THE ATRYPIDINE BRACHIOPOD *DAYIA NAVICULA* (J. DE C. SOWERBY)

by E. V. TUCKER

ABSTRACT. The atrypidine brachiopod *Dayia navicula* (J. de C. Sowerby) is described and a neotype is designated. The musculature is reinterpreted and shown to differ from previous interpretations. Comparisons are made between *Dayia navicula* s. str. and other forms referred to the species. Between the Ludlow and the Lower Devonian the shells increase in size and incurvature of the umbo becomes less marked.

PRIOR to 1881 the brachiopod now designated *Dayia navicula* rested uneasily in palaeontological works first under the style of *Terebratula navicula* and later *Rhynchonella? navicula*. M'Coy in 1846 anticipated in part the probable relationship between this form and the atrypids when he referred it to *Atrypa navicula*. In 1881 Davidson, studying material skilfully prepared by the Revd. N. Glass, recognized the distinctiveness of the brachidium and erected the new genus *Dayia*. Since then material referred to the species *D. navicula* has received attention especially in the hands of Kozłowski (1929, p. 179) and Alexander (1947). The latter undertook a morphological study of the characteristic British form but her conclusions contain certain misconstructions.

In stratigraphy, *Dayia navicula* has been widely used as an index of Ludlovian rocks, particularly for the Leintwardine Beds (formerly the *Dayia* or Mocktree Shales of Elles and Slater (1906)) which underlie the Upper Ludlow or Whitcliffe Beds. Straw (1937), however, noted its presence in rocks ranging from the *nilssoni* zone into the base of the Upper Ludlow at Builth. This extended range was re-emphasized by Earp (1938) and Shirley (1939 and 1952) for other parts of Wales and the Welsh Borderland. Davidson (1869, p. 191) in the monograph of Silurian brachiopods records Wenlock occurrences given in Murchison's 'Siluria' but only the general locality of Builth is mentioned.

A similar stratigraphical range has been suggested in continental Europe. Barrande (1879) records the species from the Upper Ordovician of Bohemia but this claim needs re-examination. In Scandinavia, Lower Ludlow forms, although smaller than the typical *Dayia navicula*, closely resemble certain British Elton Bed (Lower Ludlow) forms. Koslowski's description (1929, p. 179) and illustrations of Podolian specimens from the Marnes de Dźwinogród, now believed by Jaeger (1965) and others to be post-Ludlovian and possibly Gedinnian in age, indicate close agreement with the characteristic British form. The existence of other sub-species, or at least variants of *Dayia navicula*, is suggested, however, by the work of Bouček (1940) and Shirley (1962). Shirley emphasizes the differences between varieties from the Schistes de Liévin and the Köbbinghauser Schichten of the Artois basin and Westphalia respectively, which have previously been referred to as *Dayia navicula*, and the characteristic British forms; a view endorsed by the present writer. This misidentification and the usage of *Dayia navicula* as a Ludlovian index fossil is partly responsible for the discordant views which have been expressed on the correlation of French-Rhenish and British successions.

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In her account, Alexander referred (1947, p. 305) to a specimen in the Geological Survey collection as holotype. This specimen does not match Sowerby's illustration in Murchison's Silurian System (1839, pl. 5, fig. 17) however, differing in size, detail of ornamentation, nature of ventral umbo, and in its geographical location. Search elsewhere has failed to reveal the type specimens and they are presumed to have been lost. To assist future comparison a neotype for *Dayia navicula* is designated here, the morphology is re-described, the musculature reinterpreted and some aspects of variation in the genus are outlined.

The material on which the study is based has been collected by the writer, chiefly from the Leintwardine Beds of Downton Gorge (Herefordshire) and various Silurian inliers in the Welsh Borderland, particularly those of Woolhope and Usk, and from the Elton Beds and Whitcliffe Beds. These personal collections were supplemented by collections housed in the Geological Survey Museum (GSM) and Mrs. Alexander's collections of silicified specimens in the Sedgwick Museum, Cambridge (SM). (Manuscript notes of Alexander suggest that this collection was made near Greenway Cross (Nat. Grid. SO/461 827), although repeated visits to the same locality by the present writer have revealed few specimens of *Dayia navicula*. The fauna indicates a Lower Leintwardine age for the beds.) The source of foreign material is indicated in the appropriate section.

SYSTEMATIC DESCRIPTION

Superfamily DAYIACEA Waagen 1883
Family DAYIIDAE Waagen 1883
Subfamily DAYIINAE Waagen 1883
Genus DAYIA Davidson 1881

Type species. Terebratula navicula (J. de C. Sowerby) 1839.

Diagnosis. Small, strongly inequivalve, pedicle valve larger; hinge line gently curved; shell generally elongated medially but sometimes spherical. Brachial valve with sulcus expanding to one-third of shell width at anterior margin; weakly inflated laterally. Pedicle valve highly arched transversely, smoothly curved medially. Umbo normally incurved. Lateral commissure dorsally curved, anterior commissure sulcate. Surface ornamentation of very fine costae and weak growth-lines, indistinct.

Spires directed towards sides of pedicle valve but contained within the first coil. In the pedicle valve a platform of secondary callus supported the diductor muscles. Muscle fields deeply impressed, of chevron form. Adductor scars ill-defined. Prominent median septum in the brachial valve extends to three quarters valve length and separates well-developed adductor muscle fields. A septalium divides a subdued cardinal plate at the centre of the hinge-line.

Range. Silurian (Ludlovian, possibly Wenlock) to Devonian (Gedinnian). *Dayia* has been recorded from many Western European countries along a belt from the Dingle peninsula in south-west Ireland to Podolia in the U.S.S.R., and from Scandinavia. It is not known from extra-European areas.

Discussion. The pre-Ludlovian records of *Dayia* require re-investigation. *Dayia cymbula* (Davidson) has been recorded from the Caradoc Beds of Hendre Wen (North Wales) and from the Drummuck Group (Ashgillian) near Girvan. Reed (1917) described a variant '*girvanensis*' associated with it near Girvan. Externally there are many similarities between these forms and *Dayia navicula*. The musculature of the pedicle valve differs in detail however and the teeth are more prominent. Dental plates, observed by Davidson, are lacking in *Dayia*. The nature of the brachidium of *Dayia cymbula* is not known.

