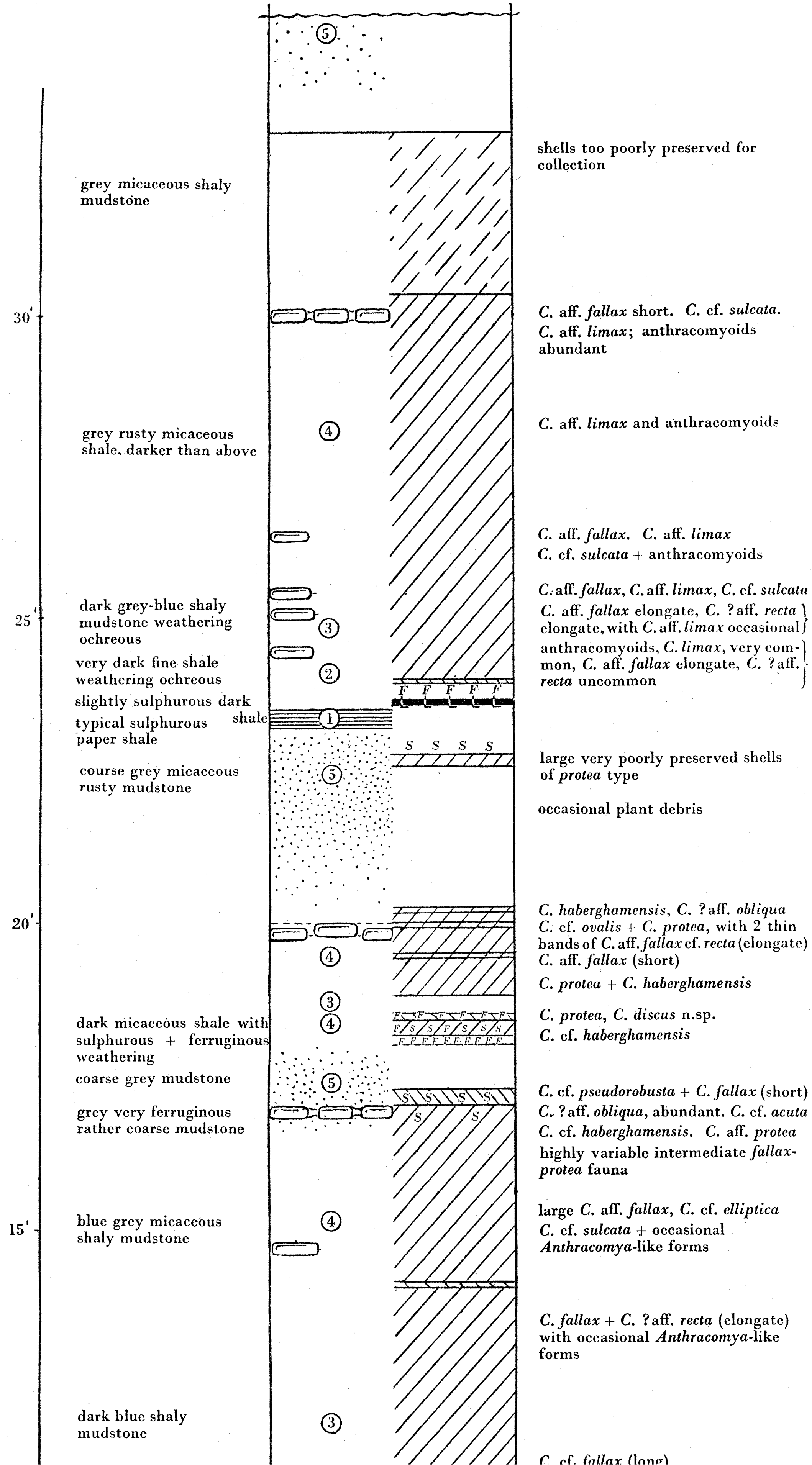
(*a*) (*b*)

FIGURE 7. Scale section of the measures between the Soft Bed and Middle Band Coals at (*a*) Honley Station cutting and (*b*) the western end of Springwood Tunnel, Huddersfield, $2\frac{1}{2}$ miles to the north-north-east, showing together lithological variation and details of the shell bands. The numbers in the grid on the left-hand side of the sections refer to the lithological grades described in the text. On the right-hand side the following conventions are used: ▬ Measures rich in non-marine lamellibranchs; ▒ Non-marine lamellibranchs sparse; ▭ Barren measures; ⊟ Shale with *Lingula*.

Lithology and rhythmic sedimentation

Lithologically and palaeontologically the measures fall naturally into the three divisions marked in the centre of figure 7*a*. Each of these can be regarded as a rhythmic unit characterized by a gradual increase in grain size towards a high grade followed by a rapid change to a low (fine-grained) grade. *Lingula* occurs at the base of the upper division in dark grey slightly pyritous shale immediately overlying typical grade 1 shale. The full sequence, shale with *Lingula* to coal, followed by *Lingula* again, is seen in the upper division. A fuller development of the middle division is seen 3 miles to the north-north-west at the

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES



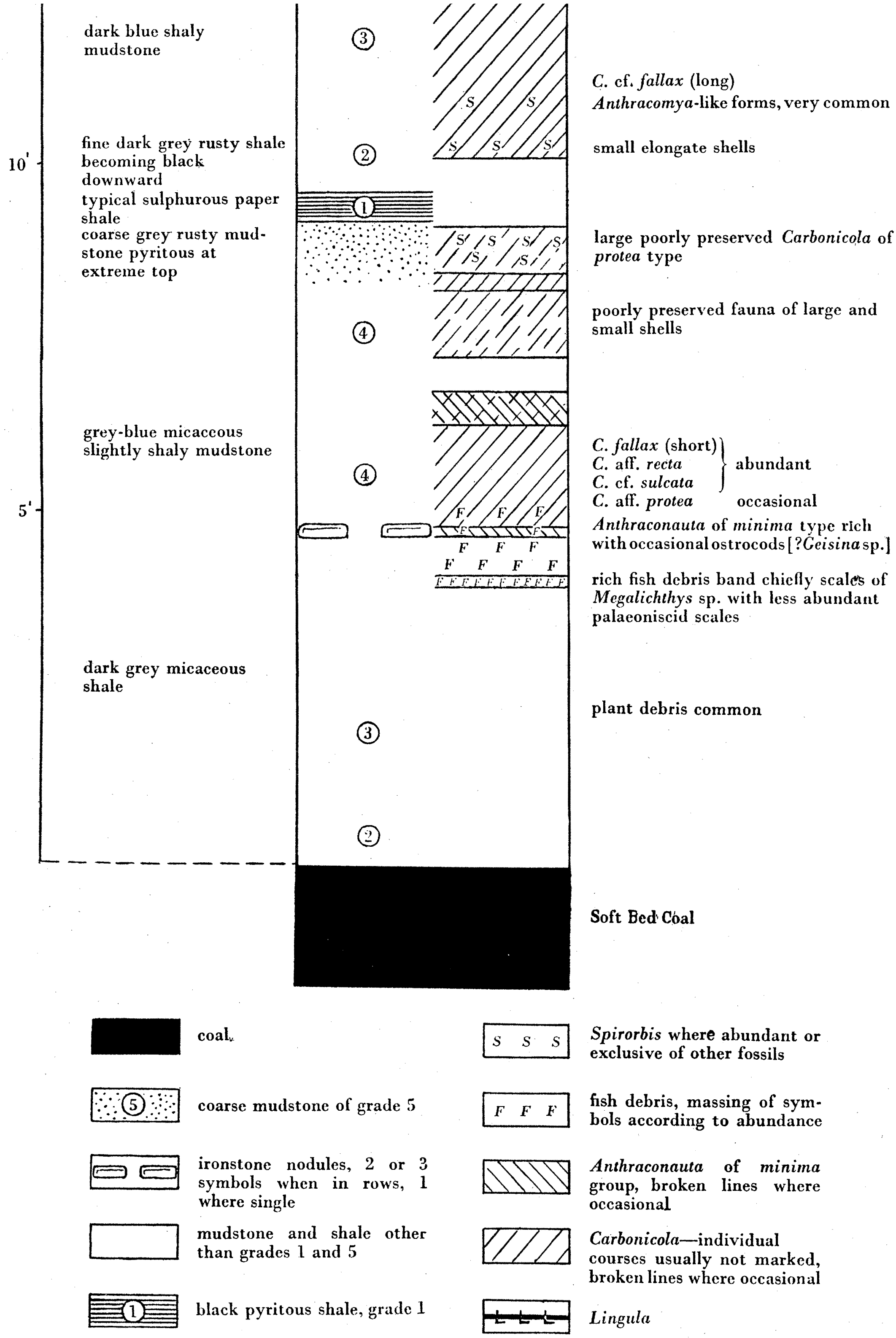


FIGURE 7*c*. Scale section of the succession at Honley Station cutting, on which are shown, partly by means of symbols, on the left hand details of the lithology, and on the right hand palaeontological features. The numerals on the left-hand side refer to the selected grades of shale and mudstone described on p. 12 (compare figure 7*a* and the tabulated summary on p. 47). For *Anthracomya* read *Anthraconaia* and for anthracomyoid read anthraconaioid.

western end of Springwood Tunnel, Huddersfield, where *Lingula* and *Orbiculoidea* have been found at its base, making a second newly recorded *Lingula* band 14 ft. above the Soft Bed Coal (figure 7*b*).

Pyrite is present in small nodules at the extreme top of the lower division and in the succeeding grade 1 of the middle division. It is again similarly distributed at the junction of the middle and upper division immediately below the *Lingula* band, and yet again at the base of a small oscillation in the middle division (see details in figure 7*c*).

Neither at Honley nor in any other section in the Soft Bed-Bassy Mine succession seen by the writer have organic remains been found in the richly pyritous shales of grade 1, although fish scales are frequently present in the lower slightly coarser portions of these bands. It is not unreasonable to suppose therefore that biochemically toxic conditions obtained during the formation of the pyrite, possibly through the action of anaerobic bacteria in shallow stagnant or boggy water during a pause in sedimentation. The pyrite may, on the other hand, have been formed from marine sulphates by the reducing agency of decomposing organic matter from the Coal Measure delta during an initial seepage phase of a marine incursion, when conditions were temporarily unsuitable for life. Whether stagnancy or marine action is responsible for the presence of the pyrite, and the writer considers both causes may have operated to some extent, the rapid change to a fine-grained, apparently deeper, water shale with a pene-marine fauna immediately above the pyritous horizons is striking. It is clear that there has been a change, and probably a pause in sedimentation.

It appears therefore that there are one complete and two incomplete rhythmic units of Coal Measure type, such as have been illustrated and discussed by Officers of the Geological Survey in Lancashire (Wright, Sherlock, Wray, Lloyd & Tonks 1927, p. 9; and Tonks, Jones, Lloyd & Sherlock 1931, p. 11). The full sequence, pene-marine band, non-marine shell band, barren shale and mudstone, sandstone, fireclay and coal seam is seen in the upper division while in the lower and middle divisions the rhythmic unit appears shortened in the terrestrial direction. In these latter there is seen the usual gradual coarsening of grain size until, it has been suggested, possibly after a condition of stagnancy was reached, subsidence took place comparatively rapidly and there followed an incursion of the sea into the deltaic area.

Wright, Tonks, Wray and others have shown in the Pennine region that the Coal Measure rhythm gradually changes in development and proportion from the Millstone Grit, where emphasis lies essentially on the marine bands, non-marine lamellibranchs being scarce, to the Middle Coal Measures where marine bands are scarce and non-marine shell bands comparatively abundant. The rhythm in the Middle Coal Measures is also shorter than that in the Millstone Grit, and non-marine shells are usually limited to a thickness of a few inches in the roof of a coal seam; although they may occur higher in the rhythm few thick bands have been reported. Here in the Lower Coal Measures above the Soft Bed Coal we have the intermediate case where pene-marine bands are closely associated with rich non-marine lamellibranch bands, the latter extending through a *considerable thickness* of the unit cycle. Here successive communities of lamellibranchs lived in an environment apparently changing in a known direction. There is in these beds, therefore, probably a unique opportunity for studying possible environmental effects on observed variation at successive horizons.

2. Detailed description of the faunal succession

(I) Lower Division, 0 ft. to 8 ft. 9 in. above the coal

Details of the distribution of fossils other than *Carbonicola* are shown in figure 7*c*. Small *Anthraconauta* of the *A. minima* (*auctorum*) group are poorly preserved and have not yet been fully studied.

(i) Band A (figures 8, 9), 4 ft. 6 in. to 6 ft. 6 in. above the coal

In the lower 1 ft. 6 in. shells of *Carbonicola* run in four courses, between and above which specimens occur more sparsely. Nearly all are small, but larger shells occur occasionally amongst them and there is at least one thin leaf of large shells only. Extreme poorness of preservation and the nature of the exposure have prevented collection of the latter. The collection of small shells through small thicknesses revealed no discernible difference in faunal character, and in the following account all shells collected through 1 ft. 6 in. of grey-blue, coarse, slightly shaly mudstone are considered together.

Most specimens are slightly crushed laterally. Shelly material is frequently not preserved, or the shell may be represented by a thin ferruginous rind.

Small shells comprise over 95 % of the collected fauna. They are shown arranged in series on the directional skeleton, plane I, in figure 8. With few exceptions they are referable to *Carbonicola fallax* (figure 8*a* the norm), *C.* aff. *fallax* (*b* and *c*), *C.* aff. *recta* (*d*, *e*, *f* and *g*) and *C.* cf. *sulcata* (*j* and *k*). Of the larger shells (figure 9), (*f*) is slightly more elongate and smaller than the holotype of *C. protea* (centre, figure 2), while (*d*) and (*e*) show further elongation and are referable to *C.* aff. *protea*. It appears from plotting height against length (figure 10) that most of the smaller shells are unrelated to those over 30 mm. long, since the former have considerably greater relative height than the latter and their increase in height with growth is greater.

(*a*) *Small shells*

Although considerable variation is found, certain distinctive characters are impressed on the fauna as a whole:

(1) With a few exceptions the shells are smaller, and 80 % of them are shorter than the holotype of *C. fallax* (which has a height/length ratio of 46·5 for internal mould, and 47·5 or 48 % with shell thickness over the umbo). The modal H/L ratio for these shells is 51 %.

(2) The lower border of 95 % of the shells is straight or very nearly straight (e.g. as in figure 8*c*). Slight reflexion of the lower border is often present in the *C.* aff. *recta* series. Figure 8*p* shows the most curved lower border found.

(3) Growth lines as a rule are straight and parallel. Increase in size was accompanied by a considerable increase in relative height (compare in order figure 8*b*, *a* and *c*; *g*, *d*, *e* and *f*; *h*, *j* and *k*).

(4) A ridge or carina of varying definition is present in all but the smallest shells and is most clearly defined in the posterior third of the shell. This originates from a slight swelling well behind the umbo and passes obliquely backward, typically having a crest which is curved convex dorsally, towards the posterior inferior angle. It is always more strongly marked on the internal mould than on the shell. In the larger shells referable to *C.* aff. *recta* it is present in the earlier stages of growth but appears to flatten out in the later stages.

Analysis of the variation.

Figure 8 shows the norm and sixteen variants selected to illustrate the variational trends. In the distribution diagram (bottom left) are shown the positions of the remaining sixty-two specimens (white circles) having their positions controlled by their resemblance to the figured specimens (black circles).

The norm (figure 8*a*), slightly smaller than the holotype of *C. fallax*, has a strong carina with weakly defined crest. Anterior to the carina is a definite shallow sulcation.

Series 1*a and* 1*b* show simple elongation and shortening of the norm respectively. Elongation is accompanied by a slightly more rounded lower border; with shortening, on the other hand, the lower border is straighter and the truncation more nearly rectangular (figure 8*c*).

Series 2. Figure 8*d* shows the complete straightening of the lower border with more rectangular truncation so that an approach is made to *C. recta*. Considered as a secondary norm two series are derived from (*d*), both of which show rectangular truncation. Series 2*a* show shells with increasing relative height; (*e*) is very near *C. recta* but (*f*) has greater height and both are smaller. Most of the shells in this series have an anterior end higher and considerably shorter than is found in the holotype. The two small, more elongate shells of Series 2*b* appear to be young specimens (compare also *b*, series 1*a*). Figure 9*c* with reflected lower border differs from the *C. recta* series in having slightly more oblique truncation and is considered as a further development of series 2*a*–*d*.

Series 3 (figures 8*i*, *j* and *k*). The shells show progressive arching of the dorsal margin and increase in relative height. Growth lines are straight and parallel. In general the higher shells referable to *C.* cf. *sulcata* are larger and some have slightly reflected lower borders. The carina is strong with well-curved crest. The known limit of this serial trend above the Soft Bed is expressed in figure 8*k*. A few forms which are slightly longer than the norm, although near it, are shown as the short series 3*a*. Figure 8*h* obviously could be considered in direct series with (*i*), (*j*) and (*k*) without passage through the norm. Fairly good transitions however are found between (*h*) and the norm, so that the present arrangement is reasonably natural.

Series 4. A few shells (*l* and *m*) show tilting of the growth lines with blunting of posterior truncation, so that on their outline they are comparable with *Anthracosia aquilina* (sensu lato). With progressive shortening this series is little removed from series 3, the main distinction being seen in the growth lines.

Series 5. A tendency towards *C. limax* is seen in two shells, the more extreme of which is illustrated, *C.* cf. *limax*, (*q*). It appears to show closer relationship with the elongate *C.* aff. *recta* forms than with the norm of the diagram.

Series 6. Figure 8*n* shows the impression of a rare form having short *Anthraconaia*-like outline. It is flattened laterally so that the anthracomyoid form may be accentuated (see section on crushing, p. 11).

Series 7. Figure 8*p* shows some increase in the rounding of the lower border but without loss of truncation, so that there is but slight approach towards the outlines of W. B. Wright's *C. elliptica-faba* group.

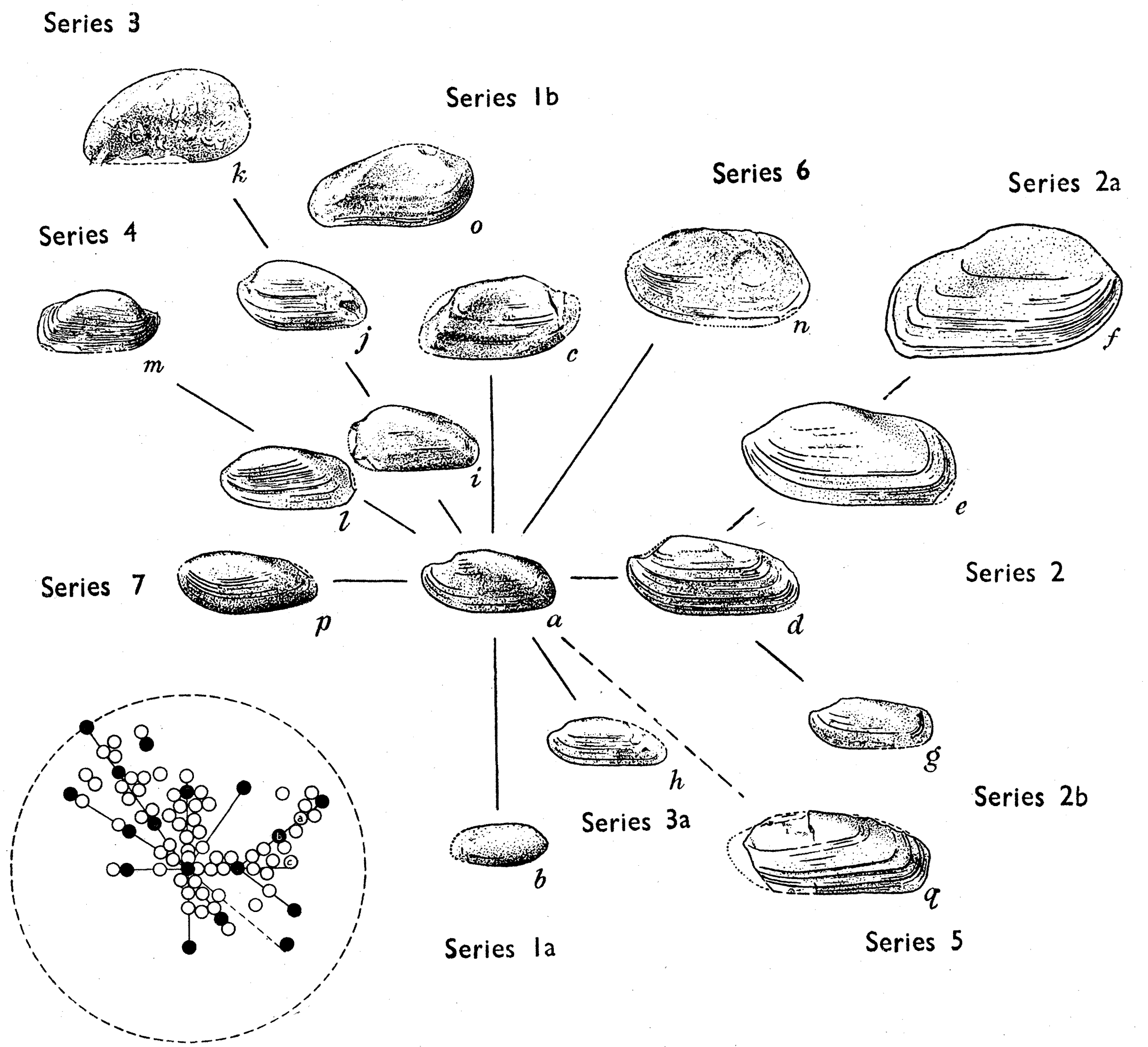


FIGURE 8. The small shells of band A of the lower division, 4 ft. 6 in. to 6 ft. 6 in. above the Soft Bed Coal, Honley. The distribution diagram is shown inset, where black circles distinguish the figured variants and the small letters refer to three shells in figure 9. Figures are slightly reduced.

