

MANTLE CANAL PATTERNS IN
SCHIZOPHORIA (BRACHIOPODA) FROM
THE LOWER CARBONIFEROUS OF
NEW SOUTH WALES

by JOHN ROBERTS

ABSTRACT. The brachiopod *Schizophoria verulamensis* Cvanara, from the Lower Carboniferous of the Gresford district, New South Wales, has distinctive mantle canal patterns in small, medium, and large specimens. The different patterns are interpreted as stages in the ontogeny and are thought to result mainly from the growth and enlargement of the genitalia.

Changes in the morphology of the canals in pedicle valves throughout six horizons in the Lower Carboniferous sequence show a trend, probably genetically controlled, towards the earlier maturity of the genitalia. The superimposition of larger or mature mantle canal systems on smaller or immature systems indicates that the canals are impressed by periodic resorption, and it is argued that this probably took place during the winter when there was a stable mantle canal system and little shell deposition. In large specimens there are connexions between the vascula genitalia, vascula media, and lateral canals in the pedicle valve, and between the vascula genitalia and vascula myaria in the brachial valve. It is suggested that the connexions may have increased the amount of oxygenated coelomic fluid circulating over the gonads, possibly causing them to ripen earlier.

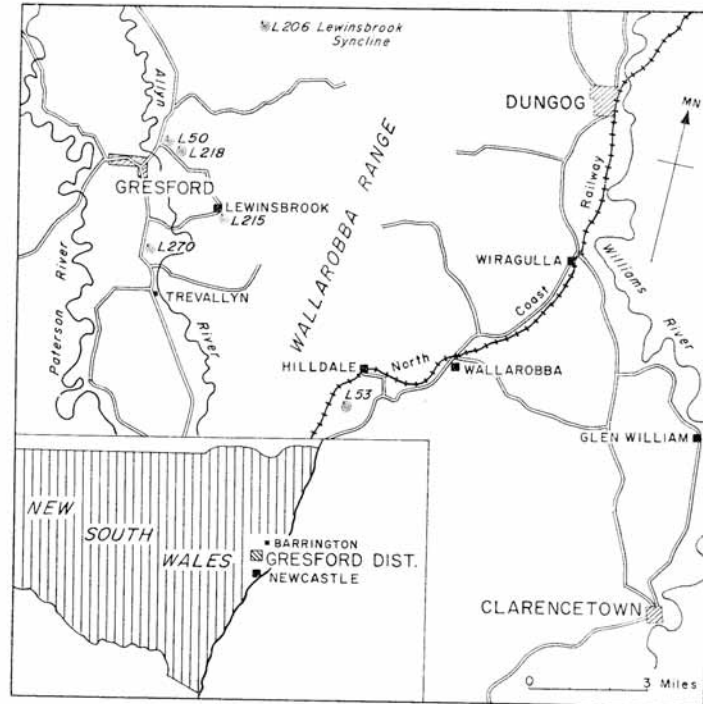
Pathological variations in the mantle canals are described, and it is shown that the canals are able to adjust to injuries or defects in the shell.

THE mantle canals in living brachiopods are extensions of the body cavity into the mantle. Their function is mainly respiratory and in articulates they also act as receptacles for the gonads. In both living and fossil brachiopods the pattern of canals is frequently impressed on the inner surface of the shell, particularly that of older specimens. In fossil brachiopods impressions of the mantle canals are common in orthoids and strophomenoids, are rarely seen in the spiriferoids and chonetoids, and only recently have been observed in two species of productoids from the Lower Carboniferous of the Bonaparte Gulf Basin, northwestern Australia. As a result their use in systematics is limited.

Schuchert and Cooper (1932) described the morphology of the mantle canals in the orthoids and used the canal patterns as a basis for the separation of a new subfamily. Öpik (1934) further demonstrated their use in his study of the Clitambonitidina, and proposed a detailed terminology for the various parts of the mantle canal system. Williams (1956) was the first to present a comprehensive review of the mantle canal patterns in articulate brachiopods. He modified Öpik's terminology and showed that the mantle canal patterns in articulates could be referred to standard types which were probably derived from Cambrian forms. Williams (1956) and Williams and Rowell (1965) illustrated many different types of mantle canal patterns.

The present study deals with the morphology, development, and probable genetic changes in the mantle canals of the Lower Carboniferous orthoid *Schizophoria verulamensis* Cvanara (1958). Extremely well-preserved material has made possible the recognition of a sequence of young, mature, and old stages in the mantle canal system of *S. verulamensis*. These stages have in turn led to the recognition of a trend towards an earlier maturity of the reproductive system during the Lower Carboniferous, and a

method of impression or superimposition of the mantle canals which had not previously been recognised in the Brachiopoda. Because of the exceptionally fine preservation it has also been possible to recognize an intricate interconnexion between the various parts of the mantle canal system, a feature not recognized in Williams's and Rowell's treatment of mantle canal patterns.



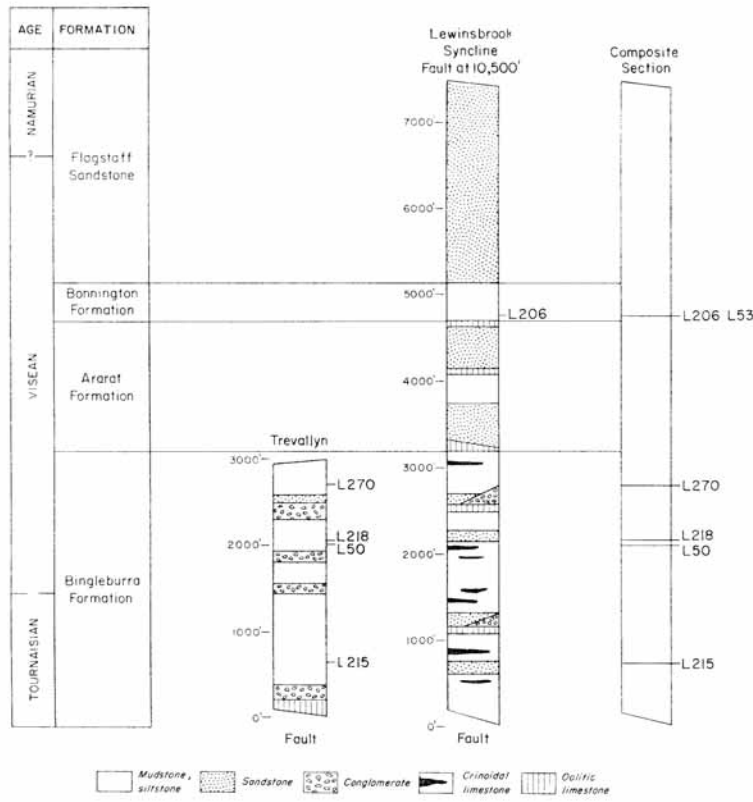
TEXT-FIG. 1. Locality of the Gresford District, N.S.W.