Dayia navicula (J. de C. Sowerby)

Plates 118–21

1839	*Terebratula navicula* Sowerby, p. 611, pl. v, fig. 17.
1846	*Atrypa navicula* (Sowerby); M'Coy, p. 40.
1848	*Hypothyris navicula* (Sowerby); Phillips, p. 281.
1852	*Hemithyris navicula* (Sowerby); M'Coy, p. 204.
1859	*Rhynchonella*? *navicula* (Sowerby); Lindström, p. 366.
1869	*Rhynchonella*? *navicula* (Sowerby); Davidson, p. 191.
1881	*Dayia navicula* (Sowerby); Davidson, p. 291.

Neotype. A specimen collected by the writer and deposited in the Geological Survey Museum (GSM 103291) is selected as neotype (Pl. 118, fig. 2). Sowerby's type locality is vaguely defined. The neotype is from the Lower Leintwardine Beds of Downton Gorge, Herefordshire (Nat. Grid SO/431 733) approximately 55 ft. above the base.

Occurrence. *Dayia navicula* is present throughout the Leintwardine Beds of the Welsh Borderland, being most common in western areas. It extends upwards into the Lower Whitcliffe Beds, especially in adjacent parts of Wales. Closely allied forms also occur in the Elton Beds of these areas and at similar levels in Scandinavia whilst other variants range upwards into Lower Devonian rocks of central Europe.

Dimensions of neotype. Length 10·4 mm., width 8·0 mm., thickness 7·2 mm.

Diagnosis. As for the genus. The umbo characteristically is gibbous and rests upon the brachial valve, effectively sealing the foramen. The diductor muscle platform is prominent in the pedicle valve and the chevron scars occupy much of the shell width.

Description. Considerable shape variation can be recognized. Ontogenetic studies demonstrate a progressive relative increase in elongation with age. (Pl. 118, figs. 1–5). This is generally accompanied by a deepening of the sulcus in the brachial valve and accentuation of umbonal incurvature in the pedicle valve. This incurvature ultimately caused pedicle atrophy during maturity (Tucker 1965). In juvenile growth stages the sulcus remains shallow and smoothly curved transversely. It becomes steeper sided in mature forms, where there is an equal division between forms with a deep, flat-bottomed sulcus and those more sharply angular. Variation in mature shells is expressed also by differences in degree of elongation and degree of incurvature of the ventral umbo. Most shells have a pronounced elongation (the width to length ratio exceeding 1 : 1·2) but

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EXPLANATION OF PLATE 118

Figs. 1–5. *Dayia navicula* (J. de C. Sowerby). All un-numbered specimens in author's collection. Lower Leintwardine Beds, Downton Gorge, Herefordshire. National Grid: SO/431 733. Dorsal, anterior, and lateral views of five growth stages. Fig. 2 is designated neotype (GSM 103291) (all × 4).

some retain more squarish outlines. All mature shells have a strongly incurved umbo but this is accompanied by excessive elevation of the posterior part of the ventral valve in some specimens, producing an acute transverse arch which accentuates elongation of the shell.

Dentition. The teeth diverge at an angle of less than 160°. Their length is almost one-quarter the shell width. They are most prominent posteromedially, hence articulation is best defined towards the centre-line where the inward and partly downward facing edge of each tooth locks into a laterally opening notch within the sockets (see text-fig. 1*g*). Thickening of the inner socket-ridge beneath, and to a lesser extent above, the socket is accompanied by a swelling into the visceral cavity, intensifying the socket and assisting articulation. The stages of development of the inner socket ridge are demonstrated by the pattern of growth lines shown in text-fig. 3*d*.

The crenulations on the dorsal surface of the teeth referred to by Alexander (1947, p. 307), are rarely apparent although similar features, lying on the inner face, have been observed on one silicified mould in her collection. There is no clear indication of these features in the micro-structure of other, calcareous, shells.

Lophophore supports. These comprise crura and laterally directed spires united by a comparatively simple jugum (see text-fig. 1).

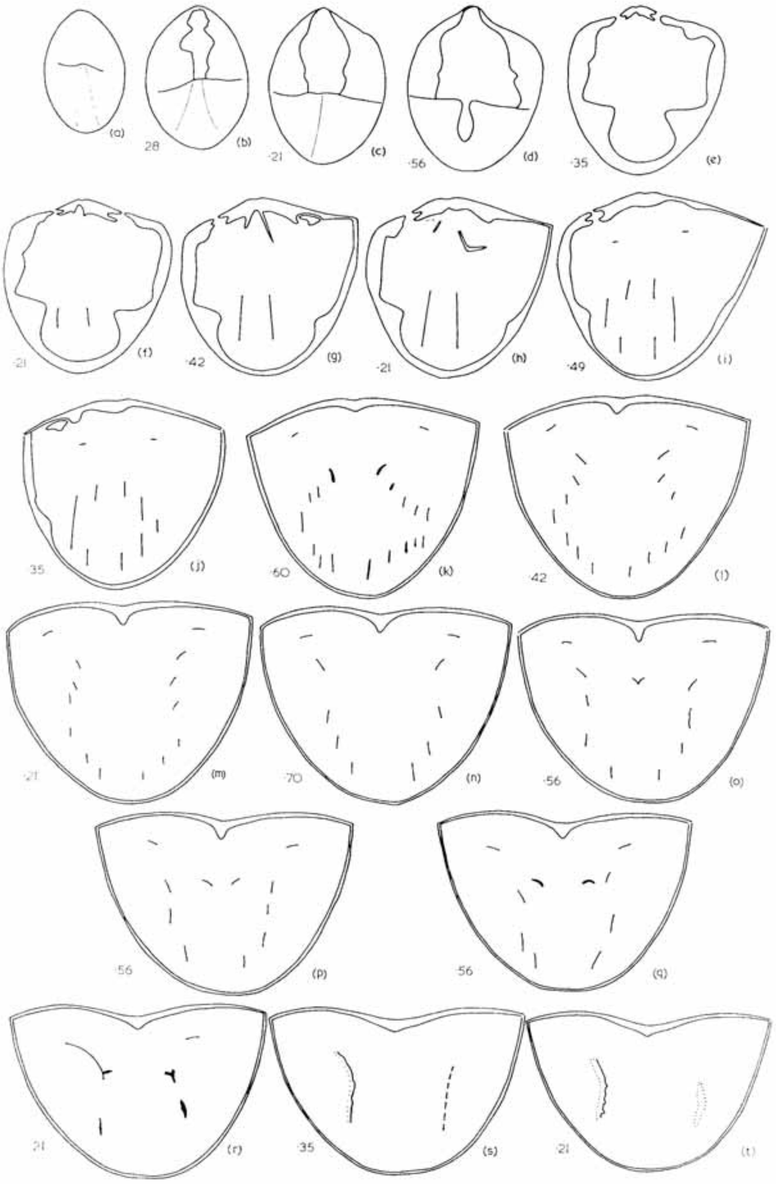
The crura arise from the inner margin of, and fuse with, geniculiform inner shell surfaces which flank a septalium in the cardinal plate. Geniculation commences on a level with the hinge axis and immediately adjacent to the shell mid-line. Its development is reflected in the micro-structure of the shell where a close relationship is seen to exist with the development of the septalium, beneath which concentration of growth-lines indicates a retarded rate of shell secretion (see Pl. 121, figs. 1, 2; text-fig 3).

