

CORTEZORTHINAE, A NEW SUBFAMILY OF SILURO-DEVONIAN DALMANELLID BRACHIOPODS

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ABSTRACT. Cortezorthinae is proposed for the Siegenian-Eifelian septate dalmanellid *Cortezorthis* gen. nov., its Silurian to Lower Devonian aseptate precursor *Protocortezorthis* gen. nov., and their derivatives, *Reeftonia* Allan and *Cariniferella* Schuchert and Cooper. New species are *Protocortezorthis windmillensis* and *Cortezorthis cortezensis* from Nevada and *Cortezorthis maclareni* and *C. bathurstensis* from the Canadian Arctic. *Cortezorthis maclareni* is type species of *Cortezorthis*; '*Dalmanella*' *fornicatimcurvata* is designated type species of *Protocortezorthis*.

Protocortezorthis windmillensis is a temporal and morphologic intermediate between fully differentiated members of *Protocortezorthis* and of *Cortezorthis*. Its incipient median septum is recapitulated in early growth stages of *Cortezorthis*, and its dorsal adductor field is variable between patterns typical of both older and younger forms.

The new subfamily Cortezorthinae arose from an as yet undesignated Silurian species of *Isorthis*. The Silurian members of *Protocortezorthis* developed distinctive ventral musculature, in part reminiscent of the rhipidomellids. The Devonian members of the Cortezorthinae (*Cortezorthis*, *Reeftonia*, and *Cariniferella*) evolved away from standard isorthisoid muscle patterns and also showed some convergence toward rhipidomellid internal morphology.

RECENT attempts to cast dalmanellid taxonomy in a phylogenetic scheme (Boucot, Johnson, and Walmsley 1965; Boucot, Gauri, and Johnson 1966) and efforts made here bring into focus some broad generalities regarding Devonian dalmanellids. The broad compass of the Dalmanellidae of Williams and Wright (1963) and of Wright (1965) includes several distinctive subfamilies in the Silurian and the Early and Middle Devonian, but members of the subfamily Dalmanellinae are unknown in Devonian beds. Devonian representatives of the family are limited to the isorthis and resserellids. The latter group and the Dicaelosiidae died out during the Emsian or Eifelian. Thus most of the Devonian genera fall into three major groups, Rhipidomellidae (emend. Boucot, Gauri, and Johnson 1966), Schizophoriidae, and Dalmanellidae.

Walmsley, Boucot, and Harper show, in a manuscript in preparation, that *Isorthis* may have been derived from *Dalmanella*. The family assignment of the cortezorthinids hinges on the derivation of *Schizophoria* and we believe the evidence still favours its having arisen from *Hinantia* or *Salopina* rather than from *Isorthis*. This is supported by the nature of the internal morphology of the earliest *Schizophoria* species of early Gedinnian age, discussed later in this paper, which have unfaceted ventral diductor impressions and a narrow ventral myophragm, plus dorsal cardinalia that are characterized by strong brachiophore supporting plates that are not associated with prominent adductor muscle bounding ridges. These are features typical of *Salopina*, but not of *Isorthis*. Therefore Isorthisinae, once regarded as belonging to the Schizophoriidae (Schuchert and Cooper 1932), must be transferred to the Dalmanellidae and the Cortezorthinae, which had its origin in *Isorthis*, is similarly placed.

If the isorthisoids are to be dissociated from the schizophoriids, the major split of

the punctate orthoids at the superfamily level recognized by Alikhova (1960) probably has real significance and is adopted here.

SYSTEMATIC PALAEOONTOLOGY

Suborder DALMANELLOIDEA
 Superfamily DALMANELLACEA Schuchert 1913
 [= Rhipidomellacea Alikhova 1960]
 Family DALMANELLIDAE Schuchert 1913
 Subfamily CORTEZORTHINAE nov.

Diagnosis. Aseptate or septate Dalmanellidae with fixed ventral adductor and unfaceted ventral diductor scars (see appendix of definitions) and progressively divergent brachiophores in Devonian member genera.

Discussion. The new subfamily Cortezorthinae is erected primarily to include the new genera *Cortezorthis* and *Protocortezorthis* defined below, but includes the previously named genera *Reefonia* and *Cariniferella* as well. *Protocortezorthis* is thought to have been derived out of one of the Silurian species of *Isorthis*, but since an understanding of *Cortezorthis* morphology, ontogeny, and direct ancestry is necessary for elucidation of the subfamily, further discussion is deferred until later in this paper.

Genus CORTEZORTHIS gen. nov.

Plates 19–20

Type species. *Cortezorthis maclareni* Johnson and Talent sp. nov.

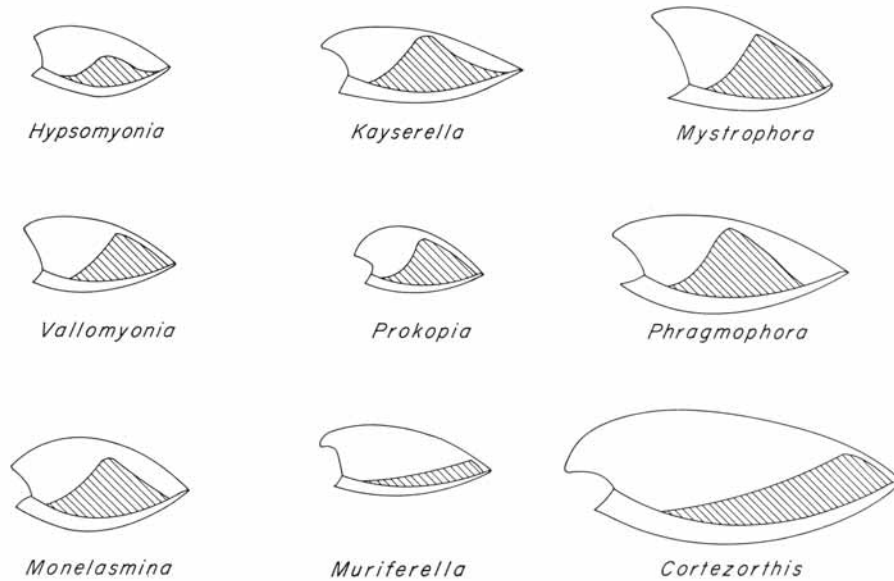
Diagnosis. Ventral muscle-field lacking broad myophragm. Brachial valve with rhomboidal adductor muscle-field and discrete postero-lateral bounding ridges; fulcral plates lacking; median septum long and triangular. Both valves may bear peripheral radial septa.

Discussion. *Cortezorthis* is an unusual dalmanellid even amongst dalmanellids with a dorsal median septum, which themselves are uncommon and at present still relatively poorly known. Most of the septate dalmanellids are small shells and the only genus previously brought to light that attains a size comparable to that of other Palaeozoic dalmanellids is *Phragmophora* Cooper 1955. The known representatives of *Phragmophora* are not particularly large for dalmanellids and are considerably smaller than the largest specimens of *Cortezorthis* as represented by *C. maclareni*, *C. bathurstensis*, and *C. cortezensis* described below.

The median septum of *Cortezorthis* is distinctive in being very long and relatively low triangular through its entire length, distinguishing it from the median septum of other known septate dalmanellids, except *Muriferella*, since they all bear a relatively high triangular structure (text-fig. 1).

The second distinctive morphologic element of *Cortezorthis* is its peripheral radial septa (see appendix of definitions). These appear first in the antero-medial regions, and in the brachial valve they closely adjoin the median septum. The smallest specimens that bear radial septa have a single pair next to the median septum. In larger specimens the

radial septa become better developed around the antero-lateral periphery with generally decreasing strength away from the mid-line. Since the peripheral radial septa are so extravagantly developed in some forms it is surprising to find that they are wholly absent in others; the evidence at hand suggests that their presence or absence within the genus is merely of specific value since forms that lack them come from different localities and different stratigraphic positions and have fairly clear-cut minor external peculiarities of form that distinguish them from species bearing radial septa.



TEXT-FIG. 1. Schematic longitudinal sections at the mid-line of the Devonian septate dalmanellid genera showing brachial valve, outline of median septum, and outline of exterior of pedicle valve.

Among forms with radial septa and those that lack them, there seems to be little difference in the thickness of the median septum, the shell in general, and the strength of development of the muscle bounding ridges or the anterior elevated edge of the adductor platform in the brachial valve. On the other hand, the unnamed species from Novaya Zemlya (Pl. 20, figs. 21-27) has a very faintly impressed dorsal musculature. Its median septum is relatively thinner than in either *C. cortezensis* or *C. maclareni* and so are the radial septa; so the possession or absence of a well-developed anterior elevated edge for the dorsal adductor scars appears to be a feature of no more than specific value.

In the pedicle valve most species lack a myophragm dividing the ventral diductors, although in a few specimens the adductor tracks are well defined. The largest specimen of *C. cortezensis*, however, has a fairly prominent ventral myophragm and is uncommon in that regard. Judging from the variation amongst the named and unnamed species of *Cortezorthis*, the internal feature of consistent taxonomic value in the pedicle valve appears to be short dental lamellae in combination with discontinuous, anteriorly

convergent muscle bounding ridges. In the brachial valve all medium and large-size specimens bear a long, low median septum and all that attain a relatively moderate size bear a rhomboidal adductor muscle-field with the postero-lateral bounding ridges of the posterior adductors discontinuous with the brachiophore bases and set within them (Pl. 19, figs. 21–23; Pl. 20, figs. 18, 28).

COMPARISON

Relation to Muriferella. There are similarities in the median septa of *Cortezorthis* and *Muriferella* Johnson and Talent (in press), but the latter genus has well-defined fulcral plates and an elongate dorsal adductor muscle-field, both of which are lacking in *Cortezorthis*. The two genera occur together in Nevada and in the Canadian Arctic and in collections bearing small *Cortezorthis* (e.g. Pl. 20, figs. 3–7) the broad muscle scars and divergent brachiophores of *Cortezorthis* at once distinguish it from *Muriferella* (cf. Johnson and Talent, in press, pl. 9, figs. 6–10).

Relation to Phragmophora. *Cortezorthis* gen. nov. somewhat resembles *Phragmophora* in the configuration of the pedicle muscle impressions and in the possession of a dorsal median septum. In the pedicle valve *Phragmophora* (Cooper 1955, pl. 12, fig. 19) bears a short, transverse muscle-field laid out on the same plan as that of *Cortezorthis*. The antero-lateral bounding ridges are shorter and converge much more sharply than in *Cortezorthis*. In the ventral valve of *Phragmophora* there is a notodeltidium (Cooper 1955, pp. 51, 52, pl. 14A; Biernat 1959, pl. 5). The structure is not present in *Cortezorthis* although some of the shells examined are exceptionally well preserved. Instead, the apex of the pedicle valve may be filled internally with a deposit of shell material that partially closes the apex of the delthyrium.

In the brachial valve, *Cortezorthis* structures are dissimilar in general layout to those of *Phragmophora*. The brachiophores and cardinal process are difficult to compare. Basically, the cardinal process of *Phragmophora* is bilobate (Cooper 1955, pl. 12, fig. 24; Biernat 1959, p. 44, fig. 16) and the myophore of the best-preserved specimen of *Cortezorthis* (pl. 19, fig. 2) is relatively similar to the quadrilobate one of *Phragmophora schnuri* illustrated by Biernat (1959, p. 44, fig. 16c). However, the shaft of the cardinal process of *Cortezorthis* is not cleft as is the shaft in *Phragmophora*. The median septum of *Phragmophora schnuri* is much higher and decidedly more precipitous in the slope of its posterior edge (text-fig. 1). Moreover, the septum does not extend to the anterior margin. In *Cortezorthis*, small shells bear a median septum that is no more than a ridge. Larger specimens of *Cortezorthis* bear a median septum that is long, low, and triangular and which does extend to the anterior margin of the valve (text-fig. 1). In addition, the brachiophores of *Phragmophora* appear to be somewhat more slender and more strongly ventrally directed than they are in *Cortezorthis*. The well-formed triangular notothyrial platform of *Cortezorthis* is not developed in *Phragmophora* as illustrated by Cooper (1955, pl. 12B) nor in the specimens illustrated by Biernat (1959, pl. 6, figs. 9–11). Biernat (1959, p. 52) noted that fulcral plates are lacking in small specimens (ephebic stage) of *Phragmophora*, but are present in gerontic shells. The latter suggestion is undoubtedly based on a misinterpretation of fulcral plates which, when present, are best seen in small specimens. The gerontic build-up of shell material in and around the sockets to form an anterior overhanging lip should not be confused with true fulcral plates.

Taken together, the configuration of the cardinalia and median septum of *Phragmophora* suggest that the genus was derived from *Prokopia* (Havlíček 1953) rather than *Cortezorthis* and its allies. *Prokopia* is a very small, thick-shelled form that lacks fulcral plates but bears a high triangular median septum that descends precipitously ventrally along its posterior edge. Wright (1965, pp. H338–9) proposed a subfamily Prokopiinae to include *Prokopia*, *Phragmophora*, and *Monelasmina*. However, as shown by Cooper (1955, pp. 53–54) *Monelasmina* is a schizophoriid genus and is therefore not closely related to *Prokopia*.

