LOWER CARBONIFEROUS NON-MARINE LAMELLIBRANCHS FROM EAST FIFE, SCOTLAND

by G. M. BENNISON

ABSTRACT. *Carbonicola antiqua* Hind (*non* Brown) and *C. elegans* (Kirkby) are redescribed from the Calciferous Sandstone Series of East Fife, and *Anthraconaia? kirki* sp. nov. proposed. Variation of the shells at different localities is discussed and the significance of faunal associations is assessed.

THREE species of non-marine lamellibranch have been described from the Calciferous Sandstone Series (Lower Carboniferous) of East Fife. Of these, two were referred to *Carbonicola* and one to *Naiadites* by Hind (1894–6). Detailed work has shown that the two species of *Carbonicola* were correctly referred to that genus by Hind, and that they are morphologically more primitive than other representatives of the genus, as well as occurring at a lower horizon. Examples of *Anthraconaia?* are also described here. The strata from which the shells described are derived are of Viséan age (Currie 1954), and are extremely variable. They thin from about 4,000 feet on the coast of East Fife, to little more than 200 feet in the Lomond Hills 15 miles away. Rapid lateral thinning of individual beds, local unconformities cutting out parts of the succession, slumping of shales, and the lenticular form of the false-bedded, ripple-marked sandstones all show that deposition was in water shallow enough to be affected by currents or wave action. Occasional coal seams indicate temporary emergence. Lack of precise knowledge of the stratigraphy of the beds is a serious limitation to palaeontological study. Text-fig. 1 shows the localities mentioned.

Certain detailed correlations postulated by Kirkby cannot be sustained, though little can be suggested in their place. The Randerstone shore section is low in the Calciferous Sandstone Series—Kirkby equates his Limestone 5 with Bed 618 of the Pittenweem to Anstruther section—but it is doubtful if Limestone 10 is the equivalent of Bed 649. They differ in lithology and in fauna and form part of different successions. Nor can the postulated correlation of the beds with *C. antiqua* at Kilminning and Kilrenny Mill be upheld. Variation in the shells differs at these localities and the beds are lithologically distinct. Summarized detailed successions are as follows:

KILMINNING	KILRENNY MILL
10–12 ft. shale	8 ft. shales and sandstones
10 in. hard red limestone with abundant *C. antiqua*	3 in. cementstone
3 in. calcareous sandstone	5 in. mudstone with *C. antiqua*
+5 ft. massive sandstone	1 in. clay
	6–10 in. hard, yellow, calcareous sandstone with many *C. antiqua*
	4 ft. 9 in. sandy shale

CARBONICOLA IN THE LOWER CARBONIFEROUS

Lower Carboniferous *Carbonicola* differ from most Westphalian forms in having tilted growth lines. These reflect a progressive change in the direction of growth and

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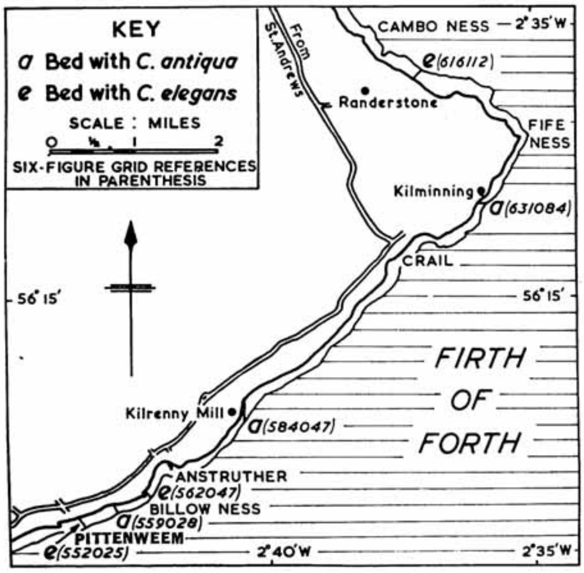
result in low umbones directed towards the anterior in the adult shell. In some specimens the umbo is not the highest part of the dorsal margin. The postero-dorsal margin, which is typically arched, becomes strongly arched in some variants. The hinge is edentulous, a condition not typical in *Carbonicola*, although noted in the Namurian species *C. pervetusta* (Bennison 1954, p. 41). Further, Eagar (1946, p. 7), describing small forms from the *Anthraconaia lenisulcata* zone of the Coal Measures, has observed that teeth are ill defined and that dentition is represented mainly by swellings and depressions in the hinge-plate. Trueman and Weir (1951, p. 106) state that the edentulous condition occurs 'not infrequently' in *Carbonicola*: in this case it may be indicative of a primitive condition.



TEXT-FIG. 1. Sketch map to show the location of non-marine lamellibranch beds in east Fife.

Despite a superficial similarity to *Anthracosia*, due to the tilted growth lines and the low umbones, and, despite the vertical anterior umbonal slope of the internal mould, these *Carbonicola* are seen to differ fundamentally from *Anthracosia* in that the internal moulds do not have a robust median dorsal ridge. By implication, the hinge-plates cannot be bevelled as in *Anthracosia*. It is the structure of the dorsum which distinguishes *Anthracosia* from *Carbonicola* (Trueman and Weir 1951, p. 105), although 'the dorsal structure indirectly affects some aspects of external shape—e.g. umbonal tilt and outline of dorsal plan'. Thus in the Lower Carboniferous there are early members of the Anthracosiidae resembling *Carbonicola* in essential characters but bearing a superficial similarity to *Anthracosia*.

Carbonicola antiqua Hind

Plate 25, figs. 1, 2, 6–8

? *Pachyodon nucleus* Brown 1843, p. 394, pl. 16, fig. 1.
Carbonicola antiqua Hind 1894, p. 79, pl. 11, figs. 28–30.
Non *Carbonicola antiqua* (Brown); Trueman and Weir 1947.