Schizophoria verulamensis Cvancara is one of the most common brachiopods in the Lower Carboniferous (Tournaisian and Viséan) of New South Wales, and has been collected from every known fossil horizon in the Gresford district, about 35 miles north-west of Newcastle (text-fig. 1). The majority of the specimens described in this paper are preserved in indurated grey siltstone; the rest occur in medium-grained lithic sandstone. They are exceptionally well preserved, and have very finely detailed impressions of the mantle canals and setal follicles. Internal moulds only are figured in the plates because the impressions of the canals, represented by ridges, are particularly prominent when illuminated by an oblique light source.

Schizophoria verulamensis is especially well represented in collections from the following localities (with grid references): L. 53 Greenhills (46609790), L. 206 Lewins-

brook syncline (46279968), L. 270 Trevallyn (45729864), L. 218 Gresford Quarry (45809912), L. 50 Gresford Quarry (45789913), L. 215 Lewinsbrook (46089882).

With the exception of L. 53 Greenhills, which is on the Paterson One-Mile Sheet, the grid references are taken from the Dungog One-Mile Sheet. The stratigraphic positions



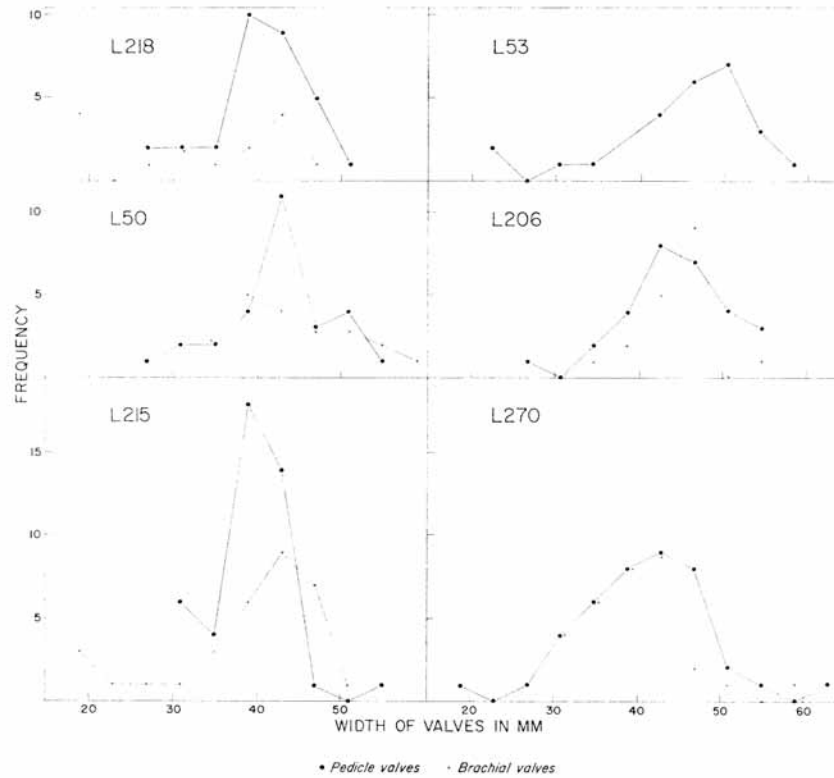
TEXT-FIG. 2. Diagrammatic stratigraphic sections of the marine rocks at Trevallyn and in the Lewinsbrook Syncline.

of the horizons are shown in text-fig. 2 on diagrammatic stratigraphic sections of the marine rocks in the north-western part of the Gresford district. All of the collections are housed in the Geology Department, University of New England, Armidale, N.S.W.

The stratigraphy of the Gresford district has been described by Roberts (1961 and 1965c) and the faunas by Roberts (1963, 1964, and 1965a and b), Campbell and Roberts (1964), and Brown, Campbell, and Roberts (1965).

The specimens of *Schizophoria verulamensis* were collected from a single horizon at each fossil locality except L. 53, where two horizons were sampled. An attempt was

made to collect randomly at each locality, and all the specimens collected were examined in the laboratory. Width-frequency plots for pedicle and brachial valves are given in text-fig. 3. The samples are characterized by the almost total absence of small specimens, and the presence of a large number of disarticulated valves, features which suggest that the populations had been affected by current action and sorting prior to burial.



TEXT-FIG. 3. Width-frequency polygons for *Schizophoria verulamensis* Cvancara specimens from six localities in the Gresford district.

The post-mortem modification is also borne out by the unequal numbers of pedicle and brachial valves and small number of articulated shells collected from each locality. These figures are given in Table 1. The collection from L. 270 is the only sample having a comparable number of pedicle and brachial valves and also contains the greatest number of articulated shells, suggesting that it is perhaps the closest to a life assemblage.

Further evidence that most of the assemblages are death assemblages is provided by the occurrence, at L. 218, L. 270, and L. 206, of shell beds containing large numbers of

mature specimens of *Schizophoria* to the virtual exclusion of smaller specimens and other small species. The L. 53 horizon contains several other large species as well as *Schizophoria*, but also has very few small species. Smaller species and polyzoan debris accompany the *Schizophoria* specimens at L. 215 and L. 50.

TABLE I

Locality	Disarticulated valves		Articulated shells
	Pedicle valve	Brachial valve	
L. 53	25	6	—
L. 206	28	18	1
L. 270	31	30	10
L. 218	30	23	1
L. 50	25	20	5
L. 215	54	31	7

MANTLE CANALS

The mantle canals in living brachiopods are situated in the mesenchyme layer of the mantle and are lined with ciliated epithelium. They are filled with coelomic fluid, which is rapidly circulated by the ciliated epithelium (Hyman 1959, p. 593), the circulation in some species being facilitated by a median ridge dividing the in- and out-flowing currents. The coelomic fluid contains free coelomocytes, including a spherical type which has a respiratory function and may be equivalent to a red blood corpuscle (Hyman 1959, p. 557). The pigment in the 'respiratory cells' absorbs oxygen and on reduction releases it to oxygenate the tissues.

