THE EOSPIRIFERIDAE

by A. J. BOUCOT

ABSTRACT. The impunctate, spire-bearing family Eospiriferidae contains the subfamilies Eospiriferinae and Cyrtiinae. The Eospiriferinae appear in the Upper Llandovery and persist until the Eifelian; whereas the Cyrtiinae appear in the Upper Llandovery and persist with certainty until the close of the Ludlow, but there is a single specimen from beds of Emsian age in Czechoslovakia. The family is characterized by the possession of radial filar ornamentation externally combined with a spiriferoid form. Internally, the brachial valve is characterized by having long crural plates on either side of a linear, unstriated diductor attachment area. The interior of the pedicle valve is relatively generalized.

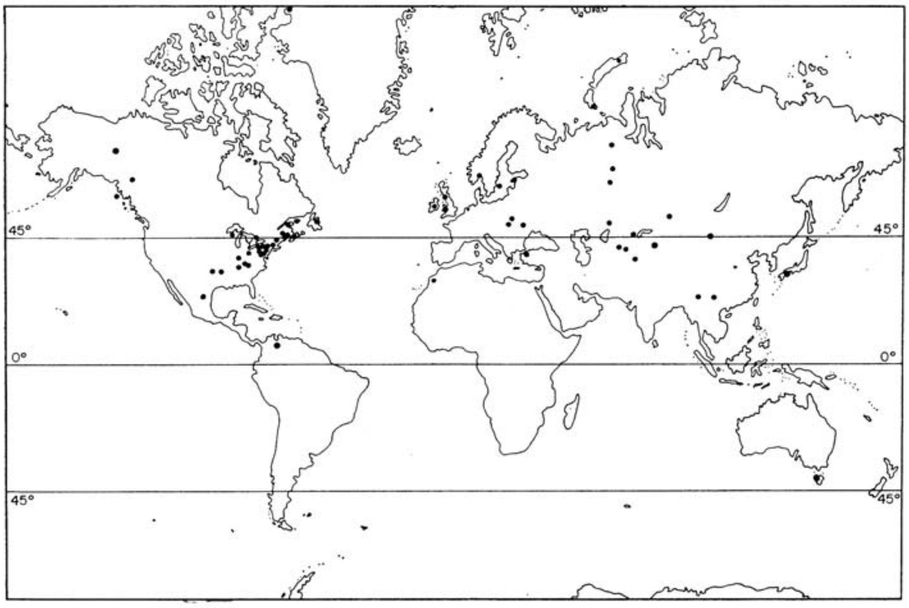
The eospiriferids disappear from the Western Hemisphere at the end of the Gedinnian, but continue on into the Eifelian in part of the Old World. In the Old World, the eospiriferids are absent from the Rhenish facies of the Devonian, as well as the Devonian of South Africa and Antarctica.

The genus *Plicocyrtia* is proposed for laterally plicate cyrtiinids, and the genera *Havlicekia*, *Macropleura*, and *Nikiforovaena* for eospiriferinids with external forms differing substantially from previously described members of the subfamily. The genera *Najadospirifer* and *Pinguispirifer* are rejected from the Eospiriferidae on the basis of differing internal structures and external fine ornamentation.

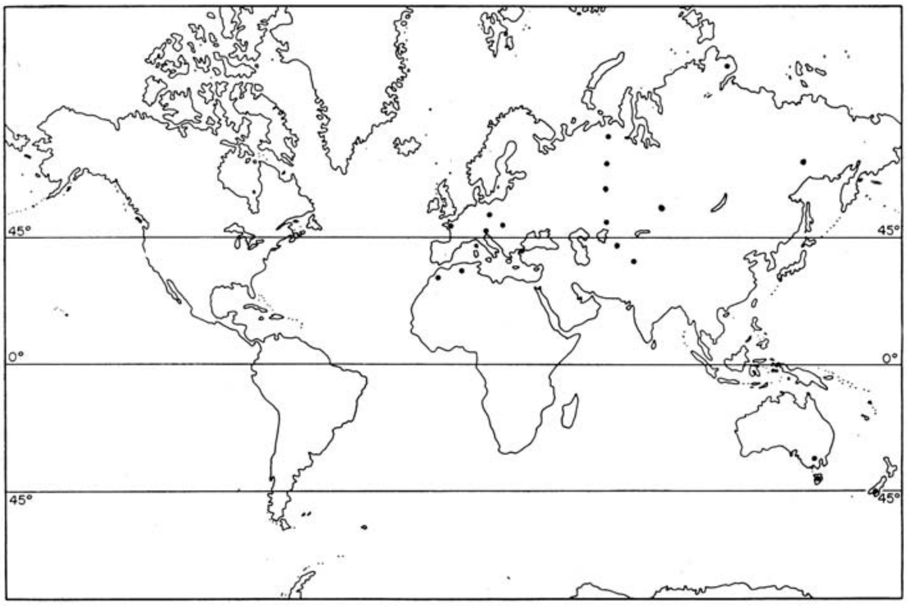
The evolution of plicated eospiriferids from unplicated forms is discussed.

In the course of a study of Silurian and early Devonian spiriferids, it became apparent to the writer that the eospiriferids were morphologically so far removed from any of the subfamilies of the Spiriferidae (King 1846) that they should be assigned to a separate family, the Eospiriferidae. The eospiriferids, world-wide in distribution (text-fig. 1), are of value in subdividing the Silurian. They appear, near the end of Llandoverian time, fully developed on both sides of the North Atlantic. No closely related precursors of the eospiriferids have been reported from strata of Lower or Middle Llandoverian age, but strata of those ages will doubtless eventually produce closely related genera and species. The disappearance of the family was relatively slow in Bohemia, the Carnic Alps, northern France, North Africa, the region of the Bosphorus, central Asia, the Appalachians, and New Zealand, with members of the family in some areas persisting into the Middle Devonian (text-figs. 2, 3), but was relatively rapid in the Malvinokaffric facies of South America and South Africa (text-fig. 1) and in the Rhenish facies of Germany ('*Spirifer*' *solitarius* Krantz possesses neither the internal nor external characteristics of an eospiriferid), Belgium, southern England, Poland, and Nova Scotia, where representatives of the family may be found in the late Silurian but not in the early Devonian. From the first appearance of the family in late Llandoverian time two lineages, here assigned to the subfamilies Eospiriferinae Schuchert and LeVene 1929 (emended) and the Cyrtiinae Fredericks 1924, are distinct and well developed.

The writer acknowledges with pleasure the criticisms of Dr. J. E. Hede, Lund University; Dr. Valdar Jaanusson, Uppsala University; Dr. Jean Berdan and Dr. Charles Merriam, U.S. Geological Survey; and Dr. T. W. Amsden, Oklahoma Geological Survey, each of whom read the manuscript. Photographs of *Nikiforovaena ferganensis* were provided by Dr. O. Nikiforova, Leningrad, and specimens of *Janius insignis* by Dr. Hede. Ing. Jose Carrillo Bravo, Petroleos Mexicanos, Tampico, Tamaulipas, provided the collections from which the Ciudad Victoria eospiriferids were extracted. Dr. M. A. Rzonsnitskaya, Leningrad, made a number of useful comments regarding Soviet stratigraphy and eospiriferids. Prof. D. Nalivkin, Leningrad, arranged for the writer to study the material in the Tscherny-

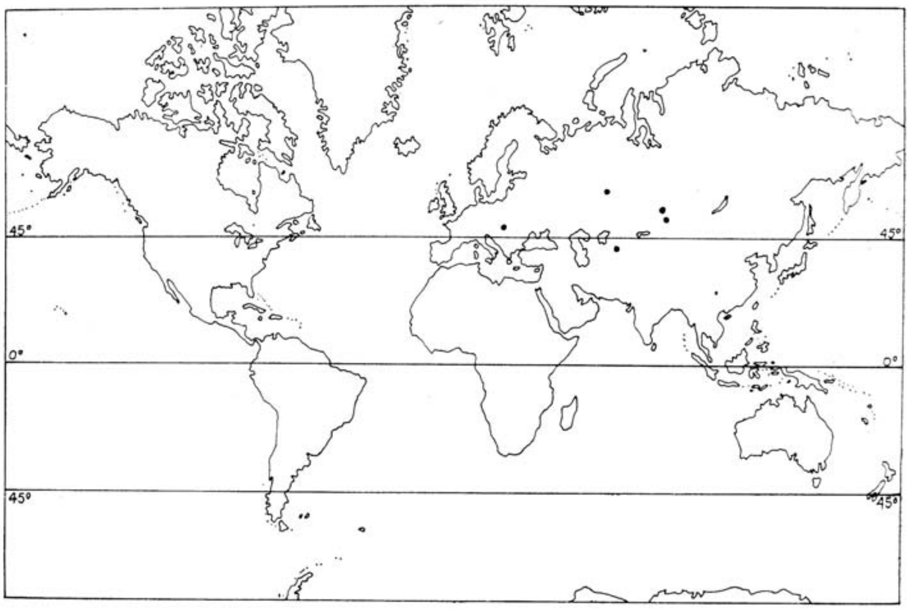


TEXT-FIG. 1. Known distribution of eospiriferids in strata of Llandoverian to Gedinnian age.



TEXT-FIG. 2. Known distribution of eospiriferids in strata of Siegenian to Emsian age.

chev Geological Museum. Dr. V. Havlíček, Prague, discussed the manuscript with the writer and pointed out the peculiar ornamentation of '*Eospirifer*' *secans* and '*E.*' *turjensis*. Dozent Dr. F. Prantl, Prague, made available for the study the rich collections in the National Museum. Mr. Winfried Haas, Bonn, gave the writer an opportunity to collect *Eospirifer* and *Cyrtia* from strata he is studying in the Istanbul region. Dr. Brian Norford, Geological Survey of Canada, Ottawa, provided information on the occurrence of *Cyrtia* in the Silurian of British Columbia. Much of the research for this paper was supported by a National Science Foundation grant to the Massachusetts Institute of Technology (DSR contract 298).



TEXT-FIG. 3. Known distribution of eospiriferids in strata of Eifelian age.

SYSTEMATIC DESCRIPTIONS

Superfamily SPIRIFERACEA King 1846

Family EOSPIRIFERIDAE Schuchert and LeVene 1929 (nom. transl. Boucot, herein, et Eospiriferinae Schuchert and LeVene 1929)

Diagnosis. Impunctate spiriferids with fine ornamentation consisting of fila which bifurate anteriorly and which originate anteriorly by implantation. The fila do not have spinose anterior terminae and are crossed by concentric growth-lines which may or may not be nodose. The delthyrium is either completely or partially closed by discrete deltidial plates which in large specimens become medially conjunct, enclose a foramen, and in many specimens are then overlain by an outer layer which simulates a pseudodeltidium. In the brachial valve long crural plates support the discrete hinge plates. Discrete chilidial plates may be present and in large specimens may be medially conjunct. The area of diductor attachment is unstriated. The ribbon-like crura and primary lamella form an obtuse angle where they join above the short jugal process. In the pedicle valve long dental lamellae are present.

Comparison. The Eospiriferidae may be distinguished from the contemporaneous Delthyrinae and Kozlowskiellininae by the presence of long crural plates in the brachial valve, and by the absence of a striated diductor attachment area in the brachial valve and of external striations terminating anteriorly over the edge of each growth lamella as a fringe of minute spines. The Cyrtinopsidae possess crenulated growth lamellae that are unstriated radially.

Distribution. World-wide in strata of Upper Llandoverian to Eifelian age.

Subfamilies. Eospiriferinae Schuchert and LeVene 1929 (emended) and Cyrtiinae Fredericks 1924.

Subfamily EOSPIRIFERINAE Schuchert and LeVene 1929 (emended)

Diagnosis. Members of the Eospiriferidae having a convex, but not pyramidal, pedicle valve and a triangular, but not narrowly elongate, delthyrium. The deltidial plates are usually narrow, border the delthyrial cavity, and are inserted normal to the interarea. In some specimens the deltidial plates may coalesce to form a pseudodeltidium.

Genera:

Eospirifer Schuchert 1913, *in* Zittel-Eastman, *Textbook of Paleontology*, **1**, 2nd ed., p. 411.
Striispirifer Cooper and Muir-Wood 1951, *J. Washington Acad. Sci.* **41**, 6, p. 195 (= *Schuchertia* Fredericks 1926).
Janius Havlíček 1957*b*, p. 247.
Havlicekia gen. nov.
Macropleura gen. nov.
Nikiforovaena gen. nov.

Genera rejected:

Najadospirifer Havlíček 1957*b*, p. 246. Restudy of topotype material shows that the type species of this genus possesses short crural plates and a striated area for diductor attachment in the brachial valve; the fine ornamentation consists of coarse spinules distributed along growth lamellae in a fashion similar to that of the reticularids.
Pinguispirifer Havlíček 1957*b*, pp. 246–7. Restudy of topotype material shows that the type species of this genus does not possess low, eospiriferid-type crural plates or a smooth, narrow notothyrial chamber for diductor attachment in the brachial valve. The musculature of the pedicle valve is unlike that of the Eospiriferidae. The finely striate ornamentation is not well enough preserved on the specimens studied to suggest the familial affinity of this genus.

Distribution. World-wide in strata of Upper Llandoverian to Eifelian age.

Genus EOSPIRIFER Schuchert 1913

Plate 97, figs. 1–15

Type species. Spirifer lineatus J. de C. Sowerby 1825, *Mineral Conchology*, **5**, p. 151, pl. 493, figs. 1–2.

Diagnosis. Eospiriferinids having unplicated flanks, fold, and sulcus, as well as an elongate hinge line one-half to almost equal the maximum width.

Comparison. Eospirifer lacks the lateral plications present in *Striispirifer*, *Macropleura*, and *Nikiforovaena*, and the anteriorly bifurcating plications on the flanks present in *Janius*. *Havlicekia* has an acuminate form, extremely high fold in the brachial valve, and striispiriferid-type plications in the early growth stages.

Pedicle exterior. Pedicle valve strongly convex, subcircular to laterally ellipsoidal in outline. Lateral margins rounded in forms where the greatest width is anterior of the posterior margin, relatively straight in forms where the greatest width is at the posterior margin. Anterior margin uniplicate. Interarea straight, posteriorly concave, and striated by growth-lines that parallel the hinge-line. Inclination of interarea catacline (for terminology of interarea inclination *see* Schuchert and Cooper 1932, p. 20), but the actual angle is distinctive for each species. The delthyrium encloses an angle of about 60 degrees. Beak straight to strongly incurved. The deltidial structures in small specimens consist of discrete plates bordering the margins of the delthyrium. With increase in size the deltidial plates may coalesce medially to enclose a pedicle foramen, and in larger specimens an outer layer of shell material completely covers the conjunct deltidial plates and foramen, simulating a pseudodeltidium (Beecher and Clarke 1889, pl. 6, figs. 9, 11). When large, the deltidial structures are striated by growth-lines paralleling the hinge-line. Sulcus well developed, gently rounded to subrectangular in cross-section. In some variants the peri-

EXPLANATION OF PLATE 97

Figs. 1–6. *Eospirifer radiatus* (Sowerby, 1825). Mulde marl; Djupviks fiskläge, Eksta, Gotland. U.S.N.M. No. 84363. 1, Anterior view (×1). Note the relatively broad, low fold and sulcus. 2, Side view (×1). Note the incurved interarea of the pedicle valve. 3, Posterior view (×1). 4, Posterior view (×2). Note the narrow deltidial plates bordering the delthyrium and inclined normal to the interarea. 5, Brachial view (×1). Note the finely striate radial ornamentation and the lack of lateral plications. 6, Pedicle view (×1).