Type material. The specimen figured by Brown as *Pachyodon nucleus*, from Woodhall, Water of Leith, near Edinburgh, is lost. I have studied faunas from Brown's type locality collected by Geological Survey officers, but found nothing with which *nucleus* could be identified. As the identity of Brown's species cannot be determined it is impracticable to sustain the name *nucleus*. Brown was correct (1849, p. 178, pl. 23, fig. 31) in renaming his Coal Measures form *Pachyodon antiquus* as *senex* on referring that species to the genus *Unio*, for the name *Unio antiquus* was preoccupied by Sowerby's (1833) species. The correct name for *C. antiqua* Brown, as used by Trueman and Weir (1947), is therefore *C. senex* (Brown). No homonymity occurs, however, in the case of *C. antiqua* Hind. Hind's specimens are syntypes and his first figured specimen (1894, pl. 40, fig. 28, B.M. L.46889) is here selected as lectotype.

Diagnosis. Shell ovate to subtriangular. Umbones low, anterior end short, *c.* 20 per cent. of the length or less. Growth lines tilted. Tumid, thickness over 40 per cent. of the length. Posterior bluntly rounded or obliquely truncated. Lower border gently rounded, or straight for the posterior two-thirds of its length.

Dimensions

	L (*mm.*)	*H* (*mm.*)	*A* (*mm.*)	*T* (*mm.*)
Pl. 25, fig. 1 (L.46889) (Hind, pl. 11, fig. 28) . . .	24·0	14·5 (60·4%)	4·2 (18·3%)	est. 5·9 (single valve) (*c.* 49%)
Pl. 25, fig. 2 (L.46890) (Hind, pl. 11, fig. 29) . . .	25·3	15·4 (60·9%)	4·5 (17·7%)	12·6 (49·6%)

Description and discussion. The syntypes are rather larger than the mean for the topotype material from Kilminning collected by the author, but the values for H/L and A/L are very close to the modes of the community. The lectotype is near the norm of the community and is typical in every way except in the detail of the posterior-umbonal slope, which is less strongly arched than in some variants, and the umbo, which is more pronounced than in the majority of adult specimens. The growth lines are only moderately tilted. The figured syntype represents a common variant with low umbones, highly tilted growth lines and a rather bluntly truncated posterior end. Variation in the community is discussed below. *C. antiqua* is edentulous and in no case have teeth or dental sockets been found; this is in accord with Hind's original description although his figured hinge-plate (1894, pl. 11, fig. 28*a*) does not provide clear evidence of this.

Comparison. C. elegans is the only other species of Lower Carboniferous lamellibranch which resembles *C. antiqua. C. elegans* occurs 250 feet below and 950 feet above *C. antiqua* and their ranges, though not fully known, must overlap. The two species do not occur together. They can be readily distinguished, chiefly on account of a large discrepancy in the value of H/L, and by features fully discussed in the emended description of *C. elegans*.

C. antiqua and *C. elegans* differ from *C. pervetusta*, the earliest form assigned to *Carbonicola* by the writer, in the following features: the umbones are low and directed towards the anterior; the growth lines are tilted; the shells are more tumid; the anterior end is short—A/L = 20 per cent. or less; the shells normally attain a greater size; and the range of variants is different.

Distribution. The syntypes are from red limestone at Kilminning, between Fife Ness and Crail. This species also occurs in two beds at Kilrenny Mill, and sparsely at a higher horizon between Pittenweem and Anstruther. It is restricted, therefore, to the lower part of the Calciferous Sandstone Series. The habitat of *C. antiqua* is discussed below.

Carbonicola elegans (Kirkby)

Plate 25, figs. 3–5, 9–12

Pleurophorus elegans Kirkby 1880, p. 586.
Carbonicola elegans Hind 1895, p. 81, pl. 20, figs. 12–15, 15*a*.

Type material. C. elegans was first described without figures from the No. 10 Limestone of Randerstone. Hind subsequently figured three complete specimens and a broken shell showing the hinge-plate, giving the locality as 'East of Pittenweem'. The evidence indicates that Hind was in error as to the locality of these specimens. Hind does not state that they are Kirkby's original material, but he acknowledges (1895, p. 82) the loan of material from Kirkby's collection. *C. elegans* occurs east of Pittenweem in a dwarf fauna from Bed 386 of Kirkby's Pittenweem–Anstruther section, but it seems improbable that the figured shells came from that locality. The writer has not found any specimen there as large as the figured shells, nor have any been observed in Kirkby's material in the Hancock Museum. The red limestone matrix of the figured shells is quite unlike pale grey ironstone of Bed 386, but is indistinguishable from the No. 10 Limestone, Randerstone. *C. elegans* is also found in Bed 649, at Billow Ness, 1 mile east of Pittenweem but much nearer to Anstruther. It is almost impossible to obtain a good specimen from this bed because of the nature of preservation of the fossils and it is unlikely that 'East of Pittenweem' refers to this locality. The writer is of the opinion that the figured shells are from the No. 10 Limestone, Randerstone, but that there is insufficient evidence to show whether they were Kirkby's original material.

EXPLANATION OF PLATE 25

Figs. 1–2. *Carbonicola antiqua* Hind. Calciferous Sandstone Series, red limestone, Kilminning, Crail, Fife, ×2. 1, Lectotype, L.46889, complete shell. 2, Syntype, L.46890, right valve.

Figs. 3–5. *Carbonicola elegans* (Kirkby). Calciferous Sandstone Series, Limestone 10, Randerstone, Fife. 3, L.47165, left valve, ×2. 4, L.47163, right valve, ×2. 5, L.47164, internal mould, ×2½.

Figs. 6–8. *C. antiqua*. Calciferous Sandstone Series, calcareous sandstone, Kilrenny Mill, Anstruther, Fife. 1001, internal mould, lateral, anterior, and dorsal views, ×2.