Relation to Monelasmina. *Cortezorthis* differs from *Monelasmina* (Cooper 1955, pl. 11; Pedder 1959) by attaining a much greater size, but more importantly in a comparison of *Monelasmina* with small specimens of *Cortezorthis* that are in the same size range, *Cortezorthis* differs most markedly by the lack of a high triangular median septum. In addition, *Monelasmina* bears long bilobate ventral diductor scars even at an early growth stage. *Monelasmina* is a schizophoriid genus, and it appears possibly to have been derived directly from a late species of *Salopina* or from *Sphenophragmus* Imbrie (1959) rather than *Cortezorthis*.

Relation to Hypsomyonia. *Hypsomyonia* Cooper is a septate Devonian dalmanellid whose phylogenetic relations are still uncertain, thus necessitating comparison with *Cortezorthis*. *Hypsomyonia* (Cooper 1955, p. 52, pl. 11, figs. 1–11) even though minute, bears a relatively high triangular median septum and an anteriorly elevated muscle platform. Large specimens of *Cortezorthis* bear an anteriorly elevated adductor platform and this is probably the source of their assignment to *Hypsomyonia* (McLaren in Fortier *et al.* 1963, p. 320); however, as is the case with *Monelasmina* and *Prokopia*, small specimens of *Cortezorthis*, the same size as Cooper's illustrated specimens of *Hypsomyonia*, differ very markedly by the lack of a high, triangular median septum or an elevated adductor platform in *Cortezorthis*.

Relation to Dalmanellopsis. The genus *Dalmanellopsis* Khalfin (1948) was thought possibly to be a septate dalmanellid. Khalfin (1948, pp. 208, 209) described a long ridge or septum in the brachial valve of the type species *D. septiger*. Examination of a specimen of *D. septiger* sent by Dr. R. T. Gratsianova revealed that the structure in question is only a low medial ridge and not a true median septum. *Dalmanellopsis* appears to be a valid genus most closely related to *Salopina* (Boucot, Gauri, and Johnson 1966) and not a synonym of *Levenea* as it was regarded by Alikhova (*in* Sarycheva 1960, p. 191) and Wright (1965, p. H334).

Cortezorthis maclareni sp. nov.

Plate 19, figs. 1–20, Plate 20, figs. 28, 29

1963 *Hypsomyonia?* sp. A, McLaren in Fortier *et al.*, p. 320.

Diagnosis. *Cortezorthis* with a strong narrow fold (carina) on the pedicle valve and a deep, subangular, narrow sulcus on the brachial valve. Internal margins of both valves bear radially arranged septa.

Exterior. Brachial valves are transversely suboval to sub-semicircular while pedicle valves may be transversely shield-shaped or subpentagonal in outline. The valves are

unequally biconvex in lateral profile with the pedicle valve slightly more convex than the brachial valve. The over-all aspect is relatively lenticular. The beak of the pedicle valve is short, pointed, and only slightly incurved over a low, triangular, nearly flat interarea. The ventral interarea is low apsacline to orthocline and is equal to approximately two-thirds of the maximum width of the valves. It is cleft medially by a triangular open delthyrium, enclosing an angle of about 60° . The interarea commonly shows fairly well-developed horizontal growth lines that start a short distance lateral to the edges of the delthyrium which are unstriated. The beak of the brachial valve is small, inconspicuous, and moderately incurved. The dorsal interarea is relatively long, equalling the width of the ventral interarea, and is flat and anacline. The cardinal angles are obtuse and relatively smoothly and strongly rounded. Maximum width is commonly near midlength or slightly posterior to it. Small shells and the posterior portions of larger ones bear a relatively strong narrow fold on the pedicle valve and a well-marked narrow sulcus on the brachial valve. However, toward the anterior of larger specimens the fold on the pedicle valve begins to broaden and become less elevated and the anterior commissure becomes slightly flattened or deflected toward the brachial valve, forming a broad, indistinct, curved margin that is slightly dorsally deflected, in effect, a reversal of the sulcation pattern, but the fold and sulcus developed posteriorly are of an entirely different order of magnitude considering the relative height : width ratio of the features.

The ornament consists of numerous, fine, subangular costellae that increase in number anteriorly by intercalation, principally along the sides of shallow interspaces. On some specimens, particularly in the proximity of the fold and sulcus, the angular costellae break down into numerous very fine costellae of about equal size. Fairly well-developed concentric growth lines are present at a few irregular intervals across the shell. There are commonly 10–15 costellae in a space of 5 mm., 10 mm. anterior to the beak of the brachial valve in the mid-region.

Interior of pedicle valve. Beneath the level of the delthyrium, in its apex, there is a somewhat variable but more or less well-developed pad of secondary shell material that fills the apex of the valve and closes off the apical one-quarter to as much as one-third of the delthyrium. Commonly the external face of the pad of shell material visible within the apex of the delthyrium is seen to bear several lamellae or growth lines that have a concave edge facing the hinge line, in effect rounding the apex of the delthyrium. The hinge teeth are relatively ponderous and triangular in cross-section, in the plane of the commissure. Their inner edges bear crural fossettes and are directed somewhat more strongly laterally than the edges of the delthyrium. The lateral edges are almost parallel to the median plane. Short dental lamellae are present in small specimens, but are made completely obsolescent by deposition of shell material beneath the hinge teeth and in the umbonal cavities so that the hinge teeth appear to connect directly with the inner surface of the valve. A pair of relatively thin, subangular, muscle bounding ridges originate at the base of the hinge teeth and curve slightly inward toward the mid-line to partially enclose the diductor muscle impressions antero-laterally.

In plan view the ventral muscle impression is roughly elongate-oval. The adductor scars are located centrally and are relatively broad, low, and very faintly impressed. The diductors are more or less triangular with their long sides lying subparallel to the mid-line. Some specimens have the submedian and lateral diductor lobes differentiated (pl. 20,

fig. 29) and the *vascula media* extend anteriorly in a radial fashion from the submedian lobes. In a few specimens the submedian lobes are separated by a very narrow myophragm, but in most there is an elongate trapezoidal track medially that is only faintly elevated. There may be a rounded median groove that runs from nearly the anterior edge of the diductor muscle field to the peripheral crenulations. Peripherally the interior bears two sets of crenulations which are most strongly developed anteriorly and which become slightly less pronounced laterally. There is an inner group of relatively widely spaced, short, high, radially aligned, septa, but these do not reach to the edge of the valve. Outside of these and right at the margin of the valve there is a finer set of more numerous crenulations. The crenulate peripheral portion of the interior may be very finely papillose, evidently mirroring the development of the endopunctae.

Interior of brachial valve. The sockets are relatively deep, expanding antero-laterally. They are bounded posteriorly by the inner edges of the interarea and medially by the lateral edges of the brachiophores. Basally they are impressed into thick shell material between the brachiophores and the hinge line. On some specimens the anterior edge of the base of the socket is free of the base of the valve overhanging a small cavity suggesting that the socket base could be classified as a fulcral plate. However, the brachiophore base at this point is not in contact with the base of the valve, but is also free. The angle between the long axis of the brachiophore and the plane of the base of the socket at the distal end is about 90°. The brachiophores diverge widely and are relatively ponderous plates of subrectangular cross-section. They project toward the antero-lateral extremities of the pedicle valve rather than being inclined strongly ventrally. The bases of the brachiophores neither converge toward the midline nor diverge from it, but

EXPLANATION OF PLATE 19

- Figs. 1–20. *Cortezorthis maclareni* gen. et sp. nov. All specimens are from a single collection, GSC loc. 26513, lower part of lower member of Blue Fiord Formation, south-western Ellesmere Island. Collected by D. J. McLaren, 1955. 1, Interior of brachial valve $\times 3$, GSC no. 19106. Note the anteriorly raised adductor muscle platform, the stout median septum, and peripheral septa. 2, Interior of incomplete brachial valve $\times 3$, GSC no. 19107. Note the distinctly quadrilobate cardinal process, the stout median septum, and the peripheral septa. 3, Internal margin of part of brachial valve $\times 5$, GSC no. 19108. Note the peripheral septa and the smaller intercalated marginal crenulations. 4, 5, Interior of pedicle valve $\times 3$ and $\times 2$, GSC no. 19109. Note deeply incised crural fossettes on the inner edges of the hinge teeth. 6, 7, Rubber internal mould and interior of pedicle valve $\times 1.5$. GSC no. 19110. Note the low, angular, anteriorly convergent, muscle bounding ridges and the strong peripheral septa. 8–10, Ventral, posterior, and anterior views $\times 1.25$, GSC no. 19111. Note loss of narrow fold and sulcus near the anterior commissure. 11, Interior of pedicle valve $\times 1$, GSC no. 19112. 12, 13, Rubber internal mould and interior of pedicle valve $\times 1.5$, GSC no. 19113. Note the bluntly rounded posterior end of the mould of the muscle impression owing to shell material deposited in the apex of the valve. 14, 15, Dorsal and ventral views $\times 2$, GSC no. 19114. Note the angular appearance of the costellae. 16–20, Posterior, anterior, dorsal, ventral, and side views of the holotype $\times 1.5$, GSC no. 19115. Note the reversal of the fold and sulcus at the anterior commissure.
- Figs. 21–23, *Cortezorthis* aff. *bathurstensis* Blue Fiord Formation, 100 ft. above base, south bank of Sutherland River, lat. 76° 19', long. 92° 51', Prince Alfred Bay area, Devon Island, collected by A. R. Ormiston, Aug. 1961. 21, Interior of brachial valve $\times 2$, GSC no. 19593. Note the stout median septum and the absence of peripheral septa. 22, 23, Two aspects of brachial valve interior $\times 3$, GSC no. 19594.
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maintain a fairly consistent angle from their ventral edges to their bases. Medially between the posterior ends of the brachiophores the notothyrial cavity is almost completely filled by a ponderous triangular pad of shell material bearing the cardinal process. The cardinal process is composed of a very short, broad, rounded shaft and a quadrilobate myophore that faces approximately the same direction as does the dorsal interarea. Both medial and lateral lobes are crenulated or are lamellose, but the median pair is commonly grooved further anteriorly. A thick, long, triangular median septum extends from the base of the anterior edge of the notothyrial platform to the anterior commissure of the valve. The median septum may be relatively narrow at its base and be thicker midway toward its ventral edge where it again becomes relatively thin and blade-like.

The adductor muscle-field is suboval and commonly slightly transversely so, or from this configuration there may be a slight tendency toward a rhombohedral outline and in most specimens the anterior edge of the adductor scars converges toward the median septum at a high angle. The postero-lateral edges of the adductor muscle-field are limited by a pair of relatively strong, straight bounding ridges that lie well within the inner edges of the bases of the brachiophores. The anterior edges of the adductor muscle scars are commonly strongly elevated above the base of the valve. The anterior and posterior adductor pairs are separated by faint, low, rounded ridges that extend anteriorly subtending an angle of about 70–75° between them and the median plane. The anterior adductor impressions are commonly radially grooved with the grooves becoming stronger toward the overhanging edge of the platform where the grooves may become very deep and are separated by elongate lobes or rods of shell material. Similar elongate rods or pustules develop fairly strongly on some specimens at the anterior end of the postero-lateral bounding ridges as well as lateral to them beneath the sockets and brachiophores. The area beneath the anterior edges of the adductor platform may be relatively smooth, but grooves deepen again anteriorly toward the periphery where a double set of septa and crenulations is developed similar to those already described for the pedicle valve. The anterior end of the median septum and the strongest radial septa, which commonly are the next adjacent pair, are irregular and deeply pitted, mirroring at least in part the development of longitudinal grooves on the septa that parallel their ventral edges.

Shell structure. The shell is thick and is endopunctate.

Occurrence. The type lot and the only specimens certainly assignable to *C. maclareni* are from Geological Survey of Canada locality 26513 from the south side of Eids Fiord, south-western Ellesmere Island and were collected by Dr. D. J. McLaren in 1955. According to McLaren (*in Fortier et al.*, 1963, p. 320) the collection horizon is about 600 ft. above the base of the lower member of the Blue Fiord Formation.

Figured specimens. GSC numbers 19106–16.

Cortezorthis maclareni loc. 26513

Figured Specimens

Measurements in mm.

	<i>Length</i>	<i>Width</i>	<i>Thickness</i>
Holotype GSC 19115	18.0	19.9	8.5
Paratype GSC 19114	11.0	14.8	5.0
Paratype GSC 19111	19.1	21.5	9.1
Paratype GSC 19116	9.6	11.5	5.3

<i>Unfigured Specimens</i>					
<i>Length</i>	<i>Width</i>	<i>Thickness</i>	<i>Length</i>	<i>Width</i>	<i>Thickness</i>
11.4	14.0	6.0	18.8	20.3	10.0
12.7	15.3	6.3	18.6	21.0	10.5
13.7	16.6	6.6	18.0	22.0	8.0
14.2	17.5	7.0	19.0	22.7	8.5
16.4	19.5	7.7	20.6	23.6	9.2
17.7	19.7	9.2	23.4	25.4	11.4
18.3	20.0	10.3	21.2	25.5	6.4

Cortezorthis bathurstensis sp. nov.