The pattern of the mantle canals varies in different brachiopod groups (Williams 1956), and there is usually a different pattern in the pedicle and brachial valves. In most cases the canals originate as wide branches from the body cavity; some of these divide repeatedly until they extend to the proximal ends of the setal follicles around the edge of the mantle; other form sac-like receptacles and act as gonocoels.

Most living brachiopods have a complicated system of mantle canals extending throughout the mantle, providing a large surface area through which oxygenation of the coelomic fluid can take place. An adaptation to increase the surface area of the mantle canals is illustrated by Williams and Rowell (1965, fig. 24) in which the mantle canals in the inarticulate *Glottidia* subtend gill ampullae into the mantle cavity.

In some fossil groups, however, the mantle canals have a relatively small surface area, and respiration may have been largely carried out by the lophophore. The lophophore in modern articulates has a plentiful supply of coelomic fluid provided by the coelomic canal and the small brachial canal (Williams and Rowell 1965, fig. 30). The small brachial canal gives off a branch to each of the filaments on the lophophore which have a large surface area and are ideally suited to respiration. Spiriferoids, for example, had narrow pinnate mantle canals with a small surface area combined with a large spiral lophophore. The lophophore probably had a large surface area suitable for oxygen exchange, was bathed in a stream of fresh water brought in by the moving filaments, and was an ideal organ for respiration as well as food gathering. Mantle canals appear to be poorly developed in the productoids, which probably also had a spiral lophophore

(Williams 1956, fig. 5 (6); Brunton 1966, figs. 8 and 9), and the lophophore may have acted as the main respiratory organ. Chonetoids occasionally exhibit mantle canals (Muir-Wood 1962, pl. 6, fig. 7), but they too probably used a spiral lophophore for respiration as well as for food gathering.

The mantle canals are also the receptacles for the gonads in living articulate brachiopods, and so the gonads are continuously bathed in oxygenated coelomic fluid.

Blood vessels, which are distinct from the mantle canals, extend from the body cavity into the mantle canals and run along the margins nearest the mantle cavity (i.e. along the inner margins of the mantle canals). These vessels, which are only seen in living brachiopods, follow all the branches of the mantle canals and extend to the margin of the mantle, and also form anastomosing blood sinuses to the gonads (Hancock 1859, pl. 55, fig. 1; pl. 63, fig. 1; and pl. 56, fig. 4). The blood system in brachiopods is an open system, the blood returning to the body cavity by way of tissue spaces. The blood itself is generally free of cells (Hyman 1959, p. 558) and consists of a colourless lymph-like fluid. Because the blood seeps back to the coelomic cavity before being recirculated it is probably coelomic fluid from which the coelomocytes have been filtered off. The blood system is responsible for the supply of nutriment to the organs within the body cavity, the gonads, and to the mantle, especially to the cells at the growing edge of the mantle. Waste products are probably transported by the blood as it filters through the tissues back to the coelome, where they are removed by the nephridia. The blood must also contain dissolved minerals, mainly calcium carbonate, for deposition as shell material by the cells at the growing edge of the mantle.

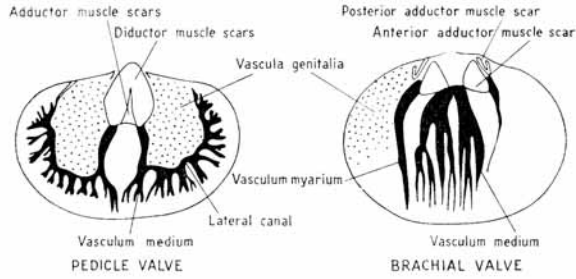
MANTLE CANALS IN *SCHIZOPHORIA VERULAMENSIS*

The morphology of the mantle canal impressions in both valves of *Schizophoria verulamensis* is shown in text-fig. 4. In the following description of the mantle canal system I propose to use the term 'canals' for the impressions of the mantle canals on the inner surfaces of the valves so as to avoid another descriptive term.

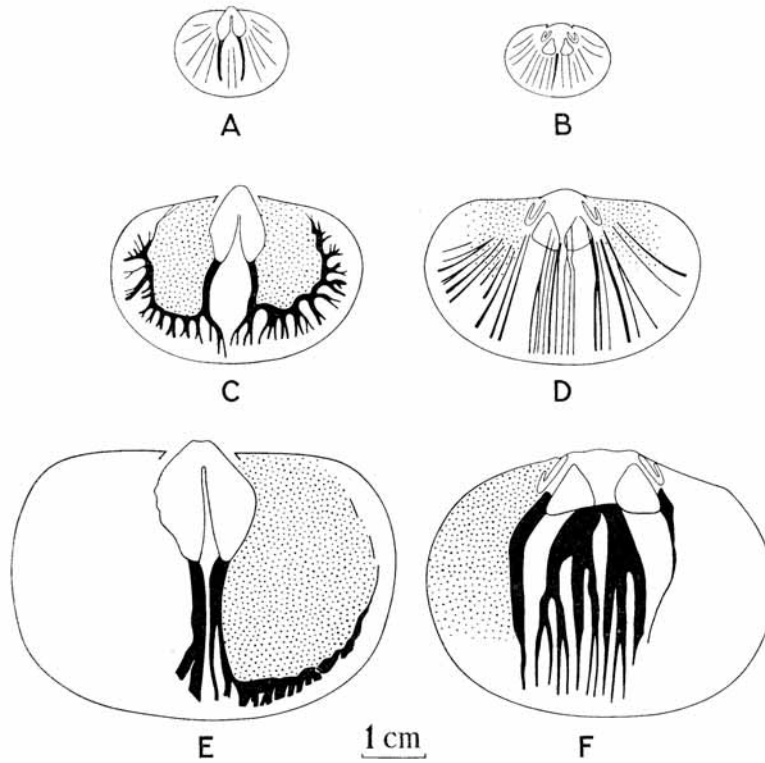
The mantle canals of small and apparently sexually immature specimens of *Schizophoria verulamensis* consist of small canals of *vascula media* and *vascula myaria* as well as a large number of narrower linear canals originating from the anterior and antero-lateral margins of the muscle field and extending to the margins of the valve (text-fig. 5 *a, b*). There is no differentiation of *vascula genitalia*.