Figs. 9–12. *C. elegans*. Topotype material. 9–11, R.10.2, internal mould, anterior, lateral and dorsal views, ×2. 12, In the collection of Dr. A. Wattison, internal mould showing muscle scars and pallial line, ×2½.

Figs. 13–14. *Anthraconaia? kirki* sp. nov. Calciferous Sandstone Series, mudstone, Kilrenny Mill, Anstruther, Fife. ×2½. 13, holotype, S.13440, 14, paratype, S.13442.

(Figs. 1–5 reproduced by permission of the British Museum (Nat. Hist.). Reg. nos.: prefix L denotes British Museum (Nat. Hist.); prefix S denotes Hunterian Museum, Glasgow; prefix R denotes University of St. Andrews collection. Remaining specimen in the author's collection.)

Dimensions

	L (*mm.*)	*H* (*mm.*)	*A* (*mm.*)	*T* (*mm.*)
Pl. 25, fig. 3 (L.47165) (Hind, pl. 20, fig. 15)	17·6	8·5 (48·3%)	3·3 (18·7%)	est. 6·2 (35·2%)
Pl. 25, fig. 4 (L.47163) (Hind, pl. 20, fig. 13)	17·8	8·4 (47·2%)	3·7 (20·2%)	est. 6·0 (33·7%)

Description and discussion. Hind's specimens are larger than the mean for the topotype material from Randerstone. Shell ovate, elongate with H/L less than 50 per cent. Anterior end short, *c.* 20 per cent. of the length. Very fine, tilted growth lines. Moderately tumid. Lower border gently curved, posterior end rounded or obliquely truncated. Antero-umbonal slope concave. Slight carinate feature running downwards and backwards from umbo. Umbones low and directed towards the anterior. Edentulous. *C. antiqua* is thick shelled where it occurs in limestone and calcareous sandstone, but it is much thinner shelled where it is found in shale.

Comparison. C. elegans resembles *C. antiqua*, but the modal value of H/L is some 12 per cent. less. Growth lines are finer in *C. elegans* than in most variants of *C. antiqua*, and in no case have variants of the former with very coarse growth lines been observed. *C. elegans* and *C. antiqua* have not been found in the same bed; this mutual exclusion may indicate that they are biospecies. The variation of A/L in *C. antiqua* encompasses the variation of A/L in *C. elegans*, so that length of the anterior end is not a diagnostic character. The shape variation is more restricted in *C. elegans* and no variants with pronounced arching of the dorsal margin, nor variants which are skew ovals (due to the lowest part of the ventral margin being near the posterior end) such as are found in *C. antiqua*, have been observed.

Distribution. C. elegans has been recorded from Beds 386 and 649, separated by 1,200 feet of strata, of the Pittenweem–Anstruther shore, as well as from the No. 10 Limestone, Randerstone. It is clear from the correlation proposed by Kirkby (1880, p. 572), as modified by Kirk (1925, p. 369), that Bed 649 and the No. 10 Limestone must be at nearly the same horizon, but that they are not precise equivalents has been shown above.

Anthraconaia? kirki sp. nov.

Plate 25, figs. 13, 14

Holotype. Hunterian Museum, Glasgow, no. S.13440. *Paratype* no. S.13442.

Diagnosis. Small, elongate with a mean value for H/L approximately 40 per cent. for the four specimens measured. Anterior end short, not exceeding 20 per cent. of the length. Umbones low, anterior-umbonal slope concave. Hinge-line long and extending the greater part of the length of the shell. Posterior end rounded and slightly expanded. Greatest height of shell about one-third of the length from the posterior end. Ventral border gently curved. Growth lines fine, numerous, tilted. No distinct carina, but a swelling runs obliquely backwards and downwards from the umbo towards the posterior-inferior angle.

Dimensions

	L (*mm.*)	*H* (*mm.*)
Pl. 25, fig. 13 (S.13440), holotype .	9·6	3·3 (34·4%)
Pl. 25, fig. 14 (S.13442), paratype .	10·8	4·6 (43%)
S.13441	*c.* 12	6·0 (50%)
1139	14·9	5·7 (38%)

Only four measurable specimens have so far been obtained. Measurements of the length of the anterior end (not given here) are in the region of 1·5–2·5 mm., representing a value of 20 per cent., or less, for A/L.

Description. In two specimens both valves are present with the umbones in contact but they are agape. It is not possible to estimate tumidity as no specimens were obtained showing the original convexity. The angle β appears to be relatively low, just exceeding 100°, but the angle γ cannot be estimated from the limited material available. No evidence is available on the interior of the shell.

Comparison. A.? kirki is similar to the more elongate forms of *Anthraconaia* such as *A. williamsoni* or to *A. bellula* from the Millstone Grit. The following characters suggest the affinity of *A.? kirki* to *Anthraconaia*: the hinge-line and ventral margin are subparallel; the shell is expanded posteriorly; and it possesses an ill-defined carinal feature. Further, it forms a small percentage of a non-marine lamellibranch fauna. It seems preferable to refer this species to the genus *Anthraconaia* with a query, for Dr. J. Weir has pointed out to me that it is far removed in time from the typical *Anthraconaia* of the *adamsi–salteri–modiolaris* group, and that vital knowledge of the internal characters is lacking.