Plate 20, figs. 1-13

Diagnosis. *Cortezorthis* lacking radial septa.

Exterior. The valves are transversely shield-shaped to suboval in outline. They are biconvex in lateral profile, with the pedicle valve having the greater convexity. There is a short, pointed, incurved ventral beak and a low, subcarinate, transverse profile; however, no median carina is developed. The brachial valve bears a well-defined median sulcus that is relatively sharp at the umbo and broadens out to something of a medial flattening anteriorly. The ventral interarea is low, triangular, and apsacline, and equal to about half the maximum width of the valves which is attained a little posterior to midlength anterior to obtuse, rounded cardinal angles. The delthyrium is open and triangular, enclosing an angle of about 60°. The dorsal interarea is low, triangular, and well developed. It is flat and anacline on smaller specimens to nearly orthocline on large ones.

The ornament consists of fine, rounded costellae that increase in number anteriorly by bifurcation and by implantation. The costellae on the postero-lateral flanks are somewhat finer than those on the median half of the valve. A few costellae that originate at the posterior become enlarged anteriorly and give a faint indication of parvicostellation on some specimens. Concentric growth lines are not developed.

Interior of pedicle valve. The hinge teeth are prominent and of triangular cross-section on small specimens, but become blunted and directed dorso-laterally on large ones. Crural fossettes are present. The ventral diductor scars are short and cordate on small- to moderate-sized specimens with a very faint low myophragm dividing the scars; poorly developed short muscle bounding ridges that converge slightly toward the midline enclose them laterally. The largest specimen has a long, well-developed myophragm that may be anteriorly split. Adductors are not discernible, but the diductor scars become strikingly elongate and are bounded by long, well-defined, sharp, anteriorly convergent muscle bounding ridges. The interiors are crenulate over half or more of the smallest specimens, but only peripherally on the largest ones. The crenulations on the best preserved, moderate-sized specimens are rounded to very slightly flattened, simple, rod-like structures. Peripheral radial septa are not developed.

Interior of brachial valve. The presence of some very small specimens, the smallest being 4 mm. in maximum dimension, allows for the discussion of small- and large-stage brachial valves. The small specimens are very strongly convex, having something of the appearance of a small brachial valve of *Schizophoria*, but the median sulcus is a point of external distinction. The brachiophores are triangular and plate-like, diverging antero-laterally

at roughly 60° and diverging slightly toward the base of the valve. The sockets are formed between the plate-like brachiophores and the inner posterior margin of the valve, and the slightly overhanging interarea. There appears to be a slight thickening on the lateral sides of the brachiophores to form the base of the socket, but fulcral plates are not developed. The cardinal process is a small rhomboidal callosity at the apex of the notothyrium supported by a very short, thin ridge in the notothyrial cavity. The adductor impressions are broadly pyriform with short, discrete, blade-like, muscle bounding ridges set close to the bases of the brachiophores and diverging parallel to them in a radial fashion. The anterior adductors are rounded and blend imperceptibly with the interior of the valve. There is a small ridge-like median septum that begins approximately at the anterior margin of the dorsal adductor impressions and extends to the anterior commissure with almost no perceptible increase in height. In the smallest specimen the septum has a height approximately one and a half times its width and is considerably less than 1 mm. in height.

In a moderate-sized specimen the brachiophores, although still plate-like, develop anterior extensions that project beyond their bases which are joined with the valve interior, and they diverge a little more strongly antero-laterally. The cardinal process is a serrated, chevron-shaped, undivided shaft with its base in the notothyrial cavity and not extended anteriorly as a myophragm. At this stage no ancillary struts are developed forming a notothyrial platform. This is a specimen about 1 cm. across.

The largest available brachial valve, approximately 25 mm. across, has fully developed brachiophores that are bent a little, so that they diverge strongly laterally. There is a fully developed notothyrial platform against which the posterior adductors are well defined. The notothyrial platform continues as a well-defined, broad, rounded myophragm to about the middle of the adductor impressions where it becomes elevated as a median septum. The septum is relatively thin and rises in height anteriorly, but does not reach the anterior commissure. The posterior adductors are slightly longitudinally grooved in a manner similar to that of *Cariniferella*, and the blade-like bounding ridges are well defined lateral to the posterior adductors. The anterior adductors are bounded by straight to slightly curved elevated ridges that converge sharply towards the mid-line. No peripheral radial septa are developed.

Comparison. *Cortezorthis bathurstensis* differs from *C. maclareni* by the absence of radial septa internally, by a thinner shell, and by the absence of a median carina on the pedicle valve.

Occurrence. This species is present at GSC localities 67145 and 59036 in the upper part of the Stuart Bay Formation on Bathurst Island. Their age is probably Emsian.

Material. There are 22 specimens in the paratype collection of which five are illustrated that include GSC numbers 19595-9.

Cortezorthis cortezensis sp. nov.

Plate 20, figs. 14-20

Diagnosis. Large, flatly biconvex *Cortezorthis* with peripheral radial septa and lacking a median ventral carina.

Exterior. The valves attain medium to large size and are transversely suboval in outline and unequally biconvex in lateral profile, with the pedicle valve a little more convex; lateral flanks of the pedicle valve are relatively flat. Cardinal angles are obtuse and rounded behind the maximum width which is attained near midlength. The brachial valve has a shallow, poorly defined sulcus. The ventral beak is short and only faintly incurved so that the narrow triangular interarea is relatively low, flat, and apsacline. The delthyrium is open, and relatively broad, enclosing an angle of nearly 90°. The dorsal interarea is flat and anacline. The exterior ornament consists of numerous rounded costellae that increase in number anteriorly by intercalation and bifurcation and which tend to bow slightly with their convex sides toward the mid-line.

Interior of pedicle valve. The hinge teeth are short, stubby, triangular extensions of the interarea and are widely divergent, directed somewhat anteriorly and laterally. They are joined to the base of the valve by parallel thickenings of shell material, but dental plates are absent except for the most rudimentary sort of short, faintly differentiated, ridge-like extensions that support the base of the teeth distally. Even on very small specimens it is almost always impossible to detect any separate plate-like structure. Crural fossettes are not present. In the smallest specimens the ventral diductor impressions are trigonal and rounded posteriorly with a slightly elevated anterior margin. Poorly defined divergent vascular tracks extend antero-laterally. In the larger specimens strong muscle bounding ridges develop and converge rather abruptly toward the midline coincident with the development of a relatively prominent rounded myophragm between the diductor scars.

Interior of brachial valve. The brachiophores are plate-like and broadly divergent, defining sockets at the base of the valve without fulcral plates. The cardinal process is too poorly preserved to characterize accurately on the available specimens, but the notothyrial platform is fully developed into a ponderous structure that continues anteriorly as a myophragm to the middle of the dorsal adductors where it joins with a relatively thick, low, median septum that increases in height anteriorly and reaches to the anterior margin of the valve. The posterior adductors are subtriangular and relatively broad with some longitudinal striation and well-developed discrete bounding ridges. In one specimen a pair of myophragms subnormal to the mid-line delimit the posterior and anterior adductors. The anterior adductors are larger than the posterior ones and are situated on a slightly elevated platform whose anterior edges are nearly straight and which converge sharply toward the mid-line, but become less pronounced just before joining the median septum. The interior is crenulated peripherally and bears radial septa that are most prominently developed near the midline anteriorly.

Comparison. *Cortezorthis cortezensis* differs from *C. bathurstensis* by the presence of peripheral septa internally, although on the exterior the outline and profile are very similar. Internally the structural features are a little better developed in *C. cortezensis* and probably this is due to the development of a thicker shell. The ventral beak is a little less strongly incurved in *C. cortezensis* with the interarea tending to be more flat and the delthyrium broader. *C. cortezensis* differs from *C. maclareni* in lacking a median carina on the pedicle valve externally and in the relatively shorter and broader ventral diductor impressions. The two species are very similar in the brachial valve interior although

C. cortezensis does not develop the internal pustules and radial ridges that are especially prominent in *C. maclareni*.

Occurrence. All of the specimens of *Cortezorthis cortezensis* are from the *Eureka-Spirifer pinyonensis* zone of Emsian age.

Material. There are 38 specimens from the west side of the Cortez Range (USNM loc. 10754), four from the east side of the Cortez Range (USNM loc. 10752), and one from the northern Simpson Park Range of central Nevada. Four specimens are illustrated under USNM nos. 141450-3.

10752—Wenban Limestone, east slope of Cortez Range, elev. 7950 ft., 1000' N., 700' W. of SE. cor. of sec. 4, T. 26 N., R. 48 E., Cortez quad., Eureka Co., Nevada. Collectors: A. J. Boucot and E. F. Lawrence, 1963; A. J. Boucot, H. K. Erben, and K. L. Gauri, 1965.

10754—Wenban Limestone, west slope of Cortez Range, elev. 6875 ft., 800' N., 2900' E. of SW. cor. of sec. 21, T. 26 N., R. 48 E., Cortez quad., Eureka Co., Nevada. Collectors: A. J. Boucot and H. Masursky, 1963.

10762—McColley Canyon Formation, elev. 6800 ft., 2450' W., 650' N. of SE. cor. of sec. 16, T. 25 N., R. 49 E., Horse Creek Valley quad., northern Simpson Park Range, Eureka Co., Nevada. Collector: J. G. Johnson, 1957.

OCCURRENCE OF *CORTEZORTHIS*

Cortezorthis cortezensis is present at two localities in the Cortez Range (USNM localities 10752, 10754) and in the northern Simpson Park Range (USNM locality 10762), all in Eureka County, central Nevada. These occurrences are from the *Eureka-spirifer pinyonensis* zone that Johnson (1962, p. 166) and House (1962, p. 253) have concluded is of Early Devonian and probable Emsian age. Johnson's study of the Lower Devonian brachiopods in central Nevada (in preparation) presents additional evidence from the brachiopods and from the conodonts (Walliser in Johnson in prep.) pointing to an Emsian age.

An unnamed species of *Cortezorthis* is present in the lower part (late Siegenian) of the *Monograptus yukonensis* zone in collections of Dr. A. C. Lenz from Yukon Territory, Arctic Canada (Boucot, Gill, Johnson, Lenz, and Talent 1966). These have a fully developed median septum and peripheral septa, but a primitive dorsal adductor scar as in some specimens of *Protocortezorthis windmillensis* (Pl. 21, figs. 3, 9) and are thus intermediate in development between *P. windmillensis* and *C. cortezensis* of the Nevada Lower Devonian.

Cortezorthis bathurstensis is present at two localities near the top of the Stuart Bay Formation on Bathurst Island (G.S.C. localities 59036 and 67145). *Cortezorthis* sp., bearing radial septa, is present in the Disappointment Bay Formation of Bathurst Island (G.S.C. locality 59037). All three collections from Bathurst Island appear to be within the interval Emsian-Eifelian and the former two are tentatively assigned to the Lower Emsian.

Cortezorthis aff. *bathurstensis* is present 100 feet above the base of the Blue Fiord Formation on Sutherland River, Devon Island, in collections made by Dr. Allen Ormiston (Pl. 19, figs. 21-23). These beds also are of Emsian age according to G. Klapper who has studied the conodonts.

Cortezorthis maclareni occurs in the lower part of the Blue Fiord Formation on Ellesmere Island. The collection horizon is of Emsian or Eifelian age (G.S.C. locality

26513). An unnamed species lacking radial septa occurs in the mid-Blue Fiord Formation on Ellesmere Island (G.S.C. locality 26522).

A single specimen from south-eastern Novaya Zemlya (Pl. 20, figs. 21–27) comes from beds reported to be of early Eifelian age (Cherkesova, written communication March 1965).

Genus *PROTOCORTEZORTHIS* gen. nov.

Plate 21, figs. 1–22

Type species. Orthis fornicatimcurvata Fuchs 1919.

Diagnosis. Ventral muscle field narrow, with thin bounding ridges that converge toward the midline anteriorly. Diductor impressions separated by a narrow, well-defined, rounded myophragm. Dorsal cardinalia with fulcral plates present or absent. Notothyrial platform present. Median septum absent.