Fig. 7. *Eospirifer* cf. *radiatus* (Sowerby, 1825). Chesuncook limestone. U.S.G.S. locality No. 3249-SD, islet about 3 miles south-east from mouth of Quaker Brook, Chesuncook Lake, Piscataquis County, Maine. U.S.N.M. No. 125257. Impression of interior of pedicle valve (×1). Note the relatively long dental lamellae.

Figs. 8–10. *Eospirifer radiatus* (Sowerby, 1825). Chicago formation; Chicago, Illinois. 8, Posterior view of internal impression (×1). Note the long, slender, crural plates and the unstriated area of diductor attachment. U.S.N.M. No. 125255B. 9, Impression of interior of pedicle valve (×1). Note the relatively long dental lamellae. U.S.N.M. No. 125255A. 10, Impression of interior of pedicle valve (×1). Note the long dental lamellae and the variability present between the muscle impressions of this specimen and that illustrated in figs. 7 and 8. U.S.N.M. No. 125255B.

Fig. 11. *Eospirifer radiatus* (Sowerby, 1825). Racine dolomite; Bridgeport, near Chicago, Illinois. Posterior view of impression of interior (×3). Note the relatively long crural plates and the unstriated area of diductor attachment. U.S.N.M. No. 8409.

Fig. 12. *Eospirifer radiatus* (Sowerby, 1825). Racine dolomite; Racine, Wisconsin. Anterior view of cardinalia and dental lamellae (×3). Note the laterally flaring hinge plates supported by long crural plates which enclose the narrow, unstriated area of diductor attachment. U.S.N.M. No. 9762.

Fig. 13. *Eospirifer radiatus* (Sowerby, 1825). Waldron shale; Waldron, Indiana. Calcined preparation (×2) showing short jugal process (outlined in India ink below) directed towards interior of pedicle valve at the junction of the primary lamella of the spire and the crura. Note the change in direction of curvature where the primary lamella and the crura fuse. M.C.Z. No. 9425B.

Figs. 14, 15. *Eospirifer radiatus* (Sowerby, 1825). Racine dolomite; Wisconsin. 14, Dolomitized interior showing spire, jugal process, and crura (×2). Note the short jugal process and the obtuse angle included by the crura and the primary lamella. M.C.Z. No. 9426. 15, Dolomitized interior showing spire, jugal process, and crura (×2). Note the short jugal process. M.C.Z. No. 9426.

phery and anterior margin tend to become plicated in larger specimens, but normally no lateral plications or plications in the sulcus are present. Fine ornamentation consists of radial fila intersected, in well-preserved specimens, by concentric growth-lines. The intersections tend to be nodose. Strong growth-lines uncommon, but if present are few in number.

Brachial exterior. Valve gently convex, subrounded to laterally elongate in outline. A low fold with a gently rounded to subrectangular cross-section is present. Interarea orthocline to gently apsacline, very short in comparison with that of the pedicle valve.

Pedicle interior. Delthyrium bordered by two strong dental plates that extend about one-third the length of the shell and support stubby hinge teeth. Almost no secondary material is deposited around the plates except for a small amount in the apex of the valve and the extremities of the umbonal cavities. The dental lamellae diverge from the mid-line at an angle of about 20 to 30 degrees. The muscle field, very poorly impressed except for a low myophragm, extends about one-third of the distance to the anterior margin. Myophragm laterally bounded by anteriorly expanding diductor impressions which are longitudinally striate and posteriorly enclose the small, elliptical adductor impressions. Anterior and lateral periphery of valve smooth.

Brachial interior. The cardinalia consist of discrete hinge-plates supported medially by long crural plates. Area of diductor attachment smooth. A low myophragm about one-third the length of the valve bisects the feebly impressed muscle field. Anterior and lateral margins smooth. The dental sockets are closed postero-laterally and flare antero-laterally. The ribbon-like crura make an oblique angle with the primary lamellae. A short jugal process is directed toward the pedicle valve near the junction of the crura and the primary lamellae. St. Joseph (1935, pp. 322–3; pl. xv, fig. 10, text-fig. 3) reports a band connecting the jugal processes medially, but the writer found no evidence of one.

Species:

Eospirifer consobrinus Poulsen 1943, pp. 52–54, pl. 6, fig. 104.
Spirifer contortus Barrande 1879, pl. 107, fig. ii.
Spirifer davousti de Verneuil 1850, *Bull. Soc. Geol. France*, 2nd ser., **7**, p. 781 (probably the same as *togatoides*).
Spirifer devonicans Barrande 1879, pl. 4, fig. 19.
Eospirifer eastoni Gill 1949, pp. 98–99, pl. 3, figs. 20, 21, 23.
Eospirifer fusus Borisyak 1955, p. 72, pl. 12, fig. 10.
Spirifer grandis Hedstrom 1923, pp. 10–11, pl. 2, figs. 5–9.
Spirifer (Eospirifer) ignobilis Khodalevitch 1939, p. 109 (English), p. 66 (Russian), pl. 27, fig. 3.
Spirifer insidiosus Barrande 1879, pl. 72, fig. iii.
Spirifer lineatus J. de C. Sowerby 1825, *Mineral Conchology*, **5**, p. 151, pl. 493, figs. 1–2.
Spirifer marklini de Verneuil 1848, *Bull. Soc. Geol. France*, 2nd ser., 5, p. 344.
Eospirifer parahentius Gill 1950, pp. 247–8, pl. 1, figs. 1–6.
Spirifer plicatellus var. *globosus* Salter 1848, *Mem. Geol. Surv.* **11**, i, p. 382.
Eospirifer praesecans Havlíček 1959, pp. 52–53, pl. 9, figs. 1–4, 6.
Spirifer (Eospirifer) pseudoindifferens Nalivkin 1930, pp. 111–12, pl. viii, fig. 7.
Eospirifer quinqueplicatus Poulsen 1934, pp. 18–19, pl. 2, figs. 17–19.
Spirifer radiatus-obsoletus Foerste 1909*b*, p. 14, pl. 2, fig. 10.
Eospirifer subradiatus Wang 1956, pp. 577–8, pl. vii, c, figs. 1–2.
Spirifer subsinuatus A. Romer 1855, *Beitr.* **3**, p. 3, pl. 2, fig. 5.

Spirifer tenuistriatus Shaler 1869, *Bull. Mus. Comp. Zool.* **1**, 4, p. 70.
Spirifer togatoides Paeckelmann 1925, pp. 128–9, pl. 6, fig. 1*a–e*.
Spirifer togatus Barrande 1848, *Haid. Naturw. Abh.* **ii**, pp. 167–8, pl. 15, fig. 2.
Eospirifer tuvaensis Chernychev 1937, pp. 79–80, pl. v, figs. 18–21.

Distribution. The distribution lists have been prepared to give complete geographic and stratigraphic coverage of the world; however, space does not permit including every reference from the literature for any given area. The following abbreviations are used: Sil. (Silurian), Dev. (Devonian), Lland. (Llandovery), Wen. (Wenlock), Lud. (Ludlow), Skal. (Skalian), Ged. (Gedinnian), Sieg. (Siegenian), Ems. (Emsian), Cobl. (Coblenzian), Eif. (Eifelian).

In North America, widely distributed in strata of Upper Llandoverian to Ludlovian age:

Northern Newfoundland: *E. radiatus*, Pike Arm fm., U. Lland. (C_6) to Wen. (Shrock and Twenhofel 1938, p. 262).

Northern Greenland: *E. radiatus*, *E. consobrinus*, *E. quinqueplicatus*, U. Lland. (C_3 or younger) (Poulsen 1934, pp. 18–19; 1943, pp. 52–54).

South-western Ontario: *Eospirifer sp.*, De Cew fm., Wen. (Bolton 1957, p. 141). *E. radiatus*, 'Irondequoit' fm., Rochester fm., Ancaster chert of Goat Island member of Lockport fm., Wen.; Wiarton member of Amabel fm., Guelph fm., Lud. (ibid., tables 7, 8, 10, 11, 12).

Gaspé: *E. radiatus*, La Vieille fm., Wen., and West Point fm., Lud. (Northrop 1939, p. 190).

Anticosti Island: *E. radiatus*, Jupiter fm., U. Lland. (C_3 to C_6), and Chicotte fm., Wen. (Twenhofel 1928, p. 219).

Coastal New Brunswick: *Eospirifer sp.*, Long Reach fm. and Mascarene series, U. Lland. (C_6) to Wen. (identified by writer).

Coastal Maine: *E. radiatus*, Eastport region, U. Lland., and Ames Knob fm., U. Lland. (C_5) to Wen. (Beecher and Dodge 1892, p. 417).

Northern Maine: *E.* cf. *radiatus*, Limestone Hill (Somerset Co.) and Chesuncook ls. (Piscataquis Co.), Wen. (identified by writer). *E. radiatus*, Aroostook Co., Wen. (Twenhofel 1941, p. 172; list probably also includes collections from a Lud. horizon).

Yukon: *E. radiatus*, unnamed beds, U. Lland. (C_3 or younger) to Lud. (Kindle in Cairnes 1914, p. 73).

New Hampshire: *E.* cf. *radiatus*, upper quartzite of Clough fm., U. Lland. (C_4 to C_6) (Boucot and Thompson 1958, pp. 362–3).

Massachusetts: *E.* cf. *radiatus*, quartzite of Bernardston fm., U. Lland. (C_3 or younger) to Lud. (Boucot, MacDonald, Milton, and Thompson 1958, pp. 860–1).

New York: *E. radiatus*, U. Lland. (Irondequoit ls. [C_5 to C_6], Williamson sh., [C_5 to C_6], Wolcott ls. [C_3 or younger], Reynales ls. [C_3 or younger]), to Wen. (Rochester sh., Herkimer ss.) (Gillette 1947, p. 20). Unknown in Lud. strata in New York.

Pennsylvania: *E. radiatus*, Clinton sh., U. Lland. (C_3 or younger) to Wen. (Lesley 1890, p. 1028).

Maryland: *E. radiatus*, Rose Hill fm., U. Lland. (C_3 or younger), to Rochester fm., Wen. (Prouty and Swartz 1923, pp. 452–3).

Indiana: *E. radiatus*, Waldron sh., Wen. (Hall and Clarke 1893, pl. 21, figs. 11–13, 26); Osgood fm., U. Lland. (C_6) (Tillman 1961); Louisville ls., Wen. (Nettleroth 1889), pl. 29, figs. 13–16).

Wisconsin: *E. radiatus*, Racine dolomite, Wen. (Hall and Clarke 1893, pl. 21, figs. 14–18).

Oklahoma: *Eospirifer sp.*, Clarita member of Chimneyhill fm., U. Lland. (C_4) to Wen. (Amsden 1957, p. 23).

Arkansas: *Eospirifer sp.*, St. Clair fm., U. Lland. (C_3 or younger) to Lud. (Amsden 1957, p. 23; Thomas 1926, p. 390–3).

Kentucky: *E. radiatus*, West Union bed, U. Lland. (C_3 or younger) (Foerste 1909*b*, pp. 14–15).

Ohio: *E. radiatus*, Massie Clay, Wen. (Foerste 1935, p. 153).

Tennessee: *E. foggi*, Lobelville fm., Wen.; 'Lego ls.', U. Lland. (C_3 or younger) to Wen. (Foerste 1935, pp. 172, 178, 197).

State of Tamaulipas, Mexico: *Eospirifer sp.*; vicinity of Ciudad Victoria (J. Carrillo, collections Ca 1689B, Ca 1684), U. Lland. (C_3 or younger) to Lud.

In Europe widely distributed in strata of Upper Llandoverian to Emsian age:

Norway: *E. marklini*, Oslo region, L. Lland. (6c) (Kiaer 1908, p. 589). If it could be confirmed, this would be the earliest known eospiriferid occurrence, but after examining three specimens that presumably formed most of Kiaer's material, this earliest reported occurrence appears dubious. One specimen, labelled '*Spirifer sp.*' (Pal. Mus. Oslo No. 52361), is the pedicle valve of a *Stricklandia*. The second, labelled '*Spirifer marklini*' (Pal. Mus. Oslo, uncatalogued), is indeed *Eospirifer marklini*, but an old note with the specimen suggests that it came from Gotland rather than from Oslo. The third, labelled '*Spirifer marklini*' (Pal. Mus. Oslo, uncatalogued), is also *Eospirifer marklini*, but again the locality is in serious doubt. Dr. Gunnar Henningsmoen, curator of the Palaeontological Museum in Oslo, writes (1961) regarding the two specimens of *E. marklini*: 'As to the two other specimens, it is correct to say that their horizon is unknown, and their localities uncertain. They are thus no proof of a Lower Llandoverian occurrence of *Eospirifer marklini*.'

Gotland: *E. marklini*, *E. globosus*, L. Visby marl, U. Lland., to Slite group, Wen. (Hede 1921, p. 94). *E. radiatus*, U. Visby marl, U. Lland.; Hogklint ls., Slite group, Halla ls., Mulde marl, Wen. (Hede 1927*a*, p. 53; 1927*b*, p. 51; 1936, p. 41; 1940, p. 66).

Podolia: *E. radiatus*, Kitaygorod fm., U. Lland., and Borshchov fm., L. Ged. (Nikiforova 1954, p. 135). *E. togatus*, schistes marneaux a Strophomenides, Wen., to Schiste d'Onut, Ged. (Vascautanu 1931, p. 504, 532).

Carnic Alps: *E. togatus*, Capolago, Ems. (Gortani 1915, pp. 130–2).

Czechoslovakia: *E. togatus*, Tachlowitz, e2, Wen. or Lud.; Konieprus, f2, and Mnienian, f2, L. Ems. (Barrande 1879, pl. 5, figs. 10–16). *E. praesecans*, L. Lud. and Wen. (Havlíček 1959, p. 53). *E. contortus*, Lud. (ibid., p. 56). *E. togatus insidiosus*, Koneprusy ls., L. Ems. (ibid., p. 43). *E. devonicans*, Kopanina beds, Lud. (ibid., p. 57).