COMMUNITIES OF *CARBONICOLA*

I. *Carbonicola antiqua*

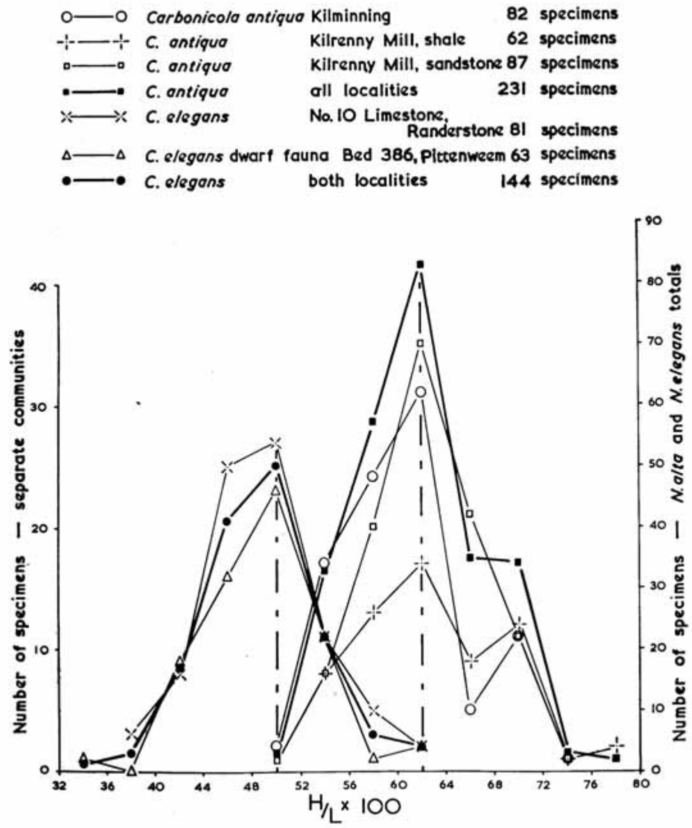
1. *Kilminning. Carbonicola antiqua* is abundant in a 10-inch bed of red limestone at Kilminning, Fife, from which the syntypes were obtained. Specimens are poorly preserved and difficult to extract, but over 100 were examined and over ninety measured. The mean values for length, height, and length of anterior end of the shells from this collection are less than those for the collections from shale and sandstone at Kilrenny Mill.

	L	*H*	*A*	*d*	*No. of specimens*
Kilminning limestone . .	20·6	12·4	3·9	8·6	91
Kilrenny Mill shale . . .	22·0	13·8	5·1	9·7	62
Kilrenny Mill sandstone . .	23·1	13·6	4·7	..	13

(Measurements in mm., only external measurements have been utilized.)

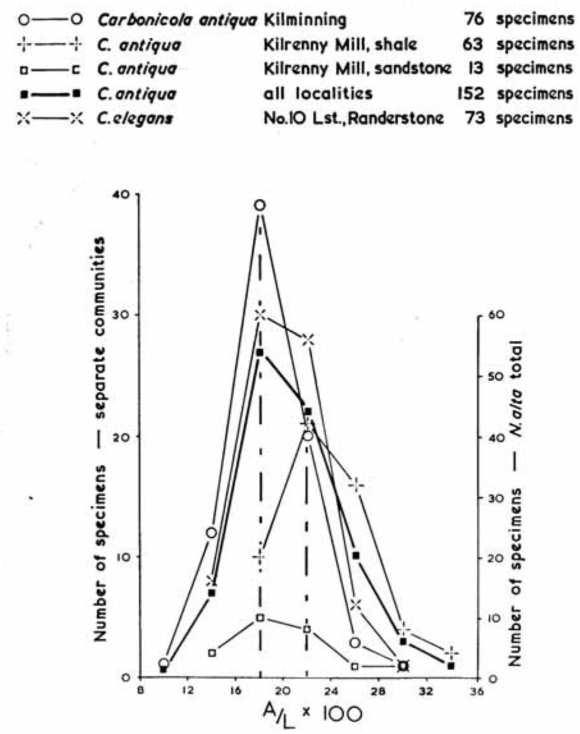
The abundance of shells in the Kilminning limestone and their eroded nature suggests that they have been sorted by wave or current action. The relatively high percentage of small forms (less than 15 mm. in length) may be due to this sorting effect and the small range of variation in size confirms that this is not a life assemblage.

	% of specimens with L less than 15 mm.	*% of specimens with L less than $\frac{2}{3}$ mean value*	*Range of value of L (mm.)*
Kilminning Limestone . .	17%	2% (less than 13·7 mm.)	13·4–28·2 (diff. 14·8)
Kilrenny Mill shale. . .	6%	6% (less than 14·5 mm.)	9·3–31·4 (diff. 22·1)
Kilrenny Mill sandstone . .	1%	1% (less than 15·4 mm.)	14·5–25·9 (diff. 11·4)



TEXT-FIG. 2. Graphs to show the ratio of length (L) to height (H) in collections of *Carbonicola antiqua* and *C. elegans* from east Fife.

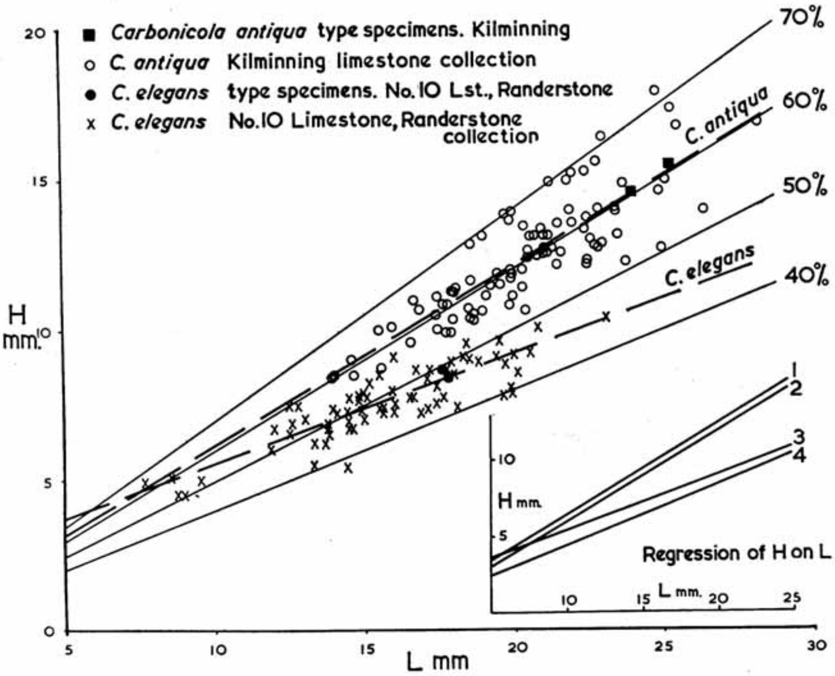
The variation graph for H/L (text-fig. 2) shows a modal value of 62 per cent. for the Kilminning shells, with a variation of 12 per cent. on either side of the mode. The other collections show close agreement, both in mode and range of variation. The variation graph for A/L (text-fig. 3) shows that the Kilminning shells have a different modal value and a different range of variation from the Kilrenny Mill collections; the modal value for A/L is approximately 4 per cent. lower in the case of the Kilminning collection. Two factors might affect the proportions of the shells. The shells are rather small and if