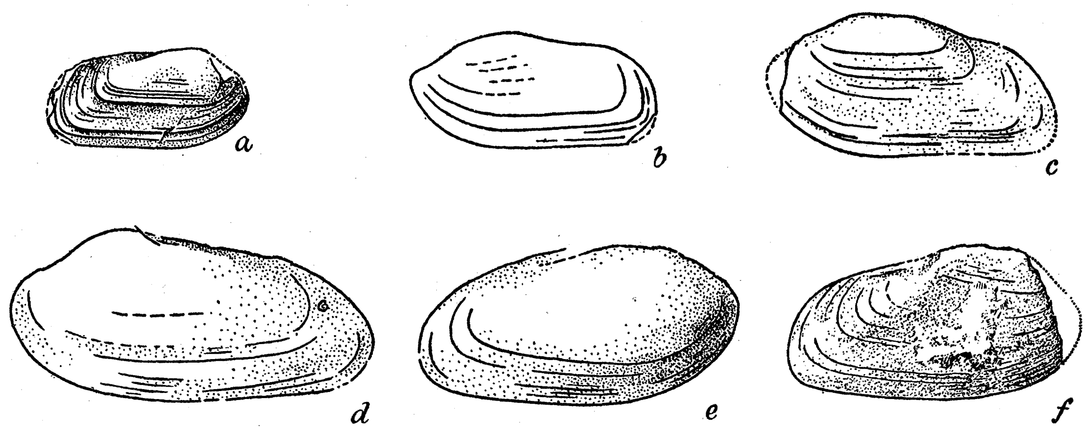


FIGURE 9. The large shells of band A of the lower division of the sequence above the Soft Bed Coal at Honley (see figure 8). The positions of the shells figured as (*a*), (*b*) and (*c*) are shown in small letters on the distribution diagram of figure 8, (*b*) being a tracing of figure 8*e*. The remaining shells are not included in the variation diagram.

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

Summary

The three-fold trend of the fauna is indicated in the concentration of circles in the distribution diagram (figure 8, inset); *C. fallax* and shorter forms, short *C.* aff. *recta*, and *C.* cf. *sulcata*. Elongate and *Anthraconaia*-like shells are rare.

The size, growth lines and distribution of the variants indicate that growth usually took place uniformly along the lower border with increase in height/length ratio with advancing age. This tendency and the presence of the carina form the two most striking characteristics of the fauna.

Measurements suggest the separation of a small shell group from a large one which is weakly represented in the material collected. Whether the larger forms of the *C.* aff. *recta* series and the smaller shells of series 1 and 3 belong strictly to the same Linnean species is not clear. Compare in figure 10 the concentration of the dots about the length of 20 mm. and again to a smaller degree between 25 and 30 mm.

(*b*) *Large shells*

In figure 9 are drawn three larger forms (*d*), (*e*) and (*f*) for comparison with the larger shells of the *C.* aff. *recta* series (see position of 9*c* in figure 8). They may be related* but in the writer's opinion the more curved lower border of (*d*), (*e*) and (*f*), their finer growth lines and more rounded and oblique truncation suggest that these forms may belong to a different species.

(ii) Band B, 7 ft. to 8 ft. 9 in. above the coal

Owing to scarcity and poorness of material, no detailed study has been attempted. Those specimens which have been collected are similar to variants seen in band A.

In the upper 3 in. no small shells were found, but occasional large relatively deep forms are referable to *C.* aff. *protea*.

(iii) Summary of the fauna of the Lower Division

Shells are present in the coarser grades only (grades 4 and 5) of the rhythmic unit. Small shells are much more abundant than large and have a high height/length ratio. They form a distinctive fauna composed principally of *C. fallax*, aff. *recta* and cf. *sulcata* elements. Large shells are occasionally found with the smaller shells, and they occur exclusively although sparsely in the uppermost portion of the rhythmic unit.

(II) Middle Division

(i) Band A, 10 to 17 ft. above the coal

(*a*) *General account*

Collection has been made throughout the band and separately through smaller thicknesses. The approximate lithological grade of the shale and details of shell length and height for each selected interval are shown in tabular form below. Except in the uppermost horizon, where evidence from thin leaves of shells points to the separation of a large sized *C. protea* shell group (*p*) from a smaller sized *C. fallax* group (*f*), the material through each interval appears homogeneous (figure 11).

* Compare the position of the holotype of *C. recta* on figure 10 and the positions of the larger shells.

As table 1 shows, at the five levels chosen in successively coarser beds there is a progressive increase in the calculated modal value of the height/length ratio of the shells. This increase is apparently continued in both large and small shell groups of the uppermost interval, at the top of which large shells occur exclusively.

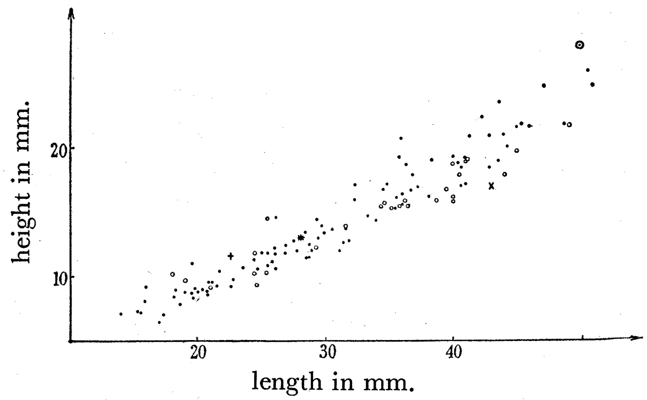


FIGURE 11. Measurements of shells in the middle division of the sequence at Honley. The small circles show shells collected 10 ft. 9 in. to 11 ft. 3 in. above the coal, the dots those from 11 ft. 3 in. to 16 ft. 1 in. above the coal.

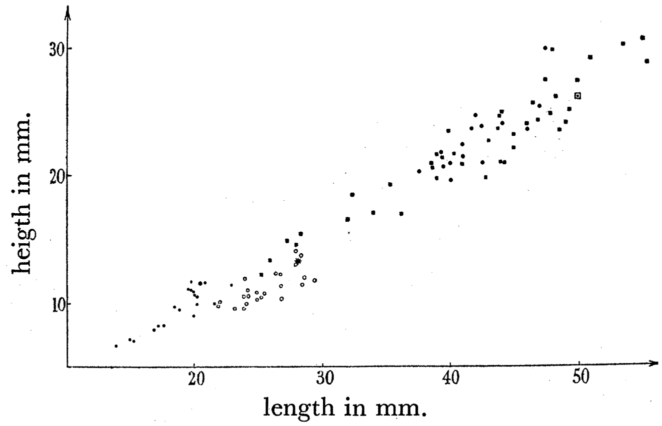


FIGURE 13. Measurements of shells in band C of the middle division of the sequence at Honley, showing speciation. Dots, *C.* cf. *fallax* 19 ft. 6 in. above the coal; open circles, *C.* aff. *fallax*; and squares, *C. haberghamensis*, both 20 ft. above the coal.

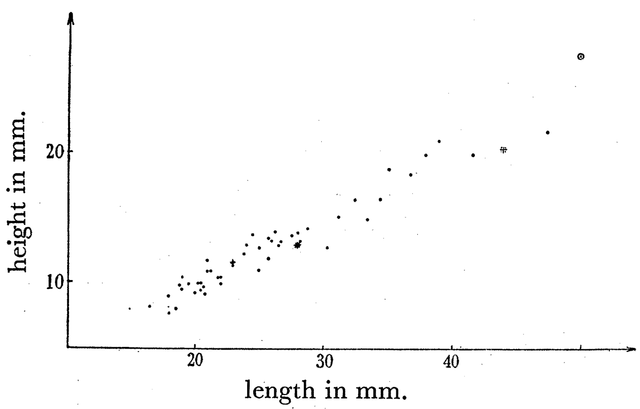


FIGURE 10. Measurements of shells in the lower division of the sequence at Honley, 4 ft. 6 in. to 6 ft. above the Soft Bed.

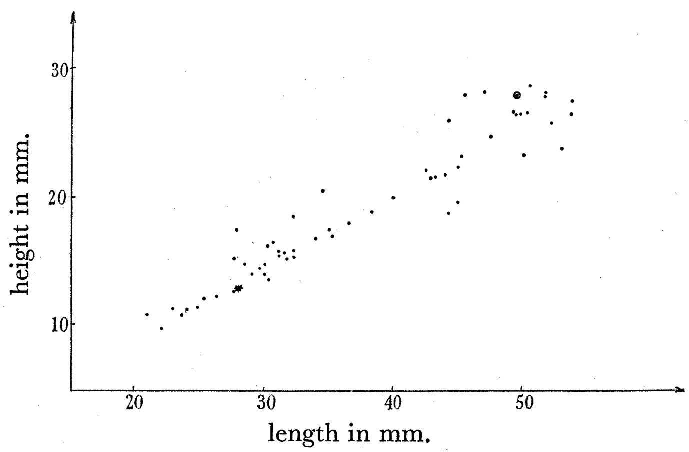


FIGURE 12. Measurements of shells from the middle division of the sequence at Honley, 16 ft. 3 in. to 17 ft. above the coal.

On the graphs of figures 10–13 symbols show the positions which would be occupied by type specimens as follows: ∗ holotype of *Carbonicola fallax*; + paratype of *C. fallax*; ⊙ holotype of *C. protea*; ⊡ holotype of *C. recta*; ⁜ holotype of *C. haberghamensis*; × holotype of *Anthraconaia lenisulcata*.

This increase is probably not quite so smooth as the table suggests, bearing in mind the errors in sampling. Measurement of specimens from the remaining horizons has not shown any significant difference from these figures except in one case, a thin band 13 ft. 2 in. above the coal which will be referred to later.

In the lower three collected intervals the range of the H/L ratio remains unaltered, the mean may increase* slightly, and the mode increases. Subsequently with further increase in the mode the more elongate forms are eliminated and large relatively shorter forms of the *C. protea* group appear. An increase in size or mean length is shown between all but the lowest two horizons. A tendency towards increase in relative height with size was noted in the *C. fallax-recta-sulcata* fauna of the lower division, and it is apparent in the shells intermediate between *C. fallax* and *C. protea* found chiefly in the upper portion of this band (figure 14*K*, *L* and *G*). That the increase in relative height is due not only to an increase in size is clear from table 1 and figure 11.

TABLE 1

height above coal	grade	no. of specimens	mean L	range of H/L %	mean H/L %	calculated modal H/L %
16 ft. 3 in. to 17 ft. 0 in.	4 (→5)	57 33*p*	37·9 44·2	43·6–63	51 52·9	50·9*p*
		24*f*	29·7	42·3–55	48·2	48·4*f*
16 ft. 0 in. to 16 ft. 1 in.	4	12	36·4	43·5–54	47·2	*c.* 47
13 ft. 9 in. to 16 ft. 0 in.	3–4	22	32·5	38·8–56	44·5	46
13 ft. 3 in. to 13 ft. 9 in.	3 (→4)	32	26·0	37·1–58	44·4	44
10 ft. 9 in. to 11 ft. 3 in.	3 (→2)	26	32·1	37·8–57·2	44·6	42·4

Throughout the 7 ft. band shells are found continuously, usually in rich courses separated by a few inches of shale or mudstone in which they are less common. Except at 16 ft. above the coal several courses have been collected together.

In the lowest collected horizon, 65 % of the shells are referable to *Anthraconaia* on their outline and grade perfectly with *Carbonicola*. In the succeeding horizons *Anthraconaia*-like forms are much less common, occurring in diminishing numbers, chiefly among the smaller shells and grading with the *Carbonicola* fauna. In the highest horizon Anthraconaias are absent and there is an abundance of large shells of the *C. protea* group having their mode centred around *C.* cf. *pseudorobusta* (figure 19*E*, *H*) with a smaller group mostly referable to *C.* aff. *fallax*. In the lower and middle horizons of the band the variation is very great, a large and small shell group being usually indistinguishable.

These changes, notably that from *Anthraconaia* to *Carbonicola*, are reflected to some extent in a slight progressive increase in the mean proportionate length of the anterior end (A) at successive levels and in more fluctuating changes in the mean proportionate thickness or obesity (T).

TABLE 2

height above coal	mean length	mean A/L %	mean T/L %
16 ft. 3 in. to 17 ft. 0 in.	44·2 (33*p*)	26·5 (20*p*)	27·7 (22)
	29·7 (24*f*)	24·5 (29*f*)	25·3 (21)
16 ft. 0 in. to 16 ft. 1 in.	36·4 (12)	22 (7)	26·2 (7)
13 ft. 9 in. to 16 ft. 0 in.	32·5 (22)	23·4 (12)	21·8 (18)
13 ft. 3 in. to 13 ft. 9 in.	23·8 (17)	20·8 (8)	30·5 (12)
10 ft. 9 in. to 11 ft. 3 in.	34·4 (23)	19 (10)	—

The figures in brackets refer to the number of specimens available for measurement.

* A collection of thirty-one specimens with mean length of 35 mm., made subsequently from 13 ft. 9 in. to 14 ft. 9 in. above the coal, had a mean H/L ratio of 47·1 % and a mode of 47·2 %.

Thickness or obesity varies considerably, the highest value, 30·5 %, being found where the shells are small. Young shells of the *fallax* group are typically rather obese, but it is usual to find a loss of obesity with increase in size. The slight increase in obesity in the uppermost horizon results from the introduction of large forms with swollen subumbonal region, *C.* cf. *pseudorobusta* and *C.* cf. *obliqua.*

(*b*) *The fauna at successive horizons*

The following notes are merely a supplement to the graphs and variation diagrams, figures 11, 12 and 14 to 19.

(1) 10 *ft. to* 11 *ft.* 3 *in. above the coal.* Preservation is poor and nearly all the shells are crushed laterally. Figures 14 and 15 should be compared with figures 29 and 31, where a similar fauna is more fully illustrated. The *Anthraconaia*-like shells, comprising 65 % of the fauna, and probably about 90 % at the extreme base of the band, have certain characteristics:

(*a*) They are typically elongate, having their upper and lower borders subparallel and the umbo not usually raised above the hinge line.

(*b*) The posterior superior angle β is always large and well rounded.

(*c*) The hinge line is frequently slightly curved.

(*d*) They grade with *Carbonicola* including forms near *C. limax.** There are a few shells with imperfectly preserved hinge lines which may be referable to *C.* cf. *limax* or an *Anthraconaia*-like shell.

It should be noted that (*a*) and (*b*) are features of *Anthraconaia lenisulcata* and *A. bellula*, while (*c*) and (*d*) are also characteristic of the latter (Wright 1934, 1937). Although none of the shells is near the holotype of *A. bellula* a few are near its variants above the Six-Inch Mine in Lancashire (Wright 1937). Figure 14*h* and *i* and another shell unfigured (S. 12398) appear to be fairly near *A. lenisulcata* but are somewhat smaller.

Carbonicola (figure 14*e*, *d*, *f*, *k* and *j*) is highly variable. The shells will later be compared with a similar fauna from the base of the upper division. Large relatively high forms (figure 14*G*) showing some approach to *C. protea* are rare and are not included in the variation diagram.

Figure 11 suggests that the distinctive characters of the fauna, elongation and *Anthraconaia*-like outline tend to become manifest with accumulated growth from a smaller more generalized form in somewhat the same manner as a totally different character, sharpness and bluntness, appears in a relatively coarse mudstone fauna from the lower division.†

(2) 11 *ft.* 3 *in. to* 13 *ft.* 9 *in. above the coal.* The *Anthraconaia*-like fauna appears to change gradually to one of *Carbonicola* in which the *C. fallax* and *C.* cf. *recta* elements, mostly elongate, predominate (figure 14*S*, *U*). Although highly variable the fauna of this horizon has certain characteristics; the lower border is straight or nearly straight in 65 % of the shells and growth lines are usually parallel; posterior truncation is typically blunt while some of the *recta*-like shells show a slight carinal swelling (figure 14*P*, *O*).

In the collection from 13 ft. 3 in. to 13 ft. 9 in. above the coal there are in addition at least five shells intermediate between *C. fallax* and *C. protea* which are not included in

* The transition will be fully illustrated in the description of shells from the upper division.

† It should be noted, however, that there are in this case apparently two groups of shells.

BIOLOGICAL SCIENCES THE ROYAL B SOCIETY PHILOSOPHICAL TRANSACTIONS OF

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

figure 14. Two similar forms, one of which is illustrated (figure 14*G*), were found in the lowest collected interval of table 1. Collection from a horizon 13 ft. to 13 ft. 3 in. above the coal has revealed a thin band of *C. fallax-protea* including *C.* aff. *protea* (figure 14*N*). Twelve measurable specimens from this horizon have a mean *H*/*L* ratio of 46·6 % (with probably a higher modal value), the only discrepancy with table 1 so far discovered.

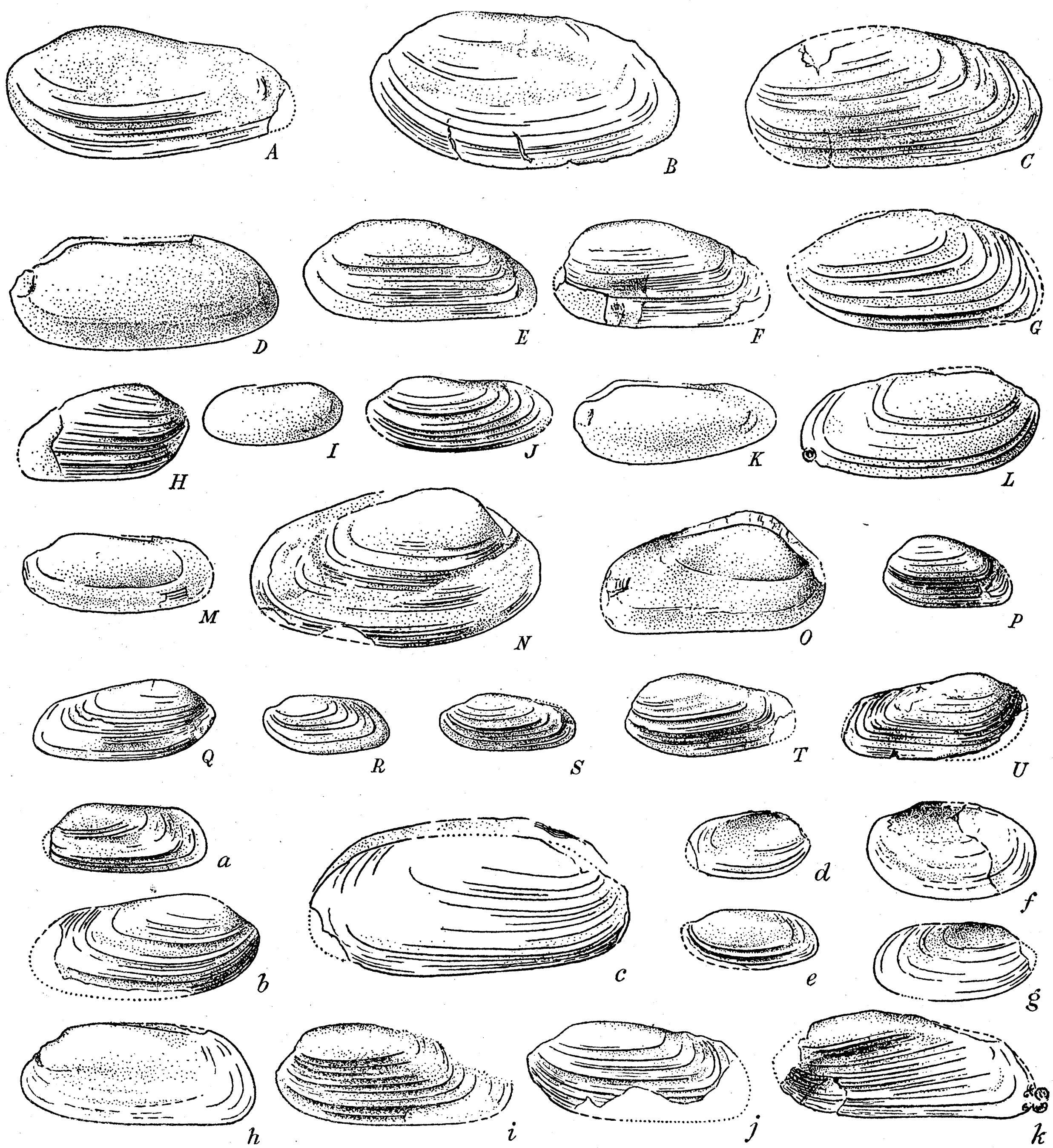


Figure 14. Shells from band A of the middle division of the sequence above the Soft Bed Coal, Honley; *A*–*M* (excluding *G*), 13 ft. 9 in. to 16 ft. 1 in. above the coal; *N*–*V*, 13 ft. to 13 ft. 9 in. above the coal; *a*–*k* (including *G*) 10 ft. 9 in. to 11 ft. 3 in. above the coal. Distribution diagrams of the latter two horizons are drawn as figures 15 and 16 where the positions of these shells are shown by letter reference.