Harz Mts.: *E. togatus*, Kalk des Joachimskopfes, Ems. (Kayser 1878, p. 161). *E. togatus* var. *subsinuata*, Kalk des Schneckenberges und Badeholzes bei Magdesprung, Ems. (ibid., p. 162).

Great Britain: *E. radiatus*, widely distributed in U. Lland, to early Lud.

Urals: *E. ignobilis*, U. Marginalis beds, Ged. (Khodalevitch 1939, p. 109). *E.* cf. *radiatus*, Striatus beds, Lud. (ibid., pp. 67–68).

Brittany: *E. davousti*, calcaire d'Erbray, Ems. (Barrois 1888, p. 145).

Outside of Europe scattered occurrences in strata of Silurian to Middle Devonian age (unrecognized in South Africa and South America; its absence in South America is probably due to the almost total lack of information concerning shelly Silurian strata in that continent):

Altai Mts.: *E. pseudotogatus* Khalfin 1948, *Pseudotogatus* horizon, concluded to be Sieg. (Khalfin 1948, p. 220).

Kuznetsk Basin: *E. secans*, Baskukan beds, M. Dev. (Eif. or U. Ems.) (Rzonsnitskaya 1952, p. 35).

Burma: *E.* cf. *radiatus*, Namhsim ss., Sil. (Reed 1906, pp. 108–9).

New Zealand: *E. togatus*, Baton River beds, probable Ems. (Shirley 1938, pp. 476–9).

Asia Minor: *E. togatoides*, Pendik Schichten (Bosphorus region), Ems. (Paeckelmann 1925, pp. 128–9).

North Africa: *E. togatus*, Gisement du Kilometre 30 (Algeria), Sieg. (LeMaitre 1952, pp. 117–18). *E.* cf. *togatus*, French Morocco, L. Dev. (Termier 1936, p. 1144). *E. radiatus*, Morocco, Sil. (Gigout 1951, p. 45).

Turkestan: *E. togatus*, Marginalis beds, Lud. (Nikiforova 1937*b*, p. 49). *E. davousti* and *E. pseudoindifferens*, highest Eif. (Nalivkin 1930, pp. 110–11).

Kazahkstan: *E. radiatus* and *E. fusus*, U. Lland. (Borisyak 1955*b*, pp. 70–72).

China: *E. subradiatus*, Sil. (Wang 1956, pp. 577–8).

Australia: *E. eastoni*, beds at Sandy's Creek (Victoria), early Dev. (Gill 1949, pp. 98–99).

Tasmania: *E. parahentius*, Bell Shale, Early Dev. (Gill 1950, pp. 247–8).

Turkey: *Eospirifer*, Chamosite horizon near Cumakoy (NW. of Aquiran) in Istanbul region, U. Lland.

Tuva: *E. tuvaensis*, Sil. (Chernychev 1937, pp. 79–80; pl. v; figs. 18–21).

T'ien-Shan: *Eospirifer sp.*, locality 14 of Arpishmebulag Series, Sil. and early Dev. (identified from photographs kindly provided by Prof. G. Regnell, Lund).

Genus MACROPLEURA gen. nov.

Plate 98, figs. 1–8; plate 99, figs. 1–9; plate 100, figs. 1–5

Type species. Delthyris macropleurus Conrad 1840, *4th Ann. Rpt. New York Geol. Surv.*, p. 207.

Diagnosis. Transversely elongate to elliptical eospiriferinids possessing a broad, flat fold and a limited number (usually three to six) of lateral plications on each flank, separated by broad, rounded interspaces.

Comparison. Macropleura differs from *Striispirifer* and *Nikiforovaena* in that the latter two, although having a relatively broad fold, also have a large number of lateral plications which are not separated from each other by broad interspaces. *Eospirifer* has flanks that are either smooth or faintly plicated anteriorly, never approaching the folded state attained by *Macropleura*. *Macropleura* lacks the anteriorly bifurcating plications which characterize *Janius*. *Havlicekia* has smooth flanks in large specimens, in contrast to the plicate condition of *Macropleura*.

Exterior. Shells subequally biconvex (the brachial valve having a slightly greater degree of convexity), transversely elongate, and elliptical in outline. Maximum width extends from the straight hinge-line to about the midlength. Lateral margin relatively straight in posterior part, evenly curved in anterior part. Anterior margin evenly curved laterally, but straight medially. The brachial valve bears a broad fold with circular to rectangular cross-section. The fold rises from the descending anterior portion of the valve at an angle of about 20 degrees and first becomes prominent near the umbo. The pedicle valve has a corresponding sulcus. Lateral to the fold are three to four rounded costae on each flank, separated by broad, rounded interspaces of about the same width as the costae. Interarea of pedicle valve catacline to steeply apsacline, very long, concave posteriorly. Interarea of brachial valve orthocline, very short. Lateral margins of interarea striated by ornamentation identical with that on the body of the valve. Beak of pedicle valve suberect. Deltidial plates are usually not preserved, and the delthyrium, which encloses an angle of about 60 degrees, is left open. However, in well-preserved specimens a pair of narrow deltidial plates, normal to the interarea, line the sides of the delthyrium and are either apically conjunct or almost so. No specimens have been observed in which the delthyrium was completely covered. The observed specimens correspond to stages 1 and 2 of Beecher and Clarke (1889, p. 79, fig. 4), and no specimens have been observed that

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Figs. 1–5. *Macropleura macropleura* (Conrad, 1840). New Scotland formation; Helderbergs, New York, M.C.Z. No. 9259. 1, Brachial view (×1). Note the fine striations. 2, Anterior view (×1). Note the broad, rounded fold and sulcus, and the weakly crenulated anterior commissure. 3, Posterior view (×1). Note the rounded lateral plications separated by broad, rounded interspaces. 4, Pedicle view (×1). Note the relatively broad sulcus and the broad interspaces between the plications. 5, Side view (×1). Note the incurved, relatively short interarea of the pedicle valve.

Figs. 6–8. *Macropleura macropleura* (Conrad, 1840). New Scotland formation; North American Cement Quarry, Alsen, New York. U.S.N.M. No. 137738, Zimm Collection, Acc. No. 167820. 6, Anterior view (×1). Note the relatively rectangular cross-section of the fold and the crenulated anterior commissure. 7, Pedicle view (×1). Note the crenulated anterior and lateral margins. 8, Side view (×1).

approximate their stages 3, 4, and 5. The fine ornamentation consists of radiating fila which originate both by bifurcation and implantation and are crossed by concentric growth lamellae. A few of the concentric growth lamellae are very pronounced and frill-like, but the majority are mere lines whose intersections with the radial fine ornamentation may become nodose in well-preserved specimens. Anterior commissure uniplicate and strongly crenulate. Anterior portion of pedicle valve projects up as a tongue to meet the fold of the brachial valve.

Pedicle interior. Relatively small, pointed hinge teeth occur on the inner margin of the hinge line, where they are supported by plate-like dental lamellae which diverge from the midline at an angle of about 20 to 30 degrees. Dental lamellae convex medially, thickened in large specimens by the deposition of secondary material in the umbonal cavities and the delthyrial cavity. Muscle field triangular in outline, extending anteriorly about one-third of the distance to the anterior margin, bisected by low, rounded myophragm. On either side of myophragm are elongate, anteriorly expanding, longitudinally striate diductor impressions, which posteriorly surround the small, elliptical adductor impressions. In some specimens a thick pad of secondary material floors the rear of the delthyrial cavity and may have been the site of the pedicle callist. The sides of the upper portion of the delthyrial cavity are striated and bear a series of indentations that parallel the sides of the delthyrium and probably served to help seat the deltidial plates. The interior of the valve is strongly plicated by the impression of the external ornamentation.

Brachial interior. The cardinalia consist of a narrow chamber that occupies the position of the cardinal process and is laterally flanked by discrete, inclined hinge-plates tilted basomedially. The hinge plates are supported basally by long crural plates. The floor of the dental sockets is relatively flat. A low myophragm extends from the notothyrial cavity to about midlength. The adductor field is not noticeably impressed.

Species:

Spirifer (Eospirifer) admirabilis Nikiforova 1937*b pars.* p. 49, pl. 10, figs. 1, 2, 4, *non* fig. 3.
Spirifer altaicus Tschernychev 1893, pp. 25–26, pl. 4, figs. 5–6.
Eospirifer balchaaschensis Nikiforova 1937*a*, pp. 26–27, pl. ii, figs. 6–7.
Eospirifer? bascuscanicus Rzonsnitskaya 1952, p. 43, pl. i, fig. 12 (inspection of the holotype shows the presence of eospiriferid-type fine ornamentation).
Spirifer perlamellosus J. Hall var. *densilineata* Chapman 1908, pp. 223–4, pls. iv–v.
Spirifer eudora Hall 1861, *Ann. Rpt. Wisconsin Geol. Surv.*, pp. 25–26.
Spirifer geronticus Foerste 1909*a*, p. 92, pl. 2, fig. 30.
Spirifer gibbosus Hall 1861 *non* Barrande 1879, *Ann. Rpt. Wisconsin Geol. Surv.*, p. 25.
Delthyris macropleura Conrad 1840, *4th Ann. Rpt. New York Geol. Surv.*, p. 207.
Spirifer macropleuroides Clarke 1907, *Bull. 107, New York State Mus.*, p. 259.
Spirifer niagarensis oligoptychus Roemer 1860, p. 68, pl. 5, fig. 8.
Spirifer pollens Barrande 1848, *Haid. Naturw. Abh.* **2**, pp. 182–3, pl. 17, fig. 6.
Spirifer rollandi Barrois 1886, pp. 182–4, pl. v, fig. 1.
Spirifer sibiricus Tschernychev 1893, pp. 24–25, pl. 4, fig. 4.
Spirifer sinuosus Hedstrom 1923, pp. 12, 13, pl. 4, figs. 1–9.
Spirifera striolata Lindstrom 1861, *Ofversigt Kongl. Vetenskapsakad., Forh.*, Arg. 17 (1860), **8**, p. 259, pl. 12, fig. 2.
Spirifer telephus Barrande 1879, pl. 73.
Spirifer uralaltaicus Gruenewaldt 1854, *Mem. savants etrang.* **7**, pp. 32–34, pl. 6, fig. 20*a–f*.
Spirifer vetulus Eichwald 1840, Lethaea Rossica, pp. 719–20, pl. 35, fig. 1.

Distribution. In North America widely distributed in strata of Wenlockian to Gedinnian age:

South-east Alaska: A form resembling *Macropleura* (erroneously compared with *J. irbitensis*), Lud. (Kirk and Amsden 1951, p. 63; pl. 10, fig. 6).

South-western Ontario: *M. eudora*, Lockport dolomite, Wen. (Williams 1919, p. 67). *M. eudora*, Wiarton, Eramosa, and Colpoy Bay members of Amabel fm., Guelph fm., Lud. (Bolton 1957, p. 58, 102; tables 11, 12). *M.* cf. *eudora*, Fossil Hill fm., U. Lland. (C_5) to Wen. (ibid., table 9).

Northern Maine: *M. macropleuroides*, Chapman sandstone (Aroostook Co.), Ged. (Clarke 1909, pp. 119–20). *M. macropleura*, Somerset Co., Ged. (Boucot, in preparation), and Aroostook Co. (Square Lake ls.), Ged. (Billings 1869, pl. 1, fig. 16).

New York: *M. macropleura*, New Scotland fm. (Helderbergs and Green Pond outlier), Ged.

Maryland and West Virginia: *M. eudora*, Rose Hill fm., U. Lland. (C_3 or younger), to Rochester fm., Wen. (Prouty and Swartz 1923, pp. 453–4). *M. macropleura*, New Scotland member, Ged. (Schuchert 1913, p. 396).

Western Tennessee: *M. macropleura*, Birdsong fm., Ged. (Dunbar 1919, p. 53). *M. niagarensis oligoptychus*, Brownsport fm., Wen. (Roemer 1860, p. 68).

Virginia: *M. macropleura*, New Scotland ls., Ged. (Butts 1940, pp. 265, 278).

New Jersey: *M. macropleura*, Coeymans ls., Ged. (Weller 1903, pp. 288, 313).

Ohio: *M. eudora*, West Union bed, U. Lland. (C_3 or younger) (Foerste 1909*b*, p. 16).

Wisconsin: *M. eudora*, Racine dolomite, Wen. (Hall and Clarke 1893, pl. 21, figs. 19–20).

Indiana: *M. eudora*, Waldron shale (Hall and Clarke 1893, pl. 21, figs. 21, 29); and Osgood fm., U. Lland. (C_5 to C_6) (Tillman 1961).

Pennsylvania: *M. eudora*, 'Niagara fm.', Sil., and *M. macropleura*, New Scotland equivalents—'Stormville shales' and 'Stormville ls.', Ged. (Lesley 1990, pp. 1010, 1016).

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Figs. 1, 2. *Macropleura macropleura* (Conrad, 1840). New Scotland formation; North American Cement Quarry, Alsen, New York. U.S.N.M. No. 137738, Zimm. Collection, Acc. No. 167820. 1, Brachial view (×1). Note the fine striations and the beaded effect due to the intersection of fine, concentric growth-lines and radial striae. 2, Posterior view (×1). Note the relatively long interarea of the pedicle valve.

Figs. 3, 4. *Macropleura macropleura* (Conrad, 1840). New Scotland formation; Clarksville, Albany County, New York. M.C.Z. No. 9427. 3, Impression of interior of pedicle valve (×1·5). Note the impression of the broad, rounded lateral plications. 4, Impression of the interior (posterior view ×1·5). Note the presence of narrow crural plates.

Fig. 5. *Macropleura macropleura* (Conrad, 1840). Birdsong shale; just south of Camden, Tennessee. U.S.N.M. No. 137729. Interior of pedicle valve (×1). Note the stout dental lamellae, the secondary material deposited in the umbonal cavities, and the pitting of the floor of the valve in the umbonal region.

Fig. 6. *Macropleura eudora* (Hall, 1861). Waldron shale; Locality 521a, Quarry on south side of U.S. 70, 2 miles east of Pegram Station, Tennessee. U.S.N.M. No. 137730. Posterior view (×3). Note the narrow deltidial plates bordering the delthyrium and inserted normal to the interarea. The fine, beaded ornamentation is formed from the intersection of fine concentric growth lamellae and radial striae.

Figs. 7, 8. *Macropleura macropleura* (Conrad, 1840). New Scotland formation; locality 526, U.S. 40, east bank of Licking Creek, 2½ miles west of Indian Springs, Maryland. U.S.N.M. No. 126051. 7, Interior of brachial valve (×2). Note the relatively long, slender crural plates supporting the discrete hinge-plates, and the laterally directed dental sockets. 8, Interior of brachial valve (×2). Note the unstriated area of diductor attachment.