TEXT-FIG. 3. Graphs to show the ratio of length (L) to length of anterior end (A) in collections of *Carbonicola antiqua* and *C. elegans* from east Fife.

growth were allometric then the modal value of this collection would be low. A scatter diagram (text-fig. 5) does not reveal any tendency for length of anterior end to increase relatively with length and, calculating the regression of A on L, we find that the line would pass nearly through the intersection of the axes of the scatter diagram. The other factor affecting the proportions of the shells is the degree of crushing, related to the compaction of the sediment: this is noticeably less in the case of shells from the limestone than in shells from shale. The effects of crushing, if the shells are lying parallel to the bedding planes, as in this case, is to increase A/L; see Dix and Trueman (1931, p. 192) and Eagar (1947, p. 11). The second term, in a calculation of the slope of the regression line of A on L, is a measure of that slope: *C. antiqua*, Kilminning limestone $A = 0{\cdot}25 + 0{\cdot}176L$. *C. antiqua*, Kilrenny Mill shale $A = 0{\cdot}45 + 0{\cdot}256L$.

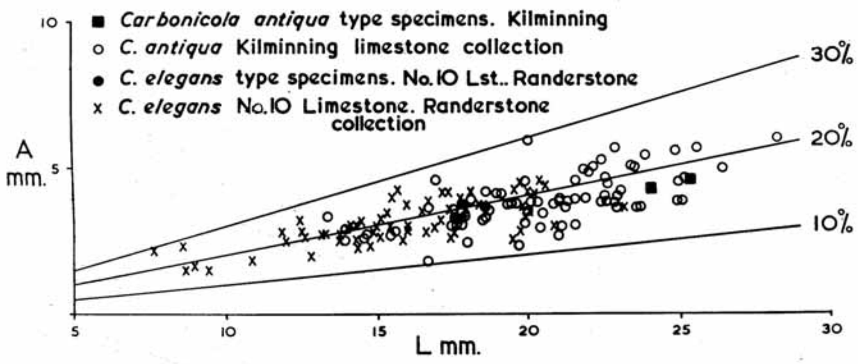
This seems to explain the discrepancy in the values of A/L in *C. antiqua*, and it seems unlikely that such a discrepancy may be attributed to evolutionary change or to a difference of habitat.



TEXT-FIG. 4. The relationship between length (L) and height (H) in *Carbonicola antiqua* and *C. elegans*. Inset: regression lines of H on L. 1 = *C. antiqua*, Kilrenny Mill shale collection, 2 = *C. antiqua*, Kilminning limestone collection, 3 = *C. elegans*, No. 10 Limestone, Randerstone collection, 4 = *C. elegans* dwarfs, Bed 386, Pittenweem collection.

In the collection from Kilminning T/L is high and variants with a bluntly rounded posterior end are relatively common. Variation in shape of shell is shown in text-fig. 6, which shows that some variants have a more pronounced dorsal arch, that some are skew ovals, and that some have an obliquely truncated posterior. The first two kinds of variants have a relatively high value for H/L, but the presence of such variants is inadequately expressed by the simple H/L ratio. A fourth measurement, the distance from the anterior end to the point of maximum downward curvature of the lower border, denoted by d, has been used (see Leitch 1940, p. 15). d/L is typically about 40 per cent., but ranges from 25 to 68 per cent.

2. *Kilrenny Mill shale*. *C. antiqua* is common in blue-grey shaly mudstone which almost immediately succeeds a highly fossiliferous calcareous sandstone. Many of the shells are excellently preserved, but they are less numerous than in the limestone of Kilminning and fewer measurable specimens were obtained. Individual shells here attain the greatest size. The shells show little evidence of sorting by wave action—although specimens often comprise single valves only—for there is here the greatest range in size and the greatest proportion of young (small, less than two-thirds the mean L) shells. This is, therefore, the most representative collection of *C. antiqua* and may approximate to a life assemblage. The assemblage includes about 8 per cent. of *Anthraconaia? kirki* and *c*. 2 per cent. of *Naiadites obesus* (R. Etheridge, jun.).