In the pedicle valve the impressions of the *vascula media* arise from the anterior margins of the diductor muscle scars and extend with only minor branching to the front of the valve. An arcuate lateral canal such as that in older individuals (text-fig. 5*c*) does not appear to have been developed and the lateral margins of the valve were presumably supplied with coelomic fluid by the narrow linear canals extending from the body cavity.

Impressions of the mantle canals are less frequently preserved in brachial valves. Small brachial valves have canals of *vascula media* originating from between the inner margins of the anterior adductor muscle scars or, more rarely, from the inner parts of the adductor scars, and extending towards the front of the valve. The *vascula myaria* are simple, straight canals arising from between the anterior and posterior adductor muscle scars and extending towards the postero-lateral margins.



TEXT-FIG. 4. Morphology of the mantle canal impressions in *Schizophoria verulamensis* Cvancara.



TEXT-FIG. 5. Mantle canal patterns in *Schizophoria verulamensis* Cvancara showing the development from small to large individuals. The pedicle valve is on the left and the brachial valve on the right.

Larger, apparently sexually mature individuals (text-fig. 5 *c, d*) have an interconnected system of *vascula genitalia* in the pedicle valve (Pl. 74, fig. 3), an incipient system of *vascula genitalia* in the brachial valve (Pl. 74, fig. 6), and more complex *vascula media* and *vascula myaria* canals.

In the pedicle valve of mature individuals the main canals of *vascula media* are well separated from one another and are much broader and more deeply impressed than in the younger form. Each of the main canals branches distally, giving off a number of canals which run to the front of the valve, and an arcuate lateral canal which extends parallel with the margin of the valve to the hinge. The lateral canal has a crenulate pattern and at the peak of each crenulation gives off a major branch, which usually subdivides several times before reaching the margin of the valve. Towards the hinge the lateral canal is irregularly crenulate and terminates in a group of diverse branches. The *vascula genitalia* cover an area enclosed by the muscle field, the *vascula media*, and the inner margins of the arcuate lateral canals, and are connected by numerous branches with the *vascula media* and lateral canals; the significance of these connexions will be dealt with below.

The *vascula genitalia* in brachial valves having the same size and presumably the same age as mature pedicle valves do not appear to be as strongly impressed as those in the pedicle valve. The genital markings consist of pit-like depressions or incipient interconnected canals on the postero-median parts of the valve, and give rise to numerous branching canals, similar to those of the *vascula media* and *vascula myaria*, which extend to the lateral margins (Pl. 74, fig. 6). There are up to ten canals of *vascula media*, and ten canals of *vascula myaria* extending with variable bifurcation towards the anterior margin. Both the *vascula media* and *vascula myaria* leave tracks on the anterior adductor muscle scars.

In the largest and probably gerontic specimens (text-fig. 5 *e, f*) the mantle canal system is frequently more strongly impressed on the inner surface of the shell and is characterized by even broader main canals and an expansion of the *vascula genitalia*.

EXPLANATION OF PLATE 74

Schizophoria verulamensis Cvancara

- Fig. 1. ×1. F.7145a. Internal mould of pedicle valve showing the connexions between the *vascula media* and *vascula genitalia*; L. 215 Lewinsbrook.
- Fig. 2. ×1. F.7145r. Internal mould of pedicle valve; note the truncation of the narrow canals by the main canals of *vascula media*; L. 270 Trevallyn.
- Fig. 3. ×2. F.4677a. Internal mould of pedicle valve showing a sexually mature mantle canal system superimposed over an immature system; L. 215 Lewinsbrook.
- Fig. 4. ×1. F.8036. Internal mould of pedicle valve showing a third canal of *vascula media* extending to the front of the valve; L. 50 Gresford Quarry.
- Fig. 5. ×1. F.7147q. Internal mould of brachial valve showing a sexually immature pattern of narrow linear mantle canals; L. 270 Trevallyn.
- Fig. 6. ×1. F.7141a. Internal mould of brachial valve showing the early development of the *vascula genitalia*; L. 215 Lewinsbrook.
- Fig. 7. ×1. F.7153b. Internal mould of mature brachial valve showing the connexion between the *vascula genitalia* and the *vascula myaria*; L. 50 Gresford Quarry.
- Fig. 8. ×1. F.7153c. Internal mould of a mature brachial valve; note the connexion between the *vascula genitalia* and the *vascula myaria*; L. 50 Gresford Quarry.
- Fig. 9. ×2. F.7153a. Internal mould of an old brachial valve; note the narrow canals emerging from beneath the wide superimposed canals of *vascula media*; L. 50 Gresford Quarry.

In the pedicle valve the main *vascula media* canals are close together and branch distally, the arcuate lateral canals are closer to the margin than in younger specimens, and the *vascula genitalia* have the same ramifying canals as those in mature specimens, covering almost the entire inner surface of the valve (Pl. 75, figs. 4-7).

The canals of *vascula media* in the brachial valve are usually wider than in smaller specimens but do not appear to have significantly altered their positions. The *vascula myaria* are also broader and run straight to the antero-lateral margins, or are bent inwards at their distal extremities. Many small branches along the outer margins of the *vascula myaria* provide a connexion with the *vascula genitalia*. The *genitalia* have the same morphology as those in the pedicle valve. They cover broad flabellate areas on the lateral and postero-lateral parts of the valve, but have a smaller area than the *genitalia* on the pedicle valve because they are confined by the *vascula myaria*.

A system of narrow linear canals at the margins of mature shells (Pl. 74, figs. 1-3, 9; Pl. 75, figs. 1, 2) are continuous with small branching canals in the middle part of the shell (viz. the small canals between the *vascula media* in Pl. 74, fig. 3). These small branching canals are interpreted as impressions of a juvenile mantle canal system, and hence their distal parts are regarded as impressions of mantle canals, probably impressions of the termination of the canals at the proximal ends of the setal follicles. These impressions were apparently continuously recorded by a process of differential thickening at the margin. The linear canals are joined by branches of a superimposed mantle canal system (see below), indicating their function as a canal rather than the trace of a setal follicle. Had they been merely traces of setal follicles they would intercalate as new setae were introduced around the margin; when they increase, these canals branch (Pl. 74, fig. 3; Pl. 75, fig. 3).

Changes in the mantle canals. In the pedicle valve the main canals of *vascula media* extending in front of the muscle field can be divided into three intergrading morphological types (text-fig. 6):

- A. Canals convex outwards and widely separated.
- B. Canals straight and widely separated.
- C. Canals straight and close together.