The crura develop from the septalium walls as narrow rods and follow the line of the walls as they diverge at an angle of about 55°. Complete fusion and continuity of shell structure is rapidly achieved between each crus and the parent shoulder, which provides additional support.

The crura extend ventrally a distance equal to about one quarter the depth of the cavity, and curve gently with the convex edge facing anteriorly; they descend anterior to their point of origin. At their distal end they produce the primary lamellae which first extend laterally to a position near the dental sockets before descending anteriorly. Peels taken from the crura reveal lamellae of fibrous calcite parallel to the surfaces. There is complete continuity with the primary coil.

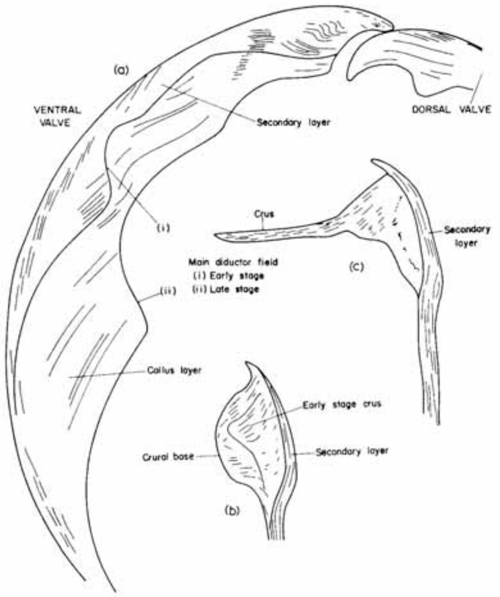
In longitudinal sections the micro-structure of the supporting crural base reveals a sharp projection within the secondary layer representing an early stage of crural development (see text-fig. 2). The base is supported on a flat spoon-shaped depression within the brachial shell.

The primary lamellae descend almost vertically at a position close to the outer socket ridge before producing the first coil. The first four or five coils are strongly flexed along their dorsal arc (text-fig. 1 and Pl. 119, fig. 10). Up to nine coils are contained in each spire, flexuring being less pronounced on each successive coil. The coils are more widely spaced dorsally than ventrally, hence the axis of rotation of successive coils migrates ventrally. Alexander (1947, p. 308) aptly describes each spire as being '. . . shaped like a sombrero with one half of the brim turned up'.



TEXT-FIG. 1. *Dayia navicula* (J. de C. Sowerby), Lower Leintwardine Beds, Downton Gorge, Herefordshire. Series of transverse sections drawn from cellulose acetate peels. × 5.

The jugum, arising from a position low on the first coil, is V-form, the apex pointing postero-ventrally. It is sharply recurved at its union with the primary coils (text-figs. 1*p*–*r*). A jugal stem points posteriorly. There appears to be perfect continuity in the micro-structure of jugum and primary lamellae.



TEXT-FIG. 2. Features of shell micro-structure in *Dayia navicula* (J. de C. Sowerby). (*a*) longitudinal section through muscle platform of ventral valve to show the position of an earlier valve floor and muscle attachment region. (*b*) longitudinal section adjacent to crus showing crural base formed of callus and 'embryonic' crus. These are in turn supported by a spoon-shaped depression in the brachial valve. (*c*) longitudinal section through crus. All × 16.

Fimbria extend from the anterior part of the primary coils and are directed anteriorly. They originate in pustule-like growths within the coils which produce surface corrugations when fimbria are not fully developed. The pustules generally point medially. Discrete pustules occur rarely on the lower part of the jugum.

Silicified specimens (Pl. 119, fig. 9) clearly show the fimbria; they attain a maximum length of over 0·175 mm.

Median septum. At its anterior end the median septum has the form of a low rounded ridge and is little more than an internal bulge complementary to the external sulcus in the brachial valve. In a posterior direction the septum is more prominent and ridge-like with broad, low, supporting buttresses on its flanks. Towards the hinge line secondary callus builds up over the median septum producing a more triangular form in cross-section before the median septum fades into the lower part of the cardinal plate, the transverse profile becoming increasingly subdued.

Ontogenetic changes of the median septum are preserved in the micro-structure of the shell (text-fig. 3*a*, *b*). Within the secondary layer calcite was secreted about the mid-line, successive growth layers being inclined from the shell outer surface laterally inwards and gently convex outwards. The following stages can be recognized in the development of the median septum from this layer:

(i) Simple fold of shell (see above);
(ii) Addition of secondary callus producing buttresses which are to serve as supports to the median septum;
(iii) Successive addition of calcite layers to produce the characteristic ridge form, there being little lateral addition of calcite at this stage;
(iv) Concentration of growth lines over crest of median septum indicating suppression of development ventrally but the addition of calcite on the flanks producing a triangular form;
(v) Extensions of process operating in (iv) to markedly increase the width; continuation of this process finally flattening out the floor of the brachial valve at the mid-line.