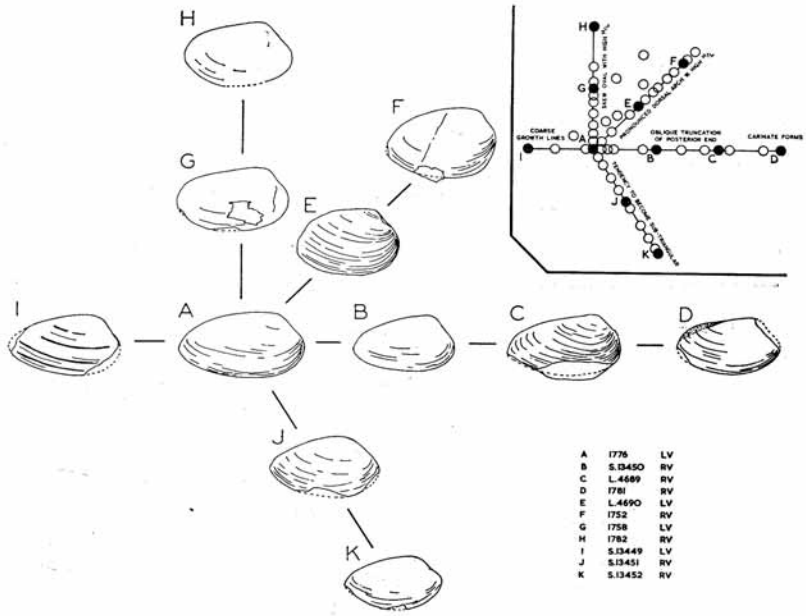


TEXT-FIG. 5. The relationship between length (L) and length of anterior end (A) in *Carbonicola antiqua* and *C. elegans*.

Variation in shape of shell is shown in text-fig. 7. It is apparent that variants with an obliquely truncated posterior end are more common than in the Kilminning collection, and a relatively large *pseudorobusta*-like variant (text-fig. 7L) is found in the Kilrenny Mill shale only. It is impossible to calculate the variation in shape of shell attributable to crushing effects and it is, therefore, questionable whether the shape variations, illustrated in text-figs. 6 and 7, represent true differences arising from adaption to environment or from evolutionary changes (Kirkby's view, that the shell beds of Kilminning and Kilrenny Mill could be correlated, has been discussed, and cannot be sustained).

3. *Kilrenny Mill sandstone*. In a calcareous sandstone of variable thickness (it is seen to thicken from 6 in. to 18 in. in a lateral distance of a few feet) *C. antiqua* is abundant. In most specimens the shell material has been dissolved away leaving excellent moulds and, although these provide information on the internal character of *C. antiqua*, comparison with the other collections is difficult. In a few specimens the shell material is partially eroded and interior and exterior dimensions can be compared. It was observed that a correction made to the measurements of internal moulds, by adding 0·6 mm. to the length and height, was justifiable. The average shell thickness is of the order of 0·3 mm. and a comparison of the mean values of L, H, and H/L for the whole collection

(with the correction applied) and the mean values obtained from the limited number of exteriors showed close similarity. No such correction was applied in the case of the anterior end, chiefly due to the difficulty of estimating the position of the umbo. The mean value of length, for this collection, is high but no very large shells have been found



TEXT-FIG. 6. Pictograph showing variation in shape of shell of *Carbonicola antiqua* from Kilminning, Fife. Inset shows distribution of variants relative to the figured specimens, which are represented by lettered black circles. For purposes of comparison all shells have been drawn as right valves. About two-thirds natural size. (Registered numbers with prefix L refer to Brit. Mus. (Nat. Hist.) specimens, with prefix S refer to Hunterian Mus., Glasgow specimens. Other specimens in author's collection.)

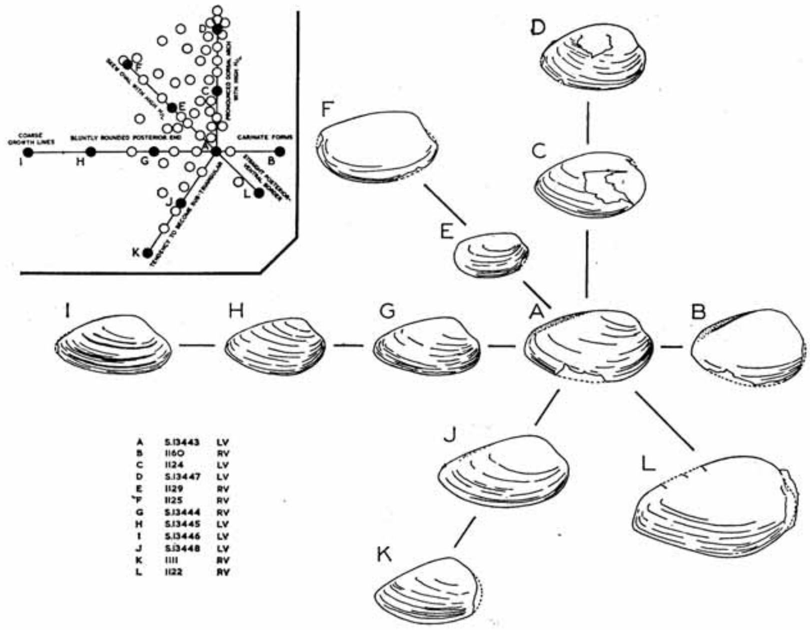
(see table above). Small shells are absent, providing evidence of sorting—as might be expected in a sediment with much detrital quartz.

4. *Bed 586 of Kirkby's main section, Pittenweem–Anstruther shore*. This exposure is covered by massive fallen blocks of sandstone. Only a few square inches of shale can be examined and, from these, three specimens of *C. antiqua* were obtained. Its presence is thus confirmed but comparison with collections from other localities is not possible.

II. *Carbonicola elegans*

1. *Kirkby's No. 10 Limestone, Randerstone*. This is the only horizon from which *C. elegans* has been obtained in sufficient numbers to permit precise comparison with *C.*

antiqua. It is the probable horizon of Hind's specimens, and the horizon from which the species was first described by Kirkby. The collection shows a wide range of variation in the value of H/L, from *c*. 36 per cent. to 64 per cent., some variants having a value for H/L comparable with the modal value of the *C. antiqua* collections (text-fig. 2). The



TEXT-FIG. 7. Pictograph showing variation in shape of shell of *Carbonicola antiqua* from shale, Kilrenny Mill, Fife. Inset shows distribution of variants relative to the figured specimens, which are represented by lettered black circles. (For location of specimens see text-fig. 6.)

modal value of the *C. elegans* collection is 12 per cent. lower than that of the *C. antiqua* collections and, since no change in mode with horizon is known in either species, this appears to be a significant difference. Further, there is a tendency for H/L to decrease with increase in size of the individual in *C. elegans* (text-fig. 4); this is shown by calculating the regression of H on L. The regression line (text-fig. 4, inset, line 3) does not, if produced, pass through the origin of the graph. The difference between the slope of this line and the regression lines calculated for the Kilrenny Mill shale and Kilminning limestone collections of *C. antiqua* (lines 1, 2) are significant.