Fig. 9. *Macropleura macropleura* (Conrad, 1840). Shale of New Scotland age; Cornwall, Orange County, New York. U.S.N.M. No. 17164. Impression of interior of pedicle valve (×1). Note the massive dental lamellae.

In Europe known from strata of Upper Llandoverian to Emsian age:

Czechoslovakia: *M. telephus*, Collines entre Luzetz et Lodenitz (e2), Wen. (Barrande 1879, pl. 4, fig. 6). *M. pollens*, same locality, Wen. (ibid., pl. 1, fig. 16). Havlíček (1959, p. 52) cites this locality as of Lower Ludlow (Kopanina) age.
Gotland: *M. striolata*, Eke marl and Hamra ls. Lud. or possibly Ged. (Hede 1921, p. 94). *M. sinuosa*, Slite group, Wen. (ibid., 1927*b*, p. 51; 1928, p. 63; 1933, p. 57; 1936, p. 41; 1940, p. 66).
Urals: *M. exsul* (without anteriorly bifurcating ribs like *J. exsul* of Barrande). Striatus beds, Lud. (Khodalevitch 1939, p. 68, pl. 27, fig. 6).
France: *M. thetidis* Le Maitre *non* Barrande, Calcaire de Chaudefonds, Ems. (LeMaitre 1934, p. 73). *M. rollandi*, same ls. (Barrois 1886, p. 182–4).

Outside of Europe and eastern North America recognized only in Asia and Australia:

Mongolia: Chernychev (1937, p. 79, pl. v, figs. 22–23) illustrates Silurian material ('*Eospirifer* aff. *radiatus*') that belongs to *Macropleura*.
Altai Mts.: *M. sibiricus*, light grey ls. of Krjukowski Grube, and *M. altaicus*, reddish ls. of same place, Eif., together with '*Goniatites*' *lateseptatus* Beyrich (Tschernychev 1893, pp. 24–26).
Kuznetsk Basin: *M. sibiricus*, Chumishsk beds, Eif.; *M. bascuscanicus*, Pesterevo beds, Cobl.; *M.* cf. *rollandi*, Salairkin beds, Eif. (Rzonsnitskaya 1952, pp. 41–43).
Turkestan and western Balkhash Land: *M. balchaaschensis*, Marginalis beds, Ged. (Nikiforova 1937*b*, pp. 48–49). *M. admirabilis* Nikiforova 1937 *pars* (pl. 10, figs. 1, 2, 4, *non* 3), Manak beds, Ged.
Kazakhstan: *E. radiatus* Borisyak *non* Sowerby, Wen. (Borisyak 1955*a*, pp. 54–55, pl. 8, figs. 1–6). Borisyak (1960, p. 270) emends the age to Lud.
Kolyma River headwaters: *M. vetulus*, Taskwan River, Sil. (Nalivkin 1936, p. 23, pl. ii, fig. 6). Rzonsnitskaya (1960, oral communication) states that this locality is U. Ems. or L. Eif.
Australia: *M. densilineata*, Sil. or L. Dev. (Chapman 1908, pp. 223–4).

Genus HAVLICEKIA gen. nov.

Plate 103, figs. 12–17

Type species. Spirifer secans Barrande 1848, *Haid. Naturw. Abh.* **II**, pp. 168–9, pl. xvi, fig. 6.

Name. The genus is named in recognition of the major contributions of Dr. Vladimir Havlíček, to knowledge of Lower Palaeozoic brachiopods.

Diagnosis. Eospiriferinids with striispiriferid-type plications in the early growth stages, smooth flanks during the later growth stages, and an acuminate form during the later growth stages, together with a very high tongue at the anterior margin of the pedicle valve which produces a very extended, uniplicate anterior margin.

Comparison. Havlicekia lacks, in the later growth stages, the lateral plications present in *Striispirifer*, *Macropleura*, and *Nikiforovaena*. The acuminate form and abnormally shaped, uniplicate anterior margin are unique among the eospiriferinids.

Pedicle exterior. Valve strongly convex, laterally ellipsoidal in outline, maximum width slightly anterior of posterior margin. Interarea catacline, straight, posteriorly concave. The delthyrium encloses an angle of about 60 degrees. The beak may be relatively straight or strongly incurved. The deltidial structures have not yet been distinguished, but are presumably similar to those present in other members of the subfamily. In the early growth stages (up to about 1–1½ cm. long) the shell bears striispiriferid-type lateral plications on the flanks, but these plications disappear beyond this early stage. The fine ornamentation consists of radial fila. Lateral margins rounded; anterior margin uniplicate and abnormally high in large specimens as a result of the acuminate form of the large shells compared with the non-acuminate form of the early growth stages. The anterior portion of the valve projects up as a long tongue.

Brachial exterior. Valve gently convex in early growth stages, strongly convex (about equal to that of pedicle valve) in large specimens. Interarea orthocline to gently apsacline, very short as compared with that of pedicle valve, and strongly incurved over that of pedicle valve. In large specimens the fold is very high anteriorly with vertical sides and U-shaped cross-section. The tremendous change in form accompanying the development of an anterior tongue in the pedicle valve and the steep-sided fold in the brachial valve is well documented by Havlíček (1959, fig. 7).

Pedicle interior. Two strong dental plates, about one-third the length of the shell, border the delthyrium and support the stubby hinge teeth. Almost no secondary material is deposited around the plates except for a small amount in the apex of the valve and the extremities of the umbonal cavities. The dental lamellae diverge from the midline at an angle of about 20 to 30 degrees. The muscle field extends about one-third of the distance to the anterior margin and is very poorly impressed except for a low myophragm. The myophragm is laterally bounded by anteriorly expanding diductor impressions which are longitudinally striate and posteriorly enclose the small, elliptical adductor impressions. Anterior and lateral periphery of valve smooth, umbonal regions crenulated by impress of external plications.

EXPLANATION OF PLATE 100

Figs. 1–5. *Macropleura eudora* (Hall, 1861). Waldron shale; Dupont, Indiana. U.S.N.M. No. 88008. 1, Side view (×1). Note the incurved beak of the pedicle valve. 2, Pedicle view (×1). Note the broad sulcus. 3, Posterior view (×1). Note the relatively short interarea of the pedicle valve. 4, Brachial view (×1). Note the broad, rounded interspaces between the lateral plications. 5, Anterior view (×1). Note the crenulated anterior commissure.

Fig. 6. *Striispirifer niagarensis* (Conrad, 1842). Clinton shale; Lockport, New York. U.S.N.M. No. 126048. Impression of interior of brachial valve (×1). Note the relatively long crural plates and the unstriated area of diductor attachment.

Fig. 7. *Striispirifer niagarensis* (Conrad, 1842). Racine dolomite; Wauwatosa Wisconsin. U.S.N.M. No. 137731. Impression of interior (posterior view, ×2). Note the long, slender crural plates and the unstriated area of diductor attachment.

Fig. 8. *Striispirifer plicatella* (Linnaeus, 1767). Wenlock limestone; Dudley, England. U.S.N.M. No. 99946. Posterior view (×3). Note the narrow deltidial plates bordering the delthyrial cavity and inserted normal to the interarea.

Figs. 9–13. *Striispirifer niagarensis* (Conrad, 1842). Clinton group; Lockport, New York. U.S.N.M. No. 3900. 9, Side view (×2). Note the slightly incurved beak of the pedicle valve. 10, Posterior view (×2). 11, Anterior view (×2). Note the rounded cross-section of the fold and sulcus, and the crenulated anterior commissure. 12, Brachial view (×2). Note the narrow interspaces between the lateral plications. 13, Pedicle view (×2). Note the broad sulcus and the narrow interspaces between the lateral plications.

Fig. 14. *Striispirifer plicatella* (Linnaeus, 1767). Mulde marl; Djupviks fiskläge, Eksta, Gotland. M.C.Z. No. 2803. Preparation of spire (×2). Note the short jugal process, and the obtuse angle included between the crura and the primary lamella.

Fig. 15. *Striispirifer plicatella* (Linnaeus, 1767). Strata of Silurian age; Gotland. M.C.Z. No. 2075. Preparation of spire (×2). Note the short jugal process, and the obtuse angle included between the crura and the primary lamella.

Brachial interior. The cardinalia consist of discrete hinge-plates supported medially by long crural plates. Dental sockets closed postero-laterally, flared antero-laterally. Area of diductor attachment smooth. A low myophragm about one-third the length of the valve bisects the feebly impressed muscle field. Anterior and lateral margins smooth, umbonal regions crenulated by impress of external plications.

Species:

Spirifer secans Barrande 1848, op. cit.
Spirifer (Eospirifer) secans var. *rarus* Khodalevitch 1951, p. 97, pl. 30, fig. 2.
Spirifer turjensis Tschernychev 1893, *Mem. Com. Geol.* **4,** 3, pp. 170–1.

Distribution. Widely distributed in the Old World; but only a single specimen known in the New World:

Czechoslovakia: *H. secans,* Koneprusy ls., L. Ems. (Havlíček 1959, p. 41). *H. turjensis,* Pridoli ls., Skal. (ibid., p. 49).
Carnic Alps: *H. secans,* Capolago, Ems. (Gortani 1915, pp. 130–2).
Kuznetsk Basin: *H. secans,* Baskuskan beds, U. Ems. or Eif. (Rzonsnitskaya 1952, p. 35).
New Zealand: *H. secans,* Baton River beds, probably Ged. (Shirley 1938, pp. 476–9).
North Africa: *H. secans,* L'Erg Djemel (Algeria), Ems. (LeMaitre 1952 , pp. 117–18).
Urals: *H. turjensis,* Wen. (Khodalevitch 1939, pp. 65–66). *H. secans* var. *rarus* Cobl. (ibid. 1951, p. 97). *H. turjensis,* L. Dev. (ibid. 1937, p. 67).
Germany: *H. secans,* Erbsloch graywacke L. Ems. (Assmann 1910, p. 152 pl. 8 fig. 13).
Indiana: *H.* cf. *secans,* Huntingdon dolomite Lud. (identified by writer in collections of Indiana University from 'N. Bluff 1/2 mi. E. of Georgetown').

Genus STRIISPIRIFER Cooper and Muir-Wood 1951

Plage 100, figs. 6–15

Type species. Delthyris niagarensis Conrad 1842, *J. Acad. Nat. Sci. Philadelphia,* **8,** p. 261.

Diagnosis. Eospiriferinids having an unplicated fold and sulcus laterally bordered by numerous costae separated from each other by narrow, V-shaped interspaces.

Comparison. Striispirifer lacks the anteriorly bifurcating costae of *Janius,* the broad U-shaped interspaces of *Macropleura,* the unplicated flanks of *Eospirifer,* and the plicate fold and sulcus of *Nikiforovaena.*

Exterior. Shells impunctate, subcircular to laterally elongate, with a spiriferiform shape. The pedicle valve is about two to three times as deep as the gently convex brachial valve. Hinge-line straight, almost equal in length to the maximum length, which is situated about one-third of the distance to the anterior margin. Lateral extremities evenly rounded to alate, anterior margin evenly rounded, crenulate, and plicate. Interarea of pedicle valve apsacline and concave posteriorly, interarea of brachial valve anacline. Interarea of pedicle valve about three to four times the length of that of the brachial valve. The interareas bear growth-lines paralleling the hinge-line. The delthyrium includes an angle of about 60 degrees and may be bordered by discrete deltidial plates, medially conjunct deltidial plates which include a pedicle foramen, or a pseudodeltidium-like structure formed by the deposition of secondary material as illustrated by Hall and Clarke (1893, p. 21, fig. 4; pl. 37, fig. 1) and Beecher and Clarke (1889, pl. 6, fig. 8). Coarse ornamention consists of radial costae separated from each other by narrow, V-shaped interspaces. Large shells carry up to fifteen costae on each side of the fold, which is about five times as wide as the first lateral costa, low, and unplicated, with circular to subrectangular cross-section. Fine ornamentation consists of radial fila intersected by fine growth lamellae.

Pedicle interior. Dental lamellae well developed, blade-like, and unthickened by secondary material except in the apices of the umbonal and delthyrial cavities. The short, stubby hinge teeth, situated on the inner side of the hinge-line, are supported by the dental lamellae. A low myophragm bisects the muscle field, which extends laterally about one-third of the length of the valve. Periphery and most of the interior crenulated by the impress of the costae. Musculature similar to that of *Macropleura* and *Eospirifer*.

Brachial interior. Similar to that of the other eospiriferinids except where the impress of the costae reflects the outer character of the shell. Relatively long crural plates support discrete hinge-plates. Area of diductor attachment smooth. A low myophragm bisects the muscle field. The crura make an obtuse angle with the primary lamellae. The short jugal process descends toward the pedicle valve near the junction of the crura and primary lamella.

Species:

Spirifer foggi Nettleroth 1889, p. 117, pl. 32, figs. 28–31.
Spirifer interlineatus Sowerby 1839, *Sil. Syst.*, pl. 12, fig. 6.
Delthyris niagarensis Conrad 1842, *J. Acad. Nat. Sci. Philadelphia*, **8**, p. 261.
Anomia plicatella Linnaeus 1767, *Syst. Nat.*, 12th ed., p. 1154.
Spirifer repertus Foerste 1909*b*, p. 16, pl. 1, fig. 14*a–b*; pl. 2, fig. 5.
Eospirifer stonehousensis McLearn 1924, pp. 84–85, pl. 9, fig. 8.
Spirifer (Eospirifer) subviator Khodalevitch 1951, p. 99, pl. 29, figs. 1–2.
Spirifer tenuis Barrande 1879, pl. 138, fig. ix.
Spirifer viator Barrande 1848, *Haid. Naturw. Abh.*, **2**, p. 181, pl. 15, fig. 3.

Species to be investigated:

Delthyris cyrtaena Dalman 1828, *K. Vetensk. Handl.*, *1827*, p. 120, pl. 3, fig. 3.

Distribution. In eastern North America widely distributed in strata of Upper Llandoverian to Ludlovian age:

Nova Scotia: *S. stonehousensis*, French River fm., Pictou Co. Maehl, 1961, (p. 52), U. Lland. (C_3 or younger). *S. stonehousensis* is also listed by McLearn (1924, p. 84) from a boulder that he believed came from the Stonehouse fm., of L. Ged. (*Podolella* and *Proschizophoria* occur in the top of the fm. near Pictou at one of Maehl's localities) and possible Lud. age, but the writer concludes that McLearn's boulder came from the French River fm.

Gaspé: *Striispirifer* cf. *niagarensis*, St. Leon fm., early Lud. (Alcock 1935, p. 50). If the material is correctly identified, it represents the only member of the genus thus far recognized in Gaspé.