Discussion. The detailed morphology of one species, *Protocortezorthis windmillensis*, is described below. The ventral adductor scars are not discernible in *P. windmillensis*, due probably to poor preservation in the few available specimens. *P. orbicularis* and *P. fornicatimcurvata*, on well-preserved specimens, exhibit well-marked, shield-shaped or cordate adductor impressions of a rather distinctive configuration (see Walmsley 1965, pl. 63, figs. 1–8). The same type of ventral adductor impression is repeated in *Reeftonia marwicki* (figs. 4, 6, 7 of Plate 22 in the present paper) and the close comparison is evident in sketches reproduced in text-fig. 2. *Protocortezorthis windmillensis* closely resembles some species of *Cortezorthis*, but differs in having more deeply impressed ventral diductors and a well-defined ventral myophragm. Brachial valves are the same except for the absence of a median septum in *P. windmillensis*, but an incipient median septum and peripheral radial septa are present medially in some specimens. In the brachial valve

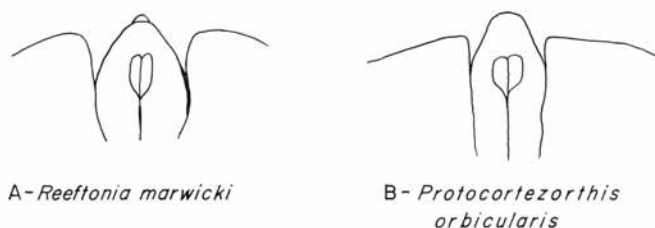
EXPLANATION OF PLATE 20

- Figs. 1–13. *Cortezorthis bathurstensis* gen. et sp. nov. All specimens from GSC loc. 67145, 85 ft. below top of Stuart Bay Formation, Bathurst Island. Collected by J. W. Kerr, 1964. 1, interior of pedicle valve ($\times 1$), GSC 19595. 2, Interior of brachial valve ($\times 1.25$), holotype, GSC 19596. 3–5, Two interior views and one exterior view of brachial valve ($\times 5$), GSC 19597. 6–8, Two interior and one exterior view of brachial valve ($\times 10$), GSC 19598. 9–13, Interior, side, anterior, posterior, and exterior views of pedicle valve ($\times 1.5$), GSC 19599.
- Figs. 14–16. *Cortezorthis cortezensis* gen. et sp. nov. Specimens from *Eurekaspirifer pinyonensis* zone, Cortez Range, central Nevada. 14, Rubber impression of interior of small pedicle valve ($\times 4$), USNM loc. 10754, USNM 141451. 15, Interior of pedicle valve ($\times 1.5$), USNM loc. 10754, USNM 141452. 16, Interior of brachial valve ($\times 2$), USNM loc. 10752, USNM 141450.
- Figs. 17–20. *Cortezorthis cortezensis* gen. et sp. nov. Specimen from *Eurekaspirifer pinyonensis* zone, northern Simpson Park Range, USNM loc. 10762. 17, 18, Ventral and dorsal views of internal mould ($\times 1$), holotype, USNM 141453. 19, Rubber replica of dorsal interior ($\times 1.25$), of specimen in fig. 18. 20, Side view of rubber replica of median septum ($\times 2$), of specimen in fig. 18.
- Figs. 21–27. *Cortezorthis* sp. From beds of early Eifelian age, south-eastern Novaya Zemlya, collected by S. V. Cherkesova. 21, 22 Ventral and dorsal views of internal mould ($\times 2$) of specimen in figs. 23–27, GSC 19117. 23–27, Dorsal, side, anterior, posterior, and ventral views ($\times 1.5$), GSC 19117.
- Figs. 28, 29. *Cortezorthis maclareni* gen. et sp. nov. Lower Blue Fiord Formation, Emsian or Eifelian, south-western Ellesmere Island, GSC loc. 26513. Collected by D. J. McLaren, 1955. Dorsal and ventral views of internal mould ($\times 3$), GSC 19116.

of *P. fornicatimcurvata* brachiophore supporting plates are present and continue antero-laterally as ridges bounding the posterior adductors. No peripheral radial septa are known in *P. fornicatimcurvata*.

Comparison. *Protocortezorthis* differs from *Reeftonia* in only a few minor modifications. *Reeftonia* has flatter and somewhat wider ventral diductors and commonly lacks a well-defined narrow ridge-like myophragm present in *Protocortezorthis*. In the brachial valve *Reeftonia* is almost identical with specimens of *P. windmillensis* that lack peripheral radial septa (see discussion of variation in *Reeftonia* below). *Reeftonia* completely lacks fulcral plates in all known representatives.

Protocortezorthis differs from *Cariniferella* in the form of the valves and in the ventral interior. In *Cariniferella* the ventral diductor scars diverge antero-laterally and lack



A-*Reeftonia marwicki*

B-*Protocortezorthis orbicularis*

TEXT-FIG. 2. Sketch drawings of ventral adductor and diductor scars in two cortezorthinid genera.

a narrow myophragm. The arrangement of the cardinalia of *Cariniferella* is close to that of the youngest forms of *Protocortezorthis*, i.e. *P. windmillensis*, and that of *Reeftonia*. The dorsal scar pattern appears to be comparable to that of *Cortezorthis* and *Reeftonia*, but the proportions of the several elements and the scar as a whole, relative to the size of the brachial valve, are different.

Species assigned to Protocortezorthis:

Protocortezorthis windmillensis sp. nov.

Isorthis slitensis Walmsley 1965, p. 467, pl. 62, figs. 23-35.

Orthis fornicatimcurvata Fuchs 1919.

Orthis orbicularis Sowerby in Murchison (1839, p. 611, pl. 5, fig. 16). This species has been redescribed and well illustrated by Walmsley (1965) leaving no doubt as to its relation to *P. fornicatimcurvata*. Specimens from the Sutherland River Formation illustrated and described by Boucot (in Boucot *et al.* 1960, p. 5, pl. 1, figs. 13-20, pl. 2, figs. 1-7) as *Isorthis orbicularis* were examined by Johnson who regards them as belonging to *Schizophoria* and close to the species *Schizophoria fragilis* Kozlowksi (1929).

Large specimens of *Schizophoria* are usually easily distinguished from *Isorthis* because of the larger brachial valve than pedicle valve in *Schizophoria* and because there commonly is a broad ventral sulcus in *Schizophoria*. Internally the brachial valve of *Schizophoria* has the posterior and anterior adductor muscle impressions separated from one another by ridges that diverge antero-laterally in contrast to ridges that are normal to the midline in *Isorthis*. However, in small specimens, *Schizophoria* is commonly subequally

biconvex without a sulcus as is *Isorthis szajnochai*. Moreover, in small specimens, ridges dividing the posterior and anterior adductor muscles are not discernible; thus small specimens must be distinguished on a different basis. In the case of the specimens illustrated by Boucot (1960), the shells are not congeneric with *I. szajnochai* because the muscle-field is long, but not anteriorly elevated and thus unlike the anteriorly elevated scar of *I. szajnochai*. Differences in the brachial valve are discussed further below. Specimens illustrated by Boucot also cannot be closely related to *Protocortezorthis orbicularis* because that form has a much less convex, but sulcate brachial valve (Walm-sley 1965, pl. 63, figs. 9–15). In the writers' opinion the ventral muscle impressions of the form illustrated by Boucot almost exactly duplicates that of *Schizophoria bisinuata* Weller (1903, p. 278, pl. 31, figs. 12–13). After examining several score specimens in Boucot's collection, from which the Devon Island forms come, the writers found that the median groove on the ventral myophragm is an inconsistent feature and that most specimens do not have it. The type of ventral musculature developed in the Devon Island form and in *Schizophoria bisinuata* has also been seen in several collections of *Schizophoria* from limestone of Helderberg age in the Klamath Mountains of California and from the McMonnigal Limestone of early Siegenian age in central Nevada (Johnson 1965). On all of the shells mentioned above it is not uncommon to find that the narrow ridge-like ventral myophragm extends anteriorly beyond the diductor muscle bounding ridges.

In the case of small brachial valves where the ridges dividing the posterior and anterior adductor impressions are not developed, *Schizophoria* and *Isorthis* of the *szajnochai* type are easily distinguished by the nature of the muscle bounding ridges. In *Schizophoria* the brachiophores are supported by high triangular brachiophore supporting plates, but muscle bounding ridges that would outline the anterior adductors are not developed. On the other hand, in *Isorthis szajnochai* and its relatives, relatively long muscle bounding ridges are present even in early growth stages and bound the anterior adductors with almost equal strength as they bound the posterior adductors. The Devon Island specimens have strong, divergent brachiophore supporting plates as is typical of *Schizophoria*, but there is no continuation as ridges lateral to the anterior adductors as in *Isorthis*.

EXPLANATION OF PLATE 21

- Figs. 1–13. *Protocortezorthis windmillensis* gen. et sp. nov. Windmill Limestone (*Quadrithyris* zone, of early Siegenian age) Coal Canyon, northern Simpson Park Range, central Nevada. 1, 2, Dorsal and anterior views of interior of brachial valve $\times 3$, USNM 147338, loc. 10758. 3, Interior of brachial valve $\times 1.5$, USNM 147339, loc. 10758. 4, Interior of brachial valve $\times 1.5$, USNM 147340, loc. 10758. 5, Interior of brachial valve $\times 2$, USNM 147341, loc. 10758. 6, 7, Rubber impression and interior of pedicle valve $\times 1.5$, USNM 147342, loc. 10758. 8, 9, Exterior and interior of brachial valve $\times 1.5$, USNM 147343, loc. 10758. 10–12, Exterior, interior, and anterior views of pedicle valve $\times 2$, USNM 147344, loc. 10758. 13, Interior of pedicle valve $\times 1.5$, USNM 147345, loc. 10757.
- Figs. 14–22. *Protocortezorthis fornicatimcurvata* (Fuchs 1919). Flaserschiefer of Hüinghäuser Schichten; railroad cut, 85 paces NE. of Hüinghäuser railroad station. USNM loc. 10596. Collected by A. J. Boucot, 1957. 14, 15, Rubber impression and internal mould of pedicle valve $\times 2$, USNM 147346. 16, 17, Internal mould of brachial valve and rubber impression $\times 2$, USNM 147347. 18, 19, Rubber impression and internal mould of brachial valve $\times 2$, USNM 147348. 20, 21, Internal mould $\times 2$ and rubber impression $\times 3$ of brachial valve, USNM 147349. 22, Rubber impression of internal mould of brachial valve $\times 3$, impression of USNM 147350.

DISTRIBUTION OF *PROTECORTEZORTHIS*

Protocortezorthis slitensis occurs in the Wenlock age Slite Marl of Gotland (Walmsley 1965, p. 469). *Protocortezorthis orbicularis* is present in the Ludlovian of the Welsh borderland (Walmsley 1965, p. 467). *Protocortezorthis sp.* is present in probable Ludlow age beds of the Caparo Formation of the Mérida Andes, Venezuela in a collection of R. Shagam, USNM loc. 12204. *Protocortezorthis fornicatimcurvata* is present in the Gedinnian of Germany (Fuchs 1919), France (Barrois, Pruvost, and Dubois 1922, p. 77), and Belgium (Boucot 1960, p. 296). It is also present in the Gedinnian Stonehouse Formation of the Arisaig area of Nova Scotia (Walmsley, Boucot, and Harper, manuscript in preparation). An unnamed species with closest affinity to *P. fornicatimcurvata* is present in the lower *Monograptus yukonensis* zone of late Siegenian age from Yukon Territory, Arctic Canada, in collections made by Dr. A. C. Lenz and examined by Johnson (see Boucot, Gill, Johnson, Lenz, and Talent 1966). The youngest reported occurrence is from the upper Pendikschichten in the Bosphorus region (Paeckelmann and Sieverts 1932, pl. 2, fig. 24). The occurrences cited above appear to be a part of the *P. fornicatimcurvata* lineage. *P. windmillensis*, a divergent species initiating the lineage resulting in *Cortezorthis*, is present in the early Siegenian *Quadrithyrus* zone of central Nevada (Johnson 1965).

Protocortezorthis fornicatimcurvata (Fuchs 1919)

Plate 21, figs. 14–22

- 1919 *Orthis fornicatimcurvata* Fuchs, p. 58, pl. 5, figs. 1–6.
 1922 *Orthis (Dalmanella) lunata* Barrois, Pruvost, and Dubois, p. 77, pl. 11, figs. 4–12; *non* Sowerby.
 1942 *Dalmanella orbicularis* Dahmer, p. 125, figs. 14, 15, 16a, b; *non* Sowerby.
 1951 *Dalmanella orbicularis* Dahmer, p. 91, pl. 7, fig. 1; pl. 9, figs. 20, 21; pl. 10, fig. 6; *non* Sowerby.
 1960 *Isorthis fornicatimcurvata* (Fuchs); Boucot, p. 296, pl. 10, figs. 6, 7.

Discussion. *Protocortezorthis fornicatimcurvata* compares closely to *P. windmillensis* described below in the form of the valves with a relatively strongly convex, subcarinate pedicle valve and a gently convex, sulcate brachial valve. In the interior *P. fornicatimcurvata* has ventral diductor scars closely comparable to those developed in *P. windmillensis*, but those on the latter appear for the most part to be slightly broader.

In the brachial valve *P. fornicatimcurvata* has brachiophores less widely divergent than does *P. windmillensis* and they are connected with brachiophore supporting plates that continue as muscle bounding ridges around the posterior adductors. Because the brachiophore supporting plates are relatively well developed the sockets are defined by fulcral plates. Medially the posterior adductors are divided by a broad myophragm that merges with the brachiophore bases forming a poorly defined notothyrial platform. The anterior adductors are bounded by discrete muscle bounding ridges that converge antero-medially.

The internal crenulations of *P. fornicatimcurvata* (Pl. 21, fig. 21) fairly closely resemble those of *P. windmillensis* and consist of somewhat swollen appearing lobes with minor lobes intercalated.

Figured specimens. USNM 147346–50.