(3) 13 *ft.* 9 *in. to* 16 *ft. above the coal.* A variation diagram has not been made. Most of the shells are intermediate in size and often in shape between *C. fallax* and *C. protea.* A second collection of thirty-one shells from 13 ft. 9 in. to 14 ft. 9 in. above the coal with mean length of 35 mm. had a mean H/L ratio of 47·1 % and a mode of 47·2 %. The larger shells include *C. protea* (figure 14*B*), *C.* aff. *protea* (figure 14*C*), *C.* cf. *acuta* (figure 14*A*) and *C. fallax-protea* (figure 14*L*, *E*). It seems clear that at this horizon increase in size was accompanied by increase in relative height. The fauna contains all the elements of the preceding collection with the following differences: (*a*) curved lower borders are common and the *C.* cf. *recta* trend is consequently weakly represented; (*b*) the *C.* cf. *sulcata* trend is slightly more strongly represented (figure 14*H*); (*c*) *Anthraconaia*-like shells are less common, the shape with little posterior depth being rarely seen in large shells (figure 14*D*) but occasionally in small ones. It appears that in some cases the shells became progressively less *Anthraconaia*-like with growth. Compare in order figure 14*I*, *J*, *K*, *L* and *G* and the early growth lines of some of the larger forms.

(4) 16 *ft. to* 16 *ft.* 1 *in. above the coal.* The fauna is one essentially of *C. fallax-protea* in which several forms have straight lower borders and may provide a transition through *C.* cf. *sulcata* (figure 14*F* and compare 14*E*). Amongst a number of such shells on a single slab one specimen of the *C.* cf. *pseudorobusta* series of the succeeding horizon occurs.

(5) 16 *ft.* 3 *in. to* 17 *ft. above the coal.* It is apparent from figure 12 that there are two groups of shells between which there is a simple linear growth relationship, most of the young of the larger group having similar dimensions to shells of the smaller. While it is usually possible to make the separation by eye there are a few difficult cases. The separation, however, is fully justified by very detailed examination and collection through this horizon. This revealed within 9 in. seven shell-bearing leaves, some of which merged with one another. Large shells of the *C. protea* group are found exclusively in the upper two leaves, while in the remainder they are present in varying proportions with smaller shells; in one very thin leaf only small shells have been found. In the lowest leaf and for 3 in. below it there is a profusion of shells showing extreme variability which appear quite inseparable. It seems likely, therefore, that a split into two Linnean species took place between the horizons 16 ft. and 16 ft. 6 in. above the coal. This effect may be the result of evolution. In view, however, of the rapidity of the change and the fact that division into a large and small shell group has been found as low as the Pot Clay Coal, at the base of the Lower Coal Measures, the writer suggests that we may be dealing with the gradual migration of a cline which split into species 'up river' or towards the shore.

(*a*) *Small shells* (figure 17)

The variation is comparatively limited. Nearly all the shells are referable to *C. fallax* (figure 19*L*) or *C.* aff. *fallax* (figure 19*K*), while some approach *C.* cf. *sulcata* (figure 19 *M*, *N*). Typically, the lower border is gently curved, and a slight carina may be developed in the more dorsally arched casts. The fauna is comparable with that of the coarse mudstone of the lower division (small shells of figure 8), differing from it principally in the absence of the *C. recta* trend and in the possession generally of considerably greater size and a more curved lower border. As in the lower division, however, the shells appear to have increased in relative height as growth proceeded. The comparison carries the suggestion that in both cases a somewhat similar suite of variations has been superimposed on different norms.

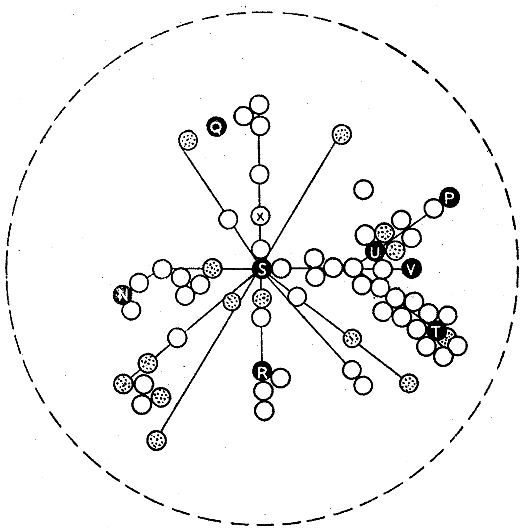


FIGURE 16. Shells 13 ft. to 13 ft. 9 in. above the coal; the positions of those from 13 ft. to 13 ft. 3 in. above the coal are shown by shaded circles (on plane I).

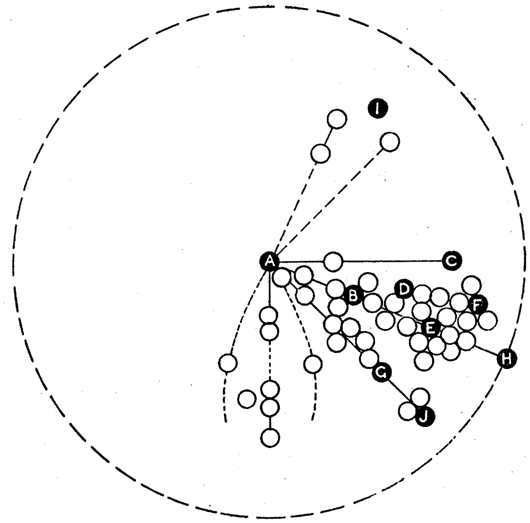


FIGURE 18. Large shells 16 ft. 3 in. to 17 ft. above the coal (on planes II and III).

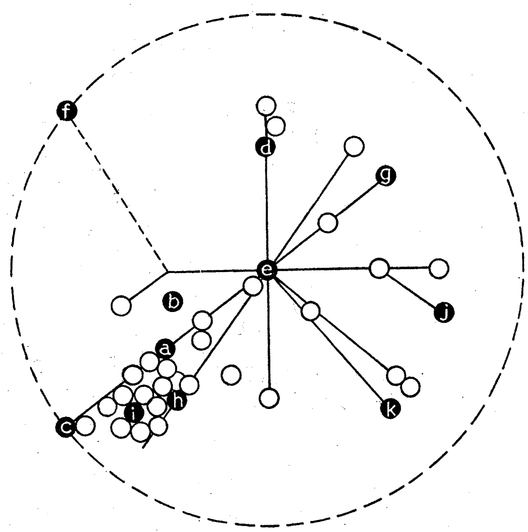


FIGURE 15. Shells 10 ft. 9 in. to 11 ft. 3 in. above the coal (on plane I).

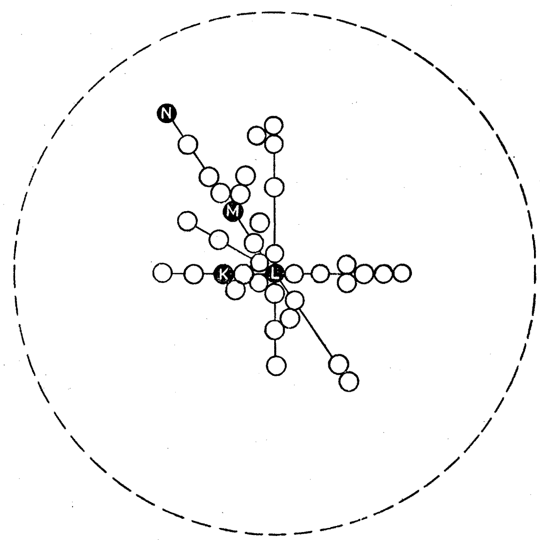


FIGURE 17. Small shells 16 ft. 3 in. to 17 ft. above the coal (on plane I).

FIGURES 15 to 18. Distribution diagrams of shells in band A, 10–17 ft. above the Soft Bed Coal, Honley. The letters in figures 15 and 16 refer to shells illustrated in figure 14; the letters of figures 17 and 18 to shells illustrated in figure 19.

(*b*) *Large shells* (figure 18)

The fauna is essentially one of large posteriorly tapered shells among which three main series may be distinguished. The first and dominant series is toward *C.* cf. *pseudorobusta* (figure 19*E*, *H*), although the shells lack the subumbonal depth of that species; the second toward *C. obliqua* (figure 19*C*, *F*), in which the periumbonal region is well swollen; and the third toward *C.* cf. *acuta* (figure 19*J*). None of the latter shells has swollen umbones, and they compare quite closely with *C. crista-galli* W. B. Wright. The dotted lines south of the norm show the projection upward of plane III of the directional skeleton with a few specimens of *C. fallax-protea* presumed to be the young of the larger group. It must be admitted that nearly the whole fauna bears a striking resemblance to one of the Pseudo-robusta subzone of the Ovalis zone.

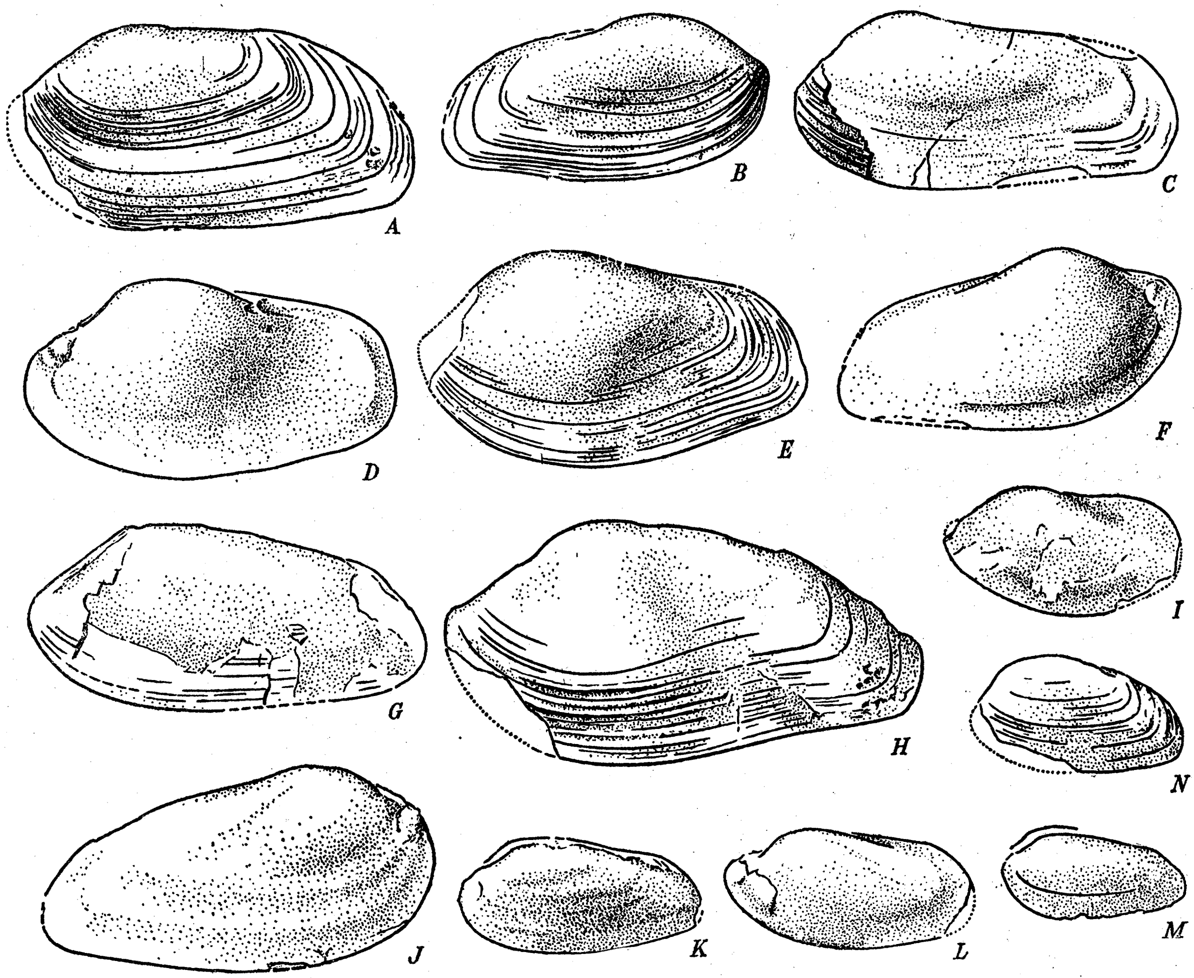


FIGURE 19. Shells from band A of the middle division of the sequence at Honley, 16 ft. 3 in. above the Soft Bed Coal. The positions of these forms are shown by letter reference on the distribution diagrams of figures 17 and 18.

There are in addition, however, a few smaller *Anthraconaia*-like shells of the *C. haberghamensis* group (figure 19*I*), which may not be in continuous variation with the remainder. They compare closely with the smaller and presumably younger shells found in a rich *C. haberghamensis* fauna 2 ft. 6 in. above this level (figures 26, 27). Since other *Anthraconaia*-like shells associated with an elongate *C. fallax-limax* fauna are present at the base of the middle division and again at the base of the upper, the chief characteristics of the two groups are summarized and contrasted below.

(1) The Anthraconaias of the finer grade shale are typically elongate, usually having a height/length ratio below 45 %.

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

Those related to *C. haberghamensis* are shorter, having a H/L ratio typically above 45 % and ranging up to 60 %.

(2) Subparallelism of the upper and lower borders is typical of the Anthraconaias of the finer shale, which usually have posterior inferior angulation.

In the shells related to *C. haberghamensis* the lower border is typically very well rounded so that it frequently passes with continuous sweep into the hinge line.

(3) There is more swelling of the umbonal region in the anthraconaioid variants of *C. haberghamensis*, and the umbo may project above the hinge line.

(ii) Band B, middle division, 18 ft. above the coal

General account

Preservation of the shells in black, slightly sulphurous shale is poor. Nearly all have been totally crushed laterally. *Spirorbis* is exceptionally abundant.

The fauna (figure 20) consists of large shells of the *C. protea* group and has distinct individuality through the presence of a striking newly recorded trend, extreme representatives of which have been assigned to a new species, *C. discus*;* figure 20*E* shows the holotype, a full description of which is given in a later section.

The most distinctive features of the community are a very high H/L and A/L ratio with subcentralization of the umbones in the more extreme forms and generally a marked loss in shell angulation.

TABLE 3

	L in mm.	H/L %	A/L %
number of specimens	17	17	11
limits of range	30–52·5	52–72	24–35
mean value	39	63·1	30·1
approximate mode	39	64	32

With the exception of a somewhat similar related fauna 8 in. to 1 ft. 3 in. above this band, the mean and modal values for H/L percentage are 9 % higher than the nearest values found for other collections at Honley, while the anterior end-length percentage is $3\frac{1}{2}$ % higher than in the *C.* cf. *pseudorobusta* fauna 1 ft. below band B, where this value is most closely approached. The fauna occurs at the extreme top of the lower rhythmic development of the middle division, being associated with a little pyrite and immediately preceding a return to a slightly lower grade. The increase in mean and modal H/L and A/L ratios observable through band A (tables 1 and 2) is thus further continued to a higher level in the rhythmic unit.

Analysis of the variation (figure 20)

Norm and series 1. The central norm differs from the holotype of *C. protea* chiefly in having slightly greater relative height (figure 20*B*). Simple shortening with slight increase in curvature of the lower border, series 1*A*, leads to an accessory norm (figure 20*C*). Simple lengthening of the central norm is shown in series 1B (figure 20*A*).

Series 2A–C. The three series, considered as derived from the accessory norm, are closely related to one another, and in each case further shortening and rounding of the lower

* The species was named only after it had been found of stratigraphical value over a wide area.

border is seen. In series 2 A (figure 20*C*, *D* and *E*) posterior truncation is first lost (compare figure 20*D* and the earlier growth lines of figure 20*C*). Further shortening from *D* to *E* leads towards subcentralization of the umbones and some elevation of the hinge line. The resultant subcircular form is *C. discus* n.sp. (figure 20*E*). In series 2 B shortening with loss of angulation proceeds without raising of the hinge line, the resultant form, figure 20*H*,

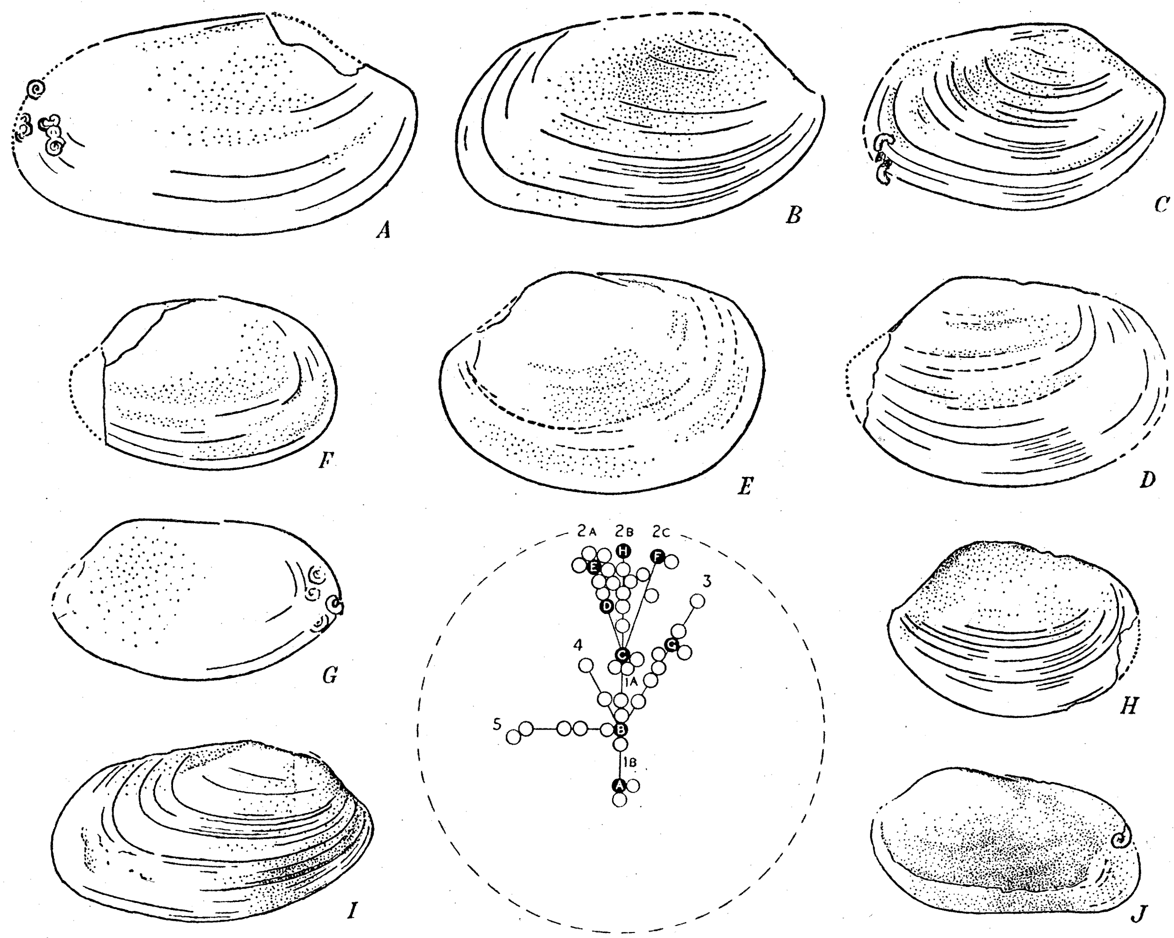


FIGURE 20. Distribution diagram with illustrated variants (*A–H*) of the fauna of band B of the middle division of the sequence at Honley, 18 ft. above the Soft Bed Coal. The shells figured as *I* and *J* are from the fauna 18 ft. 9 in. to 19 ft. 6 in. above the coal (lower part of band C), and illustrate the distribution diagram of figure 22.

comparing slightly in outline with *C. bella* Davies & Trueman. Series 2 C (figure 20*F*) shows with slight shortening some rounding of the shell angles, curvature of the hinge line and expansion to the posterior. The tendency may thus be towards extreme short forms associated with *C. haberghamensis* 2 ft. above this level.