The modal value of A/L for this collection of *C. elegans*, 18 per cent., is close to that of the *C. antiqua* collections. The more reliable comparison can be made between the two limestone faunas, the Kilminning Limestone and the No. 10, Randerstone, for in both the effects of crushing are at a minimum (text-figs. 4, 5). Calculation of the regression of A on L showed no statistically significant difference for the two species.

2. *Bed 649 of Kirkby's main section, Pittenweem–Anstruther shore*. In this bed at Billow Ness, as Kirkby remarked (*in* Geikie 1902, p. 96), *C. elegans* occurs as a small percentage of a dominantly *Naiadites obesus* fauna. Usually the posterior-dorsal area of *N. obesus* is broken off, so that the shell bears a close resemblance to *C. elegans*. Because of this preservation it is difficult to estimate how commonly *C. elegans* occurs, but prolonged collecting has yielded a few well preserved shells which can be referred to that species without doubt.

3. *Bed 386 of Kirkby's main section, Pittenweem–Anstruther shore*. A 3-inch bed of calcareous iron-rich siltstone includes dwarfed shells of *Carbonicola elegans*. The mean length of shell is less than 7 mm., less than half that of those from No. 10 Limestone, Randerstone. In measuring such small shells the operational error is liable to be high when expressed as a percentage of length or height. For this reason the same reliance cannot be placed on the H/L ratio although the modal value of 50 per cent. for this collection is comparable with that of the Randerstone shells and the regression lines (text-fig. 4 inset) are similar. The shells appear to resemble *C. elegans* in every way except size: they are, however, relatively thick shelled. It is difficult to establish whether the fauna is 'dwarfed' by adverse ecological conditions, or whether only small shells are present as a result of sorting by waves or currents. The former seems probable in view of the lithology (fine angular quartz grains are abundant and may have inhibited growth), and the range of variation in size of shell (L = 3 mm. to 11·5 mm.) does not confirm sorting effects. However, very young individuals (spat) are not present in the assemblage.

The following table shows the similarity of different collections of *C. antiqua*, differences due to relative amounts of crushing being reflected in regression equations of both

	C. antiqua			*C. elegans*	
	Kilminning	*K. Mill sh.*	*K. Mill sst.*	*No. 10 Lst.*	*Bed 386*
$\bar{L}$	20·6 mm.	22·0 mm.	23·1 mm.	15·7 mm.	6·9 mm.
$\bar{H}$	12·4 mm.	13·8 mm.	13·6 mm.	7·6 mm.	3·3 mm.
$\bar{A}$	3·9 mm.	5·1 mm.	4·7 mm.	3·1 mm.	..
$\bar{d}$	8·6 mm.	9·7 mm.	..	..	..
Mode H/L . .	62%	62%	62%	50%	50%
Mode A/L . .	18%	22%	18%	18%	..
Mode d/L . .	42%	42%	..	..	..
Correlation:					
r_{HL} .	0·854	0·893	..	0·856	..
r_{AL} .	0·651	0·793	..	0·729	..
Regression:					
H =	0·25+0·593L	0·41+0·610L	..	1·82+0·368L	0·52+0·405L
A =	0·25+0·176L	0·45+0·256L	..	0·51+0·165L	..

H on L and A on L. The greater difference between *C. antiqua* and *C. elegans* is indicated in the figures for H/L as well as the regressions.

CONDITIONS OF SEDIMENTATION

One of the features of *Carbonicola* from the Lower Carboniferous is its occurrence in rocks of widely differing lithology. It is found in calcareous, arenaceous, and argillaceous rocks. The question whether it could survive under such differing conditions of sedimentation arises. Further, if it lived in such a variety of environments, why should *C. antiqua* and *C. elegans* each occur at so few horizons, as far as is known, and be mutually exclusive of each other? In some cases, for example the No. 10 Limestone, the Kilminning limestone, and probably the Kilrenny Mill sandstone, the shells have been collected together by currents. The specimens are usually single valves and are probably not in their ecological stations. The occurrence of *C. antiqua* in the shaly mudstone of Kilrenny Mill probably provides the only reliable evidence of its ecology. The presence of large numbers of *C. antiqua* in the underlying sandstone is enigmatic, for this sediment comprises angular quartz grains cemented by calcite. The coarse texture of the rock, the variations in thickness of the bed, and the similarity in size of all the shells, together with the presence of macroscopic plant fragments, indicate turbulent conditions (Broadhurst 1959).

The habitat of *C. elegans* is even more difficult to assess. Only in the No. 10 Limestone of Randerstone is *C. elegans* abundant and here there is evidence of sorting. Petrologically, this rock could be classified as a microscopic limestone breccia. Apart from complete shells, the rock is made up largely of shell fragments of about 4 mm. diameter. It is surprising that *C. elegans* is not found in the shales immediately above the No. 10 Limestone in which *Naiadites obesus* is common, the more so since these two species occur together in Bed 649 at Billow Ness. Microscopic examination of the rock which yields the *C. elegans* dwarf fauna, Bed 386, reveals a matrix which includes 40 per cent. of angular quartz grains (0·1 mm. in diameter). This silt may have inhibited the growth of *C. elegans*.