Protocortezorthis windmillensis sp. nov.

Plate 21, figs. 1-13

1965 '*Isorthis*' cf. '*I. forncatimcurvata* Johnson; p. 371, non Fuchs.

Diagnosis. Brachial valve interior with evanescent development of an antero-medial mound of radial septa. Brachiophore supporting plates not developed.

Exterior. The shells are of approximately equal width and length and are rounded-trapezoidal in outline. The valves are unequally biconvex in lateral profile with the pedicle valve the larger. The interarea of the pedicle valve is low, apsacline, and nearly flat. It is relatively narrow, generally slightly less than half the maximum width of the valves. The delthyrium is relatively narrow at its apex with gently curved sides enclosing a broader angle toward the hinge line. The interarea of the brachial valve is narrow, band-like, and anacline. The cardinal angles are obtuse and strongly rounded. Maximum width of the valves is generally attained near midlength or anterior to it. The pedicle valves are subcarinate in transverse section and the brachial valves bear a corresponding median sulcus. Large shells are slightly emarginate at the anterior commissure.

The ornament consists of fine radial costellae that increase in number anteriorly by bifurcation and by intercalation. There are approximately 12-15 costellae in a space of 5 mm., 10 mm. anterior to the beak.

Interior of pedicle valve. The teeth are stout and triangular and diverge antero-laterally. They are supported by short, stout, divergent dental lamellae that nearly join anteriorly with sharply raised, narrow muscle bounding ridges that may be bowed gently laterally at their posterior, but which are gently convergent medially along most of their length. The muscle-field bears a very narrow, sharp, well-defined myophragm dividing the muscle-field throughout most of its length. Adductor scars are not differentiated. The interior is crenulated peripherally by the impress of the costellae.

EXPLANATION OF PLATE 22

- Figs. 1-7. *Reefstonia marwicki* Allan 1947. 1-6, Reefton beds, argillite boulder from argillites upstream from the main limestone in Lankeys Creek above junction with Stony Creek, New Zealand. USNM loc. 11731. Collected by David Ives, 1956. 7, Reefton beds, loose block about $\frac{3}{4}$ mile north of Highway 7, Lankeys Creek, New Zealand. USNM loc. 11002. Collected by A. J. Boucot, 1965. 1-3, Dorsal view of rubber impression, internal mould, and anterior view of rubber impression of brachial valve internal mould $\times 1.5$, USNM 147351. 4, Internal mould of pedicle valve $\times 1.5$, USNM 147352. 5, Internal mould of brachial valve $\times 1.5$, USNM 147353. 6, Internal mould of pedicle valve $\times 2$, USNM 147354. 7, Internal mould of pedicle valve $\times 1.5$, USNM 147355.
- Figs. 8-9. *Reefstonia alpha* (Gill 1949). Kilgower Member of Tabberabbera Formation, locality 22 of Talent (1963), Victoria, Australia. 8, Internal mould of pedicle valve $\times 1.5$, Geol. Surv. Victoria 50700F. 9, Internal mould of brachial valve $\times 2.5$, Geol. Surv. Victoria 50700C.
- Figs. 10-19. *Cariniferella carinata* (Hall 1843). 11-14, Chemung Gp., Bath, New York. Collected by F. Braun; Schuchert Collection. 15-19, Chemung Gp., Arkport, New York, collection of J. M. Clarke. 10-12, Replica of brachial valve cardinalia and muscle impressions $\times 3$, internal mould of brachial valve $\times 2$, and impression of internal mould of brachial valve $\times 2$, YPM S-1087. 13, Internal mould of pedicle valve $\times 2$, YPM 24856. 14, Internal mould of brachial valve $\times 2$, YPM 24857. 15-19, Dorsal, anterior, posterior, ventral, and side views $\times 1.25$, YPM S-1088.
- Figs. 20, 21. *Cariniferella tioga* (Hall 1867). Chemung, $1\frac{1}{4}$ miles N. of Post Creek, Elmira quad., New York, collection of H. S. Williams. 20, 21, Internal mould of pedicle valve $\times 1$, and rubber impression of internal mould $\times 1.25$, USNM 145582.

Interior of brachial valve. The sockets are widely divergent and on large shells their posterior edges are partially covered by the inner edges of the interarea. They are defined by gently curved brachiophore bases that overhang the floor of the valve. The brachiophores are widely divergent and are elongate elliptical, nearly plate-like, in cross-section. They are made slightly more convex medially by the addition of a thin pad of shell material. Brachiophore supporting plates are lacking. The notothyrial cavity is partially filled with shell material continuous with a stout, rounded to rectangular myophragm that divides the posterior half of the adductor muscle-field. The cardinal process is elongate and narrows posteriorly. The posterior adductor scars are roughly triangular and are bounded postero-laterally by more or less well-developed muscle bounding ridges that originate medial to the unsupported brachiophores. The anterior adductor scars are bounded by smoothly rounded muscle bounding ridges that curve and join medially. Anteriorly and well beyond the muscle impressions, large specimens may develop a low rod-like median septum or a mound-like group of peripheral septa medially that extend to the anterior commissure (Pl. 21, figs. 1-3). The group of septa is low and triangular in cross-section with the middle septum the highest. This medial enlargement of the internal edge of the valves fills the gap produced by non-elongation along the carinate antero-medial part of the pedicle valve.

Shell structure. The shell substance is finely punctate (endopunctate).

Occurrence. The species is known from two localities in the Windmill Limestone at Coal Canyon:

10757—West flank of Coal Canyon, elev. 6320 ft., 1600' N., 1800' W. of SE. cor. of sec. 17, T. 25 N., R. 49 E., Horses Creek Valley 15' quad., Eureka Co., Nevada.

Collectors: J. G. Johnson, M. A. Murphy, and E. L. Winterer 1957; N. G. Lane and E. L. Winterer 1962; H. Masursky 1959, 1961; A. J. Boucot 1963.

10758—East flank of Coal Canyon, big ledge, elev. 6320 ft., 1500' N., 1100' W. of SE. cor. of sec. 17, T. 25 N., R. 49 E., Horses Creek Valley 15' quad., Eureka Co., Nevada.

Collectors: J. G. Johnson 1957, 1958; M. A. Murphy and E. L. Winterer 1957; H. Masursky 1959; N. G. Lane and E. L. Winterer 1962; A. J. Boucot 1963.

Figured specimens. USNM numbers 147338-45.

Comparative morphology. *Protocortezorthis windmillensis* and *Cortezorthis maclareni* are distinct, but are closely comparable in so many internal features that a structure-by-structure comparison is worth while. In the pedicle valve of both the beak is short and the interarea narrow with strong triangular teeth to which are connected thin, blade-like, anteriorly convergent, muscle bounding ridges. In this respect the species of the two genera are exceptionally close. The muscle-field of *P. windmillensis* is relatively slightly longer and bears a strong narrow myophragm separating the diductor tracks anteriorly. In the brachial valve both bear brachiophores of the same general outline and shape that diverge at about the same angle and define sockets that are structurally the same. In addition, both species bear a triangular notothyrial platform of about the same outline. The general layout of the adductor muscle field is very similar in the two species and the similarity is accentuated by development of straight postero-lateral bounding ridges that lie inside the bases of the brachiophores. However, the muscle-field of *P. windmillensis* is not elevated anteriorly and its brachial valve differs most markedly by the absence of a

long median septum. *Protocortezorthis windmillensis* is noteworthy in its possession of an incipient median septum anteriorly as well as short coplanar peripheral septa in the medial region, closely adjacent to the midline. The structure of these anterior septa appears to be fully homologous with structures in *Cortezorthis*.

In summary, *Cortezorthis maclareni* exhibits close similarity in the general layout of all its internal structures, but some of these structures, such as the median septum, the peripheral septa, and the elevated dorsal adductor platform, are in contrast with the more conservatively built structures of *Protocortezorthis windmillensis*. The similarity, taken in conjunction with the stratigraphic and geographic positions of the two species, is taken as evidence in support of *P. windmillensis* as the ancestor of *Cortezorthis*.

The discussion of comparative morphology outlined above might easily have been made between them and the genus *Reeftonia* (Allan 1947). All of the features found similar between *P. windmillensis* and *C. maclareni*, except the development of peripheral septa, are also present in *Reeftonia*.

Genus REEFTONIA Allan 1947

Plate 22, figs. 1-9

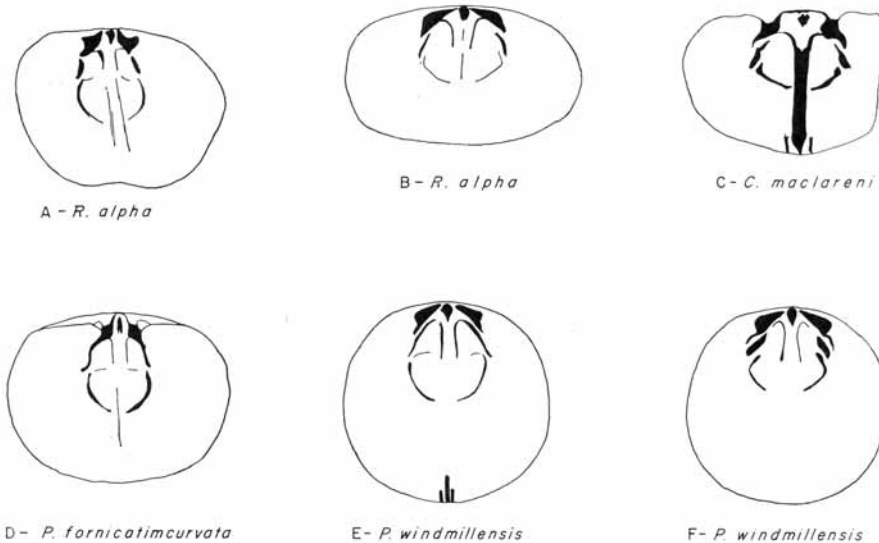
Type species. Reeftonia marwicki Allan 1947, p. 437, pl. 63, figs. 6-9.

Discussion. When erecting his new genus Allan (1947, p. 437) pointed to the absence of fulcral plates in the brachial valve and the fact that in the pedicle valve the diductor scars completely enclose the adductor impressions anteriorly as a basis for assignment of *Reeftonia* to the family Rhipidomellidae. Both features are indeed particularly important in a number of rhipidomellid genera, particularly members of the Rhipidomellinae, but similarity between *Reeftonia marwicki* and any of the more typical rhipidomellid genera finds more substance in word comparisons than in comparisons of the fossils themselves. The unequally biconvex shell, the sulcate brachial valve, and somewhat carinate pedicle valve (Allan 1947, pl. 63, figs. 6, 7) are not at all rhipidomellid in appearance. The pedicle valve diductor impressions illustrated herein are not flabellate and resemble rhipidomellid muscle scars essentially only in the outline of the adductors (text-fig. 2). It is in the brachial valve, however, that the rhipidomellid associations are most obviously distant. The sockets, though lacking fulcral plates, are constructed very differently from those typical of rhipidomellids; and the brachiophores, cardinal process, and posterior myophragm are all different. The adductor muscle scars on the rubber impression illustrated by Allan (1947, pl. 63, fig. 9) are not at all clear. The muscle scars on specimens illustrated in the present paper, however, show an adductor field similar to *Cortezorthis* and particularly to *Protocortezorthis* as exemplified by *P. windmillensis*, but unlike adductor patterns developed in any of the known rhipidomellids.

Specimens of *Reeftonia* illustrated in this paper (Pl. 22, figs. 1-9) were selected to show typical *Reeftonia* muscle scar patterns and to demonstrate the assignment of *R. alpha* (Gill) to the genus by close comparison with the type, *R. marwicki*. These illustrations do not show the variation of *Reeftonia* which is known to exist and which has been illustrated by more than 60 figures of specimens of *Reeftonia alpha* by Talent (1963, pls. 24-28). The variation is striking and is particularly pertinent to the thesis of the present paper that *Reeftonia* was derived from *Protocortezorthis*. Several of the specimens illustrated by Talent show particularly strong resemblance to *Protocortezorthis*

fornicatimcurvata while others, and among them those that are reproduced in the present paper as figs. 8 and 9 of Plate 22, show 'typical' *Reeftonia* musculature. A configuration like that of *P. fornicatimcurvata* is particularly well shown by specimens in figs. 14, 15, and 22 of plate 27 of Talent (1963) while the specimen in fig. 25 of the same plate is recognizable as a *Reeftonia* very close to the 'typical' pattern (text-fig. 3B).

The essential difference between *Protocortezorthis* of the *fornicatimcurvata* type and *Reeftonia alpha* is a tendency away from elongation of the ventral muscle scar and pre-



TEXT-FIG. 3. Sketch drawings of some dorsal internal moulds showing style of muscle impressions and bounding ridges and their variation.

sence in some specimens of *Reeftonia alpha* of a nearly obsolescent ventral myophragm. In the brachial valve, specimens of *P. fornicatimcurvata* do not show variation in the dorsal adductor muscle pattern to a *Reeftonia* type. Furthermore, in *P. fornicatimcurvata*, the posterior adductor muscle bounding ridges are smoothly continuous with the bases of the brachiophore supporting plates rather than disjunct as in *R. alpha*. Variation within the cortezorthinid pattern of dorsal cardinalia and muscle impressions is shown in text-fig. 3.