Series 3 (figure 20*G*). This is derived from the first (central) norm. Rounding of the lower border and later the shell angles (cf. figure 20*I*) and posterior retreat of the position of maximum depth lead to an anthracomyoid outline; and with swelling and elevation of the umbones these features would lead on to *C. haberghamensis*. Figure 20*G* approaches the latter species, but the umbones are insufficiently raised.* There appear to be no typical

* When laterally crushed, specimens of *C. haberghamensis* are difficult to identify since the well swollen umbonal region may be crushed in a number of ways and may not always project above the hinge line.

C. haberghamensis and the series is probably best considered as one of incipient forms developing from *C. protea*.

Series 4. The extreme posterior part of the lower border of the norm (figure 20*B*) is very slightly reflexed. Two shells show further straightening of the lower border with the same amount of reflexion and slight tendency toward rectangular form.

Series 5. Rounding of the shell angles of the first norm and slight raising of the hinge line produces forms tending towards *C.* cf. *ovalis* closely comparable with figure 27*A* and *B*. They are little removed from the rounded forms of series 2, differing from these essentially in their greater length.

From the distribution diagram it is seen that a large proportion of the fauna lies between simple short variants of *C. protea* and rounded forms with subcentral umbones associated with *C. discus*, a number of others showing a tendency towards *C. haberghamensis*. There is a striking absence of elongate shells.

The fauna is distinctive by reason of the mode of growth of the shells. At the type locality of *C. protea* there is a growth series from the direction of small elongate shells near *C. fallax* towards *C. protea*, progressively larger and relatively higher shells being found as the norm is approached (central series of plane III of the standard diagram, figure 3). In this community *C. fallax* is not present. Small apparently young shells are usually relatively high, having well-rounded lower borders and sometimes subcentral umbones. Thus while there are several forms common to both these faunas the growth series which led up to them were apparently different in most cases. Probably increase in relative height with growth took place chiefly in the earliest developmental stages in the *C. discus* fauna. Compare with figure 20*H* the early growth lines of figure 20*C*, figure 40*B*, and also young specimens of *C. haberghamensis*, figure 27*J*–*N*.

(iii) Band C, 18 ft. 9 in. to 20 ft. 3 in. above the coal

The shale (grade 3–4) is slightly finer than that of the preceding horizon and shows no appreciable change through the thickness of the band. Large shells are present throughout, while there are three courses of small shells at 19 ft. 6 in., 20 ft. and 20 ft. 3 in. above the coal. The latter are distinct from the larger group and are treated separately.

(*a*) *Small shells*

The faunas of the leaves 20 ft. and 20 ft. 3 in. above the coal appear identical and only those of the 20 ft. and 19 ft. 6 in. horizons are described below.

The lower leaf consists of a single layer of shells and is an undoubted community, no large shells having been found exactly on its horizon. The middle leaf, however, shows well-preserved ironstone moulds of small shells intimately mixed with larger moulds of *C. haberghamensis* and associated forms. That the two groups are distinct Linnean species is clear at once from a brief comparison of figure 27*a*–*j* and *k*–*r*. When height is plotted against length it is interesting to compare the clear separation of small and large shells with the less perfect separation of somewhat similar smaller and larger sized groups at the top of band A, 2 ft. 9 in. below this horizon (figures 12, 13).

Further speciation in the small shell group is apparent from a comparison of the faunas 19 ft. 6 in. and 20 ft. above the coal (figure 13 and table 4). Both faunas show comparatively limited variation which is quite different in each.

TABLE 4

level above the coal	mean length in mm.	mean *H/L* ratio	modal *H/L* %	mean *T/L* %	mean *A/L* %
20 ft. 0 in.	25·8	43·4 (24)	41·8	30 (22)	21·2 (22)
19 ft. 6 in.	19·2	50·7 (20)	48·3	26·6 (10)	24·2 (17)

The figures in brackets refer to the number of specimens available for measurement.

It seems perfectly clear that within the upper 9 in. of band C there are three distinct Linnean species (figure 13), two of which lived apparently contemporaneously. How far we are dealing with evolution and how far with the migration of pre-existent species is not at present clear. The writer, however, has evidence from other horizons in the Lenisulcata zone pointing to a similar division of the shells comparable with *C. fallax*, in each case the difference being one of smaller size and greater *H/L* ratio of the smaller group. Separation of a group of small shells from a large shell group (*C.* aff. *protea*) has been found as low as the Pot Clay Coal in Yorkshire.

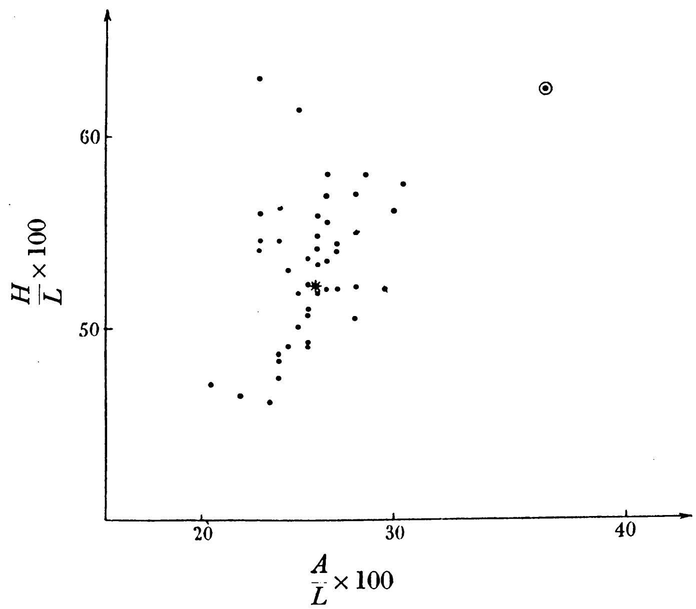


FIGURE 21. Scatter diagram of a community of *Carbonicola haberghamensis* from band C of the middle division of the sequence at Honley, 19 ft. 9 in. above the Soft Bed Coal. Symbols show the positions which would be occupied by the holotype of *C. haberghamensis* ∗, and the paratype ⊙.

(1) *Lower leaf* 19 *ft.* 6 *in. above the coal.* Preservation is poor and lateral crushing fairly common. It is clear from the distribution diagram (figure 24) that for a fauna from the Lenisulcata zone variation is unusually limited. The following points call for emphasis:

(*a*) The mode of the fauna is centred around forms which appear to be simple short variants of *C. fallax*, blunt posteriorly and with slightly more curved lower border than is typical of that species: the lower border is curved in thirty out of thirty-three shells.

(*b*) All the shells are smaller than the holotype of *C. fallax*, the majority being two-thirds of its length.

(*c*) The proportionate height of 95 % of the specimens is greater than that of *C. fallax*. The calculated mode might be greater if more specimens were available.

Many of the shells compare in outline with *C. protea* (figure 27*m–o*) and in a system of nomenclature which disregarded the criterion of size they would aptly be called *C.* aff.

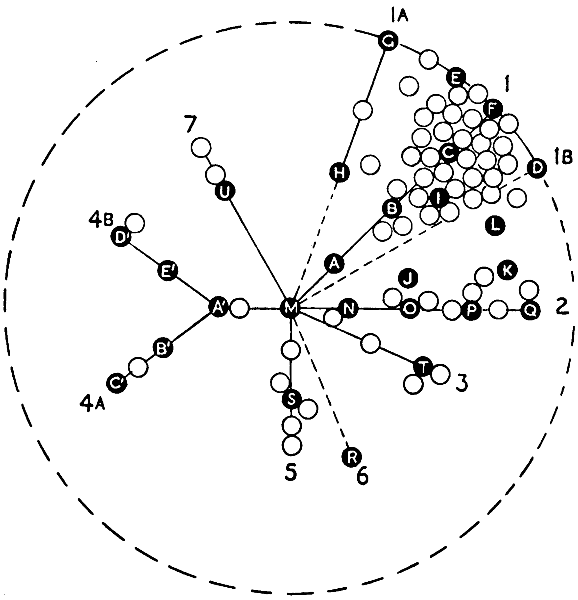


FIGURE 23. Large shells 19 ft. 9 in. to 20 ft. above the coal (on plane II).

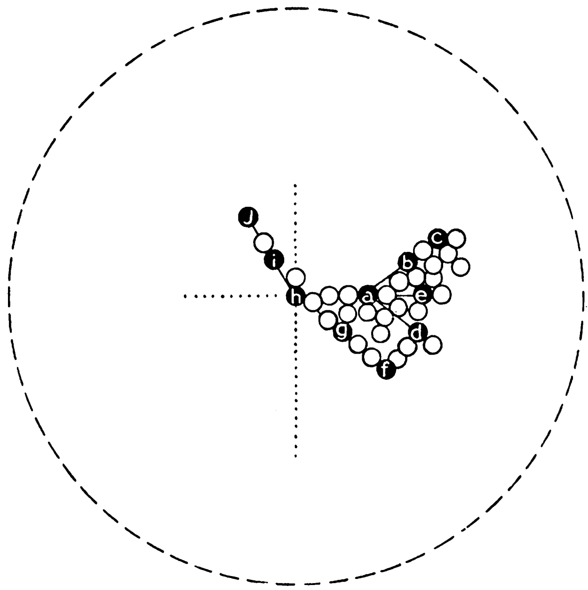


FIGURE 25. Small shells 20 ft. above the coal (on plane I).

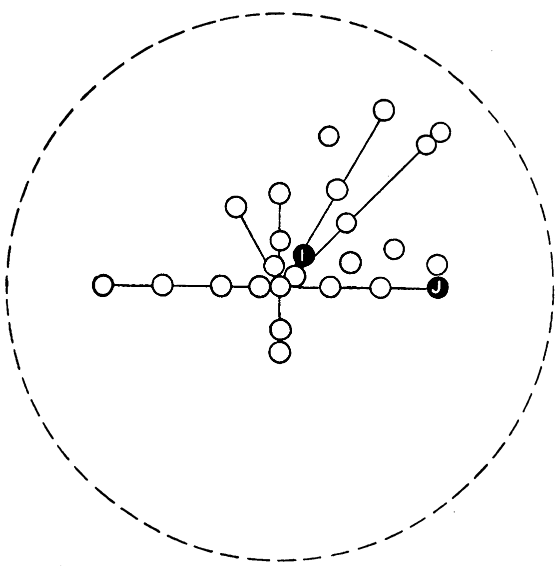


FIGURE 22. Large shells 18 ft. 9 in. to 19 ft. 6 in. above the coal (on plane II).

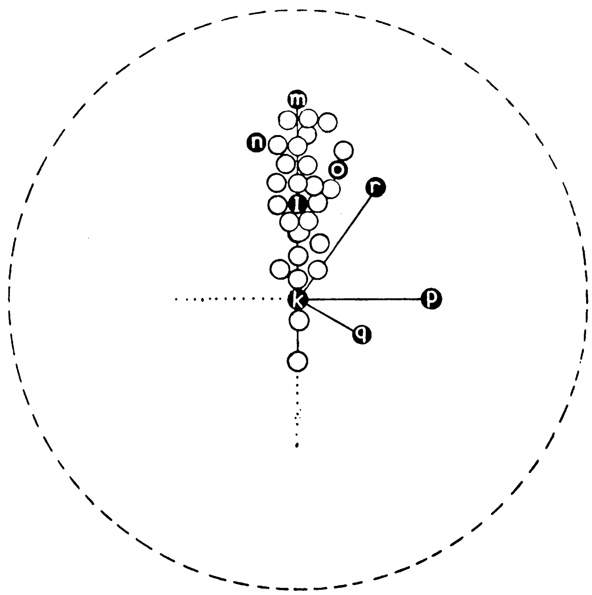


FIGURE 24. Small shells 19 ft. 6 in. above the coal (on plane I).

FIGURES 22 to 25. Distribution diagrams of shell faunas in band C of the middle division of the sequence above the Soft Bed Coal at Honley. The letters of figure 22 refer to the shells of figure 19; those of figure 23 to shells of figures 26 and 27 (letters with a dash); those of figures 24 and 25 to the small shells of figure 27.

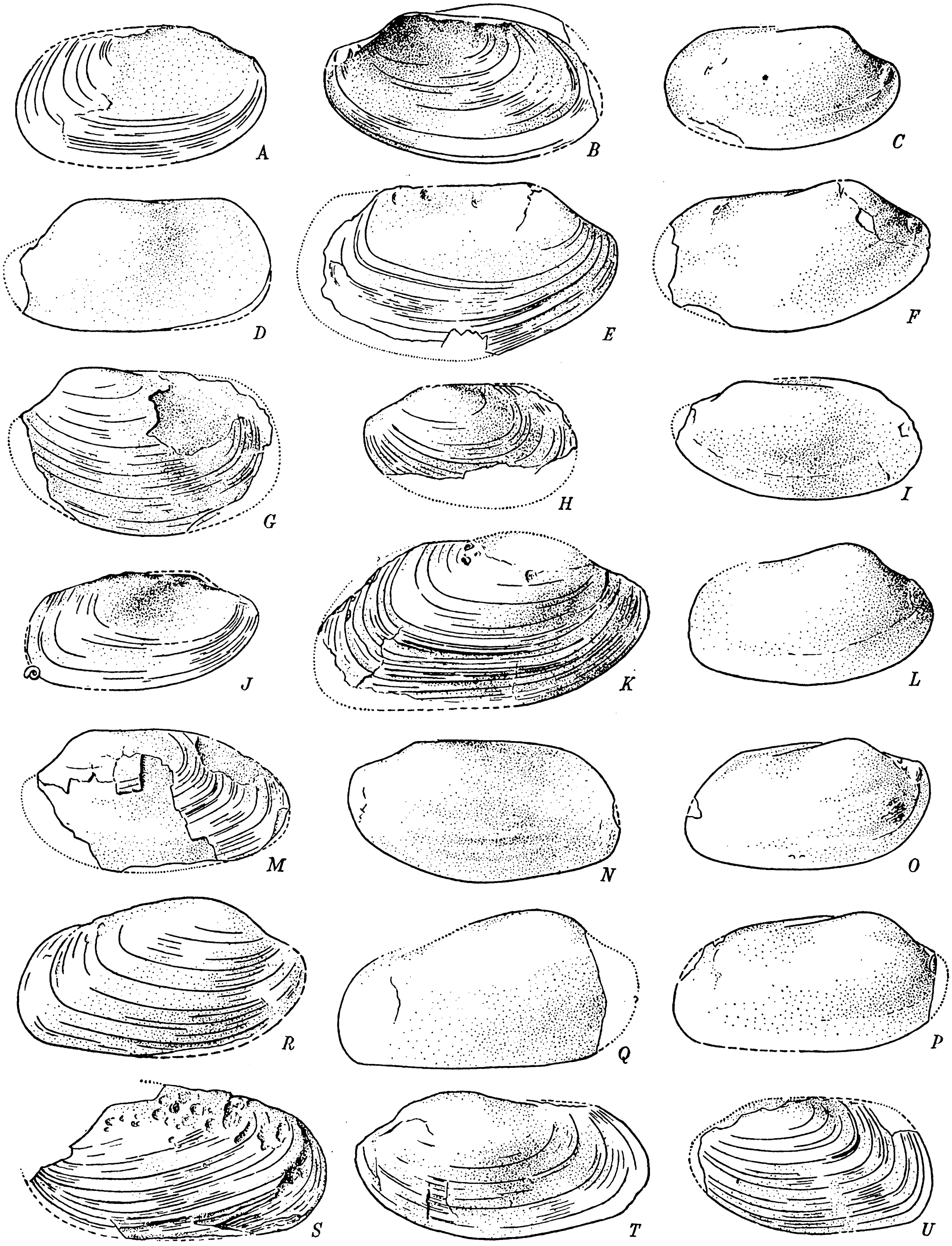


FIGURE 26. Shells from band C of the middle division of the sequence at Honley, a community of *Carbonicola haberghamensis* 19 ft. 9 in. to 20 ft. above the Soft Bed Coal, illustrating by letter reference the distribution diagram of figure 23.

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

protea (small). There appears, however, to have been usually a rapid increase in relative height with growth. They are provisionally termed here a community of *C.* cf. *fallax*.

(2) *Middle leaf* 20 *ft. above the coal*. Preservation is good, variation comparatively limited (figures 25, 27 *a–j*), and the character of the fauna well marked. The most distinctive features of the fauna are elongation, a typically straight or slightly reflected lower border with straight parallel growth lines and a short high anterior end. Posterior truncation is blunt or oblique.

With the above features the outlines of several shells resemble those of *C. obliqua* (figure 27 *a*, *f* and *g*). The shape of the solid shell, however, apart from the more obvious differences of size and associated forms, is sufficient to distinguish these shells from *C. obliqua*. In the latter (see figure 39(*b*), p. 52) there is a periumbonal bulge, anterior and posterior to which the shell tapers, tending to flatten out at the margins. In dorsal view the shells of this community are fairly tumid for about two-thirds of their length (figure 27*I*(1)–(3)). Generally there is some carinal swelling, typically strongest in internal moulds, which passes obliquely backwards from well behind the umbo towards the posterior inferior angle. Anterior to the carinal swelling there may be a flat area or very slight hollow or constriction which, when strong, is associated with the reflexion of the lower border (figure 27 *e*).

Most of the specimens are therefore referable to *C. fallax* (figure 27 *h*), *C.* aff. *fallax* and *C.* cf. *recta* (elongate) (figure 27 *b*, *d*). Figure 27 *a*, *C.* cf. *declivis* Weir & Trueman, seems the most typical form, but the similarity of the shells in all the series should again be emphasized.

(*b*) *Large shells*

Collection has been made throughout the band. The fauna at the base, 18 ft. 9 in. to 19 ft. 6 in. above the coal (figure 22), is essentially one of *C. protea* (figure 20*I*) with trends toward *C. haberghamensis* and *C.* cf. *obliqua* (figure 20*J*). Dimensionally and from the point of view of variation it is to some extent intermediate between the fauna of *C. discus* and associates 3 in. below it and that of *C. haberghamensis* into which it passes upward (table 5, showing also for comparison measurements of the types of *C. haberghamensis*). No representatives of *C. discus*, however, have been found, although *C. haberghamensis* is present.

Table 5

height above coal	mean L in mm.	mean H/L %	modal H/L %	mean T/L %	mean A/L %
19 ft. 9 in. to 20 ft. 0 in.	41·3	53	54·3 (57)	32·4 (27)	25·5 (53)
18 ft. 9 in. to 19 ft. 6 in.	43·7	55·3	56·7 (16)	—	25·3 (12)
C. haberghamensis:					
holotype	50	52		30	26
paratype	46	62		30	38

The figures in brackets refer to the number of specimens available for measurement.