The full sequence is discernible within the brachial shell just below the hinge line. Peels show darker areas of more concentrated lamellae at intervals. They increase in number posteriorly and must represent growth pauses. One shell revealed at least five and possibly six such growth pauses.

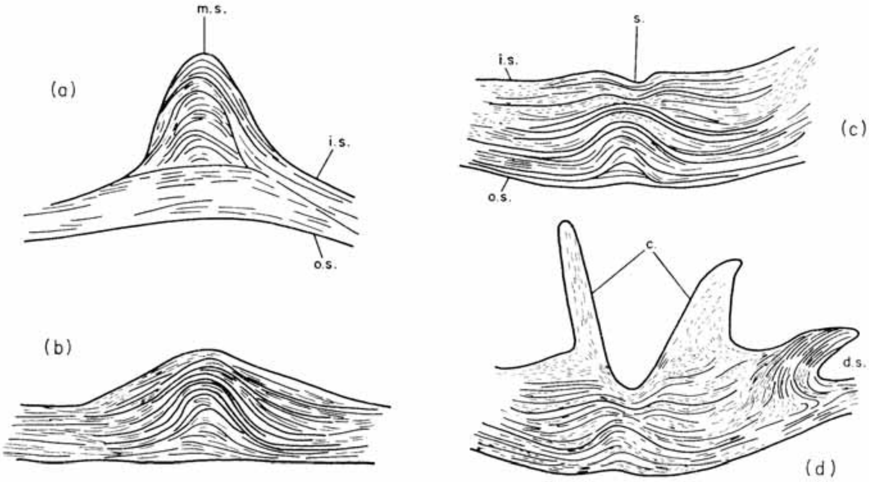
EXPLANATION OF PLATE 119

Figs. 1–7, 9–10. *Dayia navicula* (J. de C. Sowerby). 1, Upper Llanbadoc Beds, Darran, Usk, Monmouthshire. National Grid ST/327 979 (GSM 103292). Internal mould of ventral valve showing chevron diductor field, with the accessory diductor field in its apex, and the adductor muscle field. Between the adductor muscle impressions faint ridges (? vascula media) exist (× 7). 2, Lower Leintwardine Beds, Greenway Cross, near Norton, Shropshire. National Grid SO/461 827. (SM A11207). Internal mould of ventral valve showing diductor muscle field in an immature specimen (× 5). 3–4, Lower Leintwardine Beds, Greenway Cross, near Norton, Shropshire. National Grid SO/461 827. (SM A11202 and A11206). Internal moulds of brachial valve showing median septum, adductor muscle fields and position of dental sockets (both × 5). 5, Lower Leintwardine Beds, Greenway Cross, near Norton, Shropshire. National Grid SO/461 827. (SM A11655–64 one of twelve specimens bearing number 2000). Lateral view of internal mould of ventral valve showing part of chevron and vascular markings (? gonadal sacs) (× 5). 6, Lower Forest Beds, Llancayo, Usk, Monmouthshire. National Grid SO/372 036. Internal mould of ventral valve showing chevron diductor impression (× 6). 7 and 11, *nilssoni-scanicus* zone, S. side of Mynydd-y-Gaer, Denbigh Moors, Denbighshire. National Grid SH/974 715. Internal moulds of ventral valves showing chevron diductor impression. Fig. 7 is an immature specimen also showing the adductor impressions (× 4 and × 6 respectively). 9–10, Lower Leintwardine Beds, Greenway Cross, near Norton, Shropshire. National Grid SO/461 827. (SM A11655–664 (specimen numbered 2042) and A11201). Silicified specimens showing form of spiralium. 9, lateral view exhibiting pustules and fimbria on spire, photographed through the silica mould (this specimen has been cut along the left side). 10, looking from the anterior (× 7 and × 6 respectively).

Fig. 8. *Dayia* sp. Köbbinghauser Beds (Lower Devonian), Huinghausen, W. Germany. Internal mould of posterior part of ventral valve showing relatively small diductor muscle field (× 4).

Further changes can be recognized in the shell micro-structure at the mid-line but these are related to the changes in the cardinal plate.

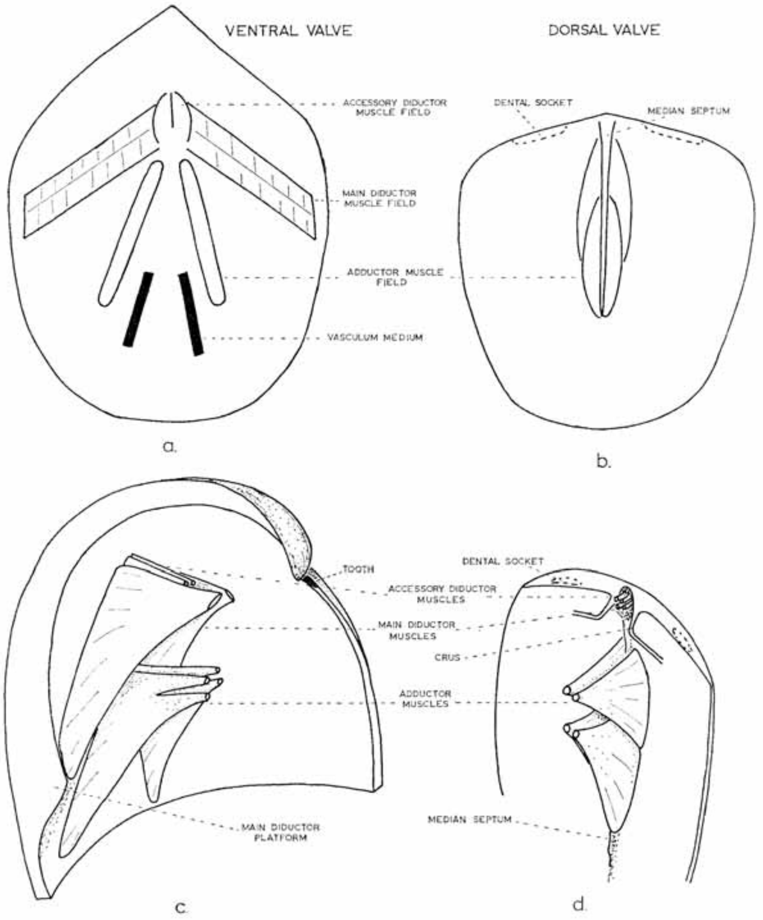
Cardinal plate. Serial sections and latex casts provide no indication of the kidney-shaped cardinal process ascribed to *Dayia navicula* by Alexander (1947, p. 307). Instead, it is seen to have the form of a flattish or gently arched area lying within the brachial hinge plate, divided by a pronounced cleft or septalium. Suppression of the median septum by lateral addition of callus, as described above, reaches its ultimate conclusion in the production of the cardinal plate. From then onwards crowding of growth-lines and growth pause at the centre-line reverses the form of the inner shell surface to produce the septalium (text-fig. 3 and Pl. 121, fig. 2). This trough is flanked by the crura and is in part a result of the development of the crura and expansion of the inner socket ridge.