South-western Ontario: *S. niagarensis*, 'Irondequoit' dolomite member and Rochester shale fm., Wen.; Lockport dolomite, Wen. (Williams 1919, pp. 51, 55, 67). *S. niagarensis*, 'Reynales' fm., 'Irondequoit' fm., Rochester fm., Ancaster chert of Goat Island member of Lockport fm., Lockport fm., Wen.; Wiarton member of Amabel fm., Wen. and Lud. (Bolton 1957, pp. 27, 31, 48, 85, 94, 109, 126, 130, 137, 139, tables 7, 8, 10, 11).

New York: *S. niagarensis*, Irondequoit ls., U. Lland. (C_5 to C_6), to Rochester shale and Herkimer ss., Wen. (Gillette 1947, p. 20).

Maryland: *S. niagarensis*, Rochester fm., Wen. (Prouty and Swartz 1923, p. 455).

Ohio: *S. niagarensis* and *S. plicatellus*, Dayton ls. U. Lland. (C_5 or younger) (Foerste 1935, p. 151).

Kentucky: *S. foggi*, Niagara group, Lud. (Nettleroth 1889, pp. 117–19).
Indiana: *S. foggi*, Liston Creek reef, Lud. (Cummings 1930, p. 209). *S. niagarensis*, Osgood fm. and Laurel ls., U. Lland. (C_5 to C_6) (Tillman 1961).
Pennsylvania: *S. niagarensis*, 'Clinton fossil ore', Sil. (Lesley 1890, p. 1024).

In Europe widely distributed in strata of Silurian and Devonian age:

Podolia: *S. interlineatus*, Kitaygorod fm., U. Lland (Nikiforova 1954, p. 136).
England: *S. interlineatus*, Wenlock shale and ls., Wen., and Aymestry ls., Lud. (Davidson 1871, pl. 9, figs. 9–12).
Czechoslovakia: *S. viator*, Collines entre Luzetz et Lodenitz (e2), Dlauha Hora (e2̣), Wohrada (e2), Listice (e2), Rochers de Kozel (e2); Wen. or Lud. (Barrande 1879, pl. 7, figs. 4–11; pl. 73, fig. iii, 1–8; pl. 138, fig. 9). *S. tenuis*, Liten to Lochkov beds, Wen. to Ged. (Havlíček 1959, p. 60).
Gotland: *S. interlineatus* (Hedstrom *non* Sowerby), Slite group, Wen. (Hede 1927*b*, p. 51; 1933, p. 57; 1936, p. 41; 1940, p. 65). *S.* cf. *interlineatus* (Sowerby) Hemse group, L. Lud. (ibid. 1927*a*, p. 53).
Norway: *S. plicatella*, Oslo region, U. Lland. (7c) and Wen. (8a, b, c) (Kiaer 1908, p. 589).
Estonia: *S.* cf. *interlineatus* Hedstrom, Jaagarahu-Kalkstein, Wen. (Luha 1930, p. 9).
Urals: *Spirifer* (*Eospirifer*) *subviator*, L. Dev. to Eif. (Khodalevitch 1951, p. 99).

Genus NIKIFOROVAENA gen. nov.

Plate 103, figs. 1–6

Type species. *Spirifer* (*Eospirifer*) *ferganensis* Nikiforova 1937*b*, p. 48 (Russian text); pp. 80–81 (English text); pl. 10, figs. 5*a–d*, 6*a–b*.

Name. The genus is named in recognition of Dr. Olga Nikiforova's major contributions to knowledge of Lower Palaeozoic brachiopods.

Diagnosis. Transversely elongate to elliptical eospiriferids with flanks ornamented by gently rounded costae separated by U-shaped interspaces, and with one or more prominent median grooves on the fold and corresponding plication or plications in the sulcus.

Comparison. *Nikiforovaena* has the lateral costae of *Macropleura*, with the addition of a groove or grooves on the fold and corresponding plication or plications in the sulcus. No other eospiriferid has this type of lateral costae combined with a grooved fold and a plicated sulcus.

Exterior. Shells elliptical in outline, laterally elongate, unequally biconvex, the pedicle valve being about one and a half times as deep as the brachial valve. Hinge-line straight, equal to maximum width. Lateral and anterior margins evenly rounded. Anterior commissure uniplicate and crenulate. Interarea striated by growth-lines paralleling hinge-line. Interarea of pedicle valve apsacline, posteriorly concave, about three to four times as long as that of brachial valve. Interarea of brachial valve anacline. Coarse ornamentation consists of costae with rounded cross-sections, separated by U-shaped interspaces on the flanks, a deep median groove or grooves on the fold, and a sharp median plication or plications in the sulcus. The tongue of the sulcus is serrated terminally by the junction of the median plication and the groove. Each flank bears about four to eight plications. Fine ornamentation consists of radial striae crossed by fine concentric growth-lines to give a reticulate effect. Delthyrium open, includes an angle of about 60 degrees. Narrow delthyrial plates may be present.

Pedicle interior. The interior of the pedicle valve has two prominent dental lamellae.

Brachial interior. No information available.

Species:

Spirifer (*Eospirifer*) *admirabilis* Nikiforova 1937*b*, p. 49 (Russian text), pl. 10, fig. 3, *non* figs. 1, 2, 4.
Spiriter bowningensis Mitchell 1921, pp. 545–6, pl. 21, figs. 21–22.
Spirifer (*Eospirifer*) *ferganensis* Nikiforova 1937*b*, p. 48 (Russian text); pp. 80–81 (English text); pl. 10, figs. 5*a–d*, 6*a–b*.
Spirifer lynxoides Nalivkin 1926, *Sketch of Turkestan Geology*, p. 34 (first figured by Nikiforova 1937*b*, p. 80, pl. 10, figs. 7*a–c*, 8–11).
Spirifer (*Eospirifer*) *tingi* Grabau 1926, pp. 37–43, pl. 2, figs. 16–21.

Distribution:

Australia: *N. bowningensis*, Lower and Middle Trilobite beds, Wen. or Lud. (Mitchell 1921, p. 546).
Japan: *N. tingi*, Stage G_2 of the Gion–Yama Series (Kuma-Kii), Wen. or Lud. (Hamada 1961, p. 29).
China: *N. tingi*, Miaokao group (eastern Yunnan), Lud. (Grabau 1926, pp. 18–19).
Turkestan: *N. ferganensis* and *N. lynxoides*, Marginalis and Isfara beds, Lud. (Nikiforova 1937*b*, p. 48, 50, 80). *N. admirabilis*, Ged. (ibid., p. 49, pl. 10, fig. 3, *non* figs. 1, 2, 4).

Genus JANIUS Havlíček 1957

Plate 101, figs. 1–13; plate 103, figs. 7–11; plate 104, figs. 9–14

Type species. *Spirifer nobilis* Barrande 1848, *Haid. Naturw. Abh.* **2**, p. 32, pl. 18, fig. 2.

Diagnosis. Eospiriferids with anteriorly bifurcating costae. The fold and sulcus may or may not be costate.

Comparison. *Janius* can be distinguished from all other members of the Eospiriferinae because it has anteriorly bifurcating costae on the flanks.

Exterior. Shells transversely elongate, elliptical in outline, unequally biconvex, with brachial valve gently convex and pedicle valve subpyramidal. The brachial valve bears a fold which is subrectangular in cross-section; the pedicle valve has a corresponding sulcus. Hinge-line straight, almost as wide as the maximum width, which is located near the midlength. Interarea of pedicle valve steeply apsacline, concave posteriorly, about five to seven times longer than that of brachial valve. Interarea of brachial valve gently apsacline. Lateral margins of interarea striate, but remainder smooth except for growth-lines which parallel the hinge-line. Lateral margins and lateral portion of anterior margin evenly rounded, but median portion of the anterior margin almost straight. Anterior commissure uniplicate and crenulate. Delthyrial cavity bordered by narrow deltidial plates which are apically conjunct and resemble those figured by Beecher and Clarke (1889, p. 79, fig. 4, no. 3). Coarse ornamentation consists of three to five costae on each flank. In some species two costae are present on the fold and one or two in the sulcus. The costae on the flanks bifurcate anteriorly. Costae rounded in cross-section, separated by U-shaped interspaces of about same width and curvature as costae. Fine ornamentation consists of radial fila and fine concentric growth-lines. The fila increase both by implantation and bifurcation. The junctions of the concentric and radial fine ornamentations are nodose in well-preserved specimens. A few prominent concentric growth-lines are present.

Pedicle interior. Relatively small hinge teeth at medial ends of the hinge-line are supported by long dental lamellae. Dental lamellae convex medially, include an angle of about 30 degrees. On the specimens studied, the muscle field is poorly impressed; it consists of diductor impressions which expand anteriorly, are separated by a low median myophragm, and posteriorly include a small pair of elongate, feebly impressed adductor impressions. Interior crenulated by impress of external ornamentation.

Brachial interior. The cardinalia consist of a small chamber (occupying the position of the cardinal process) laterally bounded by long crural plates which support the discrete hinge-plates. The hinge-plates floor the dental sockets. A low myophragm bisects the area of muscle attachment, which is very feebly impressed and appears to consist of a pair of elongate adductor impressions extending to a position just short of the mid-length. Interior strongly impressed by external coarse ornamentation. The ribbon-like crura make an oblique angle with the primary lamellae. No jugal processes were found in the three specimens of *J. schmidti* studied.

Geologic range. Highest Wenlockian (zones of *Cyrtograptus radians* and *Monograptus testis* in Bohemia) to Eifelian.

Species:

Spirifer exsul Barrande 1848, *Haid. Naturw. Abh.* **2,** p. 184, pl. 15, fig. 5.
Spirifer inconstans Hall 1862, *Rpt. Wisconsin Geol. Surv.*, p. 26, 1, **1,** 1867, p. 436, pl. 69, fig. 6.
Spirifer insignis Hedstrom 1923, pp. 13–15, pl. 5, figs. 1–24.
Spirifer nobilis Barrande 1848, *Haid. Naturw. Abh.* **2,** pp. 184–5, pl. 18, fig. 2.
Spirifer nobilis var. *fortiuscula* Barrande 1879, pl. 7, fig. 12.
Spirifer nobilis var. *irbitensis* Tschernychev 1893, *Mém. Com. Géol.* **4,** 3, pp. 55–56, pl. 8 figs. 1–5.
Spirifer racinensis McChesney 1861, *New Paleozoic Fossils*, p. 84; plates, 1865, pl. 8, figs. 3–3*b*.
Spirifer reluctans Barrande 1879, pl. 74, fig. ii (1–4).
Spirifer rostellum Hall and Whitfield 1872, pp. 182–3.
Spirifer schmidti Lindstrom 1861, *Ofver. Vetenskapsakad.*, Arg. 17 (1860), **8,** pp. 358–9, p. 12, fig. 1.
Spirifer schmidti var. *pyramidalis* Wenjukow 1899, *Mater. Geol. Russ., St. Petersburg*, **19,** pp .137–8, pl. 2, fig. 11.
Eospirifer vetuloides Nalivkin 1960, pp. 382–3, pl. 89, figs. 1–2.
Spirifer (*Eospirifer*) *weberi* Nalivkin 1930, pp. 112–13, pl. x, figs. 25–26.

Distribution. In eastern North America widely distributed in strata of highest Wenlockian and Lower Ludlovian age:

Gaspé: *Eospirifer* cf. *eudora* (resembles *J. racinensis* [McChesney]), Gascons fm. L. Lud. (Northrop 1939, p. 191; Pl. 101, fig. 10).
New Brunswick: *Janius* cf. *nobilis* in association with *Conchidium* cf. *knighti*, Gambol Brook, Bathurst–Newcastle map-area (identification of *J.* cf. *nobilis* by the writer, of *C.* cf. *knighti* by Dr. L. M. Cumming) (Pl. 103, figs. 20–22).
Northern Maine: *Janius sp.*, collections made by Dr. R. B. Neuman, U.S. Geol. Surv., on White Horse Lake, Shin Pond quadrangle, Penobscot County, L. Lud. (identifications by the writer; Pl. 103, figs. 23–24).
Illinois: *J. nobilis*, Chicago fm., Wen. and early Lud. (Hall and Clarke 1893, pl. 29, fig. 16).
Wisconsin: *J. nobilis*, Racine dolomite, Wen. (Hall and Clarke 1893, pl. 37, figs. 2–3).

Indiana: *J. nobilis*, Liston Creek reef, Lud. (Cummings 1930, p. 209). *J. rostellum* Louisville ls., Lud. (Hall and Whitfield 1872; 1875, pl. 9, figs. 11–13) (Nettleroth 1889, pl. 27, figs. 17–19; pl. 29, fig. 25).

Alaska: *J. nobilis*, unnamed beds, U. Lland. (C_3 or younger) to Lud. (Kindle 1908, p. 325).

In Europe widely distributed in strata of highest Wenlockian to Ludlovian and possibly Lower Gedinnian age:

Gotland: *J. schmidti*, Hemse group, L. Lud., and Eke group, Lud. or possibly slightly younger (Hede 1921, p. 94). (For a discussion of the age of the Eke group see Boucot 1960, p. 290.) *J. insignis*, Hemse group and Eke group, Lud. (Hedstrom 1923, p. 13).

Podolia: *J. schmidti*, Malinovetski fm., Lud. (Nikiforova 1954, pp. 136–8; Vascautanu 1932, p. 509). *J. pyramidalis*, Malinovetski fm., Lud. (Nikiforova 1954, pp. 138–9), and Skal. (Vascautanu 1932, p. 463).

Novaya Zemlya: *J. irbitensis*, Kostin Shar, Lud. (Alferov 1937, p. 10). *J. vetuloides*, U. Eif. (Nalivkin 1960, p. 383).

England: *J.* cf. *nobilis*, L. Lud. (this paper, Pl. 101, fig. 10). *Janius* Wenlock ls., Wen. (this paper, Pl. 101, fig. 9).

Czechoslovakia: *J. nobilis*, Collines entre Luzetz et Lodenitz (e2), Wen. or Lud. (Barrande 1879, pl. 7, figs. 13–15). *J. exsul* Barrande, Kopanina beds, Lud. (Havlíček 1959, pl. k2, figs. 1–5). *J. reluctans*, Listice (e2), Wen. or Lud. (Barrande 1879, pl. 74, fig. ii, 1*a*, 4; Havlíček 1959, p. 62, concludes that *J. reluctans* is the young of *J. exsul*). *J. exsul*, Lodenitz (e2) and Collines entre Luzetz et Bubowitz (e2), Wen. or Lud. (ibid., pl. 1, figs. 1, 2; pl. 76, fig. 2).

EXPLANATION OF PLATE 101

Figs. 1–6. *Janius schmidti* (Lindstrom, 1861). Probably from the Eke Group; Gotland (probably from Lau backar, Lau parish, Ronehamn map sheet). U.S.N.M. No. 126057. 1, Pedicle view (×1). Note the plications in the sulcus and the bifurcating lateral plications. 2, Brachial view (×1). Note the presence of anteriorly bifurcating lateral plications and bifurcating plications on the fold. 3, Side view (×1). Note the relatively long interarea of the pedicle valve. 4, Anterior view (×1). Note the crenulated anterior commissure. 5, Posterior view (×1). Note the narrow deltidial plates bordering the delthyrial cavity and inserted normal to the interarea. 6, Exterior of pedicle valve (×3). Note the beaded fine ornamentation formed by the intersection of the concentric growth lamellae and the radial striae.