It has been shown above that the A and B types of canals typify small- to medium-sized individuals and C type canals larger individuals, and hence the different shapes of the *vascula media* can be explained as stages in the ontogenetic development of the individual. Accompanying the change from the A to C types of canals is the enlargement of the complex network of the *vascula genitalia*, and it is suggested that this enlargement within the mesenchyme layer of the mantle gradually forced the *vascula media* canals together and the lateral canals to move towards the margin as the shell became older. Specimens having each of these types of canals are present in all of the horizons in the Gresford district.

This explanation of the development of the canals does not account for their distribution as outlined in Table 2, unless evolution has taken place.

An analysis of Table 2 is simplified if it is realized firstly that the C type canal is that seen in the largest specimens, and secondly that the L. 53 sample is dominated by large specimens (text-fig. 7). Table 2 shows a decrease in A type canals and an associated

increase in B type canals from the oldest to the youngest horizons. This trend could be explained in at least two ways: as the expression of the ontogeny, as outlined above, in which sampling errors gave the impression of a genetic change, or as a true genetic change towards the earlier maturity of the genitalia.

An examination of the width-frequency polygons (text-fig. 3) shows that the samples are essentially the same in terms of size distribution, except for L. 53. Also, the specimens from the highest stratigraphic horizon with B type canals are about the same size as specimens from the lower horizons characterized by A type canals. In the absence of genetic change the specimens having the B type canals should have been larger.

TABLE 2

	Canal types		
	A	B	C
L. 53 Greenhills	Occasional	30%	70%
L. 206 Lewinsbrook Syncline	25%	75%	occasional
L. 270 Trevallyn	65%	35%	occasional
L. 218 } Gresford Quarry	65%	35%	occasional
L. 50 }			
L. 215 Lewinsbrook	70%	30%	occasional

More conclusive evidence in favour of the genetic change is available from younger horizons (probably middle to upper Viséan) at Barrington, N.S.W., in which moderate to large specimens of *S. verulamensis* have mainly straight, sub-parallel (or B type) canals (Cvancara 1958).

The earlier maturity of the genitalia would have increased the number of larvae produced by each individual and probably significantly increased the *S. verulamensis* population to one of even greater dominance during the Viséan.

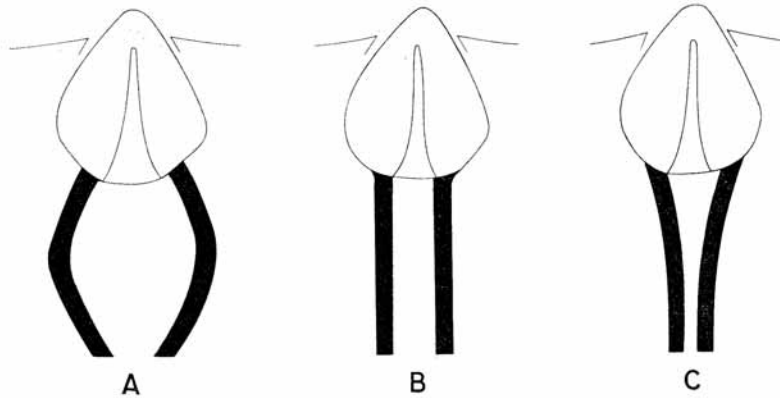
Superimposition of mantle canals. In mature specimens of *Schizophoria verulamensis*, particularly in pedicle valves, the greater part of the mantle canal system is superimposed over small radial canals. The small canals originate from the body cavity frequently branch, and run irregularly towards the front of the shell. In mature valves the posterior parts of these canals (viz. the narrow branching canals between the main *vascula media* in Pl. 74, fig. 3) are interpreted as the traces of juvenile mantle canals.

EXPLANATION OF PLATE 75

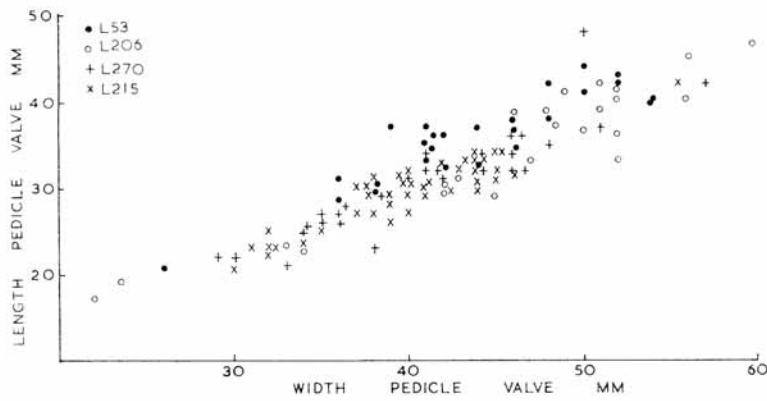
Schizophoria verulamensis Cvancara

- Fig. 1. $\times 2$. F.7152a. Internal mould of pedicle valve showing narrow canals extending from the front of the muscle field and being truncated by the superimposed mature mantle canal system; L. 50 Gresford Quarry.
- Fig. 2. $\times 2$. F.7146k. Internal mould of pedicle valve; L. 270 Trevallyn.
- Fig. 3. $\times 2$. F.4677b. Internal mould of pedicle valve; L. 215 Lewinsbrook.
- Fig. 4. $\times 1$. F.7144a. Internal mould of an old pedicle valve; L. 53 Greenhills.
- Fig. 5. $\times 1$. F.4784. Internal mould of an old pedicle valve with C-type *vascula media* and large areas of *vascula genitalia*; L. 53 Greenhills.
- Fig. 6. $\times 1$. F.7145b. Internal mould of an old pedicle valve; L. 270 Trevallyn.
- Fig. 7. $\times 1$. F.7146c. Internal mould of an old pedicle valve with large *vascula genitalia*, C-type *vascula media* and the lateral canals situated close to the margin; L. 270 Trevallyn.

Because all the canals were connected to the bases of the setal follicles (Williams and Rowell 1965) these juvenile canals are continuous with the traces, recorded at the margin, of the termination of the mantle canals at the setal follicles.



TEXT-FIG. 6. The three types of vascula media canals in the pedicle valve of *Schizophoria verulamensis* Cvancara.



TEXT-FIG. 7. Scatter diagram of length plotted against width for pedicle valves of *Schizophoria verulamensis* Cvancara from L. 215 Lewinsbrook, L. 270 Trevallyn, L. 206 Lewinsbrook Syncline, and L. 53 Greenhills.