C. antiqua and *C. elegans* are found in beds which occur in a succession which is not dominantly marine, but which includes shales and limestones with varied marine faunas. The absence of contemporaneous marine forms (but see below) from the *C. antiqua* and *C. elegans* shell beds is an indication of their non-marine habitat. Both species are found in association with *Naiadites obesus* which, elsewhere, is found in close proximity to marine forms. The only other faunal associations of these species of *Carbonicola* are with *Spirorbis* (cf. the association of *Spirorbis* with non-marine shells noted by Etheridge (1800, p. 217); see also Trueman (1942) and with ostracods. Kirkby (1880, p. 577) records the presence of numbers of *Littorina scotoburdigalensis* with *Carbonicola elegans*. Hind (1895, p. 82) notes that Etheridge believed this gastropod to be 'nearer to *Paludina*' (= *Viviparis*, a fresh-water form). Unfortunately the author has not found any specimens of it. Kirkby (*in* Geikie 1902) records only three species of ostracod in association with *C. elegans*, namely *Cytherella attenuata*, *C. extuberata*, and *Cythere superba*. Latham (1932) showed that these are among the commonest forms in the Calciferous Sandstone Series, are of long range, and occur in varied faunal associations, frequently with *Naiadites obesus* but also with *Schizodus* and other marine lamellibranchs. The known faunal associations of the two Calciferous Sandstone Series species of *Carbonicola* are summarized:

Carbonicola antiqua	*Carbonicola elegans*
Naiadites obesus	*Naiadites obesus*
Spirorbis sp.	*Spirorbis sp.*
Anthraconaia? kirki	*? Littorina scotoburdigalensis*
Cytherella sp.	*Cytherella attenuata*
Fish teeth	*Cytherella extuberata*
	Cythere superba
	Fish teeth and spines

The presence of macroscopic drifted plant fragments, occurring on the same bedding planes as the shells, indicates the proximity of land. Little can be said to account for the mutual exclusion of *C. antiqua* and *C. elegans*; the only observed difference in the matrices was the relative abundance of iron in the shell beds including *C. elegans*. The presence of one species rather than the other may well be related to salinity or temperature, environmental characters which are not reflected in the lithology.

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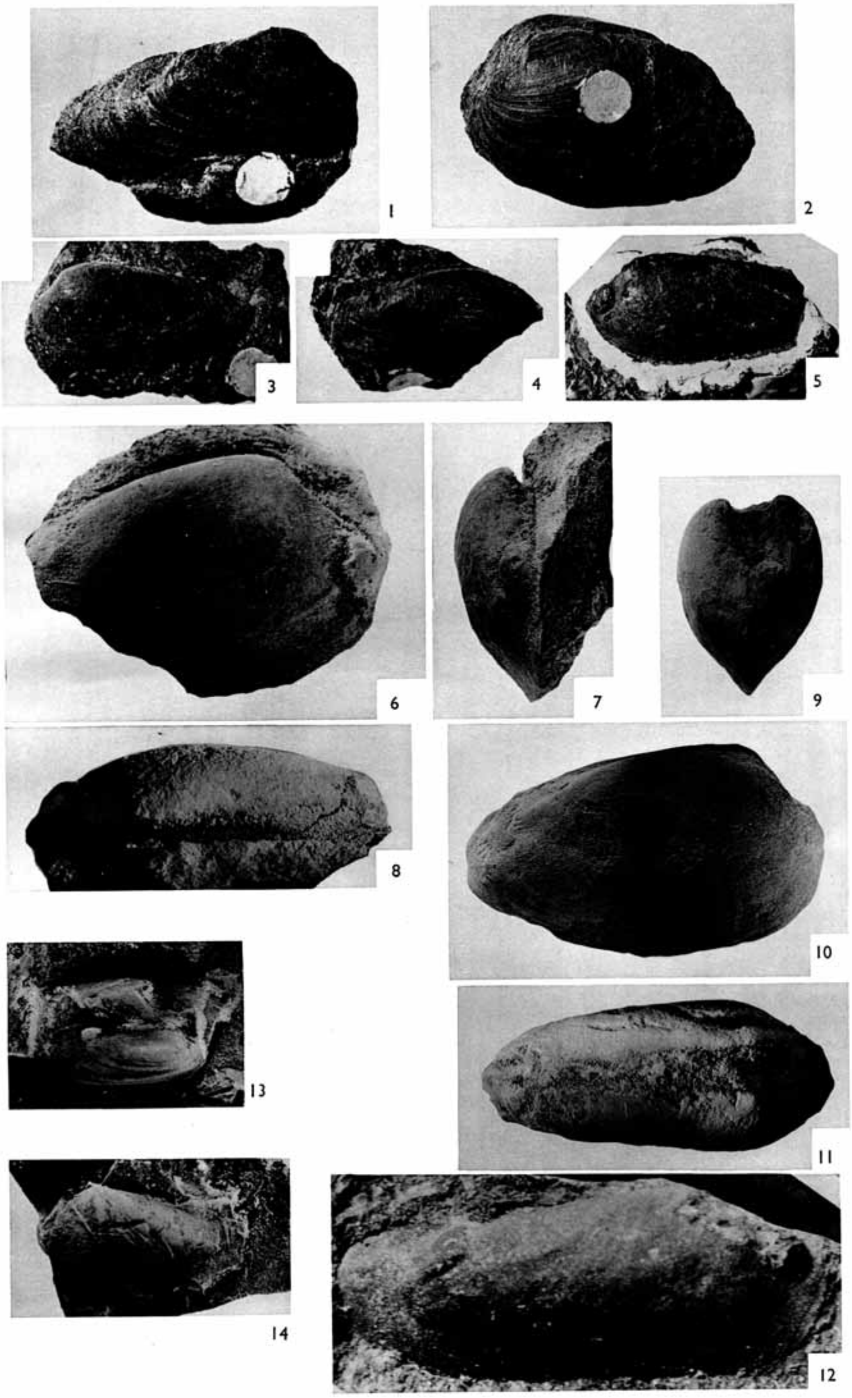

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