Figs. 7, 8. *Janius* cf. *schmidti* (Lindstrom, 1861). Racine dolomite; Racine, Wisconsin. U.S.N.M. No. 126053. 7, Posterior view of impression of interior (×1). Note the relatively long crural plates and the unstriated area of diductor attachment. 8, Brachial view of impression of interior (×1). Note the presence of anteriorly bifurcating lateral plications and bifurcating plications on the fold.

Fig. 9. *Janius* cf. *nobilis* (Barrande, 1848). Wenlock limestone; old quarry at Iron Bridge, in Benthall Wood, Grid Ref. 665/034, map sheet 118 (Shrewsbury). Boucot loc. 56GB170, U.S.N.M. No. 137739. Pedicle view (×1). Note the unplicated sulcus and the anteriorly bifurcating lateral plications.

Fig. 10. *Janius* cf. *nobilis* (Barrande, 1848). Lower Ludlow; Old quarry, 250 yards WNW. of milestone (1 mile to Hundred House) and 1 mile S. 39° E. of Church, Abberley, Worcs., G.B. Geological Survey Collection No. Gr.–249. Rubber replica (×1) of brachial valve exterior. Note the unplicated fold and the presence of anteriorly bifurcating lateral plications.

Fig. 11. *Janius* cf. *nobilis* (Barrande, 1848). Upper Gascons formation; Black Cape, Quebec. Peabody Museum, Yale Univ. No. 2850/6. Brachial view (×1½). Note the anteriorly bifurcating medial plication.

Figs. 12, 13. *Janius schmidti* (Lindstrom, 1861). Eke Group; Lau backar, Lau parish, Ronehamn map sheet, Gotland. 12, Preparation of spire (×2). Note the absence of a jugal process, and the obtuse angle included by the crura and primary lamella. U.S.N.M. No. 137732. 13, Impression of interior (posterior view, ×3). Note the relatively long crural plates and the unstriated area of diductor attachment. U.S.N.M. No. 137733.

Urals: *J. irbitensis*, Striatus beds, L. Lud., and Marginalis beds, U. Lud. (Khodalevitch 1939, pp. 64–65); L. Dev. (ibid. 1937, p. 67).
Estonia: *J. schmidti*, Lud. (Schmidt 1881, p. 49).

Outside of Europe and eastern North America recognized only in central Asia:

Turkestan: *J. irbitensis*, Marginalis beds and possibly Isfara beds, bed. and Lud. ? (Nikiforova 1937, p. 50). *J. irbitensis*, Eif. (Nalivkin 1930, pp. 108–9), together with *J. weberi* (ibid., pp. 112–13) and *J. vetulus* (ibid., p. 107).
Kuznetsk Basin: *J.* ex. gr. *nobilis*, Salairkin beds, Eif. (Rzonsnitskaya 1952, p. 39).

Subfamily CYRTIINAE Fredericks 1924

Diagnosis. The subfamily Cyrtiinae is redefined to include those members of the Eospiriferidae having a pyramidal pedicle valve, a catacline to steeply procline pedicle interarea, and an elongate delthyrium occupied by a complex deltidium. The brachial valve has chilidial plates or a chilidium.

Genera:

Cyrtia Dalman 1828, *K. Vetenskapsakad. Handl. f. 1827*, pp. 92, 93, 97.
Plicocyrtia Boucot gen. nov.

Geological range. Upper Llandoverian to Eifelian.

Geographical range. Europe, eastern North America, Tasmania, and possibly Turkestan if *C.?* aff. *petasus* (Nikiforova 1937, p. 51) belongs to *Plicocyrtia*.

Genus CYRTIA Dalman 1828

Plate 102, figs. 1–5, 12–17; Plate 104, figs. 4–8

Type species. *Anomites exporrectus* Wahlenberg 1821, *Nova Acta Reg. Soc. Sci. Uppsaliensis*, **8**, p. 64, no. 3.

Diagnosis. *Cyrtia* is characterized by unplicated flanks and an unplicated fold and sulcus.

Comparison. *Cyrtia* may be distinguished from *Plicocyrtia* by the absence of plicated flanks.

Pedicle exterior. Valve pyramidal, in outline subcircular to laterally elongate or even alate. Interarea incurved gently, catacline to steeply apsacline, unstriated but bearing the trace of growth lamellae paralleling the hinge-line. Hinge-line straight and the place of maximum width. Delthyrium narrow, occupied by a complex series of plates. In small specimens these plates appear to be a pair of narrow discrete deltidial plates. With increase in shell size the plates join medially in the apical half of the delthyrium. With further increase in size another plate fills the entire base of the delthyrium except for a small foramen. In large specimens a deposit of secondary material may be laid down over the entire structure, obscuring the foramen and giving the impression of a pseudo-deltidium. Fine ornamentation consists of fine radial fila which in well-preserved specimens are seen to be crossed by concentric growth lamellae. The junction of the concentric and radial ornamentation may be nodose. Anterior commissure uniplicate. Median sulcus prominent, gently rounded to subrectangular in cross-section.

Brachial exterior. Valve gently convex, posteriorly overhangs the pedicle valve. Interarea orthocline to apsacline. Discrete chilidial plates present on small specimens, but on large specimens may be medially conjunct. Fold gently rounded to subrectangular in cross-section. Fine ornamentation similar to that of pedicle valve. Shell impunctate.

Pedicle interior. Dental lamellae long, surmounted by stubby hinge teeth. Muscle field almost free of secondary deposits, as are the umbonal cavities. A low myophragm discernible in some specimens. Sulcus impressed upon the interior; peripheral regions smooth.

Brachial interior. Crural plates long, support discrete chilidial plates. Area of diductor attachment unstriated. Muscle field not noticeably impressed, although a low myophragm is discernible in some specimens. Periphery smooth. The dental sockets narrow posteriorly and flare rapidly antero-laterally. The crura make an obtuse angle with the primary lamellae. The short jugal processes descend toward the pedicle valve near the intersection of the crura and primary lamellae.

Species:

Spirifer approximans Barrande 1879, pl. 4, fig. 5.
Cyrtia cliftonensis Foerste 1903, *J. Geol.* **11**, p. 709; 1909*a*, p. 91, pl. 2, fig. 32.
Anomites exporrectus Wahlenberg 1821, *Nova Acta Reg. Soc. Sci. Uppsaliensis*, **8**, p. 64, no. 3.

EXPLANATION OF PLATE 102

Figs. 1, 2. *Cyrtia sp. Bilobites* zone; Locality 4·24, Duck Harbor, Edmunds Township, Washington County, Maine. U.S.N.M. No. 126083. 1, Impression of interior of pedicle valve (×3). Note the relatively long dental lamellae. 2, Impression of interior (posterior view, ×4). Note the relatively long dental lamellae and the impression of the inner face of the deltidial plate.

Fig. 3. *Cyrtia sp.* Cedarville dolomite; Mills quarry, south-west of Springfield, Ohio. U.S.N.M. No. 87495. Impression of interior (posterior view, ×2). Note the relatively long crural plates and the unstriated area of diductor attachment.

Fig. 4. *Cyrtia exporrecta* (Wahlenberg, 1821). Upper Visby marl; Shore at Gnisvärds fiskläge, Tofta parish, Klintehamn map sheet, Gotland (Boucot locality No. 56G47). U.S.N.M. No. 137734. Preparation of spire (×2). Note the short jugal process and the obtuse angle included between the crura and the primary lamella.

Fig. 5. *Cyrtia trapezoidalis* Hisinger, 1828. Wenlock limestone; Dudley, England. U.S.N.M. No. 99909. Posterior view (×2). Note the narrow chilidium bordering the upper margin of the deltidial plate.

Figs. 6–11. *Plicocyrtia petasus* (Barrande, 1848). Liten beds; Lodenice, Czechoslovakia. 6, Brachial valve (×1). Note the lateral plications. M.C.Z. No. 9428A. 7, Side view (×1). Note the lateral plication adjacent to the sulcus and the relatively elongate, slightly curved interarea of the pedicle valve. M.C.Z. No. 9428A. 8, Pedicle valve (×1). Note the lateral plications bordering the sulcus. M.C.Z. No. 9428A. 9, Exterior (×3). Note the radially striate fine ornamentation remaining on the unexfoliated portion of the shell. M.C.Z. No. 9428C. 10, Impression of interior of brachial valve (×2). Note the elongate crural plates and the unstriated area of diductor attachment. M.C.Z. No. 9428B. 11, Impression of interior of pedicle valve (×2). Note the relatively long dental lamellae and the myophragm medially dividing the muscle field. M.C.Z. No. 9428B.

Figs. 12–17. *Cyrtia exporrecta* (Wahlenberg, 1821). Probably from the Upper Visby marl; Visby, Gotland. U.S.N.M. No. 53505. 12, Exterior (posterior view, ×2). Note the discrete chilidial plates. 13, Exterior (posterior view, ×2). Note the elongate deltidium. 14, Brachial view (×3). Note the low, rounded fold, smooth flanks, and fine radial striae. 15, Side view (×3). Note the elongate, slightly curved interarea. 16, Anterior view (×3). Note the uniplicate anterior commissure. 17, Pedicle view (×3). Note the broad sulcus and the smooth flanks.

Cyrtia exporrecta ludlowensis Boucek 1940, p. 13, pl. ii, fig. 2.
Cyrtia exporrecta maior Boucek 1940, p. 14, pl. ii, fig. 3.
Cyrtia exporrecta postera Boucek 1940, p. 15, pl. i, fig. 6.
Cyrtia exporrecta spiriferoides Boucek 1940, p. 15, pl. ii, fig. 4.
Cyrtia extensa Bolton 1957, p. 71, pl. 12, figs. 3–6.
Cyrtia humilis Boucek 1940, p. 10, pl. 1, fig. 1*b*.
Cyrtia meta Hall 1867, *20th Rpt. New York State Cab. Nat. Hist.*, p. 372, pl. 13, figs. 12–13.
Cyrtia myrtia Billings 1862, *Paleozoic Fossils*, **1**, p. 165, fig. 149.
Cyrtia radians Hall and Clarke 1893, *Paleontology of New York*, **8**, pt. 2, pp. 42, 362, pl. 13, figs. 12–13.
Cyrtia tasmaniensis Gill 1948, pp. 60–61, pl. 8, figs. 23–26.
Cyrtia trapezoidalis Hisinger 1828, Pridrag till Sveriges geognosie, *Anteckningar i physik och geognosie*, **4**, p. 220, pl. 6, fig. 1*a*, *b*, *c*.
Cyrtia trapezoidalis var. *arrectus* Hall and Whitfield 1872, p. 183.

Distribution. In eastern North America widely distributed in strata of Upper Llandoverian to Ludlovian age:

Anticosti Island: *C. myrtia*, Chicotte fm., Wen. (Twenhofel 1928, p. 219).
Gaspe: *C. sp. nov.* aff. *C. exporrecta*, St. Leon fm., early Lud. (Alcock 1935, p. 50). *C.* cf. *exporrecta*, near Matapedia, Sil. (noted by writer in a collection made by Dr. Jacques Beland, Quebec Dept. of Mines).
New Brunswick: *C.* cf. *exporrecta*, Mascarene series at Back Bay near St. George, U. Lland. (C_6) to Wen.
Maine: *Cyrtia*, Shin Pond quadrangle (loc. no. BB4 of R. B. Neuman), U. Lland. (C_6) to Wen. (identified by writer), and Eastport region (Pl. 102, figs. 1–2).
New York: *C. myrtia* and *C. meta*, Irondequoit ls. and Williamson sh., U. Lland. (C_5 to C_6) (Gillette 1947, p. 20).
Kentucky: *C. arrecta*, strata of Louisville age (Wen.) (Hall and Clarke 1893, p. 28, figs. 2–3).
Ohio: *Cyrtia sp.*, Cedarville dolomite, Wen. (pl. 6, fig. 3).
Arkansas: *C. exporrecta*, St. Clair ls., U. Lland. (C_3 or younger) to Lud. (Thomas 1926, pp. 394–5).
Wisconsin: *C. radians*, Racine dolomite, Wen. (Hall and Clarke 1893, p. 39, fig. 33).
Indiana: *C. myrtia*, Liston Creek reef, Lud. (Cumings 1930, p. 209). *C. trapezoidalis*, Osgood fm., U. Lland. (C_5 to C_6) (Tillman 1961).
Ontario: *C. meta*, Lockport dolomite, Wen. (Williams 1919, p. 67). *C. extensa*, Wiarton member of Amabel fm., Wen. and Lud. (Bolton 1957, p. 71; pl. 12, figs. 3–6; table 11).
British Columbia: *Cyrtia sp.*, basal 150 ft. of Sandpile group near junction of Dall and Turnagain rivers (Geol. Surv. of Canada specimens no. 15795, 15796 from coll. No. 35174), U. Lland. (C_3–C_5).

In Europe widely distributed in strata of Upper Llandoverian to Emsian and possibly Eifelian age, but rare elsewhere:

Norway: *C. exporrecta*, Oslo region, U. Lland. (7c) and Wen. (8a) (Kiaer 1908, p. 589).
Gotland: *C. exporrecta*, U. and L. Visby marl. U. Lland.; Tofta ls. and Slite group, Wen. (Hede 1921, p. 94). *C. trapezoidalis*, Mulde marl and Klinteberg ls., Wen. and L. Lud. (ibid.).
Podolia: *C. exporrecta*, Kitaygorod fm. to Malinovetski fm., U. Lland. to Lud. (Nikiforova 1954, pp. 148–50).
Poland: *Cyrtia*, Holy Cross Mts., Lud. (Tomszykowa 1959, p. 67).
Urals: *C. trapezoidalis*, Striatus beds, Lud. (Khodalevitch 1937, pp. 69–70).
Novaya Zemlya: *C. trapezoidalis*, Lud. (Yermolaev 1937, p. 105).
Great Britain: *C. trapezoidalis* and *C. exporrecta*, U. Lland. to Lud. (observed by writer).
Czechoslovakia: *C. trapezoidalis*, Collines entre Luzetz et Lodenitz (e2), Tachlowitz (e2), and Dlauha Hora (e2), Wen. or Lud. (Barrande 1879, pl. 8, figs. 10–15). *C. approximans*, Ems. or Eif. (Havlíček 1959, pp. 73–75). *C. exporrecta exporrecta*, e2; *C. exporrecta postera*, e3; *C. humilis*, e1;

C. exporrecta ludlowensis e1; *C. exporrecta maior*, e2; *C. exporrecta exporrecta spiriferoides*, e2 (Boucek 1940, plate explanation).