Ironstone lenticles 19 ft. 9 in. to 20 ft. above the coal yield well-preserved internal and external moulds, frequently uncrushed. Although the range of variation is fairly large (figure 26), the dominant element of the fauna, comprising about 60 % of the shells shown on the variation diagram, is that of *C. haberghamensis*. Both with respect to outline (figure 26*F*), solid shape and dimensions (table 5 and figure 21) the mode of the fauna is situated very near the holotype of that species, although most of the shells are slightly

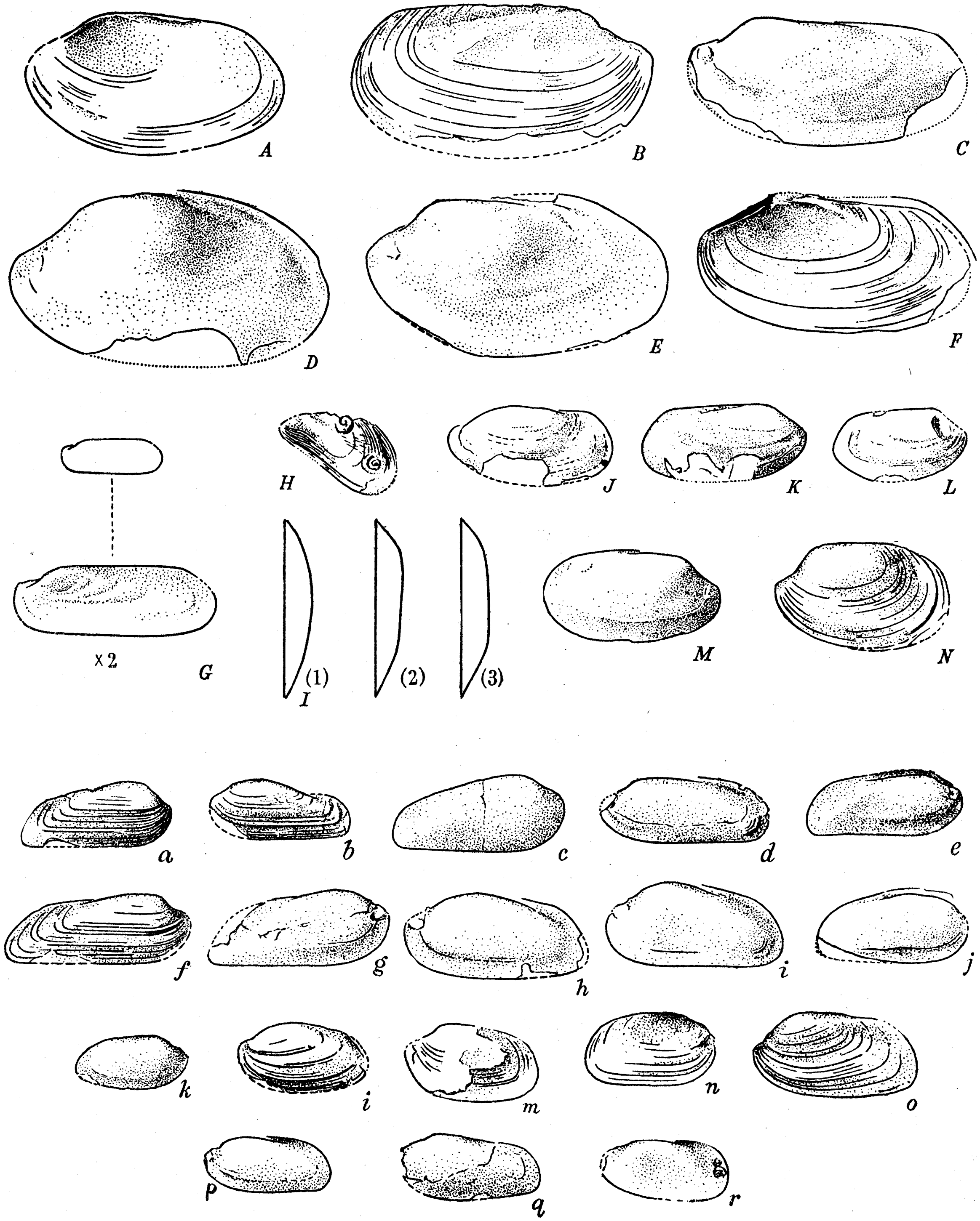


FIGURE 27. Shells from band C of the middle division of the sequence at Honley above the Soft Bed Coal. *A–F*, 19 ft. 9 in. to 20 ft. above the coal, illustrate the distribution diagram of figure 23, on which letter reference is made with a dash (*G*, *H* and *J–N*, also from this horizon, are not included in the diagram). *a–j*, 20 ft. above the coal, illustrate the distribution diagram of figure 25 (*I* showing dorsal profiles of this community). *k–r*, 19 ft. 6 in. above the coal, illustrate the distribution diagram of figure 24.

smaller. At this level, however, there has been found no shell near the paratype of *C. haberghamensis** (figure 21), which appears more comparable with certain forms associated with *C. discus*. It is worth noting that the upper limit of the *A*/*L* ratio for the fauna from 19 to 20 ft. above the coal is 30·5 %, while the value for the paratype is 38 %.

The most distinctive characteristics of the fauna are the well swollen umbo, typically, but not invariably, rising above the hinge line, and the loss of shell angulation (figure 26*A*–*I*). Forms tending towards *C. obliqua* (figure 26*M*–*Q*) appear to be in continuous variation with the *C. haberghamensis* group having the same tumid periumbonal region. The remaining variants are referable to *C. protea* (figure 26*R*), *C.* aff. *protea* (figure 26*M*), *C.* cf. *ovalis* (figure 27*B*, *C*) and rarer forms to be later described.

Analysis of the variation

Specimens illustrating the distribution diagram (figure 23) are shown in figures 26 and 27.

Norm and series 1. The norm (figure 26 *M*) differs from the holotype of *C. protea* in having greater proportionate height and increased rounding of the lower border. In series 1, *C. haberghamensis* appears to grade with this form by increase of posterior depth and loss of posterior inferior angulation (figure 26*A*), followed by inflation and raising of the umbones and greater expansion posterior to the umbo. (Compare in order figures 26*M*, 20*I*, 26*A*, *B*, *C* and *F*: the latter is identical with the holotype of *C. haberghamensis*.) The shorter varieties, series 1 A, have less swollen umbones which are scarcely raised above the hinge line. They compare with certain forms from the *C. discus* fauna, being here rather uncommon and typically small. Series 1B shows more elongate shells in which the umbonal region is strongly tumid.

Series 2. In figure 26 *M*–*Q* is seen the gradual development of a trend toward *C. obliqua* from *C.* aff. *protea* by slight elongation with subparallelism of the upper and lower borders (*N*), gradual straightening of the lower border with umbonal swelling and elevation (*O* and *P*) followed by further umbonal elevation (*Q*). Figures 26*P* and *Q* differ from *C. obliqua* chiefly in their greater height and more blunt posterior truncation. This series, next in numerical strength to *C. haberghamensis*, appears fairly closely associated with that species especially with regard to solid form, in which most members of both series differ markedly from *C. protea*. There are a number of intermediate forms which are of particular interest from the point of view of their growth lines (e.g. figure 26*J*, *K*).

Series 3 (figure 26*T*). Four shells show slight posterior tapering, broad umbonal swelling and in two cases slight constriction of the lower border (compare figure 26*T* with figure 19*B*, *E*).

Series 4 (figure 27*A*–*E*). Rounding of the lower border with raising of the hinge line produces forms comparable in outline with *C. ovalis*. From figure 27*A*, considered as an accessory norm, two series may be derived, in each of which is found further rounding of the lower border accompanied by progressive elongation in series 4A and shortening in series 4B. Both series appear closely related to *C. haberghamensis* and there are found between series 1 and 4 a few shells which cannot be placed on the diagram, one of which (figure 27*F*) is illustrated.

* The paratype of *C. haberghamensis* has been photographed (figure ix, plate 1) and is refigured on p. 51.

Series 5. Simple elongation of the norm is illustrated by figure 26*R*, which is very near but slightly more tapered posteriorly than the holotype of *C. protea*. In the shells of this series there is no appreciable periumbonal swelling.

Series 6. Figure 26*S* shows an incomplete specimen of a rare form which may approach in outline *C. retrotracta* W. B. Wright. It appears nearest figure 26*R* and shows considerable erosion in the posterior region of the hinge line.

Series 7. Three specimens show shortening of the norm, straightening of the lower border and squaring of the truncation with approach to rectangular outline (figure 26*U*). There is no periumbonal swelling.

Young forms of *C. haberghamensis* (figure 27*J*,–*N*) have already been described in the account of band A, 2 ft. 9 in. below this horizon. Amongst these and larger shells was found a very small flattened cast (figure 27 *G*). It is difficult to believe that this shell bears any relation either to those of the *C. haberghamensis* group or those of the *C. fallax* group. It resembles certain variants of *Anthraconaia bellula* from above the Six-Inch Mine of Lancashire. *Anthraconauta* cf. *minima* (figure 27*H*) and *A.* aff. *scotica* have also been found, but are rare.

Summary

To sum up, the fauna of large shells of the upper part of band C of the middle division is distinguishable essentially by those features which characterize the holotype of *C. haberghamensis*, a high well-swollen umbo and a large shell devoid of angulation. There is, however, a definite trend toward *C. obliqua* which appears closely related to *C. haberghamensis*. Other trends are weakly represented, the more important of which are the oval shell development (*C.* cf. *ovalis*) and those forms near *C. protea* longer than the norm. No shell remotely like the paratype of *C. haberghamensis* has been found at this horizon.

(iv) Band D, 22 ft. 6 in. above the coal

A small collection has been made from the thin band of large, crushed and very poorly preserved shells at the extreme top of the rhythmic unit. All appear to belong to the *C. protea* group having curved lower borders and a high H/L ratio. Smaller specimens are comparable with young forms of *C. haberghamensis* and possibly *C. discus*.

(v) Summary of the fauna of the middle division

Lithologically the middle division (grades 1–5) is divided into two rhythmic phases separated by a small oscillation (to grade 3, see figure 7*a*). In both phases small, rather elongate, shells are finally followed by exclusively large and relatively high shells.

Band A, 7 ft. thick, occupies most of the lower phase. Within it, with upward coarsening in grain size of the shale (from grade 2 almost to grade 5), there is a progressive increase in the modal H/L ratio of the shells from 42·4 to 48·4 and 51 % (for large and small shells respectively). This increase is continued to 64 % in band B (grades 4 and 5, see figure 7*a*) at the top of the lower rhythmic phase. Detailed work in band A shows that the increase is not always perfectly smooth. The following facts however are clear:

(*a*) With upward modal increase in H/L ratio there is also an increase in the mean A/L ratio: this is continued also to band B.

(*b*) There is typically, but not invariably, a slight increase in shell size upwards in the unit. Although this may account partly for the increase in H/L ratio it is certainly not entirely responsible for it.

(*c*) The fauna is dominantly *Anthraconaia*-like at the base of the band, the forms apparently in continuous variation with *Carbonicola*. Passing upward in the band the *Anthraconaia*-like forms greatly diminish in number and towards the top the fauna consists entirely of *Carbonicola*.

(*d*) Variation is greatest in the middle of band A, many of the shells being intermediate between *C. fallax* and *C. protea*. At the top of band A there is a large and small shell group which appears more or less distinct (figure 12). In band C speciation is perfectly distinct (figure 13), although small and large shells appear to have lived contemporaneously at one horizon. There is also in band C a clear division of a community of smaller shells from one consisting of *C. fallax* and associates. In both communities the variation is markedly limited and quite different for each.

(*e*) The faunas, particularly in bands C and D, have distinctive characters. The more important horizons are: *C.* cf. *pseudorobusta* at the top of band A; *C. discus* n.sp. in band B; *C. haberghamensis* in band C.

(III) Upper Division

(i) General account of the fauna and its principal changes

The succession from *Lingula* upward through fish debris and *Anthraconauta* to an *Anthraconaia*-like fauna is shown in figure 7*c* Leaves of shells continue upward for 6 ft. 3 in. in coarser shale, being abundant and better preserved in the lower portion of the band (grade 2–3). In the upper 4 ft. there is very little change in shale grade, the highest reached being about 4, which is slightly lower than that found at the top of band A of the middle division. Material collected through some thickness appears homogeneous, but evidence from thin bands suggests that variation at certain levels in the upper portion of the band may be discontinuous.

The shells show a general increase in H/L ratio when traced upward in the lower portion of the band.

TABLE 6

height above coal	number of measurable specimens	mean L	range H/L %	mean H/L	modal H/L
29 ft. 6 in. to 30 ft. 3 in.	23	26·6	40–53	47	46·4
26 ft. 0 in. to 29 ft. 6 in.	54	28·4	39–56	46·8	46·7
24 ft. 3 in. to 26 ft. 0 in.	31	23·9	37–54	44·1	42·9
24 ft. 0 in. to 24 ft. 3 in.	9	23·5	37·5–50	42·8	—

These figures for shell H/L ratios compare closely with those of shells from corresponding levels in the middle division (band A, table 1). The increase, however, is not so far continued.

The chief difference in the corresponding portions of the tables is seen in the smaller size* of the specimens from the lowest horizons of the upper division. A general tendency

* Small shells comparable in size with these occur at the extreme base of band A of the middle division where poor preservation prevents many specimens from being collected.

to increase in size with extension of the upper size limit in higher horizons is, however, present as in the middle division and is best seen in figure 28. The graph should be compared with that for corresponding levels in the middle division (figure 11). In both graphs the smaller shells of the upper and lower horizons are indistinguishable with regard to

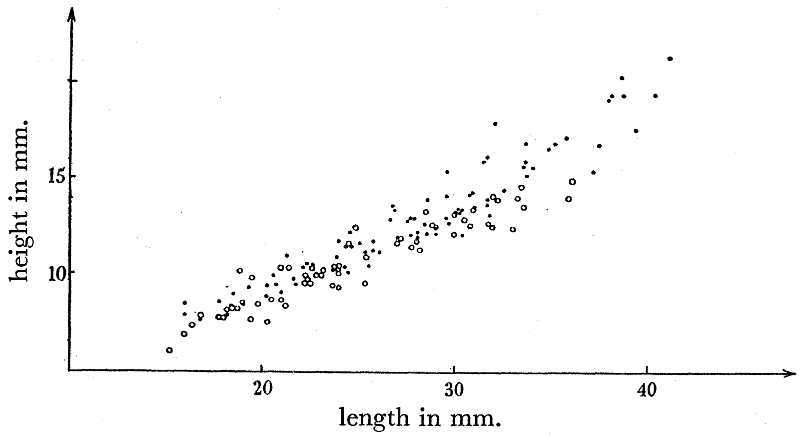


FIGURE 28. Measurements of shells from the upper division of the sequence at Honley. The circles refer to shells collected 24 to 26 ft. above the Soft Bed Coal and the dots to shells 26 ft. to 30 ft. 3 in. above the coal.

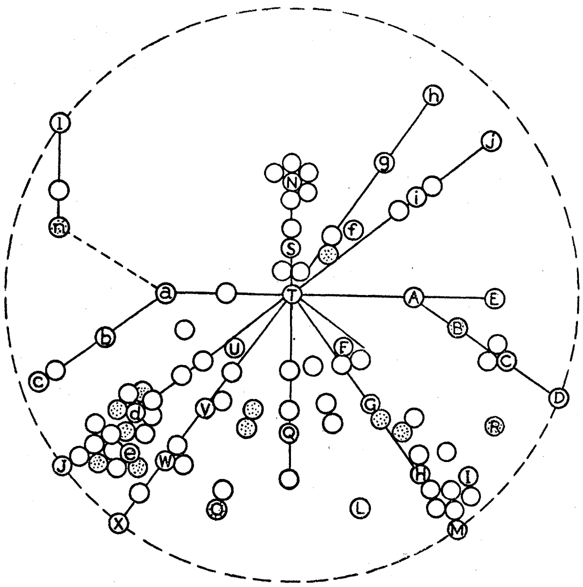


FIGURE 29. Distribution diagram (on plane I) of shells from the upper division of the sequence at Honley, 24 to 26 ft. above the Soft Bed Coal. The letters refer to the shells illustrated in figure 31. The positions of shells 24 ft. to 24 ft. 3 in. above the coal are shown shaded.

height and length, while with further growth the faunas become differentiated in the same manner. From the roughly curved paths of dots in each case it appears that the predominant mode of growth has changed in the coarser beds from one of constant or decreasing, to one of increasing H/L ratio. It is again clear that the increase in H/L ratio is due not only to increase in size.

The mean A/L ratio, 19·6 % for shells 24–26 ft. above the coal, shows no appreciable change between the selected shale intervals in table 6. Its values, with those of the T/L ratio, will be referred to in the more detailed account of faunal changes to be given later.

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

The fauna of the lowest portion of the band is dominantly *Anthraconaia*-like (figures 29, 33). Although the variation in the lowest 2 ft. is considerable, many shells compare very closely with those collected in the basal fauna of the middle division (compare figure 14). The shells pass upward into a fauna consisting almost entirely of *Carbonicola* aff. *fallax* and elongate *C.* ? aff. *recta* (figure 34), variation being continuous throughout. The change is somewhat similar to that described at the base of the middle division (figures 15, 16). In the upper 4 ft. of the band (figure 30) *Anthraconaia*-like forms recur with *C.* aff. *fallax*, *C. limax*, *C.* cf. *sulcata*, *C. fallax-protea* and occasionally *C. protea* (figure 32*a*). Several of these larger and relatively higher forms are comparable with those occurring in the middle and upper portions of band A of the middle division. The fauna of the upper division, however, has certain characteristic features which distinguish it as a whole from that of the middle division. These are best seen when the corresponding middle and upper portions of the rhythmic units are compared.

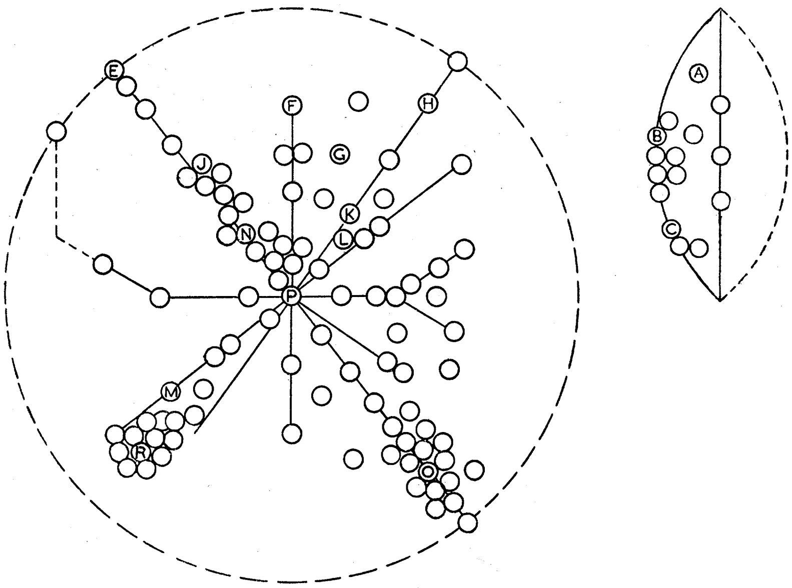


FIGURE 30. Distribution diagram (planes I and III) of shells 26 ft. to 30 ft. 3 in. above the Soft Bed Coal, Honley, the letters referring to the illustrated variants of figure 32.

(ii) Description of the fauna and its variation

The main lamellibranch fauna consists of shells of the *fallax-limax* group in which the *C. limax* element is conspicuous. Recognizable variants of *C. fallax* and *C. limax*, however, are found intergrading with a varying proportion of shells which on their outline would undoubtedly be identified as *Anthraconaia*. Many of them compare closely with forms illustrated by Wright (1934*b*), although several other varieties are newly recorded. Their relations with *Carbonicola*, particularly *C. limax*, are very close, and their general characteristics have already been described in the account of the lowest fauna of the middle division (p. 32). Some are very near *Anthraconaia bellula* and *A. lenisulcata* (Trueman 1929, p. 94), but they are all smaller than the holotype of the latter. In the following sections they are provisionally termed anthraconaioids; it is hoped to discuss their taxonomic status in a later paper.

The gradation of an anthraconaioid with *Carbonicola fallax* has been demonstrated by Wright (1934*b*). The writer would emphasize their even closer relationship with *C. limax* and shorter dorsally arched *Carbonicola*.

The holotype of *C. limax* has been photographed and refigured. Figure 37*a* shows a hinge line considerably higher in the posterior portion of the shell than is indicated in Wright's figure (figure 37*b*), while the posterior inferior angle is somewhat different.