From the discussion of *Protocortezorthis windmillensis*, earlier in this paper, it should be recalled that both points made above that distinguish *Reeftonia* from *Protocortezorthis fornicatimcurvata* (i.e. variability toward a *Reeftonia* dorsal adductor plan with discrete posterior adductor bounding ridges) also distinguish *P. windmillensis* from *P. fornicatimcurvata*.

Species assigned to Reeftonia:

Two species are known, *Reeftonia marwicki* Allan and *Cariniferella alpha* Gill (1949,

p. 95, pl. 3, figs. 1, 6, 7). Gill named a second species *Cariniferella beta* (1949, p. 96, pl. 3, figs. 2, 3, 4, 9), but Talent (1963, p. 58) has shown these to belong to a single species and has published numerous figures illustrating them under the name *Isorthis alpha* (1963, pls. 24–27). Talent (1963, pp. 58–60) erred in reporting fulcral plates in *Reeftonia alpha*. The grooves that cross the antero-lateral edges of the moulds of the sockets shown in Talent's figure 19, page 58 (1963), correspond to the edge of slightly elevated sockets constructed on the floor of the valve, but are not fulcral plates. The same mistake in concept (cf. Boucot, Johnson, and Walmsley 1965, p. 335) led Talent to remark that fulcral plates are shown in Allan's figures of *Reeftonia marwicki*.

Occurrence and Age. *Reeftonia* is known from the Reefton beds of New Zealand (Allan 1947) and from the Dead Bull and Kilgower Members of the Tabberabbera Formation of Victoria, Australia (Talent 1963, table 3). We consider both occurrences to be of Emsian age.

Figured specimens. USNM numbers 147351–5; Geol. Surv. Victoria 50700C, 50700F.

Genus CARINIFERELLA Schuchert and Cooper 1931

Plate 22, figs. 10–21

Type species. *Orthis carinata* Hall 1843, p. 267, text-fig. 121, nos. 1–1A.

Exterior. *Cariniferella* is characterized by reverse convexity in the manner of *Schizophoria*, with the brachial valve more strongly convex than the pedicle valve. However, in small shells the distinction is not great. In large specimens the pedicle valve may be nearly flat. The outline is commonly broadly transverse oval, nearly subquadrate. The pedicle valve bears a well-developed narrow median carina and the brachial valve bears a corresponding narrow sulcus that is commonly deep and well marked. The flatness of the pedicle valve combined with the considerable strength of the dorsal sulcus may combine to make the anterior margin re-entrant medially. The exterior bears a radial ornament of fine costellae that increase in number by bifurcation and by intercalation. The interarea of the pedicle valve is low, narrow, triangular, and catacline or may be slightly incurved at the beak. The delthyrium is broadly triangular and on larger specimens may be rounded rather than angular at its apex. The interarea of the brachial valve is orthocline.

Interior of pedicle valve. The hinge teeth are small, broadly divergent, and triangular in cross-section. They are situated on a thickening of shell material adjoining the palintrope and are not supported by dental lamellae. Because the teeth are so broadly divergent and because there are no dental lamellae the ventral muscle field lies entirely on the floor of the valve and the adjustor scars become well marked on larger specimens. The ventral musculature is short, broad, and cordate. The adductor tracks are commonly well defined medially and may be accompanied by a moderate development of a low rectangular myophragm that divides the diductor lobes anteriorly. The diductor impressions are fairly well marked laterally where they are slightly divergent and anteriorly where they are bounded by ridges that curve all the way around toward the mid-line. In most specimens the anterior margin of the muscle scars is raised a little above the trough corresponding to the external carina.

Interior of brachial valve. The brachiophores are widely divergent and blade-like and are connected directly to the floor of the valve, defining the inner sides of the sockets. The bases of the sockets lie at the floor of the valve and their posterior portions are bounded by the interarea. There is a well-developed notothyrial platform connecting with a stout myophragm that divides the posterior adductor impressions. A small, elongate, trilobed cardinal process is situated at the apex of the notothyrial platform.

In small specimens the muscle scars are only faintly impressed, but in large ones the posterior adductors are broad and subtriangular and may be faintly longitudinally striate. The anterior adductors are smaller and subpyriform so that the whole muscle impression narrows anteriorly. For the most part the musculature is outlined by being impressed into the shell, but short bounding ridges define the anterior adductor scars antero-laterally and the bounding ridges converge toward the mid-line. A faint pair of muscle bounding ridges adjoins the posterior adductor scars laterally. The interior of small specimens is strongly crenulated by the costellae, but in large ones only the area anterior to the muscle impressions shows their impression.

Species assigned to Cariniferella:

Orthis carinata Hall 1843, p. 267.

Orthis tioga Hall 1867, p. 59, pl. 8, figs. 20–29.

Dalmanella elmira Williams 1908, p. 56, pl. 3, figs. 6, 8, 11, 13–17.

Dalmanella virginia Williams 1908, p. 58, pl. 4, figs. 10–16.

Williams (1908, p. 59) erected a variety *beta*, believing it to represent the young of *Dalmanella virginia*. This is probably true and is reason for revocation of *beta* as a separate taxon. The specimens are here included within *Cariniferella virginia*.

Cariniferella iowensis Stainbrook 1945, p. 16, pl. 1, figs. 29–37.

Orthis dumontiana Verneuil 1850, p. 181, pl. 4, figs. 7a, b, c.

Schuchert and Cooper (1932, p. 122, pl. 18, fig. 11) figured a Belgian specimen under the name *Cariniferella dumonti*, evidently a *nomen nullum* for *C. dumontiana*. The figured specimen and a number of others accompanying it in the collection were examined on loan from the Museum of Comparative Zoology, Harvard. They are labelled *Orthis dumonti*, Koninck collection.

Occurrence and age. *Cariniferella* is fairly common in the Appalachians (Hall 1843; Williams 1908; Stainbrook 1942). It is present in the Independence Shale of Iowa (Stainbrook 1945) and in the Sly Gap beds in New Mexico (Stainbrook 1948). It is represented in the south of Belgium by *C. dumontiana* (Schuchert and Cooper 1932) and in Spain (Verneuil 1850; Comte 1938). It is probably present in Kazakhstan, Asiatic U.S.S.R., where it has been reported as *Cariniferella tioga* (Sarycheva 1960, pl. 14, fig. 9). All of these occurrences are of Frasnian age.

Figured specimens. Y.P.M. 24856, 24857; S-1087, 1088; USNM no. 145582.

COMMENTS ON CORTEZORTHINID MORPHOLOGY

Strictly held definitions of brachiopod groups may prove inconsistent because of exceptions, but a summary of observed variability of the characteristic structures can be particularly apt to the definition of a group. The three Silurian to Eifelian genera of the

Cortezorthinae compose a particularly tight-knit group characterized by ventral diductor and dorsal adductor muscle patterns that show considerable stability across generic lines (text-fig. 4), but that are not presently known to the writers to occur outside the subfamily. In the pedicle valve of *Protocortezorthis*, *Cortezorthis*, and *Reeftonia* the diductor impressions are smoothly rounded in transverse section. They narrow anteriorly between thin but well-defined muscle bounding ridges that commonly can be seen to be discrete posteriorly and not continuous with the adjacent dental lamellae (text-fig. 4A, C). Of the three, *Protocortezorthis* differs essentially in the presence of a prominent narrow myophragm. *Cortezorthis* and *Reeftonia* have the diductors relatively a little wider but less deeply impressed, and *Reeftonia* commonly has the ventral adductor scars prominently marked.

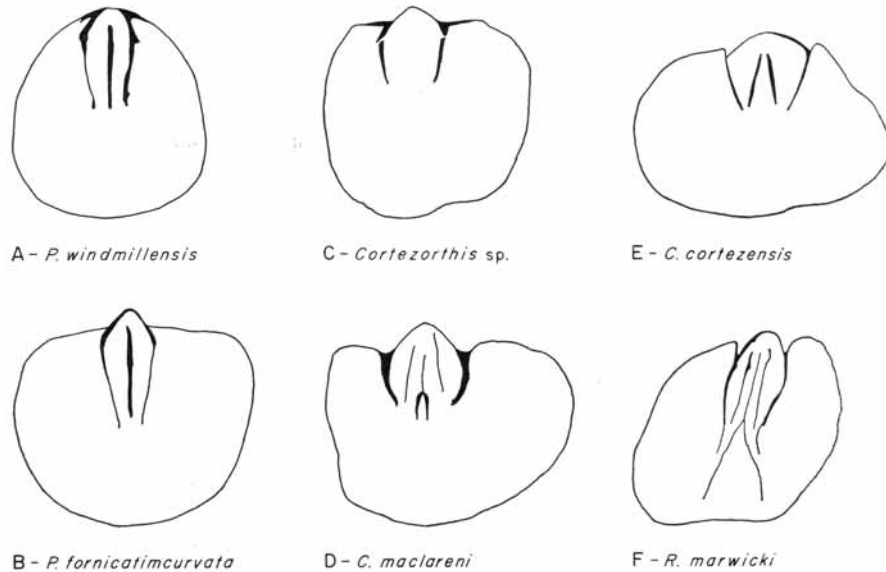
In the brachial valve these genera and *Cariniferella* have blade-like brachiophores that diverge relatively widely, but with a relatively slight ventral inclination. Between them there is a prominent myophragm, commonly rectangular in cross-section, that joins with a well-defined notothyrial platform bearing the cardinal process. In *Protocortezorthis fornicatimcurvata* the sockets are most elevated; brachiophore supporting plates support the brachiophores at the inner edges of the sockets and connect with the floor of the valve. The resultant structure is one that defines the sockets by fulcral plates. In *P. windmillensis* the sockets have similar structure, but the brachiophore supporting plates are absent and the sockets thus somewhat overhang the base of the valve. In the younger genera *Cortezorthis*, *Reeftonia*, and *Cariniferella*, the blade-like brachiophores are strongly divergent and are attached directly to the floor of the valve, defining the sockets between them and the margin of the valve. The dorsal adductor pattern is a rhomboidal one in which the posterior adductors are bounded by ridges that do not continue anteriorly around the anterior adductors. In *Protocortezorthis fornicatimcurvata* these continue from the brachiophore supporting plates, but in *P. windmillensis*, which lacks supporting plates, the bounding ridges are separate structures and this is especially true in the younger genera—*Cortezorthis*, *Reeftonia*, and *Cariniferella*. *Cortezorthis* and *Reeftonia* exhibit variation in the dorsal adductor impressions, varying between only partially differentiated and fully differentiated posterior adductor bounding ridges. It is notable that discrete, fully differentiated bounding ridges occur (apparently rarely) in *Protocortezorthis orbicularis* (Holland, Lawson, and Walmsley 1963, pl. 6, fig. 9), but understandable that they occur in that species rather than in *P. fornicatimcurvata* because the specimens of *P. orbicularis* illustrated by Walmsley (1965, see pl. 63, fig. 9; pl. 64, fig. 11) show weaker development of brachiophore supporting plates than does *P. fornicatimcurvata* (see Pl. 21, figs. 16, 19).

The subfamily Cortezorthinae differs from Isorthinae by its fixed adductors and un-faceted diductors in the pedicle valve and by the development of a distinctive pattern of dorsal adductor impressions unknown in any isorthid.

COMPARISON WITH RHIPIDOMELLIDAE

Two genera, *Reeftonia* and *Cariniferella*, that the writers include in the subfamily Cortezorthinae exhibit features of internal morphology that invite comparison with the Rhipidomellidae. The pedicle valve of *Reeftonia* bears adductor scars like those developed in the subfamily Rhipidomellinae, but since the same type of scar is developed

in *Protocortezorthis* (text-fig. 2) the feature must cross phylogenetic lines. In *Cariniferella* the ventral muscle pattern mimics the heterorthisid rhipidomellid genus *Heterorthis* (Havlíček 1950, text-fig. 10), but the stratigraphic gap is very great and to the writers' knowledge no Devonian rhipidomellid (that might serve as an ancestor) bears a ventral muscle pattern like that of *Cariniferella*.



TEXT-FIG. 4. Sketch drawings of some ventral internal moulds showing style of muscle impressions and bounding ridges and their variation.