TEXT-FIG. 3. Micro-structure of shell of *Dayia navicula* (J. de C. Sowerby) at mid-line of dorsal valve (m.s., median septum; i.s., inner shell surface; o.s., outer shell surface; s., septalium; c., crura; d.s., dental socket). (*a*) transverse section through median septum × 45 (*b*) transverse section through posterior part of median septum immediately below hinge line × 50. (*c*) transverse section through cardinal plate below crura × 50, and (*d*) including crura × 40.

Musculature. There is clear evidence for the former position of certain muscle fields but the interpretation of these fields and of the particular function of the muscles is less easy to deduce.

The pedicle valve contains a prominent chevron muscle-scar impressed on a platform produced by the addition of secondary callus to the inner shell surface. The muscle field occupies much of the shell width in mature specimens but only one-third of the width in juveniles (Pl. 119, figs. 1, 2). The apex of the chevron is directed posteriorly and extends to a point level with or even above the hinge-line; however the major part of the muscle field lies below this line. Two muscles occupied this field, one each side of the shell mid-line, and they diverged at angles between 90° and 100°. One or more narrow troughs, or sometimes ridges, cross the field parallel to its long axis. Weaker, but more numerous, corrugations cross this line obliquely subparalleling the shell mid-line. These are muscle tracks. The first set probably result from the anterior extension and migration of the muscle attachment areas during growth. This migration is demonstrated by the micro-structure of the supporting platform where the secondary addition of calcite is seen to obliterate earlier muscle fields which now lie ghost-like



TEXT-FIG. 4. Muscle fields and postulated form of muscles in *Dayia navicula* (J. de C. Sowerby).

within the layer of callus (see text-fig. 2). The oblique structures are believed to be due to the lateral extension of the muscle areas.

Situated in the apex of the chevron is a small elliptical area often divided by a trough (text-fig. 4 and Pl. 119, fig. 1). The limits of the area are strongly defined and the area must have provided an attachment region for separately functioning tissue—probably muscular.

Together, the above muscle fields are here interpreted as the diductor muscle attachment areas, the main diductors being attached to the chevron field and accessory diductors to the elliptical field. This interpretation differs from that placed upon the muscle-fields by Alexander (1947, p. 308, text-fig. 3).

Anterior of the diductor muscle platform in the ventral valve two slightly divergent troughs are weakly impressed into the shell: they are not always discernible. They extend from a position close to the lower apex of the diductor chevron halfway towards the anterior margin of the shell. The troughs exist in most growth stages but are most prominent in mature shells (Pl. 119, figs. 1, 7). These features were not recorded by Alexander; the present writer interprets them as the ventral muscle-fields of the adductor muscles.

In the umbonal region of the ventral valve other corrugations exist on the inner shell surface. Certain of these seem to have been interpreted as diductor muscle fields by Alexander but it is difficult to understand how the muscles could function mechanically if this interpretation is correct. These corrugations are possibly responses to folding of the mantle following pedicle atrophy. Alternatively they may represent pedicle attachment areas during early stages of growth, although their size tends to preclude such a simple interpretation.

No muscle scars are preserved on the cardinal plate. However, the adductor muscles left prominent impressions on the floor of the brachial valve. Although exhibiting some variation in form, these are normally elongate twin fields, the posterior field embracing half its companion (Pl. 119, figs. 3, 4). The muscle fields lie partly on the flanks of, and are separated by, the median septum which acts in part as a myophragm.

The writer's interpretation of the muscle fields is shown in text-fig. 4, together with a reconstruction of the form of the muscles as they crossed the visceral cavity. During youth the disposition of the (small) diductor muscle fields in the ventral valve and the cardinal plate in the dorsal valve permitted shell opening probably by uniform contraction of the muscles. In mature forms however the posterior arching of the ventral valve transposed part of the main diductor field to a position posterior of the hinge axis. It was inevitable therefore, that the main functional part of the muscle was that part lying below or anterior of the hinge axis and the main diductor muscles became extended anteriorly, with accompanying anterior extension of the muscle platform.

Vascular markings. Faint vascular markings are discernible between the diductor muscle field and hinge extremity in the ventral valve of mature individuals and also anterior of the muscle fields in both valves (see Pl. 119, figs. 1, 5). Saccate or lemniscate gonadal sacs can possibly be inferred from fig. 5 whilst fig. 1 shows divergent ridges between the ventral adductor scars which may indicate the former site of the vascula media. Other sinuses have not yet been recognized in *Dayia navicula*.

General micro-structure of the shell. Certain aspects of the micro-structure of the shell have already been discussed and many points of detail can be interpreted from text-figs. 2 and 3 and Plate 121.

The inner secondary layer of the shell, composed of fibrous calcite, is more prominent than the primary layer. The lamellae lie parallel or subparallel to adjacent shell surfaces, notably the inner surface. Considerable secondary callus has been added at the inner surface particularly around the median septum and on the ventral muscle platform. In the latter instance, as well as assisting change of muscle position it partly accounts for the highly arched and elevated form of the posterior region of the ventral valve. Within the umbo of the ventral valve growth layers are concentrated together as a result of growth pauses.

The very thin primary layer is frequently lost. Lamellae are closely spaced and seem to be sub-parallel to the outer shell surface, though sometimes lying obliquely to it. Alexander (1947, p. 309) suggested that the lamellae are '. . . directed forward and inward'.