Tasmania: *C. tasmaniensis*, Eldon group, Sil., as evidenced by the presence of *Encrinurus* (Gill 1948, pp. 60–61). The *Protoleptostrophia* cited by Gill 1948, pp. 64–65 from the fauna may well belong to *Leptostrophia*, but no information on the brachial interior is available for positive identification.

Turkey: *Cyrtia*, Chamosite horizon near Cumakoy (NW. of Aquiran) in the Istanbul region, U. Lland.

T'ien-Shan: *Cyrtia sp.* from locality 13 of Arpishmebulag Series, Sil. (identified from photographs provided through the courtesy of Prof. G. Regnell, Lund).

Genus PLICOCYRTIA gen. nov.

Plate 102, figs. 6–11; plate 104, figs. 1–3

Type species. Cyrtia petasus Barrande 1848, *Haid. Naturw. Abh.* **2**, p. 183, pl. 17, fig. 1; 1879, pl. 7, figs. 7–9.

EXPLANATION OF PLATE 103

Figs. 1–6. *Nikiforovaena ferganensis* (Nikiforova, 1937). Isfara beds; outcrop 1885, northern slope of the Alai Range, Fergana. Cat. No. 1841/5037 (Holotype). 1, Anterior view (×1). Note the grooved fold and corresponding rib in the sulcus. 2, Pedicle view (×1). 3, Branchial view (×1). 4, Posterior view (×1). 5, Side view (×1). 6, Fine ornamentation (×5). Note the eospiriferid-type striae.

Figs. 7–9. *Janius sp.* Strata of Ludlovian age; Junction of road and Gambol Brook (loose blocks almost in situ), Field No. CE-16, Stratum No. 30801, Tetagouche Lakes area, New Brunswick, Canada. L. M. Cumming, collector, 1957. 7, Impression of interior of pedicle valve (×2). Note the plication in the sulcus. G.S.C. No. 15152. 8, Impression of portion of exterior (×2). Note the eospiriferid-type striations. G.S.C. No. 15153. 9, Impression of interior of pedicle valve (×2). Note the anteriorly bifurcating lateral plications and the plication in the sulcus. G.S.C. No. 15154.

Figs. 10, 11. *Janius sp.* Strata of Ludlovian age; Small island near southern end of Whitehorse Lake, Shin Pond quadrangle, Maine. U.S.N.M. No. 137737. 10, Impression of exterior (×3). Note the eospiriferid-type striations and the anteriorly branching lateral plications. 11, Impression of pedicle valve interior (×3).

Figs. 12–17. *Havlicekia sp.* Lower portion of Lochkov limestone. Svaty Jan pod Skalou, small valley under the hill 'Mramor', south-west of the village. Right side of the Kacak stream, Czechoslovakia. Boucot locality No. B–60–32. 12, Posterior view (×1). 13, Pedicle view (×1). 14, Brachial view (×1). 15, Anterior view (×1). 16, Side view (×1). 17, Posterior view (×2). Note the long crural plates and the unstriated area for diductor attachment. U.S.N.M. No. 137738.

EXPLANATION OF PLATE 104

Figs. 1–3. *Plicocyrtia petasus* (Barrande, 1848). Liten beds; Lodenice, Czechoslovakia. M.C.Z. No. 9248A. 1, Posterior view (×1). Note the deltidial cover. 2, Anterior view 3, (×1). Anterior view (×1). Note the short dental lamella.

Figs. 4–8. *Cyrtia exporrecta* (Wahlenberg, 1821). Upper Visby marl; Gotland. Pal. Inst. Uppsala, Wahlenbergs samling Nr. G. 199. These figures are of the lectotype, which is here designated from the three cotypes. 4, Brachial view (×3). 5, Pedicle view (×3). 6, Posterior view (×3). 7, Anterior view (×3). 8, Side view (×3).

Figs. 9–14. *Janius insignis* (Hedstrom, 1923). Eke Group; Lau backar, 1·3 km. north-east of Church of Lau, parish of Lau, Gotland. Collected and identified by Dr. J. E. Hede. 9, Side view (×3). U.S.N.M. No. 137735. 10, Pedicle view (×3). Note the plication in the sulcus. U.S.N.M. No. 137735. 11, Brachial view (×3). Note the grooved fold. U.S.N.M. No. 137735. 12, Anterior view (×3). U.S.N.M. No. 137735. 13, Posterior view (×3). Note the ribbon-like deltidial plates. U.S.N.M. No. 137735. 14, Posterior view of internal impression (×3). Note the long crural plates. U.S.N.M. No. 137736.

Diagnosis. Cyrtiinids bearing lateral plications on either side of the fold and sulcus.

Comparison. Plicocyrtia differs from *Cyrtia* only in having lateral plications on either side of the fold and sulcus.

Pedicle exterior. Valve pyramidal, laterally elongate tending to become alate. Interarea unstriated, gently incurved, catacline to steeply apsacline. Hinge-line straight, equal to maximum width. Delthyrium narrow, elongate, filled by a convex deltidial plate. The detailed structure and mode of origin of the deltidial plate is not known. Fine ornamentation consists of fine radial fila. Anterior commissure uniplicate and crenulate. Sulcus prominent, rounded in cross-section, bordered laterally by one to three lateral plications having low, rounded cross-sections and separated by broad, U-shaped interspaces. Flanks smooth.

Brachial exterior. Valve gently convex, laterally elongate tending toward alation; posteriorly it overhangs the pedicle valve. Shell impunctate. Interarea orthocline to apsacline. The presence or absence of chilidial plates was not determined. Fold rounded in cross-section, bordered laterally by one to three plications lateral to which the flanks are smooth. Fine ornamentation same as that of pedicle valve.

Pedicle interior. Hinge teeth stubby, supported basally by the long, thin dental lamellae. Muscle field and umbonal cavities almost free of secondary deposits. A well-developed myophragm medially divides the muscle field and extends anteriorly to about the midlength. The external ornamentation is impressed upon the interior.

Brachial interior. The cardinalia consist of slender crural plates which laterally border the unstriated area of diductor attachment and basally support the discrete hinge-plates. A low myophragm bisects the feebly impressed muscle field and extends anteriorly past the midlength.

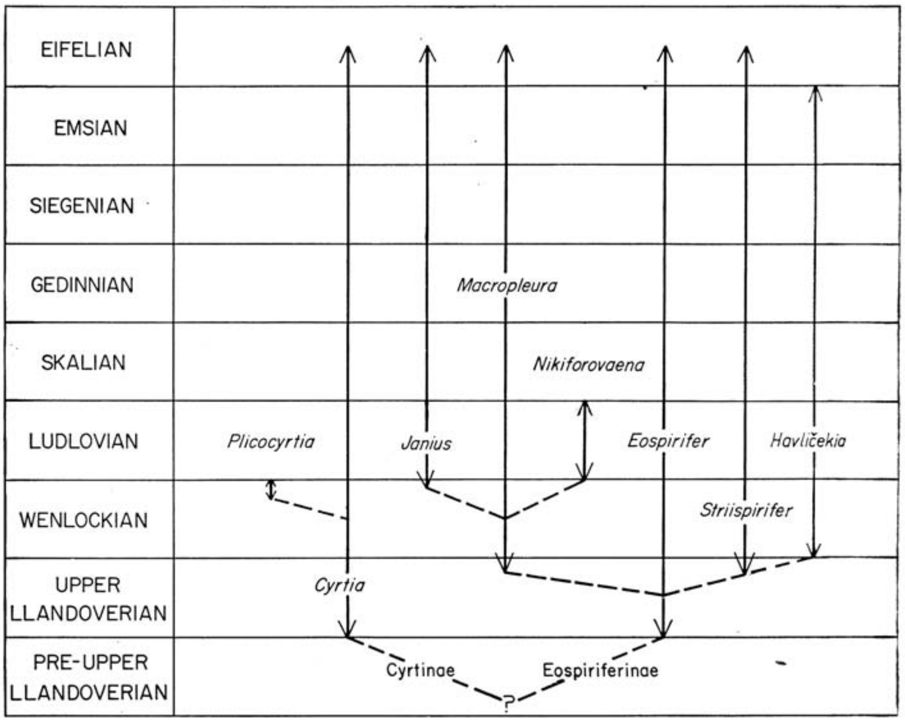
Species:

Cyrtia petasus Barrande 1848, *Haid. Naturw. Abh.* **2**, p. 183, pl. 17, fig. 1.

Distribution. Known from the Upper Liten beds (uppermost Wenlockian) of Czechoslovakia, and possibly from strata of Ludlow age in Turkestan if *C.?* aff. *petasus* (Nikiforova 1937, p. 51) belongs to the genus.

EVOLUTION OF THE EOSPIRIFERIDAE

The oldest known genera of the family Eospiriferidae (text-fig. 4), *Eospirifer* and *Cyrtia*, appear in strata of early Upper Llandovery age on both sides of the North Atlantic. The similar cardinalia, spires, interiors of pedicle valves, and fine ornamentation of both genera clearly suggest that they have a common ancestor somewhere in pre-Upper Llandoverian time. Both genera belong to the brachiopod fauna which first appears in the North Atlantic region during Upper Llandoverian time from an unknown area. Among known Ordovician or pre-Upper Llandoverian brachiopods there are no closely related genera and, in fact, no genera that could reasonably be included in the same family. The Cyrtiinae, as exemplified by *Cyrtia*, appear to have been a relatively stable stock which, for unknown reasons, did not give rise to such diverse plicated forms as those in the Eospiriferinae. The genus *Eospirifer*, for example, by the development of different types of plications on flanks and sulcus proliferated a number of genera. The gradual transition between specimens with smooth flanks (*Eospirifer*) and those with undulating plications separated by U-shaped interspaces of the *Macropleura* type, or those with V-shaped interspaces of the *Striispirifer* type, strongly suggests that



TEXT-FIG. 4. Relations of the Eospiriferidae.

Eospirifer was ancestral to both of the latter genera. It is probable that the long-lived stock of smooth-flanked eospiriferids repeatedly gave rise to forms with plicated flanks, but this cannot be demonstrated on the basis of available collections and information.

Some relevant information comes from the genus *Havlicekia*. Havlíček (1959, pp. 52–53) has concluded, on morphological grounds, that the Ludlovian species *E. praesecans* from the Kopanina beds is ancestral to the Lower Devonian form *H. secans*, as large specimens of both have the peculiarly large, steep-sided fold with U-shaped cross-section. It is more probable that *E. praesecans* is ancestral to *E. togatus togatus*, which, as described by Havlíček (ibid., pp. 42–43), is very similar to *E. praesecans*, and that *H. turjensis*, which occurs in the Pridoli beds (overlying the Kopanina beds) and also in the Urals in strata reported to be of Wenlockian age (Khodalevitch 1939, pp. 65–66), is ancestral to *H. secans*.

The Kopanina beds also contain *Striispirifer viator*, which has a steep-sided fold similar to that of *Havlicekia* and *E. praesecans*. This suggests that at least one species of *Striispirifer* was derived from a smooth eospiriferid similar to *E. praesecans* in pre-Kopanina time (presumably during the late Llandovery), and that *Havlicekia* was derived from a similar source at about the same time. From a consideration of fold cross-sections, it seems likely that species of *Striispirifer* similar to *S. niagarensis* were derived from an *Eospirifer* similar to *E. radiatus*, which suggests that *Striispirifer* is polyphyletic.

Macropleura is transitional to the later-appearing genus *Janius*, the early growth stages of which have *Macropleura*-type ornamentation. On morphological grounds, the U-shaped interspaces between the rounded plications of *Nikiforovaena* ally it closely with *Macropleura*, and it is concluded that the former was derived from the latter by the development of a plicated fold and sulcus.

The coarse ornamentation of *Plicocyrtia* suggests its origin from the unplicated genus *Cyrtia*.

From a phylogenetic point of view, the Eospiriferidae show a repeated tendency to develop forms with lateral plications in the adult (large specimen), whereas the early growth stages are usually reminiscent of an ancestral type (e.g. smooth, unplicated umbonal beak region in such genera as *Macropleura*, *Striispirifer*, and *Plicocyrtia*). *Havlicekia* suggests that the genetic processes responsible for the development of lateral plications in adults could also operate in the reverse manner, to produce lateral plications in the umbonal region in the young and smooth flanks in the adult.

'*Eospirifer*' *iorensis* Nikiforova 1937, from strata of Ludlow age in Turkestan, is undoubtedly an eospiriferid, as evidenced by its fine ornamentation. The presence of a deep groove in its fold, associated with a corresponding rib in the sulcus, separates it generically from all other members of the Eospiriferidae, but the writer does not propose a new genus to receive this unique species because its internal morphology is not clear.

Havlíček (1959, p. 231) noted that both '*Eospirifer*' *olgae* Borisyak 1955 and '*Eospirifer*' *kassini* Borisyak 1955 may belong to a group in which the brachial valve bears a sulcus containing a median plication. Inspection of Borisyak's figured specimens shows that they are too fragmentary for certainty on this point, although their fine ornamentation indicates they are undoubtedly eospiriferid.

STRATIGRAPHIC VALUE OF THE EOSPIRIFERIDAE

Members of the Cyrtiinae are known in beds of Upper Llandoverian to possible Eifelian age, and members of the Eospiriferinae from beds of Upper Llandoverian to Eifelian age. Representatives of both groups occurring in pre-Upper Llandoverian beds will probably eventually be found. *Eospirifer* itself ranges from the Upper Llandoverian to the Eifelian. In the North Atlantic region, *Macropleura* appears in uppermost Llandoverian time; it continues through Gedinnian time and possibly into the lowest Siegenian interval, although elsewhere it persisted into Eifelian time. *Striispirifer* appears in uppermost Llandoverian time and continues through to Eifelian time. *Janius* appears in uppermost Wenlockian time and continues into the Eifelian. The species of *Janius* without plicae on the fold or sulcus appear earlier (in late Wenlockian time) than those forms with such plicae (Ludlow), making it possible to distinguish between beds of latest Wenlockian to Ludlovian age on this basis. *Nikiforovaena* is known in strata of Ludlovian age. *Havlicekia* is known from strata of Wenlockian to Eifelian age.

In North America, eospiriferids are not known after the Gedinnian (New Scotland formation and its equivalents). In the Old World, eospiriferids normally occur as high as the Emsian, except in the Rhenish facies of northern Europe where they are unknown in either the Siegenian or Emsian, and in Central Asia and Czechoslovakia, where they also occur in the Eifelian. The available distribution data suggests that the family became progressively restricted geographically after the Gedinnian until, by the end of Eifelian time, they became extinct.