The brachial valves of *Reeftonia* and *Cariniferella* bear similar cardinalia with brachio-phores that define sockets without fulcral plates, and absence of fulcral plates is typical of the Rhipidomellidae. However, the evidence from the cortezorthinid lineage *Protocortezorthis*-*Cortezorthis* illustrates that fulcral plates are lost during the evolution of *Protocortezorthis*. The brachio-phore and socket arrangement of *Reeftonia* and *Cariniferella* closely duplicates that developed in *Cortezorthis* (Pl. 19, figs. 22, 23). The brachio-phores and sockets of rhipidomellids, though similar in gross aspect, differ consistently in detail from those of *Reeftonia* and *Cariniferella*. Rhipidomellid brachio-phores typically are more tusk-like or rod-like than plate-like (Boucot, Johnson, and Walmsley 1965, pl. 46, figs. 6, 7) and in most cases bear ridge-like flanges along their length (Hall and Clarke 1892, pl. 6a, fig. 10). Commonly their extremities protrude free (Boucot, Johnson, and Walmsley 1965, pl. 46, figs. 9, 10) although when connected in part to the base of the valve by brachio-phore supporting plates, the two-fold nature of the structure is usually distinguishable. Moreover, it is typical of rhipidomellids that the brachio-phores are closely set medially and crowd against the cardinal process which is

swollen distally (Hall and Clarke 1892, pl. 6a, figs. 3, 7, 10, 15, 16, 21). This is decidedly not the pattern of cardinalia developed in *Reeftonia* or *Cariniferella* or in any other cortezorthinid (cf. pl. 19, figs. 2, 22, 23; pl. 21, figs. 1-5, pl. 22, figs. 1, 3, 10, 12).

The adductor impressions in the brachial valve of rhipidomellids are almost without exception so poorly impressed that the lateral and anterior outline of the adductors is indiscernible on small specimens. Even on large ones, the scars typically are impressed rather than being outlined by muscle bounding ridges. The characteristic rhipidomellid adductor pattern is one in which the posterior adductors are small and triangular with the long sides of the triangles extending from the bases of the brachiophores along the postero-lateral sides of the muscle scars (Hall and Clarke 1892, pl. 6a, figs. 7, 15, 21). The posterior adductors in many forms developed in such cramped quarters that they were reduced even more by thickenings of the brachiophore supports (cf. Boucot, Johnson, and Walmsley 1965, pl. 45, fig. 26). The anterior adductors in rhipidomellids show a little more variation in outline from subrectangular or transversely suboval to trapezoidal, but commonly are larger than the posterior adductors and are very faintly impressed. The adductor muscle pattern described above is not developed in *Reeftonia* or *Cariniferella*. Instead they bear the cortezorthinid pattern (text-fig. 3) with discrete postero-lateral adductor muscle bounding ridges and over-all rhomboidal outline. In addition to specimens of *Reeftonia* and *Cariniferella* illustrated herein (Pl. 22) the reader may refer to a specimen of *Cariniferella* illustrated by Cooper (1944, pl. 138, fig. 36) which compares very closely with *Reeftonia* in all internal features.

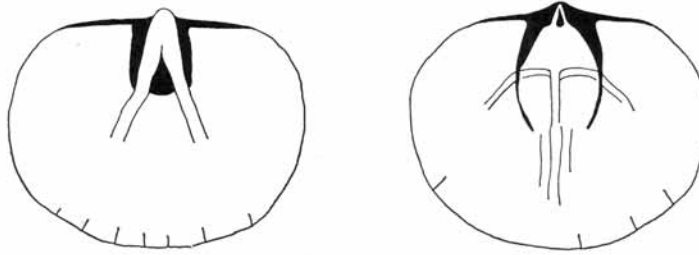
COMPARISON WITH *ISORTHIS*

Since *Protocortezorthis fornicatimcurvata* was assigned to *Isorthis* by Boucot (1960, p. 296) and *Reeftonia alpha* to *Isorthis* by Talent (1963, p. 57) it is appropriate to examine the basis for these assignments in the light of those made in this paper. *Isorthis szajnochai* bears strong, anteriorly divergent dental lamellae in the pedicle valve, bounding relatively strongly impressed, faceted diductor scars which in turn are divided by an anteriorly prominent adductor platform (text-fig. 5). In *Reeftonia*, *Cortezorthis*, and *Protocortezorthis* the dental lamellae appear to be short, but are joined with, or are closely adjacent to, long, thin muscle bounding ridges that converge anteriorly. The diductor impressions are unfaceted and the myophragm is a narrow rounded ridge rather than an anteriorly prominent platform. The muscle bounding ridges of *Protocortezorthis fornicatimcurvata* appear to be continuous with the dental lamellae so it is not surprising that a broad view of *Isorthis* should have included them. Nevertheless, in the light of the present work, the muscle bounding ridges of *Protocortezorthis*, especially *P. windmillensis*, and of *Reeftonia* and *Cortezorthis* appear to be different structures from the dental lamellae of *Isorthis szajnochai*. The elongation of the diductor scars remains as the principal similarity in the pedicle valve between *Isorthis* and the cortezorthinids.

In the brachial valve more similarity is evident since at least one species of *Protocortezorthis*, *P. fornicatimcurvata*, has fairly well-developed fulcral plates and a relatively simple quadripartite adductor muscle field defined by more or less prominent muscle bounding ridges. All of the Lower Devonian cortezorthinids have well-developed myophragms posteriorly that join a more or less prominent notothyrial platform. In *Isorthis szajnochai* this type of myophragm is not developed nor is there a prominent notothyrial

platform (text-fig. 5). Instead, the postero-medial portions of the brachiophore bases of *I. szajnochai* are relatively widely set apart defining a broad, deep, notothyrial cavity.

The morphologic differences in the brachial valve interior appear to be minor but consistent and although some variation between the isorthid pattern and the cortezorthinid pattern will make difficult the interpretation of some isolated specimens, the morphologic features of both valves taken together should be sufficient to avoid future re-combination of most members of the two groups.

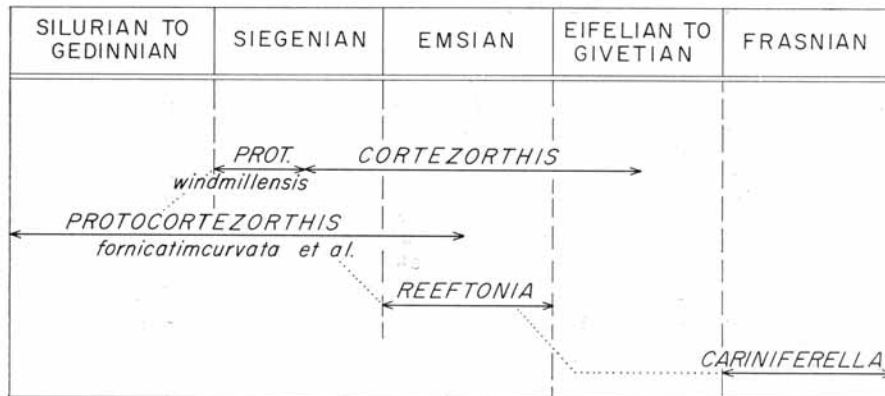


Isorthis szajnochai

TEXT-FIG. 5. Sketch drawings of internal moulds of the type species of *Isorthis*.

ORIGIN OF CORTEZORTHINAE

Three cortezorthinid genera, *Cortezorthis*, *Reeftonia*, and *Cariniferella* are so distinct morphologically that association with any of the previously known dalmanellid groups on



TEXT-FIG. 6. Stratigraphic range and inferred phylogeny of the genera composing the subfamily Cortezorthinae.

the basis of direct morphologic comparison is less than obvious. Nevertheless, demonstration that *Cortezorthis* ancestry includes an intermediate aseptate form exemplified

by *Protocortezorthis windmillensis* and that it in turn was derived from the *P. fornicatim-curvata* group of the Silurian and Gedinian allows some reasonable conclusions to be drawn regarding the origin of the new subfamily. As pointed out earlier, *P. fornicatim-curvata* and its relatives differ from typical *Isorthis* principally by the development of a distinct ventral musculature, but there are so many points of similarity between some early species such as *P. orbicularis* and *P. slitensis* shown by Walmsley that there is little reason to doubt that these early species of *Protocortezorthis* were derived from some Silurian species of *Isorthis* in the strict sense.

Acknowledgements. We are very much indebted to a number of people who have donated or loaned dalmanellid specimens. Dr. A. J. Boucot of the California Institute of Technology made collections of silicified specimens of *C. cortezensis* and of *P. windmillensis*. In addition, access to Boucot's dalmanellid collections, including '*Orthis*' *fornicatimcurvata* and *Reeftonia marwicki* proved invaluable. Dr. G. A. Cooper of the U.S. National Museum loaned specimens of *Cariniferella*. Dr. S. V. Cherkasova, Scientific Research Institute for the Geology of the Arctic, Leningrad, kindly provided the specimen from Novaya Zemlya, and Dr. R. T. Gratsianova, Institute of Geology and Geophysics, Siberian Branch Academy of Sciences, Novosibirsk, loaned specimens of *Dalmanellopsis septiger* from the Altai Mountains. Dr. J. W. Kerr of the Geological Survey of Canada collected *Cortezorthis* specimens from Bathurst Island.

Dr. A. C. Lenz of the University of Western Ontario loaned specimens from the *Monograptus yukonensis* zone of Yukon Territory, Canada. Dr. D. J. McLaren of the Geological Survey of Canada most graciously put at our disposal his collection of excellently preserved specimens from Ellesmere Island which form the basis for the type species of *Cortezorthis*. Dr. Copeland MacClintock of the Peabody Museum of Natural History loaned specimens of *Cariniferella carinata* from the Schuchert collection. Dr. Allen Ormiston of Pan American Petroleum Corporation provided specimens of *Cortezorthis* from Devon Island. Professor H. B. Whittington, Harvard University, loaned specimens of *Cariniferella doumontiana* from the Museum of Comparative Zoology. Johnson's work was done as a part of a project at Pasadena supported by a grant from the National Science Foundation, number GP-3743.

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APPENDIX OF DEFINITIONS

Faceted and Unfaceted. Among the Siluro-Devonian dalmanellids, *Isorthis*, *Levenea*, and some species of *Schizophoria* bear ventral muscle scars in which the various components, particularly the submedian and lateral diductor lobes and the adductor track, lie at prominent angles to one another. In some, the separate elements are flat or nearly flat surfaces (as in many orthoids), but flatness alone is not critical to the term as used here. Unfaceted refers to ventral muscle scars in which the various components lie in the same cross-sectional arc (or pair of arcs if a median ridge-like myophragm is present). The cortezorthinids characteristically are unfaceted and this is particularly well displayed by *Protocortezorthis* and *Reeftonia* (pl. 21, figs. 6, 15; pl. 22, figs. 4, 6, 7, 8).

Fixed Ventral Adductors. This term refers to small cordate impressions developed in some cortezorthinids (text-fig. 2) and typical of Devonian rhipidomellids as distinguished from the track-like ventral adductor site of *Isorthis* (text-fig. 5) and typical of the Dalmanellidae (Williams and Wright 1963, text-figs. 5-7). Similar distinctions can be made in a number of other brachiopod groups.

Peripheral radial septa. Except for incipient development in *Protocortezorthis windmillensis* the structures are known to the writers only in *Cortezorthis* and consist of relatively short, plate-like lobes situated radially around the internal periphery of both valves. The distal ends of the septa terminate slightly inside the valve margin where the marginal crenulations are prominent (Pl. 19, fig. 3). The height of the septa varies up to four or five times as high as thick and they generally appear first and attain greatest height in the mid-regions (Pl. 19, fig. 2).