In the umbonal region of the ventral valve the continuity of shell structure is interrupted by a number of 'suture lines', seen in transverse section as distinct seams (sometimes followed by cracks (text-fig. 1*a*–*b*)). They may be represented by inflections in the shell microstructure in longitudinal section (see text-fig. 2). The most prominent suture crosses the shell transversely and descends antero-ventrally through the secondary layer meeting the valve floor at the diductor attachment area. Two weaker sutures diverge ventrally from near the mid-line of the transverse suture; they appear to fuse anteriorly and rapidly fade away. These structures are difficult to interpret but bearing in mind the modifications affecting the muscle platform during ontogeny it is not unreasonable to suggest that they either had a similar supporting function or at least defined the limits of the muscles during some early stage of the individual's development. In this respect it is worth noting that a somewhat similar structure, a transverse plate (shoe-lifter process), is exhibited by the Ordovician brachiopod *Aulidospira* (see Williams 1962, p. 253) another member of the Dayiacea.

ALLIED FORMS

Dayia is not uncommon in rocks of Eltonian (Lower Ludlow) age in many parts of Wales and the Welsh Borderland. The major difference between these forms and *Dayia*

EXPLANATION OF PLATE 120

Variants of *Dayia navicula* (J. de C. Sowerby).

Figs. 1–3. *Dayia navicula* cf. *bohemica* Bouček, upper part of Přidoli Beds (eβ_2), Bohemia. Dorsal, anterior, and lateral views of three growth stages (all ×4).

Fig. 4. *Dayia navicula* (J. de C. Sowerby); Hemse Group (Lower Ludlow) Lau, Gotland, Sweden. Dorsal, anterior, and lateral views of a mature specimen. (×4).

Fig. 5. *Dayia navicula* (J. de C. Sowerby); Skała Beds, Ruchotina, Podolia. Dorsal, anterior, and lateral views. Ventral umbo imperfect (×4).

EXPLANATION OF PLATE 121

Microstructure of shell in *Dayia navicula* (J. de C. Sowerby). Photographs of cellulose acetate peels of calcareous shell, fig. 1 and 2 slightly retouched. All specimens from Lower Leintwardine Beds, Downton Gorge, Herefordshire. National Grid SO/431 733.

Fig. 1. Cardinal plate, showing shallow septalium (t.s. ×100).

Fig. 2. Growth line pattern associated with socket, crus (proximal end) and septalium (t.s. ×125).

Fig. 3. Pustules and fimbria on the lower part of the first coil of the spiralium (l.s. ×100).

navicula is their smaller size. Mature shells have an average length of between 7 and 8 mm. The degree of incurvature of the ventral umbo is similar although the posterior part of this valve is normally proportionately less elevated above the hinge line. Most specimens occur as internal moulds hence the external morphology is difficult to assess fully but there appear to be no fundamental differences from the typical form.

The internal structures are also the same although it has not been possible to interpret the spiralium fully. The intensity, but not always the length, of the chevron muscle scars and platform is similar, and the presence of additional impressions within the chevron supports the interpretation of the musculature. Specimens collected from the *Monograptus scanicus* zone of the Denbigh Moors (North Wales) show chevron muscle scars occupying at least two-thirds of the shell width (Pl. 119, fig. 11), a relationship which occurs in the Leintwardine Bed forms. Other specimens collected from the upper part of the Elton Beds (locally, Lower Forest Beds) near Usk possess proportionately smaller muscle fields which occupy approximately one-third of the shell width (Pl. 119, fig. 6). There is thus minor variation between the typical *Dayia navicula* and these earlier forms and also variation within the latter. It would however be premature to append varietal names until more comprehensive collections from rocks of Eltonian age are available for examination.

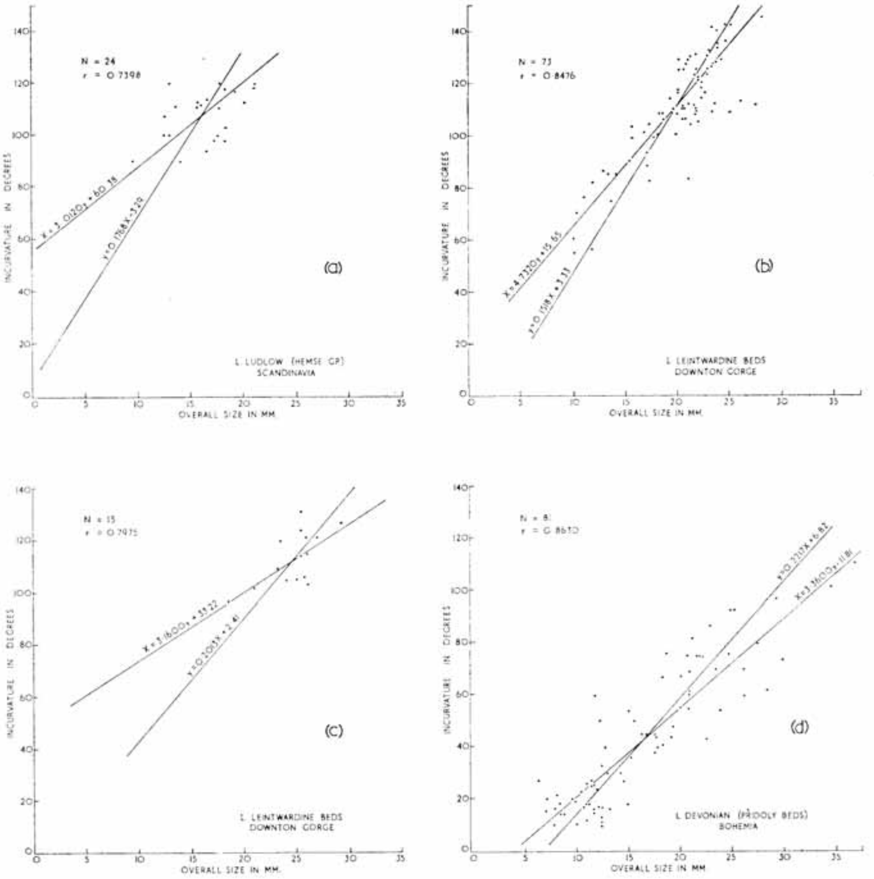
I am indebted to Dr. Anders Martinsson and Dr. H. Jaeger for providing me with specimens of *Dayia* from the Hemse Group (considered by Hede 1919 to belong to the zone of *Monograptus nilssoni*) of Scandinavia. No attempt at a full description is made here but the following points are worth noting. The average dimensions are similar to those of British Eltonian age but the posterior elevation of the ventral valve is greater than in the Usk form: the umbo is again strongly incurved (Pl. 120, fig. 4). The Scandinavian forms possibly possess closer relationships with the Denbigh Moor forms (which unfortunately have not yielded good externals although the moulds show a prominent umbonal feature). The chevron muscle field shows similar proportions to the Denbigh variety also. One characteristic feature of the Scandinavian forms is the almost horizontal disposition of the teeth; this is extremely rare in British forms. Almost all mature shells possess a deep sulcus and a strongly flexed lateral commissure.