In mature pedicle valves impressions of the small canals extend from the front of the muscle field between the large canals of vascula media, branching as they run towards the front of the valve (Pl. 74, fig. 3; Pl. 75, figs. 1, 2). In the middle and mid-anterior

parts of the valve they are truncated by superimposed larger canals: viz. the inner branch of the right-hand vasculum medium on the specimen in Plate 74, fig. 3 in which small canals extend on either side of a branch of the superimposed larger canal. Near the margins, the large canals join with the narrow linear traces left by the mantle canals at the ends of the setal follicles, and extend to the depressions left by the setal follicles. The junction between these canals results from both systems supplying the same setal follicles at the margin; the small linear marks were impressed as the shell grew, and the larger canals, which had been formed by the modification of the smaller ones, were impressed at a later time.

The superimposition of the mantle canal systems is less clear in the brachial valve. One large specimen, however, has a system of narrow linear canals beneath broad canals of *vascula media* (Pl. 74, fig. 9). The U-shaped branch on the left hand side of the *vascula media* truncates at least six of the narrow canals, and other narrow canals emerge from beneath the sites of bifurcation of the larger canals and are apparently continuous with the traces of the canals at the bases of the setal follicles.

The two main systems (i.e. the younger and older systems) described above are interpreted as impressions of the mantle canals at two different periods during the life of the shell, probable before and after sexual maturity. Because of the impression of a large or mature system on top of a smaller and probably immature system it is inferred that the major part of the canal system was impressed at certain well-spaced intervals instead of being continuously recorded on the inside of the shell.

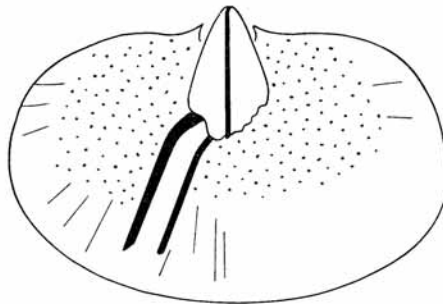
Williams (1956, p. 273) thought that mantle canals were impressed on the inner surface of the shell by differential secretion of shell material by the outer epithelium covering the canals. In *S. verulamensis* this mechanism may have been responsible for the continuous impression of the distal parts of the canals at the margin, but it could not have been responsible for the impression of the main part of the mantle canal system, because there are two and sometimes three systems superimposed over one another, unless rapid differential secretion took place at specific times; this is unlikely because it means that rather than being gradually thickened the shell would have been periodically rapidly thickened.

A more convincing explanation is that the outer epithelium over the mantle canals resorbed the shell material at specific times. Resorption is most likely to have taken place during the periods of limited shell growth when the mantle canal system had a stable morphology. During periods of rapid growth there would have been continuous reorganization of the mantle canals at the mantle edge and the development of additional setal follicles at the growing margin. To maintain efficient circulation to the margin the main canals of *vascula media* and *vascula myaria* would have enlarged by reorganizing the connective tissue in the mantle and coalescing with smaller canals. Many modern shallow-water marine organisms, particularly molluscs, cease depositing shell during the colder months of the year (Epstein and Lowenstam 1954), and hence it is reasonable to assume that the winter was the most likely time for the retardation of shell deposition and the impression of the mantle canals in *S. verulamensis*.

Abnormal mantle canals. In the pedicle valve figured in Plate 74, fig. 4, the left-hand canal of *vascula media* divides a short distance in front of the muscle field, giving a third main canal extending to the median anterior part of the valve. All three canals

branch in a similar manner to those in other valves. Functionally this additional large branch may have provided a greater supply of coelomic fluid to the growing edge of the front of the mantle. The two outer canals of *vascula media* give off arcuate lateral canals.

Another specimen showing an abnormal development of the *vascula media* (text-fig. 8) has impressions of the two main canals of *vascula media* arising from the anterior margin of the left diductor muscle scar and running, parallel with one another, to the antero-lateral part of the valve. There is no canal originating from near the right diductor scar, presumably because of some injury or functional defect to that side of the body cavity, and the *vascula genitalia* extend in front of the muscle scar. The



TEXT-FIG. 8. Pathological pedicle valve of *Schizophoria verulensis* Cvancara showing the two main canals of *vascula media* extending from the left diductor muscle scar, and the *vascula genitalia* extending in front of the right diductor muscle scar.

preservation is too poor to trace the junction of the right-hand canal with the right lateral canal. This variation indicates a certain adaptability in the organization of the mesenchyme layer of the mantle, and supports the arguments put forward above that major reorganizations took place within the mantle during the development of the species. Other features probably associated with this deformity are a deep furrow on the antero-median part of the left diductor muscle scar and an exceptionally narrow median ridge which does not expand anteriorly.

In a large pedicle valve (Pl. 75, fig. 6) branches from the arcuate lateral canal in the posterior part of the valve, instead of extending normal to the margin of the valve, turn posteriorly and run almost parallel with the margins, diverging only slightly from the main lateral canal. In other valves (Pl. 74, fig. 3) only the posterior-most branches of the lateral canal turn and run more or less parallel with the canal.

Connexion between the mantle canals. The description and figures of mantle canals of fossil brachiopods given by Williams (1956) and Williams and Rowell (1965) suggest that each of the three pairs of extensions of the coelomic cavity into the mantle—the *vascula media*, *vascula myaria*, and *vascula genitalia*—is a discrete unit, unconnected with other canals.

Larger specimens of *Schizophoria verulamensis* with well-preserved mantle canals have vascula media and arcuate lateral canals possessing well defined inner and outer margins. The vascula genitalia contained within the arc of the lateral canals is connected by many fine branches with the main vascula media canals and the arcuate lateral canals, the connexions varying from narrow constricted branches (the branches on the right-hand vasculum medium of the specimen in Pl. 74, fig. 3) to broad canals (the connexion with the right-hand lateral canal on the same specimen). In another specimen (Pl. 74, fig. 1) the branches into the vascula media canals are more pronounced and have a herringbone pattern. As well as being connected with the vascula media, the vascula genitalia are presumably connected directly with the coelomic cavity adjacent to the muscle-field.

There is no connexion with the vascula media in the brachial valve, but instead the vascula genitalia are linked with the main canals of vascula myaria (Pl. 74, figs. 7, 8). The branches are comparable with those in the pedicle valve and appear to extend along the entire outer margin of the vascula myaria canals.