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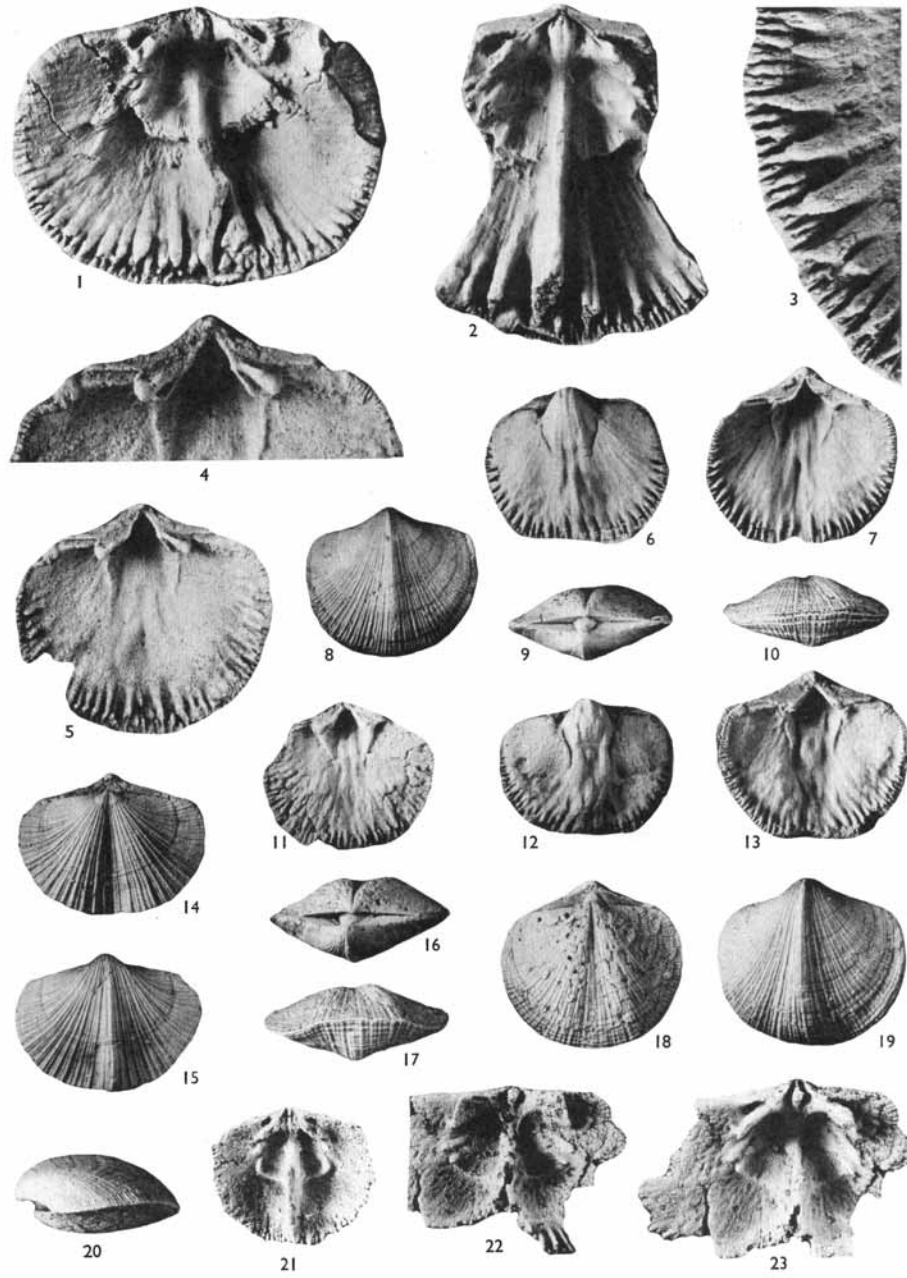
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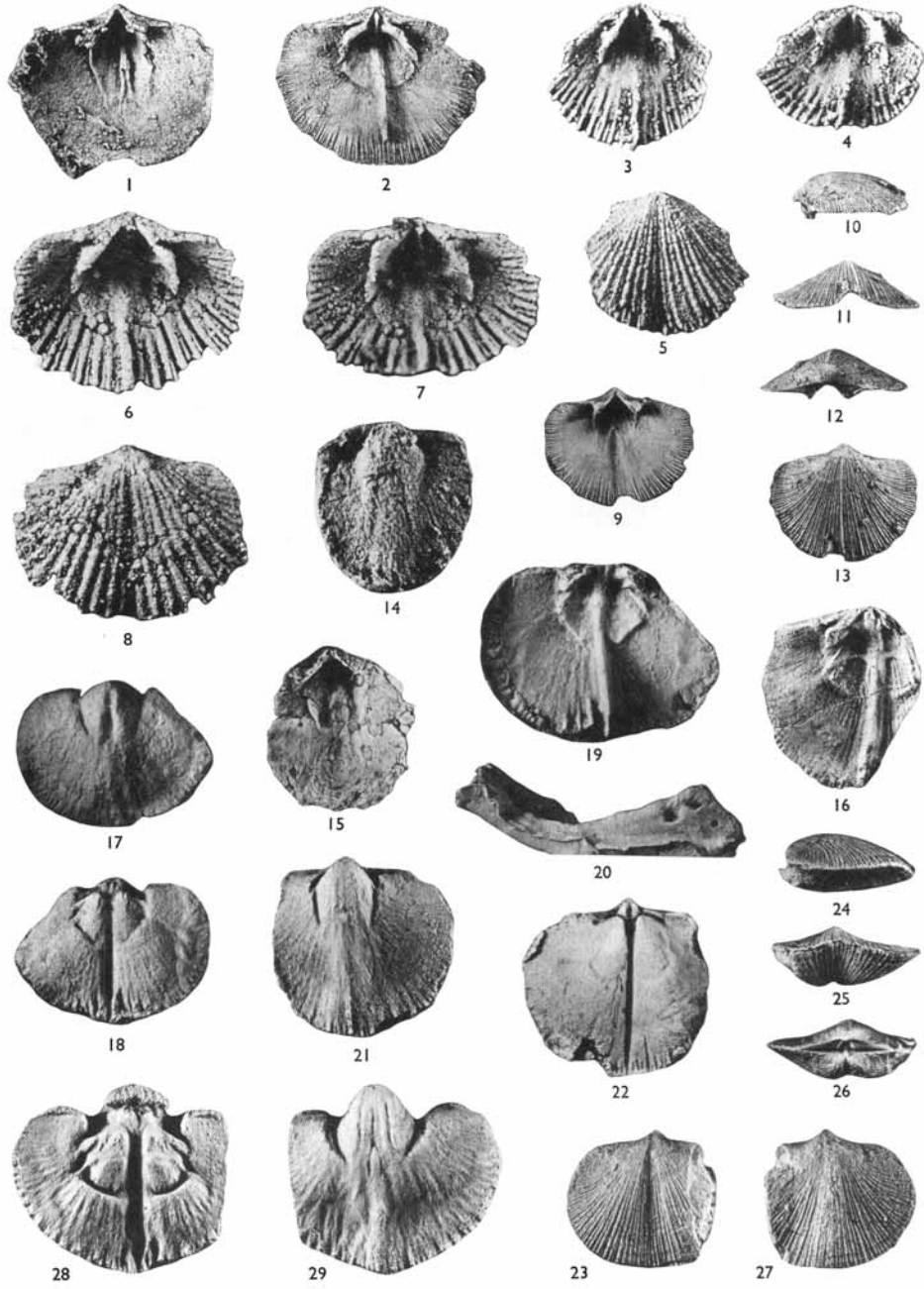
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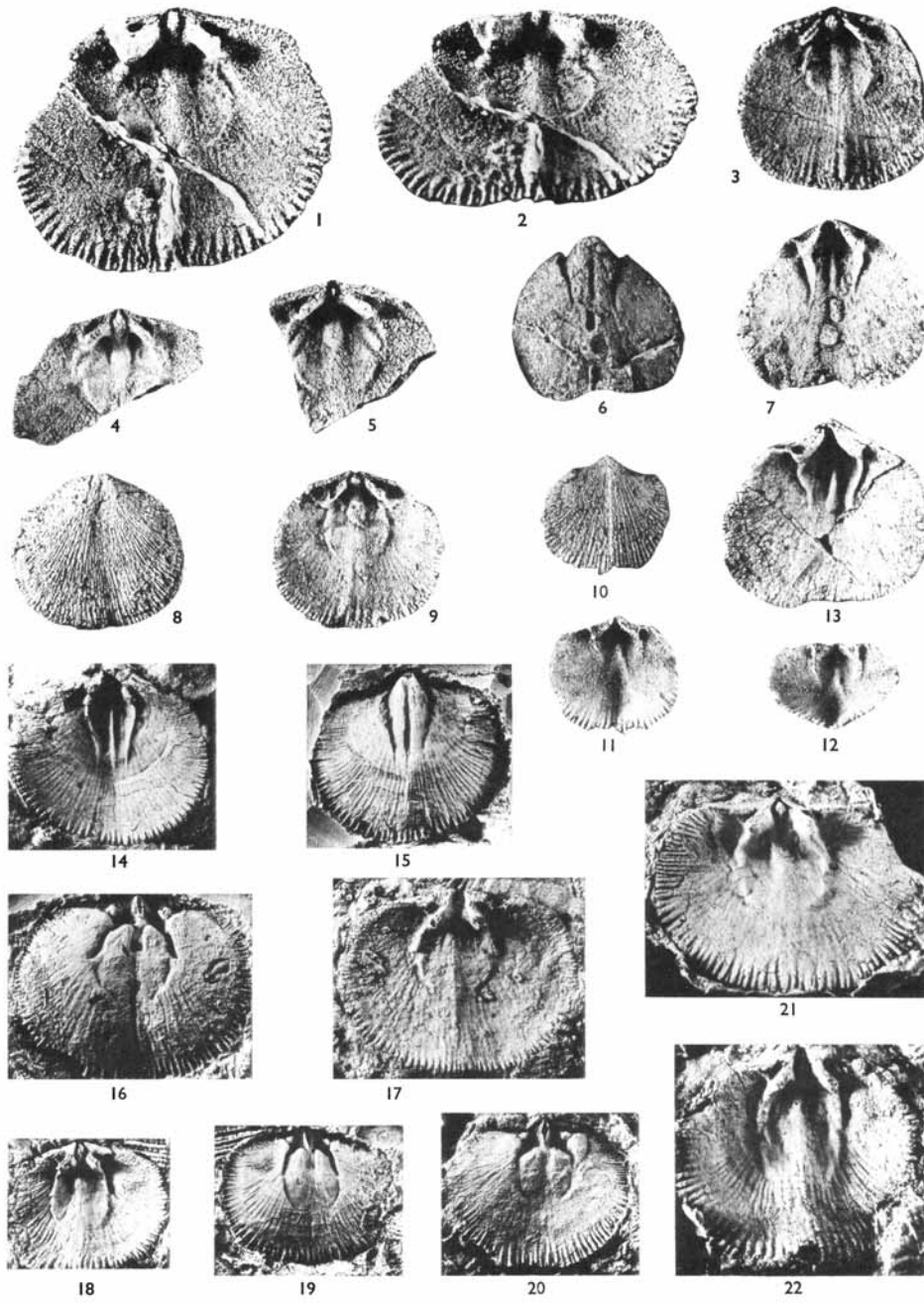
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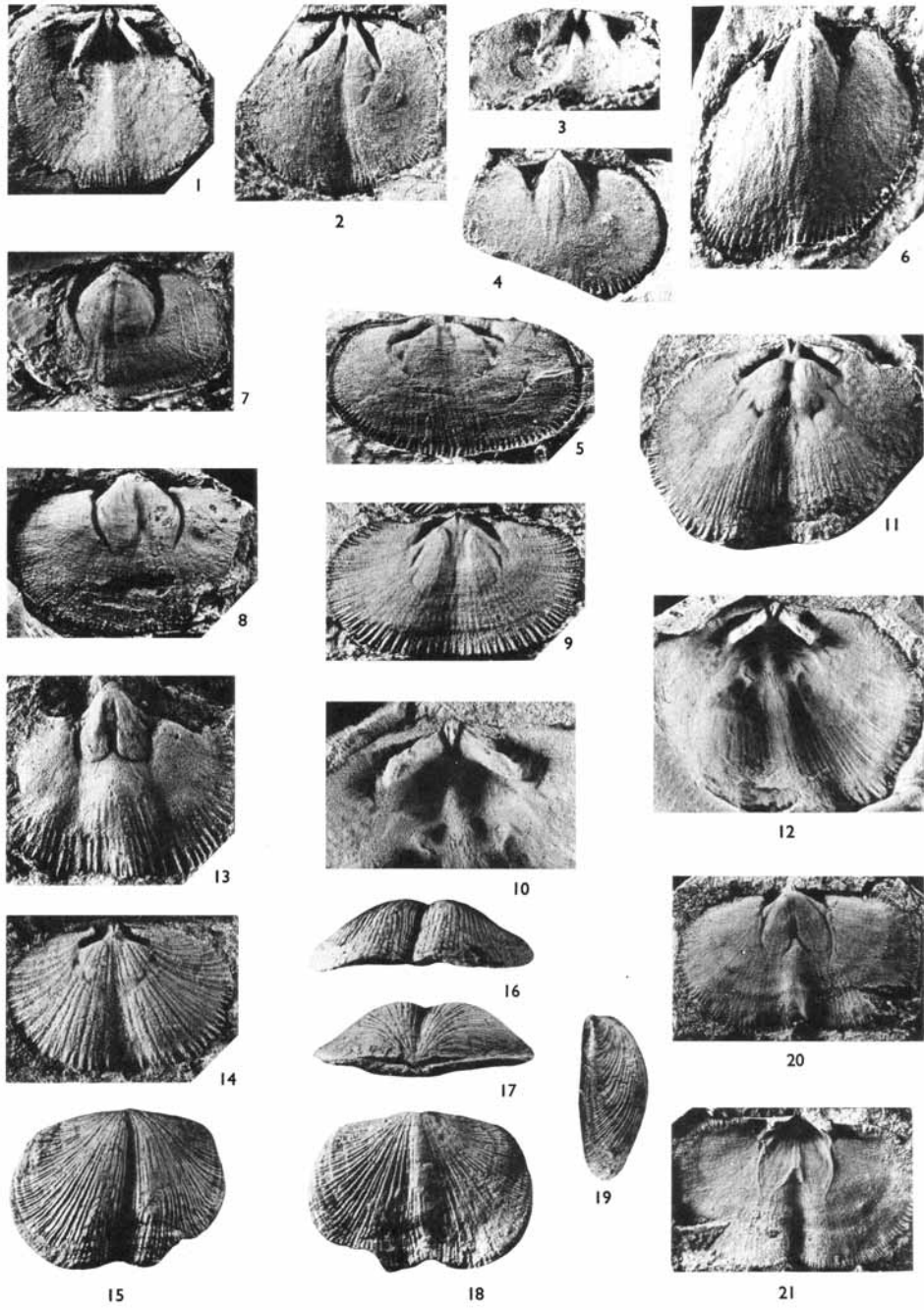
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