Few Podolian specimens of *Dayia* are available for comparison. Kozłowski's description and illustration of this form in 1929, supplemented by material loaned to the writer by Dr. O. Nikiforova, show the close similarity between it and *Dayia navicula*. Minor differences in external morphology include a squarer outline to the brachial valve resulting from the straighter hinge and the fact that maximum width is attained closer to the hinge (Pl. 120, fig. 5). The shell is relatively less wide than British examples but with a deeper ventral valve, strongly incurved but less elevated at the umbo. The species occurs in the Marnes de Dźwinogród of the Skala Formation.

Similarities exist between certain Podolian and large Bohemian specimens (see below) but the Podolian specimens are closer to the British forms.

In 1940, Bouček discussed variation within *Dayia navicula* in Bohemia. He recognized two subspecies which he named *Dayia navicula minor* and *Dayia navicula bohemica*. They are recorded from zones eβ_1 and eβ_2 of the Budňany Beds which, according to Jaeger (1962 and 1965) range from the Ludlovian into younger beds. It is clear from Bouček's illustrations that the shape of both varieties is different from the typical British form. Horný (1955, p. 438) suggested that a transition exists between the two subspecies.

A collection of Bohemian *Dayia* from the Přidoli Beds (belonging to eβ_2) have been studied by the writer. They include many growth stages. Based on external morphology alone, both Bouček's subspecies appear to be present. With the exception of one assemblage which may represent the true *minor*, mature individuals generally attain greater dimensions than the British form. The ventral umbo is less strongly incurved (see Pl. 120, figs. 1–3) and the foramen probably remained unimpaired until later in



TEXT-FIG. 5. Scatter diagrams to show the relationship between incurvature of the ventral umbo and overall size (height + width + thickness) in four assemblages of *Dayia*. Assemblages *b* and *c* occur 22 and 55 ft. respectively above the base of the Lower Leintwardine Beds. N, no. of individuals in sample; r, degree of correlation between related regression lines.

life; hence pedicle atrophy was delayed. The diductor muscle platform is weakly developed. There is a suggestion of vestigial deltidial plates in some small juvenile shells, although the observed features could result from slight curvature of the ventral interarea at the delthyrium edge. Deltidial plates are not apparent in mature shells.

The hinge-line is straighter and proportionately longer than in British forms so producing distinctly squarish cardinal extremities. The shells are less elongate and the lateral margins are more sharply angular. Surface ornamentation is similar but the costae are more prominent.

The Köbbinghauser Beds of Germany and their age equivalent the Schistes de Liévin of Artois yield '*Dayia navicula*'. This form is being studied by Dr. J. Shirley who in 1962 expressed the view '. . . that the "*D. navicula*" of these areas and Liévin differs specifically and constantly from the Middle Ludlow (i.e. *Leintwardine Beds*) form and is now to be referred to a new species *D. tenuisepta* sp. nov. (nomen nudum)'. A specimen from the Köbbinghauser Schichten is figured on Plate 119, fig. 8. It is larger than British forms but possesses relatively small and less prominent muscle attachment areas.

STRATIGRAPHICAL CONSIDERATIONS

The true nature of the sequence of faunas in the various Siluro/Devonian successions of Great Britain and Continental Europe is now more fully understood than a few decades ago and closer agreement is being reached on correlation. Following Jaeger (1962 and 1965) it is apparent that *Dayia*-bearing strata in the Rhineland, Artois, Bohemia, and Podolia are younger than the British Ludlovian. Jaeger shows that *Monograptus* extends upwards at least to the top of the Middle Siegenian in Germany and Bohemia. Teller (1964, table 5) for Poland, also shows graptolites in beds younger than the British Ludlow Bone Bed. Correlation between graptolitic and shelly facies in these areas and adjacent Podolia demonstrates the high stratigraphic level attained by *Dayia* and emphasizes the inapplicability of the genus as an index of Silurian rocks. The characteristic British forms and the, in part contemporary, Scandinavian forms are ancestral to these other varieties.

A study of assemblages separated in time brings out a fundamental change in external morphology during phylogeny. Text-fig. 5 shows the relationship between incurvature of the ventral umbo (see Tucker 1965, fig. 2) and overall size for four assemblages ranging in age from Lower Ludlow to Lower Devonian. Regression lines have been computed for each assemblage. The lower degree of correlation of samples (*a*) and (*c*) is due to the low number of individuals and lack of juvenile forms in both samples. However, it can be seen that during phylogeny individuals tended to attain greater dimensions whilst incurvature was progressively delayed and less intense. These changes are most pronounced in the assemblage of *Dayia navicula bohemica* from the Lower Devonian of Bohemia. The reduced rate of hooking would clearly postpone pedicle atrophy, a condition facilitating survival of the individual under a wider range of environment than the quiet water conditions suggested for *Dayia navicula sensu stricto* by Tucker (1965).