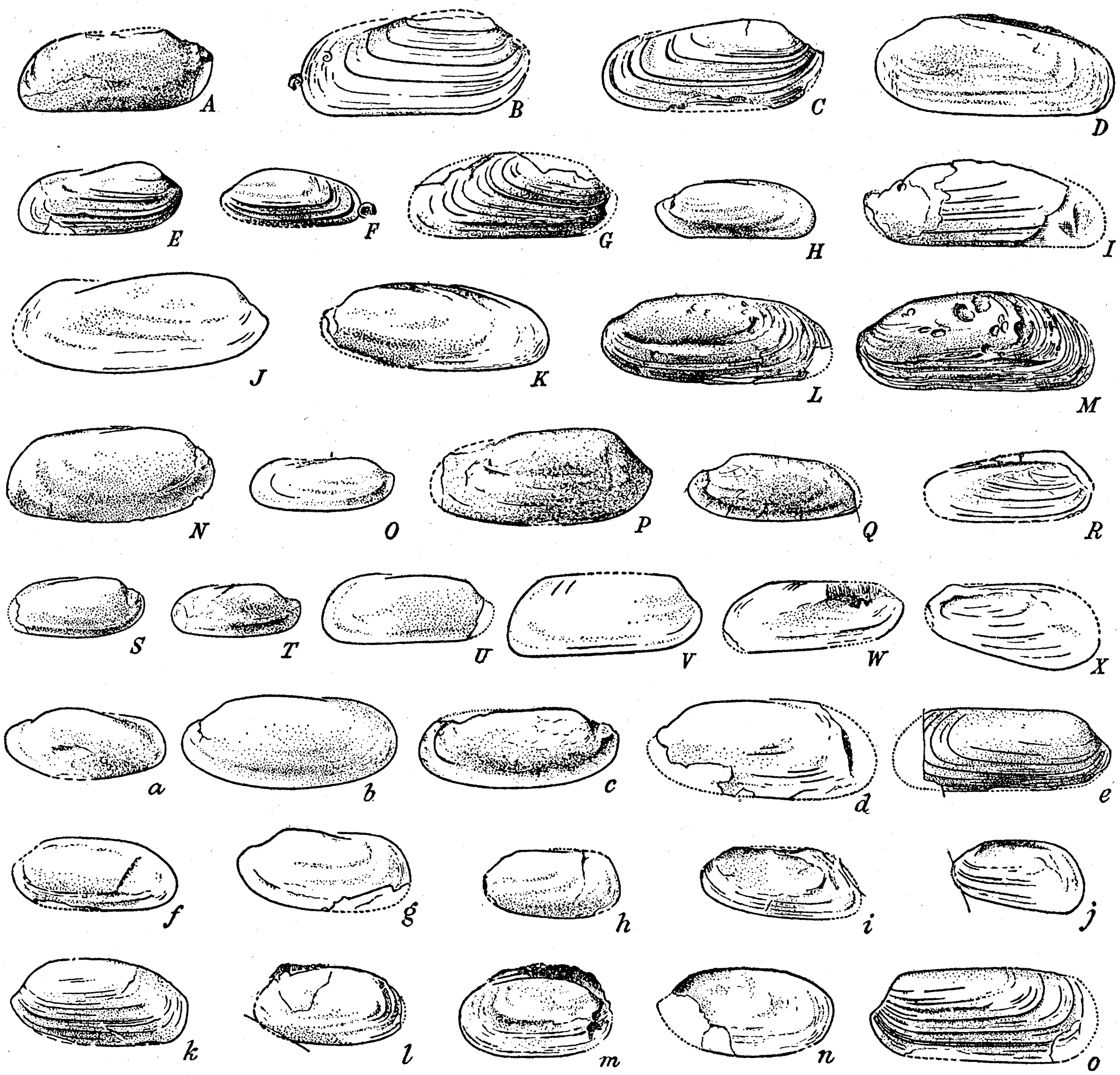


FIGURE 31. Shells from the base of the upper division of the sequence at Honley, 24 to 26 ft. above the Soft Bed Coal (with the exception of *k* which is refigured for comparison from figure 32*j*). The positions of these shells are shown by letter reference on the distribution diagram of figure 29.

Now a study of the shells of the upper division makes it clear that very slight differences in the curvature of the hinge line govern the usual interpretation of *C. limax* or an anthraconaioid shell. Such a form as figure 31*U*, with straight lower border and well-rounded or *Carbonicola*-like posterior superior angulation, requires but a slightly more curved hinge line to pass into a dorsally arched shell comparable with *C. limax*, when it would then be reorientated. Compare in order figure 31*J*, *O*, *K*, *L* and *M*. Similar transitions may be seen between a short anthraconaioid (figure 31*h*), *C*. cf. *elliptica* cf. *sulcata* (figure 31*l*) and *C*. cf. *sulcata* (figure 31*k*). (Compare in order figure 31*h*, *m*, *l* and *k*, or *h*, *m* and *n* showing differences in the curvature of the hinge line and postero-dorsal margin.)

The transitions shown on figure 33 need little further description. Figure 33*b* is clearly near *C. limax*. The shell figured as (*e*), however, could be termed an anthraconaioid, particularly if attention is paid to its younger growth stages. Yet in outline there is scarcely any essential difference between (*b*) and (*e*); furthermore, (*e*) actually compares more closely than (*b*) with the outline of the holotype of *C. limax*. Figure 33*g* is identical with

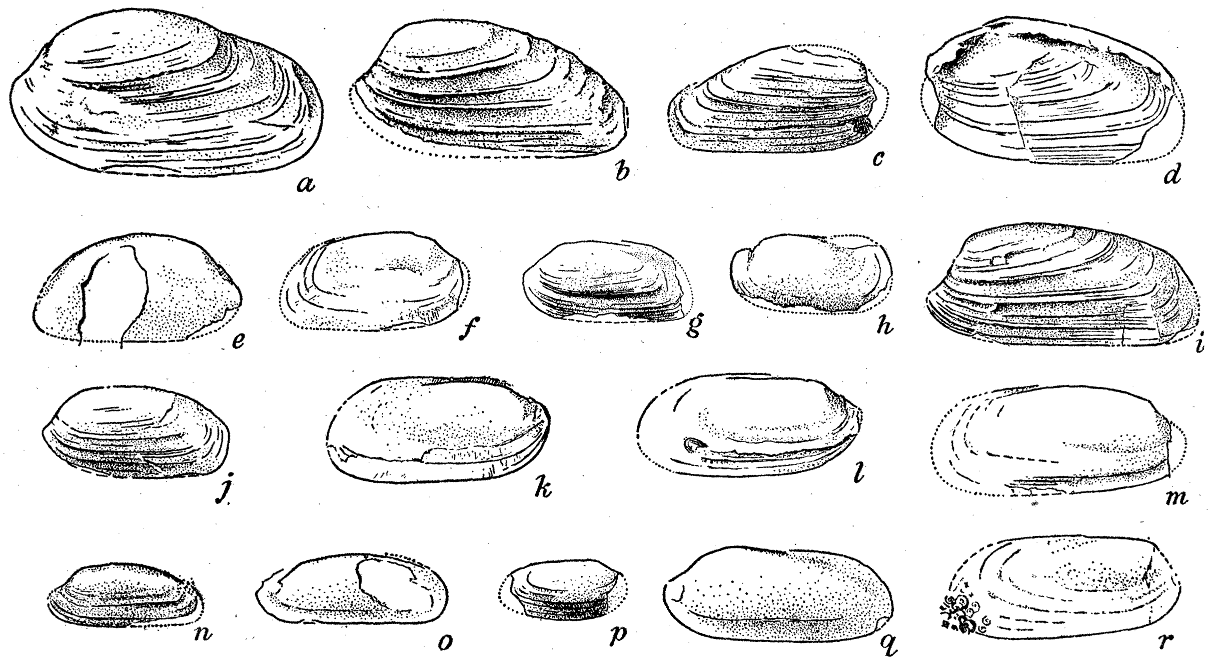


FIGURE 32. Shells from the middle and upper part of the upper division of the sequence at Honley, 26 ft. to 30 ft. 3 in. above the Soft Bed Coal. The positions of these shells are shown by letter reference on the distribution diagram of figure 30.

an early growth stage in (*e*) and could be termed *Anthraconaia* cf. *lenisulcata* (compare with figure 31*V*, *e*). Figure 33*e*, *h*, *l* and *c* all show varying degrees of difference in the curvature of the hinge line and the posterior part of the dorsal margin with straightening seen in (*e*), (*g*), (*d*) and (*a*). Similar differences may be seen in series linked up with *Carbonicola*; compare in order figure 33*g*, *h*, *f* and *b* or *h*, *g*, *i* and *k*. According to the emphasis laid on different features transitions may be traced in almost every direction as indicated by the lines drawn between the shells.

It seems, moreover, that the subtle distinction between *C. limax* and an anthraconaioid is a matter of relative growth rates and that the transition is sometimes evident in the study of a single shell. Figure 31*M* might be termed *C*. aff. *limax* or an anthraconaioid according to the emphasis laid on its several features. If the life of the animal had been somewhat shorter it would, perhaps, have been most reasonable to term it an anthraconaioid. The final shape appears to the writer nearer *C. limax*, bearing in mind that the internal mould of the shell would have a proportionately lower umbo with post umbonal slope slightly more curved. As an example of the opposite tendency developing in growth compare with it figure 31*J* whose young stages are probably near *C. limax* although the shell is now definitely an anthraconaioid.

From the above illustrations and discussion it should be clear that distinction between *C. limax* and an anthraconaioid is by no means always possible. Several poorly preserved

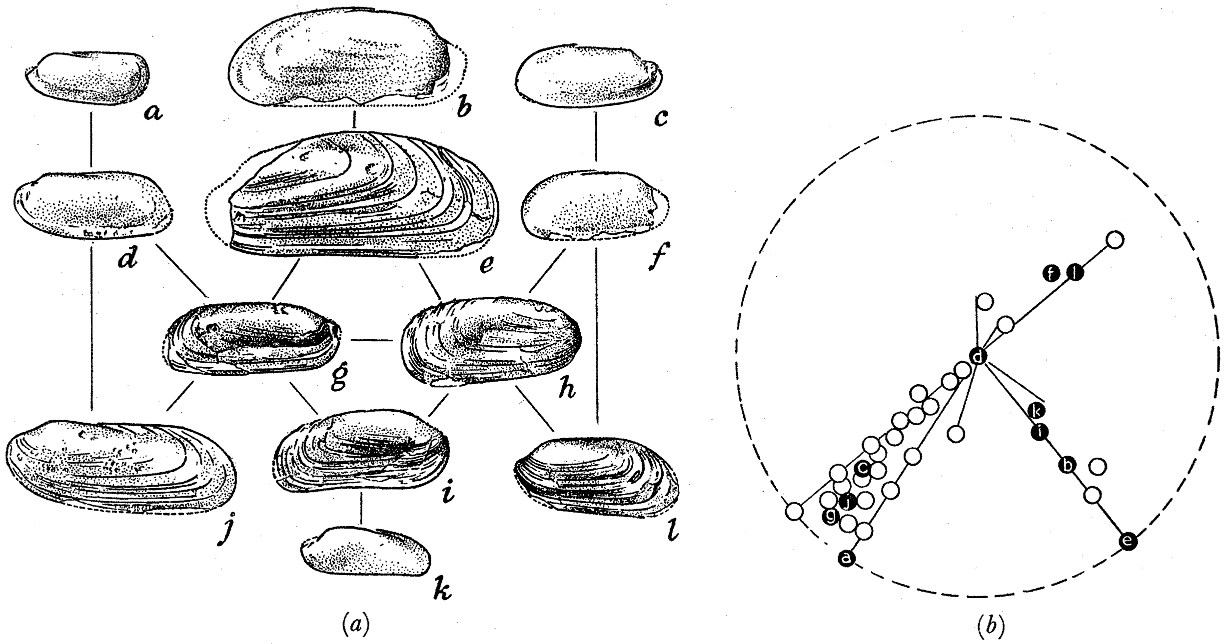


FIGURE 33

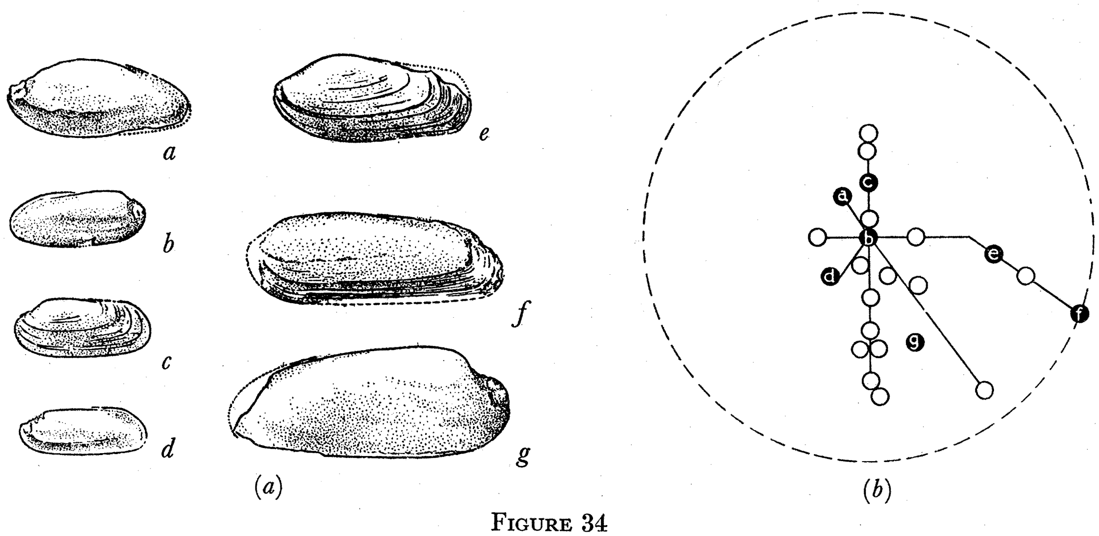


FIGURE 34

FIGURES 33, 34. Distribution diagrams with illustrated variants of shells in the upper division of the Honley sequence, in figure 33, 24 ft. 3 in. above the Soft Bed Coal and in figure 34, 25 ft. above the coal.

or indefinite types have been omitted from the distribution diagrams since they might equally well be placed with either series.

(1) *Shells 24 to 26 ft. above the coal.* The distribution diagram is shown in figure 29 and is fully illustrated (figure 31). Although the variation is very large, with the possible exception of certain short elliptical forms (figure 29*n*) it appears to be continuous.

Of the anthraconaioids the north-east and south-west series are more closely related to one another than perhaps the diagram suggests. The shells are extremely variable, but numerical strength centres around the end members of the south-west series where forms compare with *Anthraconaia lenisulcata* (figure 31*e*) and large *A.* cf. *bellula* (figure 31*d*).

The close relations of the anthraconaioids with *C. limax* (south-east series) have already been discussed. Very small shells have been omitted from the diagram. Were they included, most of them would numerically strengthen the *C. limax* series owing to the shape of their umbo, which in nearly all young shells in internal mould must form the dominant feature of the outline, although later the shell may grow into *C. fallax* or an anthraconaioid. That the *limax* series is also closely related to the elongate *C.* ? aff. *recta* series is shown by the illustrated variants.

Summary of the fauna and comparison with the basal fauna of the middle division. A comparison of figures 31*T* and 14*e* shows that the norms differ very little. Comparing the variation diagrams (figures 29, 15), the same trends are seen in both and their proportional representation is similar.

(1) Both faunas show a predominance of the anthraconaioid trend. Several variants in the two collections are virtually identical or compare very closely. (In figures 31 and 14 compare respectively *g* and *i* with *g*; *U* with *h*; *d* with *c*; *O* with *a*; and *o* with *i*.)

(2) In the upper division the series next in numerical strength is that of *C. limax*. The latter is not so strongly represented at the base of the middle division where comparable forms show a slight tendency towards *C.* cf. *acutella*. (Compare figures 31*I* and 14*k*.)

(3) In both faunas *C. fallax* is represented by forms smaller than the holotype, the norms having an H/L ratio below 45 %, and both showing slight posterior expansion; forms shorter than the norm are more common than those longer, and more common than the elongate *C.* ? aff. *recta* series. (Compare figures 31*B* and *C* with 14*j*.)

(4) Both faunas have a small proportion of short shells with curved hinge line and rounded lower border contrasting with the remainder of the variants. (Compare figures 31*n* and *l* with 14*f*.)

(5) Neither fauna shows any carinal swelling.

The close dimensional correspondence of the faunas has already been pointed out. It may also possibly be significant that in the graphs of height and length measurements, figures 28 and 11, shells are less common between the lengths 24 and 28 mm. than above or below these figures. In view of the range of the variation and the comparatively small collection made from the lower horizon the correspondence of these faunal elements from the bases of successive rhythmic units is remarkable.

(2) *Shells* 26 *ft. to* 30 *ft.* 3 *in. above the coal.* Although highly variable, the fauna has a certain individuality (figures 30, 32). The outstanding elements are the anthraconaioids, the *C. limax* series and the *C.* cf. *sulcata* series, all of which appear closely related to one another. Large shells approaching *C. protea*, shown on plane III of the direction skeleton (figure 3), have, in common with the *C. limax* and *C.* cf. *sulcata* series, an umbo slightly tilted forward and typically a curved hinge line. Throughout the fauna the lower border is generally straight or nearly straight, while the dorsal margin is frequently parallel or subparallel to it.

(1) Amongst the anthraconaioids, especially the longer forms, there is less variation in outline and less posterior expansion than in those from the lower 2 ft. of the band. *A.* ? *leni-sulcata* (figure 32*r*) is typical.

(2) Shells of the *C. limax* series are slightly more common than in the lower 2 ft., most of the shells being somewhat shorter than the holotype. With increase in H/L ratio they grade into *C.* cf. *sulcata* (figure 32*e*), or if larger into *C. fallax-protea* (figure 32*b*).

(3) Shells referable to *C.* cf. *sulcata*, absent in the lower 2 ft., are now common. The smaller forms placed in plane I of the directional skeleton compare in their shape and size with *C.* cf. *sulcata* from the coarser beds of the lower and middle divisions. With larger shells (plane III), when the form approaches that of *C. protea* (figure 32*a*) the growth lines are usually parallel or nearly parallel to the lower border in the lower half of the shell and show appreciable tilting in the upper (figure 32*b*, *c*). These specimens of *C. fallax-protea*, although comparable with those of the middle division, show less variation, having straight lower borders and typically a curved hinge line.

(4) Shells of the *fallax* series are very comparable with those in the lower 2 ft. of the band, but several shorter specimens approach diminutive *C. protea* (figure 32*f*), or a short anthraconaioid (figure 32*g*). Occasional shells referable to *C.* aff. *recta* are shorter than somewhat similar forms in the lower 2 ft. of the band. Figure 32*i*, not placed on the diagram, shows some slight resemblance to *C. retrotracta* W. B. Wright, and with the exception of the unusually low anterior end shows features typical of this fauna being nearest to the *fallax-protea* series.

To sum up: the fauna is distinguishable from that of the lower 2 ft. of the band principally by the possession of a higher H/L ratio, the addition of the *C.* cf. *sulcata* series and larger shells trending towards *C. protea*, and by the presence generally of more shells with straight or nearly straight lower borders. Anthraconaioids show more limited variation and less posterior expansion. *C. limax* is slightly more common.

(iii) Detailed changes in the fauna, 24 ft. to 30 ft. 3 in. above the coal

Of twenty specimens collected in the lowest inch of the band all are elongate anthraconaioids and are referable to the south-west series of figure 29, showing no significant difference from the forms already illustrated.

In the lowest 3 in. two-thirds of the collected fauna are anthraconaioids. The distribution of these specimens and of the remaining Carbonicolas is shown in figure 29.

A community was collected from an ironstone lenticle 24 ft. 3 in. above the coal, and a second, also in ironstone, 25 ft. above the coal. In the lower (figure 33), the fauna is 85 % anthraconaioid, while in the upper (figure 34), anthraconaioids comprise but 8 % of the fauna. The *C.* aff. *fallax* series, unrepresented in the lower, is numerically strongest in the upper community. Elongate shells with straight lower border and blunt truncation, referable to *C.* ? aff. *recta* also absent in the lower, are present in the upper community, where generally the lower border is less rounded. It is worth noting in the upper community the occurrence of a single shell (figure 34*a*), comparable with *C.* cf. *sulcata*, which is well represented in the succeeding slightly coarser shale. This faunal change, from an elongate anthraconaioid to a *C.* aff. *fallax*-elongate *C.* ? aff. *recta* fauna has already been referred to and compared with a similar change (figures 15, 16) at the base of the middle division.

A community collected midway between these horizons shows an intermediate fauna, so that the change appears to be a gradual one.

Results of the measurements of these small collections are shown in table 7.

TABLE 7

height above coal	preservation	*H/L* % range	mean *H/L* %	mean *T/L* %	mean *A/L* %
25 ft. 0 in.	uncrushed[1]	37·4–45·5	41·3 (15)	27·8 (13)	21 (10)
24 ft. 3 in.	uncrushed	37·8–48·6	42·3 (14)	26·6 (4)	15·4 (7)
	crushed	42·5–48	45·3 (9)	—	18·2 (2)
24 ft. 0 in. to 24 ft. 3 in.	crushed	37·5–50	42·8 (9)	—	17·6 (4)

The figures in brackets refer to the number of available specimens.

[1] Correction has been made for umbonal shell thickness, as discussed on p. 10.

With the transition from *Anthraconaia* to *Carbonicola* the *A/L* ratio shows a significant increase. The figures of table 7 suggest that lateral crushing may slightly increase the *H/L* ratio. Comparing the crushed shells of the 24 ft. 3 in. horizon with those of the preceding 3 in. (all crushed) there is an upward increase in the mean *H/L* ratio which may be significant.* Comparing the uncrushed shells of the 24 ft. 3 in. horizon with those 9 in. above it there is no significant change.†

The values of obesity, *T/L*, are in agreement with results from collections made through greater thicknesses. In general the ratio *T/L* is higher in a small than in a large shell and appears to be generally higher in *Carbonicola* than in an anthraconaioid.

A small collection 25 ft. 3 in. above the coal did not reveal any anthraconaioids, the fauna appearing comparable with, but slightly shorter than, that of the 25 ft. horizon.

At 26 ft. 3 in. above the coal a highly variable group of shells are mostly referable to *C. limax*, *C.* aff. *fallax*, *C.* cf. *sulcata*, *C. fallax-protea* and *C. protea* (figure 32*a*). Elongate anthraconaioids are present and it is possible that the variation is not continuous (figure 35).