Similar connexions occur in Ordovician orthid brachiopods described by Cooper (1956) (see *Chaulistomella magna* (Schuchert and Cooper), pl. 70, fig. 21; and *Mimella globosa* (Willard), pl. 89, figs. 10, 12, 14). One other possible example of an interconnected system in *Schizophoria* is given by Pocock (1966, fig. 17), who figured a specimen of *S. striatula* (Schlotheim) in which lateral branches arise from the vascula myaria and extend towards the vascula genitalia.

This type of interconnexion between the genitalia and the other mantle canals is apparently unknown in modern brachiopods. The interiors of modern brachiopods figured by Hancock (1859) show that the genitalia are either situated in the mid-part of a sac-like mantle canal, such as that in *Terebratulina caputserpentis* Linné (Hancock 1859, pl. 53, figs. 1, 2), or lie within the narrow canals of vascula genitalia or vascula media as in *Macandrevia cranium* (Müller) (Hancock 1859, pl. 53, fig. 4). In specimens with sac-like mantle canals, closest to those in *Schizophoria*, the vascula media and lateral canals are simply the lateral extremities of the gonocoel; they have no inner walls, and hence differ from the discrete canals in *S. verulamensis*. There are no connexions with the network of genitalia, but the genitalia are bathed in coelomic fluid. In *S. verulamensis*, coelomic fluid must have actually passed along the tubular network of vascula genitalia.

The connexion of the vascula genitalia with other canals in *S. verulamensis* probably increased the circulation of oxygenated fluid over the gonads, the fluid coming from the vascula media and lateral canals (or the vascula myaria in the brachial valve) as well as from within the vascula genitalia itself. The gonads in brachiopods without interconnected canals are oxygenated only by the coelomic fluid contained within the vascula genitalia, and sometimes the vascula media, meaning that there is probably less oxygenated fluid passing over them. Additional aeration could be responsible for the formation of larger gonads and possibly for a faster rate of production of sex cells, and it may also cause them to ripen earlier. In the modern brachiopod *Terebratulina caputserpentis*, already mentioned above, the gonads are bathed in the coelomic fluid of a large sac-like gonocoel, which is probably an even more efficient method of aeration.

The interconnexion of the canals seems to be a favourable attribute, and on a purely morphological basis it would seem that a system, such as that in *S. verulamensis*, would

have been more efficient for respiration and reproduction than, for example, a more restricted, discrete system such as that in the recent brachiopod *Fallax* (Williams and Rowell 1965, fig. 23D). Some of the respiratory functions of the mantle could, however, have been taken over by the lophophore in other brachiopod groups, so that there was less need to develop an interconnected system and the mantle canals acted as repositories for the gonads and as an accessory respiratory system.

The present work shows that a closer examination of living brachiopods is desirable to see if any species have an interconnected mantle canal system like that in *S. verulamensis* and other orthid brachiopods.

Interpretation of the mantle canals. The development of the mantle canals in *S. verulamensis* can be interpreted as follows. During the first period of growth, probably about one year, the shell was sexually immature and had a relatively undifferentiated system of mantle canals. In the first winter, when there was little shell growth, narrow linear canals including *vascula media* and *vascula myaria* were impressed on the inner surface of the shell, probably by resorption (Pl. 74, fig. 5). During the following summer the shell grew rapidly and became sexually mature. The rapid growth and the introduction of many setal follicles at the mantle edge, combined with the growth of the gonads, resulted in the reorganization of the mantle canal system. In the pedicle valve the *vascula media* became wider and developed complex lateral canals, and the *vascula genitalia* changed from narrow linear canals to a network of ramifying channels which branched with one another and with the main branch and lateral canal of the *vascula media* (Pl. 74, fig. 3). The changes in the brachial valve were not as marked; the canals of *vascula media* and *vascula myaria* becoming wider, and *vascula genitalia* becoming pitted near the postero-median part of the valve and also having wider canals extending to the lateral margins (Pl. 74, fig. 6). These canals were impressed during the second winter, when the shell was about two years old.

The changes in mature individuals, especially the development of the lateral canals and the network of *vascula genitalia* in the pedicle valve, must have resulted in a complete reorganization of the connective tissue in the mantle as well as the introduction of many blood vessels to the new canals and the genitalia. According to Hyman (1959, p. 533) the connective tissue of living brachiopods consists of a 'homogeneous material containing stellate mesenchymal cells that may unite into loose networks'; the mesenchyme was thus probably easily modified to allow the introduction of new or larger canals.

Further growth in the following summer resulted in an increase in size, the enlargement of the muscle-field, and a thicker shell, especially at the posterior. In the pedicle valve the *vascula genitalia* increased enormously in size, forcing the main *vascula media* canals close together (Pl. 75, figs. 4-7) and the lateral canals towards the margin, so that the impressions of the mantle canals covered almost the whole inside of the valve. In the brachial valve the *vascula media* and *vascula myaria* canals became wider and the *vascula genitalia* developed a ramifying network similar to that in the pedicle valve (Pl. 74, figs. 7, 8, 9). These enlarged canals were probably impressed during the third winter.

Little is known about the rate of growth and maturity of modern brachiopods. Rudwick (1962, p. 334; 1965, p. H209) suggested that modern articulate brachiopods

can reach sexual maturity after two or three years, and that they live for as long as seven or eight years or even longer. Amongst the inarticulates *Lingula* is sexually mature after a year or a year and a half (Chuang 1959), and *Glottidia* after only six to nine months (Paine 1963). It is therefore reasonable to suggest that *S. verulamensis* became sexually mature at about two years old, and that the mature mantle canal system was impressed during its second winter. Mantle canals of older individuals cover almost the entire surface of the shell and leave no room for the expansion of the vascula genitalia, so that after about the third year the mantle canals became stable and could not be modified during further growth of the shell. There is no indication of how long the largest shell lived.

SUMMARY AND CONCLUSIONS

The morphology of the mantle canals in *Schizophoria verulamensis* Cuvencara changes during ontogeny, mainly because of the growth of the gonads. The canals start in immature specimens as narrow linear canals over the inner surface of the valves and, with the growth of the gonads, are later modified in larger specimens into several major feeder canals which distribute coelomic fluid from the body cavity to the margins of the shell, around the areas of genitalia. In the largest shells the genitalia cover the greater part of the inner surface of the valves and have enlarged to such an extent that the large distributive canals have been forced together in the middle of the valve, or moved outwards towards the margins. The pedicle valve is affected earlier by the growth of the genitalia than the brachial valve.