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1a


1b


1c


2a


2b


2c


3a


3b


3c


4a


4b


4c


5a


5b


5c

TUCKER, *Dayia*

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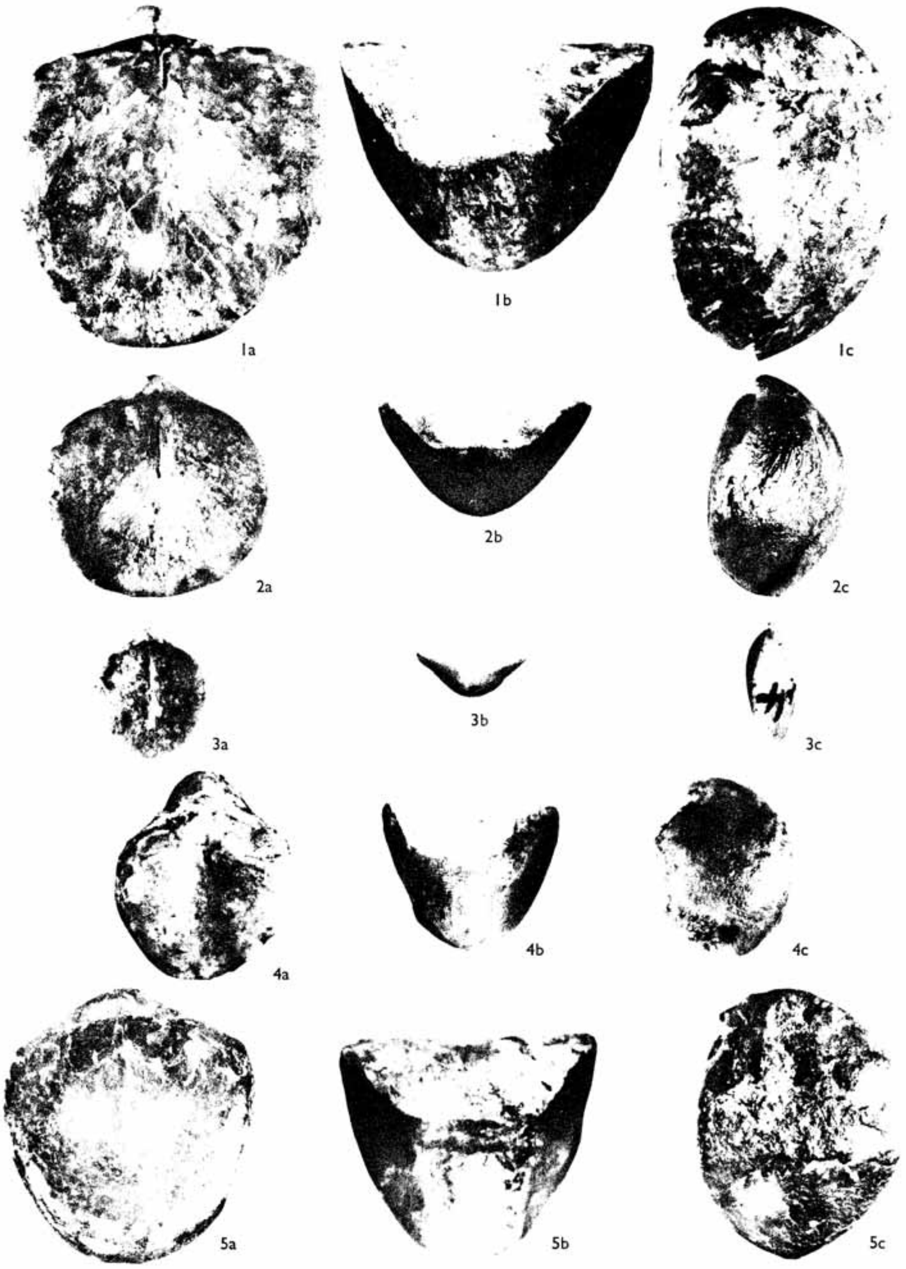
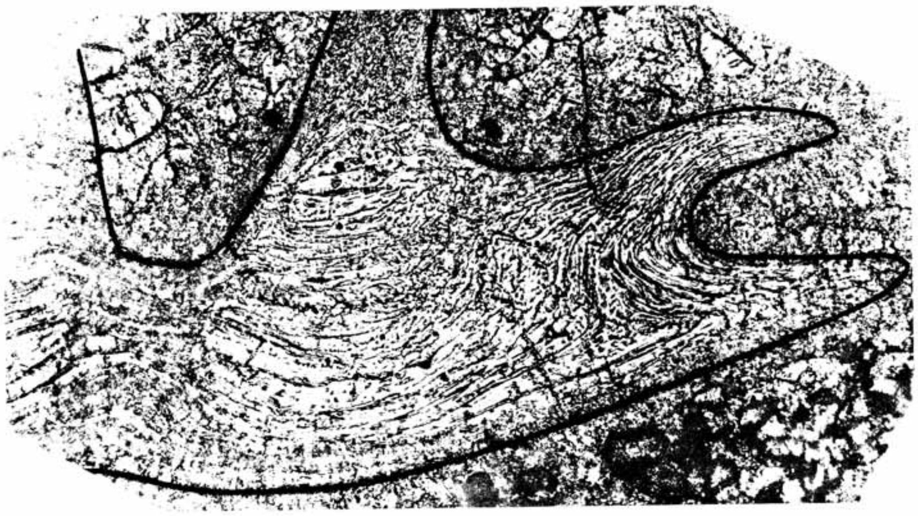
TUCKER, *Dayia*



TUCKER, *Dayia*

1



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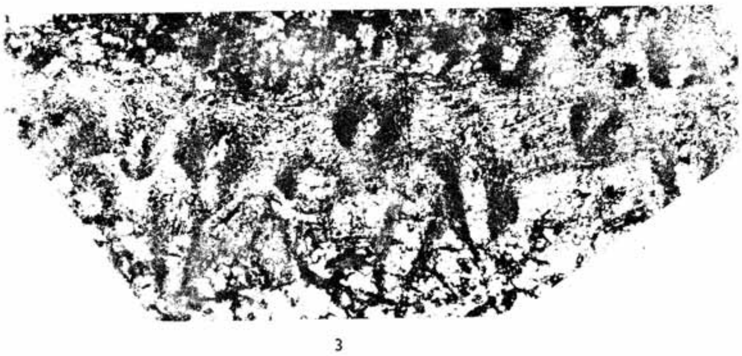

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