At 27 ft. 3 in. to 27 ft. 6 in. above the coal the fauna consists mainly of *C. limax* and somewhat elongate anthraconaioids. Oblique *Naiadites* sp. (No. S. 12399) is also present at this horizon and is obviously quite distinct from the anthraconaioids.

In the highest collected interval, 29 ft. 6 in. to 30 ft. 3 in. above the coal, a *C. limax*-cf. *sulcata*-anthraconaioid fauna has been found with *C.* aff. *fallax* (several forms with curved lower borders), *C. fallax-protea* and *C.* ? *protea* (figure 32*d*), all fairly common in the middle 3 in. of this interval, and possibly not in continuous variation with the remainder.

To sum up: the changes in the fauna in the lower part of the upper division are essentially the same as those passed through by the fauna in the lower part of the middle division. In the upper 4 ft. of the upper division there are minor faunal changes of a fluctuating nature. Somewhat elongate anthraconaioids are mingled with a fauna comparable with, but distinct from, that characterizing the middle part of the middle division.

* The increase is not significant statistically owing to the presence of the shell drawn as figure 31*n* which, *at this horizon*, may not be in continuous variation with the remainder of the fauna.

† Were crushed and uncrushed shells compared indiscriminately there would appear to be a significant decrease in the mean *H/L* ratio between the 24 ft. 3 in. and 25 ft. horizons.

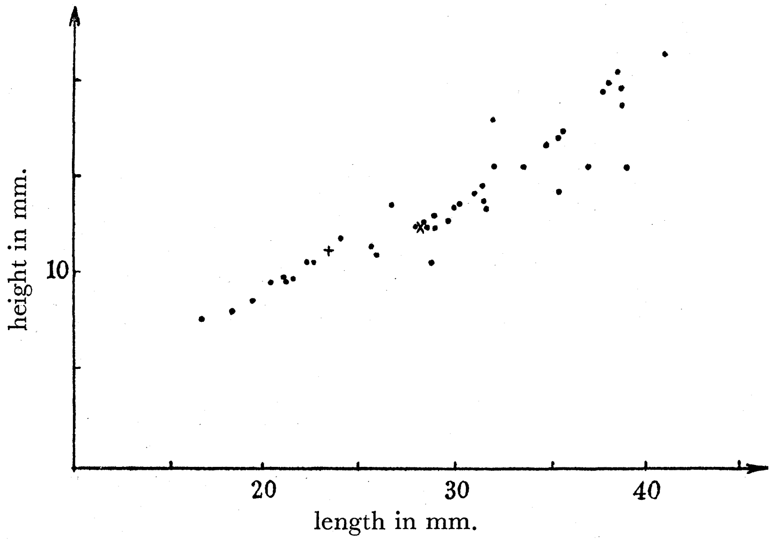


FIGURE 35. Measurements of shells in the upper division of the sequence at Honley, 26 ft. 3 in. above the Soft Bed Coal. Symbols show the positions which would be occupied by the holotype of *C. fallax* ×, and the paratype +.

(IV) A summary and comparison of the faunas characterizing each division

The following section is complimentary to the tabular arrangement of the succession shown on the opposite page.

In the lower division (grades 4 and 5) the short *C. fallax*- aff. *recta*- cf. *sulcata* fauna is easily recognizable in the field and is found at no other horizon. The large *C.* aff. *recta* is particularly distinctive. Higher in the succession, except occasionally near the base of the middle division, shells comparable with *C. recta* are relatively longer and considerably smaller than those of the lower division.

In the middle division there are the three distinctive horizons, *C. haberghamensis*, *C. discus* n.sp. and the fauna which includes *C.* cf. *pseudorobusta*. Apart from the presence of these, the highly variable fauna of the middle division is distinguishable in its middle and lower parts (grades 3 and 4) from the slightly less variable fauna in the corresponding parts of the upper division. In the lowest horizons of each division (grades 2 and 3) there is scarcely any difference in the fauna; *C. limax* is slightly more common at the base of the upper division while there is a tendency towards *C.* cf. *acutella* at the base of the middle. In the middle and upper parts of the three divisions the faunas become individualized, the greatest variation being found in the middle division. The upper division (grades 2–4) is characterized by a *C. limax*- cf. *sulcata*-anthraconaioid fauna in which hinge lines tend to be curved and lower borders are typically straight and subparallel with the hinge lines. In the middle division the lower border is generally more curved, elliptical and posteriorly tapered forms being common at certain horizons while *C. limax* is uncommon and anthraconaioids, especially in the higher levels, are rare. Shells intermediate between *C. fallax* and *C. protea* having curved lower borders are characteristic of the middle division and are distinctive in the field. Shells referable to *C. fallax-protea* are less common in the upper division and tend to have straight lower borders, often being comparable with *C. sulcata*.

3. A summary of general results

A special study has been made of non-marine lamellibranch faunas from a series of beds which, in several localities elsewhere, have yielded the most highly variable fauna known in the British Coal Measures. The following points constitute the more general results of the work.

(1) Whereas Wright (1934, 1937) emphasized the very great range of variation of Lower Coal Measure shells, more especially in the beds here investigated, it is found that if shells are examined from small thicknesses the range of variation is considerably less than is

Tabulated summary of the succession above the Soft Bed at Honley

I	II	III
Lower division	Middle division	Upper division
Top 9 ft. 0 in. above the coal	Top 22 ft. 6 in. above the coal	Top 33 ft. 0 in. above the coal
(5) *C.* ? *protea* (poor)	(5) *C.* ? *protea* (poor)	
(4)–(5) *C. fallax*- aff. *recta*- cf. *sulcata* fauna. Shells are short and typically carinate (with variable rather elongate *C. protea*). Large short *C.* aff. *recta* is distinctive. (Compare the third fauna from the base of the middle division)	(3)–(5) *C. haberghamensis*. *C.* aff. *fallax* community. Short small *C.* cf. *fallax* community	
	(5)–(4) *C. discus* n.sp.	
	(4)–(5) *C.* cf. *pseudorobusta*, *C.* cf. *obliqua* and *C.* cf. *acuta*, *C. fallax* and *C.* cf. *sulcata*	(3)–(4) Variable fauna of anthraconaioid- *C. limax*- cf. *sulcata* trends with less common *C.*? aff. *protea*. Hinge lines frequently curved and subparallel with the lower border, which is typically straight
	(3)–(4) Highly variable fauna of *C. fallax-proteas*, *C.* cf. *sulcata*, *C.* cf. *elliptica*. Most shells have curved lower borders	
	(3) Elongate small *C.* ? aff. *recta*, *C.* aff. *fallax* with shorter small shells	(3) Elongate small *C.* ? aff. *recta*, *C.* aff. *fallax* with shorter small shells
	(2) Elongate anthraconaioids, *C. limax*, occasional small short elliptical shells	(2) Elongate anthraconaioids, *C. limax*, occasional small short elliptical shells
	(1) (*Lingula* at Huddersfield)	(1) *Lingula*
Base 4 ft. 6 in. above the coal	Base 10 ft. above the coal	Base 23 ft. 6 in. above the coal

The numerals refer to the *approximate* lithological grade of the shale interval through which the fauna is summarized. At the extreme top both of the lower and middle divisions large *Carbonicola* also occur in the shale transitional directly between grades 5 and 1.

found throughout the whole range of these strata. Variation in a single community is sometimes no greater than is typical of communities of other zones, although some communities still show a remarkable range of variation.

(2) Ranges of variation in different communities differ, frequently to an extent which renders one community easily distinguishable from another.

(3) These differences in variation are to some extent linked with differences in the lithology of the rock containing the shells.

(4) In the section described in the Lower Coal Measures of Honley, near Huddersfield, three rhythmic units of Coal Measure type have been recognized.* It has been found

* The significance of the rhythmic development is discussed on pp. 14, 15.

that in each rhythmic unit or lithological division where shell horizons are developed* there is a similar shell sequence. At the base of the unit, immediately overlying a *Lingula* band, the shells are elongate, comparatively small and mostly referable on their outline to *Anthraconaia*. Traced upward in coarsening shale the fauna gives place gradually to one of *Carbonicola*. Higher in the rhythmic unit larger shells are added to the fauna, and there is a general increase in relative shell height and length of anterior end. Progressive changes in the value of these ratios are well seen in the lower part of the middle division. Large relatively high shells, referable to the *C. protea* group, are mingled with smaller shells in the middle and upper portions of the units but occur exclusively at the top of them, except in the case of the upper division.

(5) Shells apparently referable to *Anthraconaia* grade perfectly with *Carbonicola* at the base of the unit where available specimens appear to represent a homogeneous community. At certain levels in the upper parts of the units collected material suggests that communities are not homogeneous. Speciation has been proved in the upper portion of the middle division, both between large and small shell groups and within a small shell group. On one horizon two species evidently lived contemporaneously without interbreeding.

(6) Emphasis is laid on the role of relative growth rates as a differentiating factor in certain communities, more especially between faunas in fine-grained shales and those in relatively coarser shales and mudstones. The difference is seen principally in the larger shells where, it is suggested, any moulding influence of environmental origin may have had longer time to operate than in the case of the smaller shells.

(7) Although the succession is similar in each of the three rhythmic units the faunas of each may be distinguished collectively. There are also some distinctive horizons in the upper part of the middle division, the more important of which are those of *C. haberghamensis* W. B. Wright and *C. discus* n.sp. A summary of the succession is shown in tabular form on p. 47.

(8) Nearly all Wright's species and figured variants from above the Bassy Mine are at least approximated to at Honley, and several forms have been found which are identical with certain of them. A number of new variants are illustrated. Some of these show new morphological trends, others showing new links between previously known forms.

PART IV. NOTES ON SPECIES

It is proposed at present to refer only to those species which require further description or reinterpretation to clarify the nomenclature of shells in the succession at Honley.

Dimensions are given by the formula adopted by Davies & Trueman (1927). The length is first recorded in millimetres and is followed in order by height, thickness or obesity, and length of anterior end, each expressed as a percentage of the length. Registration numbers, unless otherwise stated, refer to Geological Survey collections.

Carbonicola fallax W. B. Wright

Holotype 53002A; paratype 53002B, plate 1, figure i; W. B. Wright 1934*a*, p. 13, figure 2.

Dimensions:	Holotype	28;	46·5;	25?;	25.
	Paratype	23;	50;	32?;	26.

* In the lower division shells are present only in the coarser beds towards the top, where their development falls in line with that of other units as described above.

The holotype is an internal mould well preserved in rather coarse grey shaly mudstone. The growth lines indicated on Wright's figure are not present. The 'broad rib or carina' which Wright describes as descending obliquely from the umbo towards the postero-ventral angle is especially characteristic of small shells on the horizon of the holotype and is therefore described in more detail. In the holotype the carina originates from a broad swelling well behind the umbo and passes backward with crest curved, convex dorsally, towards the postero-ventral angle, where it rapidly flattens out as it passes into the broadly compressed border of the mould. It is strongest in the posterior third of the shell and its crest lies mostly above a line from the tip of the umbo to the postero-ventral angle. Anterior to the carina in the lower central portion of the cast there is a slightly concave triangular area which can be better felt than illustrated. In material examined from the type locality and elsewhere the carina is always more strongly expressed on the internal mould than on the exterior of the shell.

Carbonicola protea W. B. Wright

Holotype 53003A, plate 1, figure ii, text-figure 36; paratypes 53003B, 53070, unfigured, 53071, plate 1, figure iii; Wright 1934*a*, p. 14, figure 3.

Dimensions: Holotype 50; 56; —; 20–22.

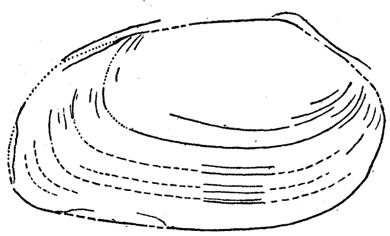


FIGURE 36. *Carbonicola protea* W. B. Wright, holotype, from above the Bassy Mine, Feniscowles, near Darwen.

The holotype consists of two valves which have been crushed flat upon one another. The postero-dorsal and posterior margins are poorly preserved and ragged and their precise outline is to some extent a matter of opinion. The interpretation of the writer differs from that of W. B. Wright only in the suggestion of a slightly more tapered posterior end. The umbo and anterior umbonal slope have been distorted with crushing. The umbo, as Wright pointed out, is 'by no means prominent'. The straight post-umbonal slope with angulation of the umbonal tip, as shown in Wright's figure, is very unusual in *C. protea*, whether crushed or uncrushed. In the original uncrushed shell the umbo was probably flatter and more pitched forward (see figure 3) than it now appears (figure 36 traced from the photograph and showing interpretation in dotted lines).

Carbonicola limax W. B. Wright

Holotype 53007, plate 1, figure iv, text-figure 37(*a*); W. B. Wright, 1934*a*, p. 17, figure 6A.

Dimensions: Holotype 28; 41*; 24?; 20 (measured by the writer).

The holotype is an internal mould on which traces of the shell remain as a thin ferruginous rind. Over the umbo the shell appears to have been very thick. Although the height of the posterior portion of the shell and the shape of the postero-ventral angle is clear the

* The height is given by Wright (1934*a*) as 46·5 %. The height measured on his figure is 36·5 %.

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

exact contour of the postero-dorsal outline is not clearly seen owing to poor preservation. It has been interpreted as continuously curved, as originally defined by Wright. There is no doubt, however, that the height in the posterior third of the shell is considerably greater than is shown in Wright's figure, and that the postero-ventral angle is now drawn more correctly than in his figure. The writer's interpretation of the posterior end has received support from a number of specimens since collected above the Bassy Mine and the Soft Bed Coal, some of which are illustrated on the south-south-east series of the standard diagram (figure 1). The lower umbo of the holotype by comparison with adjacent shells is explained by the unusual shell thickness over the immediate umbonal region. No specimen comparable with Wright's figure has been seen by the writer.

The refiguring shows a lower border slightly reflexed (compare south-south-east series of figure 1), while the anterior lobe is deeper than is shown in Wright's figure. Growth lines appear slightly tilted at one-third of the height from the ventral margin. The writer can see no evidence for the growth lines which Wright has drawn.

(*a*) (*b*)

FIGURE 37. *Carbonicola limax* W. B. Wright. (*a*) tracing from Wright's original figure; (*b*) refiguring by the writer.

The mould shows over its lower central portion a flat or very slightly concave area which is best seen when the shell is viewed obliquely from the anterior end. Posterior to this the curved broken line on figure 37(*b*) indicates a turn on the surface of the cast defining the posterior limit of the flat area.

It is noteworthy that in spite of the discrepancy between Wright's figure and that of the writer the original description of the species requires no modification except with regard to the affinities of *C. limax* (see lower section). Several poorly preserved shells in the collection of the Geological Survey labelled by Wright *C.* aff. *limax* all have posterior ends comparable with that shown in the refiguring, and there can be little doubt of Wright's original conception of the species.

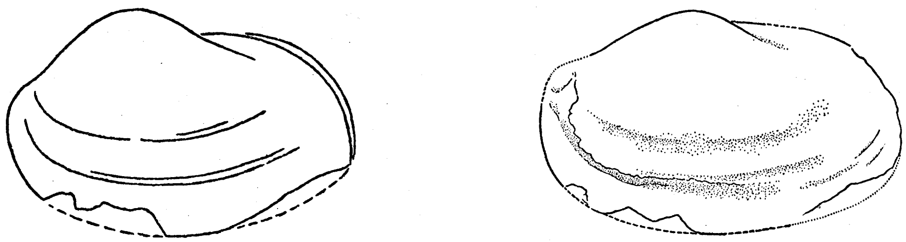
No paratype was chosen by Wright but he figures 'an allied form' labelled *C.* aff. *limax*, 53072 (Wright 1934*a*, figure 6B). This specimen (plate 1, figure v) is an internal mould, and except over the umbo and the postero-dorsal slope the outline is obscured. Growth lines are present near the edge of the exposed cast and suggest a reflexed lower border. The shape of the solid mould, however, is well seen. It is concave, whereas Wright's figure, with presumed growth lines, suggests convexity. There is an indefinite carinal swelling which originates on the dorsal slope well behind the umbo and passes obliquely backwards towards the posterior inferior angle with weakening definition. It is possible that shell thickness over the umbo may have been accentuated by crushing.

Affinities: C. limax was originally described by Wright as 'merely a humpbacked variant of *C. fallax* and *C. aquilina*'. Studies by the writer at Honley and elsewhere show that *C. limax* is very closely related to an elongate group of *Anthraconaia*-like shells or anthraconaioids, members of which are comparable in outline with *Anthraconaia lenisulcata* and certain variants of *A. bellula* (p. 40). *C. limax* may also, however, grade with larger and relatively higher forms which retain the curved hinge line.

Carbonicola haberghamensis W. B. Wright

Holotype 53005, plate 1, figure viii; Wright 1934*a*, p. 16, figure 5A; paratype 53006, plate 1, figure ix, text-figure 38(*a*), (*b*).

Dimensions:	Holotype	50;	52;	30;	26.
	Paratype	46;	63;	30;	38.



(*a*) (*b*)

FIGURE 38. The paratype of *Carbonicola haberghamensis* W. B. Wright. (*a*) Wright's original figure; (*b*) refiguring by the writer.

On the holotype, which is an incomplete internal mould, there are no suggestions of the growth lines which Wright's figure indicates. Wright's interpretation of the outline corresponds with the modal shape of the fauna collected both at the type locality near Burnley, Lancashire, and at a corresponding horizon at Honley in Yorkshire.

The paratype differs greatly from the holotype. It is a short oval shell (figure 38(*b*) and plate 1, ix) with a hinge line considerably higher than is indicated by Wright. It appears that the shell was tilted when it was originally drawn. The anterior end is higher and the posterior end, with evidence of traces of growth lines, is more fully rounded. The shell is broadly swollen in the upper central region but lacks the periumbonal swelling which characterizes the holotype of *C. haberghamensis* and most of the associated fauna. In the community of *C. haberghamensis* at Honley no shell remotely like the paratype has been found although a few comparable forms occur 1 ft. 3 in. below this level, associated with *C. discus* n.sp. At the type locality, where the writer's collection includes forms from below a horizon of ironstone lenticles, which yielded most of the specimens, occasional shells are somewhat similar. Bearing in mind the solid shape, and the very high H/L and A/L ratios, it seems likely that its affinities are with *C. discus* rather than *C. haberghamensis*.

Carbonicola obliqua W. B. Wright

Holotype 53004, plate 1, figure vi; Wright 1934*a*, p. 15, figure 4A–C. Paratypes 53073, plate 1, figure vii, text-figure 39(*a*) and (*b*), and 53074, unfigured.

Dimensions:	Holotype	44;	47;	33;	27	(quoted from Wright).
	Paratype 53074	37·5;	47·5;	30;	26	(measured by the writer).

The paratypes, one of which is figured above, both show the distinctive solid form which characterizes the species. There is a marked umbonal and post-umbonal bulge, anterior and posterior to which the shell tapers in dorsal profile tending to flatten out towards the margins (figure 39(*b*)).

The lower border of paratype 53074 is gently curved, as are the growth lines of the holotype at a quarter of the height from the ventral border. Shells near paratype 53074 are found in continuous variation with *C. haberghamensis* at Honley, but no shell identical with the holotype has yet been found above the Soft Bed or Bassy Mine Coals. *C. obliqua* and *C. haberghamensis* both have the same characteristic periumbonal bulge, and it seems likely that the two are related.

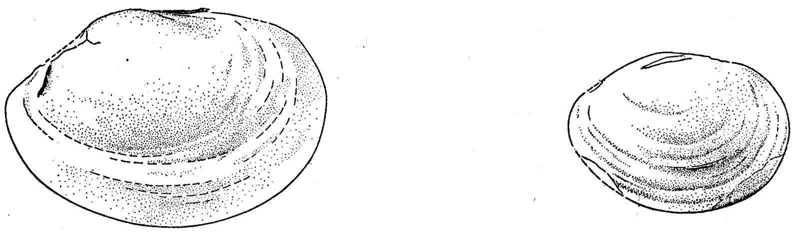
(*a*) (*b*)

FIGURE 39. *Carbonicola obliqua* W. B. Wright. Paratype 53074. (*a*) lateral view; (*b*) dorsal view.

Carbonicola discus n.sp.

Holotype S. 12396, plate 1, figure x, text-figure 40(*a*). Paratype S. 12397, plate 1, figure xi, text-figure 40(*b*). Both specimens are in the collection of the Hunterian Museum, Glasgow.

Dimensions: Holotype 42·5; 69; 22; 33.
Paratype 30; 71; —; 33·5.



(*a*) (*b*)

FIGURE 40. *Carbonicola discus* n.sp. (*a*) holotype; (*b*) paratype.