An analysis of the distortion to the main vascula media caused by the enlargement of the vascula genitalia in pedicle valves from six horizons throughout the Lower Carboniferous sequence indicates a trend, probably genetically controlled, towards the earlier maturity of the genitalia.

The main part of the mantle canal system was impressed periodically by the resorption of shell beneath the mantle canals rather than by differential secretion as suggested by Williams (1956). Resorption most likely took place during the winter when there was limited shell growth and a stable mantle canal system, recording several distinct mantle canal patterns during the development of the individual.

Larger specimens of *S. verulamensis* have the vascula genitalia connected by numerous small branches with the vascula media and lateral canals in the pedicle valve and the vascula myaria in the brachial valve. This type of connexion has not been observed in recent brachiopods. It is thought to have increased the circulation of oxygenated coelomic fluid over the gonads, and may have been responsible for their earlier ripening.

The mantle canals in pathological specimens indicate that not only was modification possible during ontogeny, but the mantle canal system could also be adapted to the effects of injuries or defects in the shell during life.

Acknowledgements. This work was begun at the University of Western Australia and finished at the Bureau of Mineral Resources. I am indebted to Drs. K. S. W. Campbell and P. J. Coleman for their interested discussion of the problem, and to Drs. J. J. Veevers, J. M. Dickins, and K. S. W. Campbell for reading the manuscript. This paper is published with the permission of the Director, Bureau of Mineral Resources, Geology, and Geophysics.

REFERENCES

- BROWN, D. A., CAMPBELL, K. S. W., and ROBERTS, J. 1965. A Viséan cephalopod fauna from New South Wales. *Palaeontology*, **7**, 682-92.
- BRUNTON, C. H. C. 1966. Silicified productoids from the Viséan of County Fermanagh. *Bull. Brit. Mus. (Nat. Hist.) Geol.* **12**, 175-243.
- CAMPBELL, K. S. W., and ROBERTS, J. 1964. Two species of *Delepinea* from New South Wales. *Palaeontology*, **7**, 514-24.
- CHUANG, S. H. 1959. The breeding season of the brachiopod *Lingula unguis* (L.). *Biol. Bull.* **117**, 202-7.
- COOPER, G. A. 1956. Chazyan and related brachiopods. *Smithson. misc. Coll.* **127**, 1-1245.
- CVANCARA, A. M. 1958. Invertebrate fossils from the Lower Carboniferous of New South Wales. *J. Paleont.* **32**, 846-88.
- EPSTEIN, S., and LOWENSTAM, H. A. 1953. Temperature-shell-grown relations of Recent and interglacial Pleistocene shoal-water biota from Bermuda. *J. Geol.* **61**, 424-38.
- HANCOCK, A. 1859. On the organization of the Brachiopoda. *Phil. Trans. Roy. Soc. Lond.* **148**, 791-869.
- HYMAN, L. H. 1959. *The Invertebrates: Smaller coelomate groups*, **5**, 1-783. McGraw-Hill, New York.
- MUIR-WOOD, H. M. 1962. *On the morphology and classification of the brachiopod Suborder Chonetoida*. Brit. Mus. (Nat. Hist.), London, 1-132.
- ÖPIK, A. A. 1934. Über Klitamboniten. *Acta et Commentationes, Univ. Tartu*, **26**, 1-239.
- PAINE, R. T. 1963. Ecology of the brachiopod *Glottidia pyramidata*. *Ecological Monographs*, **33**, 187-213.
- POCOCK, Y. P. 1966. Devonian Schizophoriid brachiopods from Western Europe. *Palaeontology*, **9**, 381-412.
- ROBERTS, J. 1961. The geology of the Gresford district, N.S.W. *J. Proc. roy. Soc. N.S.W.* **95**, 77-91.
- 1963. A Lower Carboniferous fauna from Lewinsbrook, New South Wales. *Ibid.* **97**, 1-31.
- 1964. Lower Carboniferous brachiopods from Greenhills, New South Wales. *J. geol. Soc. Aust.* **11**, 173-94.
- 1965a. Lower Carboniferous faunas from Wiragulla and Dungog, New South Wales. *J. Proc. roy. Soc. N.S.W.* **97**, 193-215.
- 1965b. A Lower Carboniferous fauna from Trevallyn, New South Wales. *Palaeontology*, **8**, 54-81.
- 1965c. Lower Carboniferous zones and correlations based on faunas from the Gresford-Dungog district, New South Wales. *J. geol. Soc. Aust.* **12**, 105-22.
- RUDWICK, M. J. S. 1962. Filter-feeding mechanism in some brachiopods from New Zealand. *J. Linn. Soc. Lond. Zoology*, **44**, No. 300, 592-615.
- 1965. In *Treatise on Invertebrate Paleontology*. Part H, Brachiopoda. Ed. R. C. Moore. Univ. Kansas Press.
- SCHUCHERT, C., and COOPER, G. A. 1932. Brachiopod genera of the Suborders Orthoidea and Pentameroida. *Mem. Peabody Mus. Nat. Hist.* **4** (1) 1-270.
- WILLIAMS, A. 1956. The calcareous shell of the Brachiopoda and its importance to their classification. *Biol. Rev.* **31**, 243-87.
- and ROWELL, A. J. 1965. In *Treatise on Invertebrate Paleontology*. Part H, Brachiopoda. Ed. R. C. Moore. Univ. Kansas Press.

JOHN ROBERTS
Bureau of Mineral Resources, Geology
and Geophysics
Canberra City, A.C.T.
Australia

Typescript received from author 1 May 1967



5



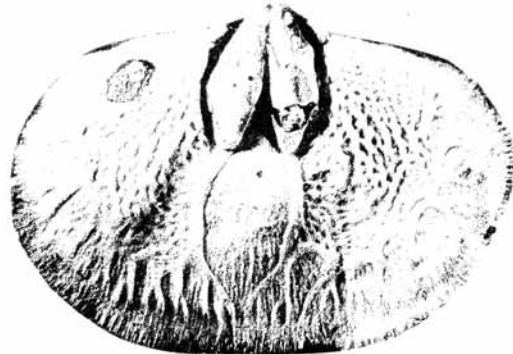
1



2



6



3



7



4



9



8

ROBERTS, *Schizophoria*