Description. Shell oval, tending to subcircular. The umbo is subcentral and scarcely rises above the hinge line, which is slightly curved. The anterior umbonal slope is straight or slightly re-entrant and passes with well-rounded angle into the sweep of the lower border, which is continued backward and upward with increased curvature into the posterior margin. The upper posterior angle is well rounded. Growth lines are approximately concentric with the umbo, which is more nearly central in the earlier stages of shell growth, so that the young of *C. discus* are slightly comparable in outline with *C. bella* Davies Trueman. The position of the maximum depth of the holotype is posterior to the umbo midway along the length of the shell. The line joining the anterior and posterior extremities of the outline is almost parallel to the hinge line and lies just within the dorsal half of the shell.*

The holotype is gently swollen beneath the umbo in the upper central portion of the shell but is slightly crushed round the lower margins. The maximum thickness appears to have been beneath the umbo at rather less than two-thirds of the height of the shell. Specimens are found typically crushed flat.

* The orientation of *C. discus* is partly dependent on the mode of curvature of the hinge line and posterior dorsal margin which, in the shells associated with the holotype, varies considerably in this respect. If the hinge line is not raised the umbo may appear rather prominent.

Locality and horizon. East bank of cutting 100 yd. north of Honley Railway Station, near Huddersfield. 1 in. sheet 86, 6 in. sheet Yorks 260.

The types were collected from a 4 in. shell band in slightly pyritous shale 18 ft. above the Soft Bed Coal at the top of the lower development of the middle rhythmic unit of the measures between the Soft Bed and Middle Band Coals (figure 7*a*).

Grateful thanks are due to Professor Trueman for criticizing the manuscript and especially for his advice and helpful suggestions at all times during the progress of the work in the laboratory; also to Dr J. Weir and Dr D. Leitch for advice and discussion. Through the kindness of Dr C. J. Stubblefield the writer has been able to examine Wright's type specimens and much other material collected chiefly from the Lower Coal Measures of Lancashire and now registered in the collections of H.M. Geological Survey.

The writer is grateful to the Geological Society of London for a grant from the Daniel Pidgeon Fund to defray costs of the field work; also the Executive Committee of the Carnegie Trust from whom he was in receipt of a grant during the writing of the paper.

REFERENCES

Bromehead, C. E. N., Edwards, Wilfrid, Wray, D. A. & Stevens, J. V. 1933 The geology of the country around Holmfirth and Glossop. *Mem. Geol. Surv.*

Davies, J. H. & Trueman, A. E. 1927 A revision of the non-marine lamellibranchs of the Coal Measures and a discussion of their zonal sequence. *Quart. J. Geol. Soc.* **83**, 210.

Hudson, R. G. S. & Dunnington, H. V. 1938 A boring in the Lower Coal Measures and Millstone Grit at Bradford. *Proc. Yorks Geol. Soc.* **24**, 129.

Hudson, R. G. S. & Dunnington, H. V. 1939 A borehole section in the Carboniferous at Fairweather Green, Bradford. *Proc. Yorks Geol. Soc.* **24**, 206.

Leitch, D. 1936 The *Carbonicola* fauna of the Midlothian fifteen foot coal; a study in variation. *Trans. Geol. Soc. Glasg.* **19**, 390.

Leitch, D. 1940 A statistical investigation of the Anthracomyas of the Basal Similis-Pulchra zone in Scotland. *Quart. J. Geol. Soc.* **96**, 13.

Leitch, D. 1941 Naiadites from the Lower Carboniferous of Scotland; a variation study. *Trans. Geol. Soc. Glasg.* **20**, 208.

Tonks, L. H., Jones, R. C. B., Lloyd, W. & Sherlock, R. L. 1931 The geology of Manchester and the south-east Lancashire coalfield. *Mem. Geol. Surv.*

Trueman, A. E. 1929 Some new carboniferous lamellibranchs. *Ann. Mag. Nat. Hist.* Ser. 10, **4**, 82.

Wray, D. A. 1929 The Carboniferous succession in the central Pennine area. *Proc. Yorks Geol. Soc.* **21**, 228.

Wray, D. A. & Trueman, A. E. 1931 The non-marine lamellibranchs of the Upper Carboniferous of Yorkshire and their zonal sequence. *Summ. Progr. Geol. Surv. for* 1930, Part III, p. 70.

Wray, D. A. & Trueman, A. E. 1934 The fauna of the Lower Coal Measures in West Yorkshire. *Summ. Progr. Geol. Surv. for* 1933, Part IV, p. 37.

Wright, W. B., Sherlock, R. L., Wray, D. A., Lloyd, W. & Tonks, L. H. 1927 The geology of the Rossendale anticline. *Mem. Geol. Surv.*

Wright, W. B. 1934*a* The fresh-water fauna of the Lower Coal Measures of Lancashire. *Summ. Progr. Geol. Surv. for* 1933, Part II, p. 8.

Wright, W. B. 1934*b* Variation of fresh-water shells in the Lower Coal Measures of Lancashire. *Summ. Progr. Geol. Surv. for* 1933, Part II, p. 24.

Wright, W. B. 1937 The Anthracomyas of the Lancashire Coal Measures and the correlation of the latter with the Coal Measures of Scotland. *Summ. Progr. Geol. Surv. for* 1936, Part II, p. 10.

Description of Plate 1

Type Specimens from the Lower Coal Measures of Lancashire and Yorkshire.

Figure i. *Carbonicola fallax* W. B. Wright. A, holotype; B, paratype. From above the Bassy Mine, Feniscowles, Darwen, Lancs. Geol. Surv. Collection nos. 53002A and 53002B. ×1·07. (See p. 48.)

Figure ii. *Carbonicola protea* W. B. Wright. Holotype. From above the Bassy Mine, Feniscowles, Darwen, Lancs. Geol. Surv. Collection no. 53003A. ×0·93. (See p. 49.)

Figure iii. *Carbonicola protea* W. B. Wright. Paratype. Horizon and locality as in figure ii. Geol. Surv. Collection no. 53071. ×1·08. (See p. 49.)

Figure iv. *Carbonicola limax* W. B. Wright. Holotype. From above the Lower Foot Mine, Dimple, Egerton, Lancs. Geol. Surv. Collection no. 53007. ×1·07. (See p. 49.)

Figure v. *Carbonicola* aff. *limax* W. B. Wright. Horizon and locality as in figure iv. Geol. Surv. Collection no. 53072. Natural size. (See p. 50.)

Figure vi. *Carbonicola obliqua* W. B. Wright. Holotype. From 20 ft. to 30 ft. below the Rambler or Middle Mountain Mine of Ravenhead Brickworks, Holland Moor, near Wigan. Geol. Surv. Collection no. 53004. Natural size. (See p. 51.)

Figure vii. *Carbonicola obliqua* W. B. Wright. Paratype. Horizon and locality as in figure vi. Geol. Surv. Collection no. 53073. ×1·04. (See p. 51.)

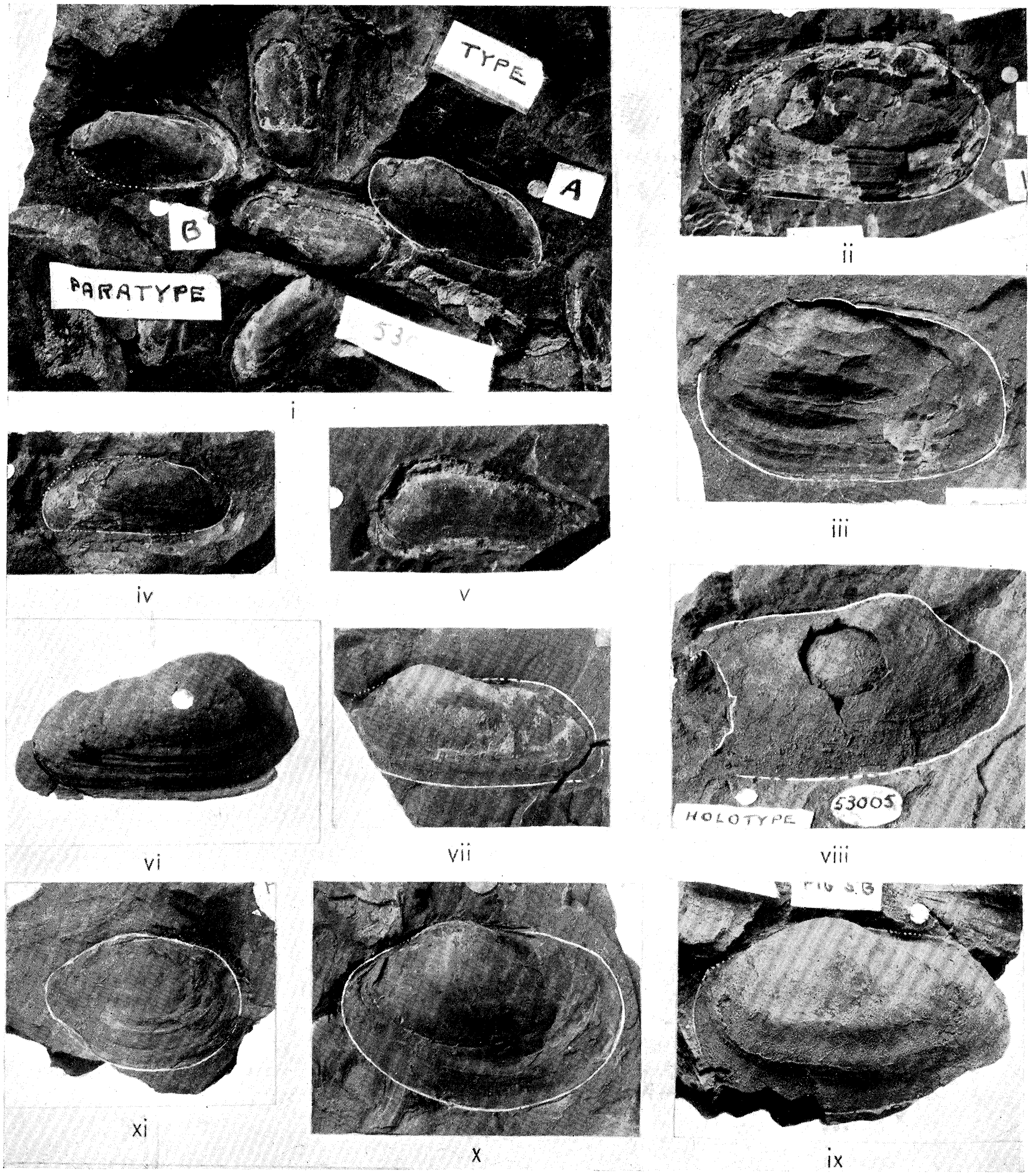
Figure viii. *Carbonicola haberghamensis* W. B. Wright. Holotype. From above the Bassy Mine, New Barn Clough, Habergham Eaves, Burnley. Geol. Surv. Collection no. 53005. ×1·09. (See p. 51.)

Figure ix. *Carbonicola haberghamensis* W. B. Wright. Paratype. Horizon and locality as in figure viii. Geol. Surv. Collection no. 53006. ×1·1. (See p. 51.)

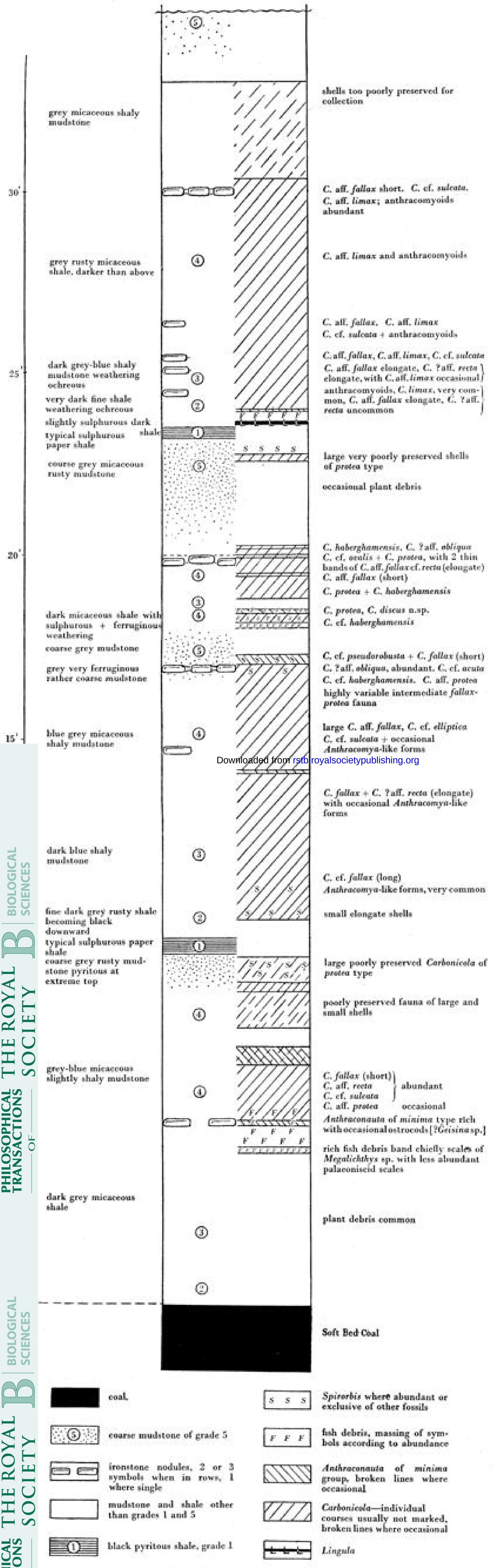
Figure x. *Carbonicola discus* n.sp. Holotype. From 18 ft. above the Soft Bed Coal, railway cutting, Honley Station, near Huddersfield. Hunterian Museum Collection, Glasgow, no. S. 12396. ×1·04. (See p. 52.)

Figure xi. *Carbonicola discus* n.sp. Paratype. Horizon and locality as in figure x. Hunterian Museum Collection, Glasgow, no. S. 12397. ×1·05. (See p. 52.)

In most of the figures a thin white line has been drawn to mark presumed position of the outline of the shell.



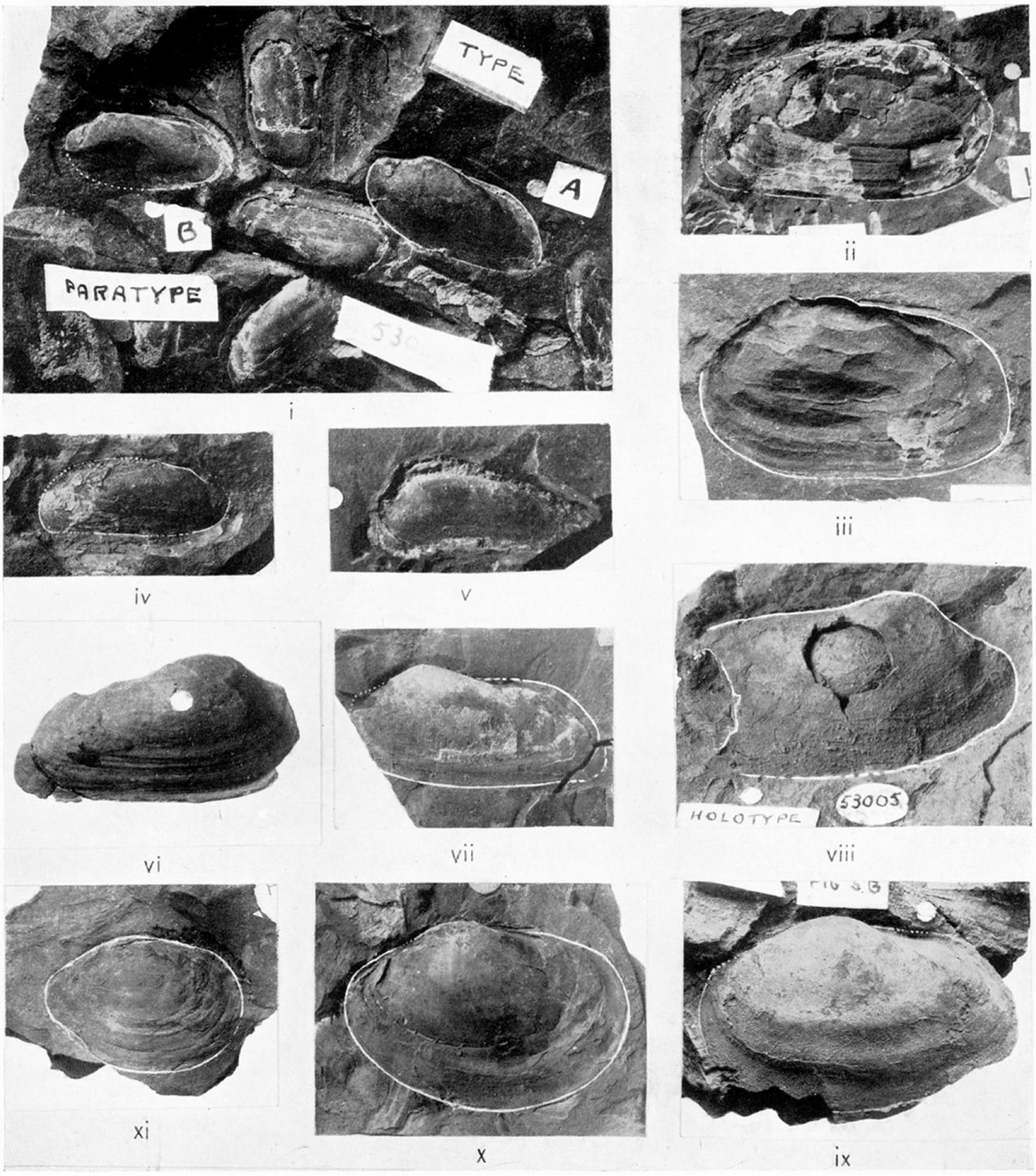
(*Facing page* 54)



PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

…URE 7c. Scale section of the succession at Honley Station cutting, on which are …wn, partly by means of symbols, on the left hand details of the lithology, and on …right hand palaeontological features. The numerals on the left-hand side refer …he selected grades of shale and mudstone described on p. 12 (compare figure 7a … the tabulated summary on p. 47). For *Anthracomya* read *Anthraconaia* and for …racomyoid read anthraconaioid.

(Facing page 14)



Description of Plate 1

Type Specimens from the Lower Coal Measures of Lancashire and Yorkshire.

Figure i. *Carbonicola fallax* W. B. Wright. A, holotype; B, paratype. From above the Bassy Mine, Feniscowles, Darwen, Lancs. Geol. Surv. Collection nos. 53002 A and 53002 B. × 1·07. (See p. 48.)

Figure ii. *Carbonicola protea* W. B. Wright. Holotype. From above the Bassy Mine, Feniscowles, Darwen, Lancs. Geol. Surv. Collection no. 53003 A. × 0·93. (See p. 49.)

Figure iii. *Carbonicola protea* W. B. Wright. Paratype. Horizon and locality as in figure ii. Geol. Surv. Collection no. 53071. × 1·08. (See p. 49.)

Figure iv. *Carbonicola limax* W. B. Wright. Holotype. From above the Lower Foot Mine, Dimple, Egerton, Lancs. Geol. Surv. Collection no. 53007. × 1·07. (See p. 49.)

Figure v. *Carbonicola* aff. *limax* W. B. Wright. Horizon and locality as in figure iv. Geol. Surv. Collection no. 53072. Natural size. (See p. 50.)

Figure vi. *Carbonicola obliqua* W. B. Wright. Holotype. From 20 ft. to 30 ft. below the Rambler or Middle Mountain Mine of Ravenhead Brickworks, Holland Moor, near Wigan. Geol. Surv. Collection no. 53004. Natural size. (See p. 51.)

Figure vii. *Carbonicola obliqua* W. B. Wright. Paratype. Horizon and locality as in figure vi. Geol. Surv. Collection no. 53073. × 1·04. (See p. 51.)

Figure viii. *Carbonicola haberghamensis* W. B. Wright. Holotype. From above the Bassy Mine, New Barn Clough, Habergham Eaves, Burnley. Geol. Surv. Collection no. 53005. × 1·09. (See p. 51.)

Figure ix. *Carbonicola haberghamensis* W. B. Wright. Paratype. Horizon and locality as in figure viii. Geol. Surv. Collection no. 53006. × 1·1. (See p. 51.)

Figure x. *Carbonicola discus* n.sp. Holotype. From 18 ft. above the Soft Bed Coal, railway cutting, Honley Station, near Huddersfield. Hunterian Museum Collection, Glasgow, no. S. 12396. × 1·04. (See p. 52.)

Figure xi. *Carbonicola discus* n.sp. Paratype. Horizon and locality as in figure x. Hunterian Museum Collection, Glasgow, no. S. 12397. × 1·05. (See p. 52.)

In most of the figures a thin white line has been drawn to mark presumed position of the outline of the shell.