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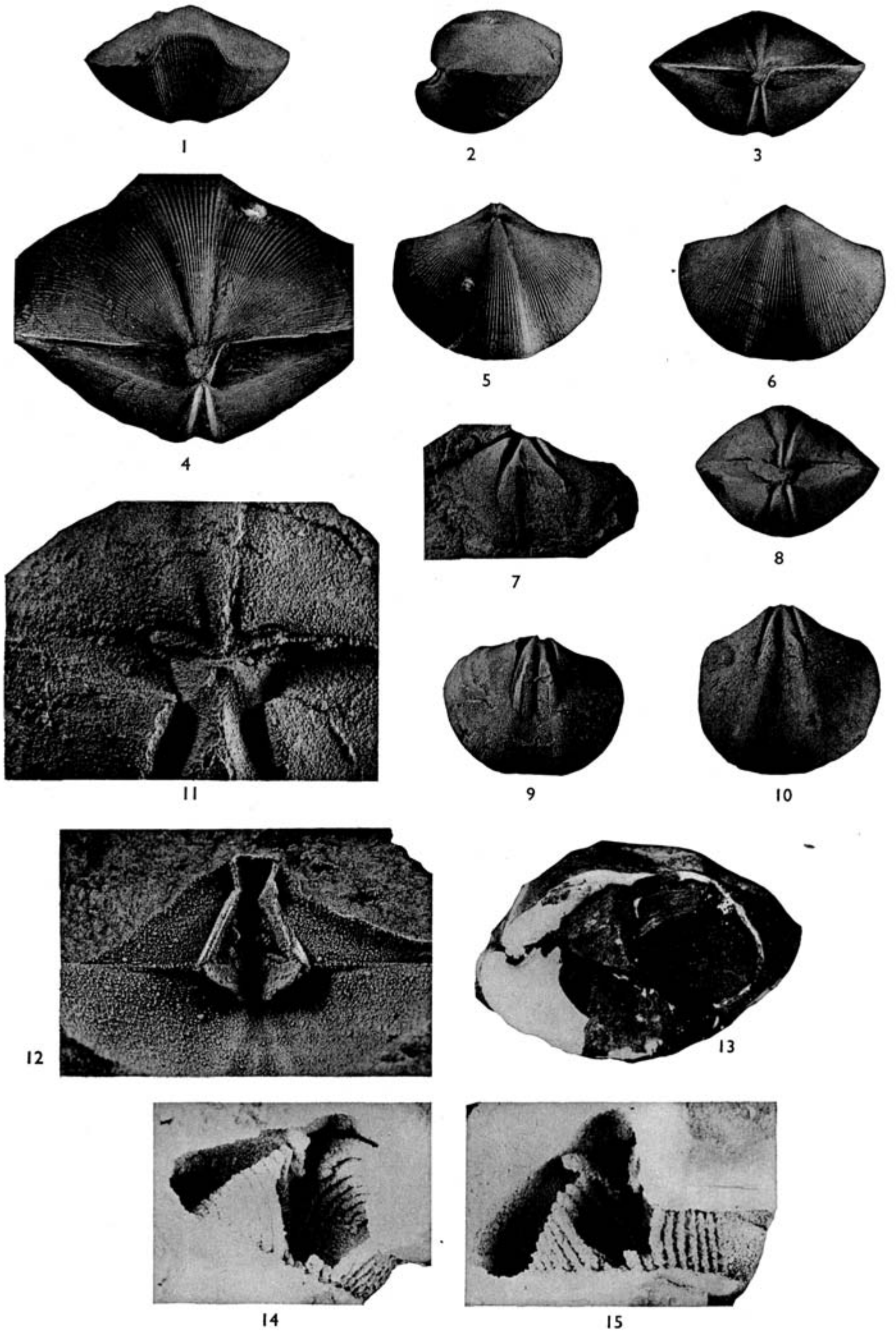

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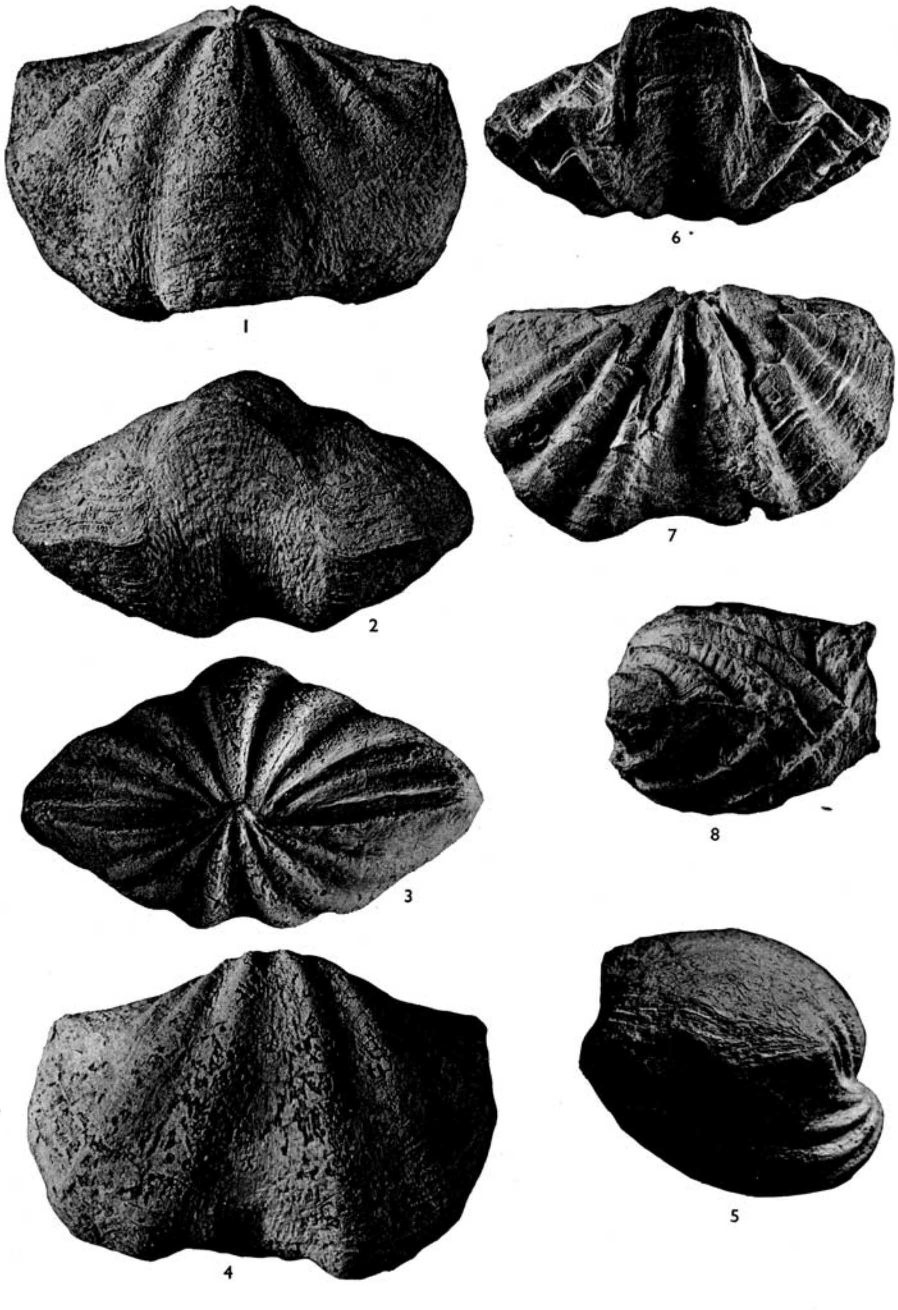

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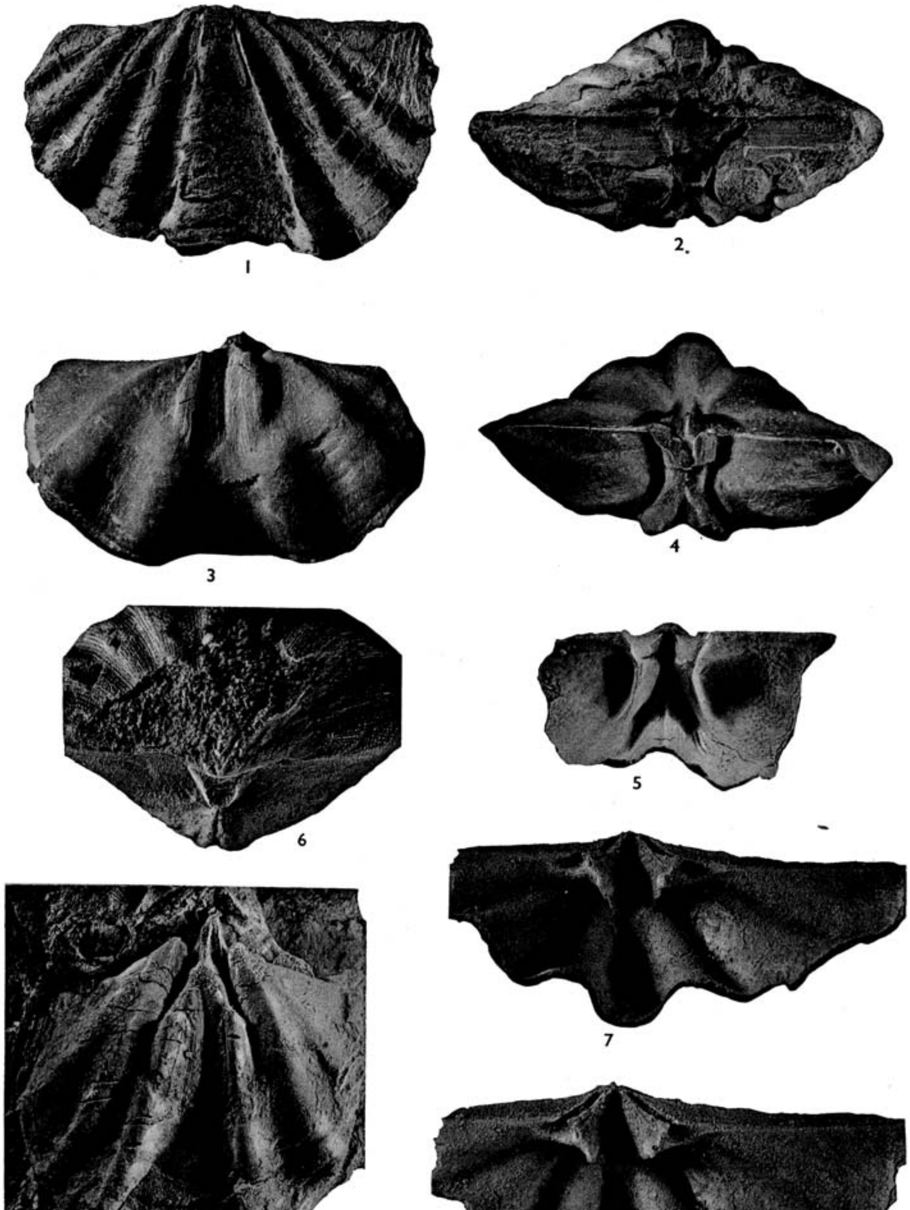

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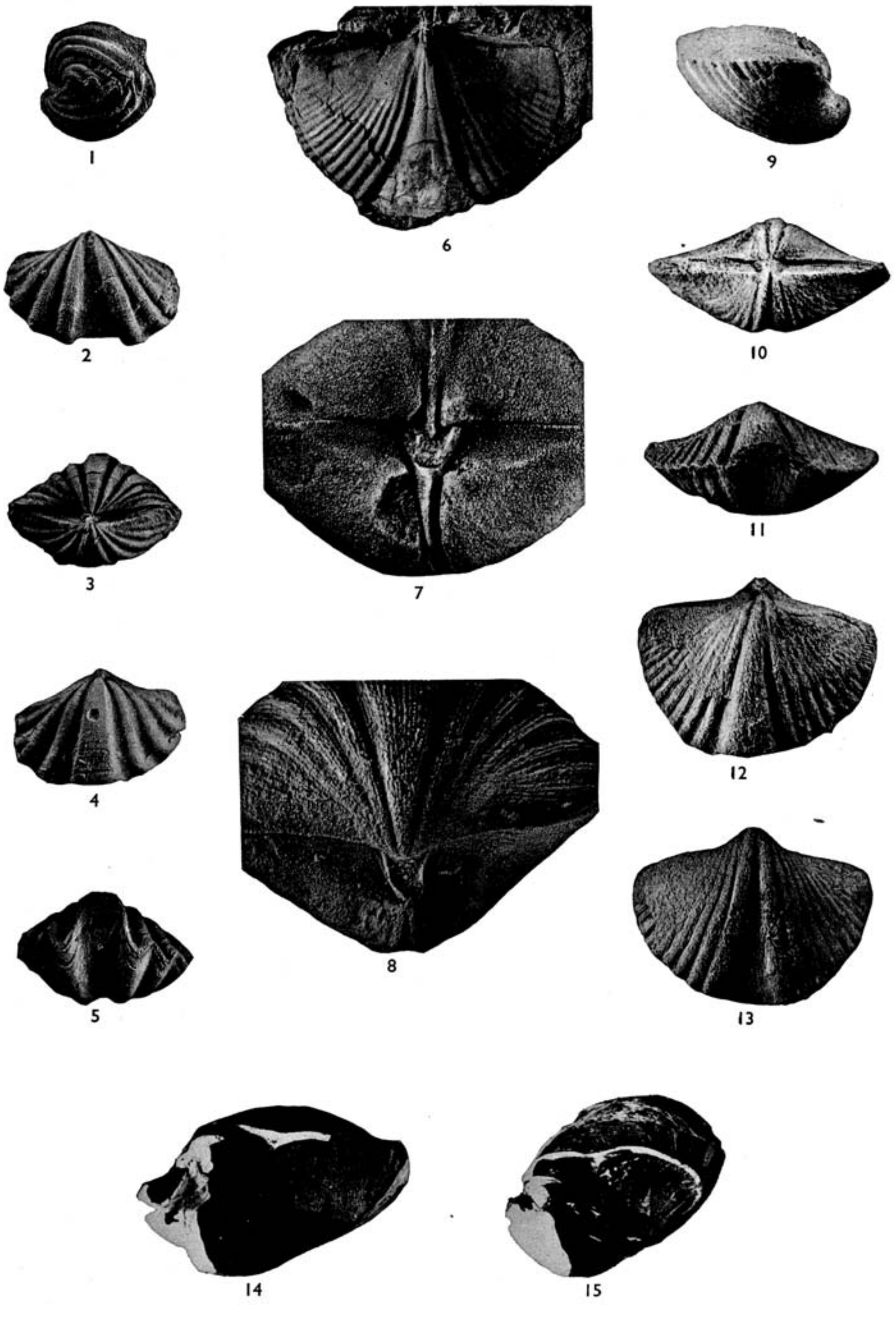

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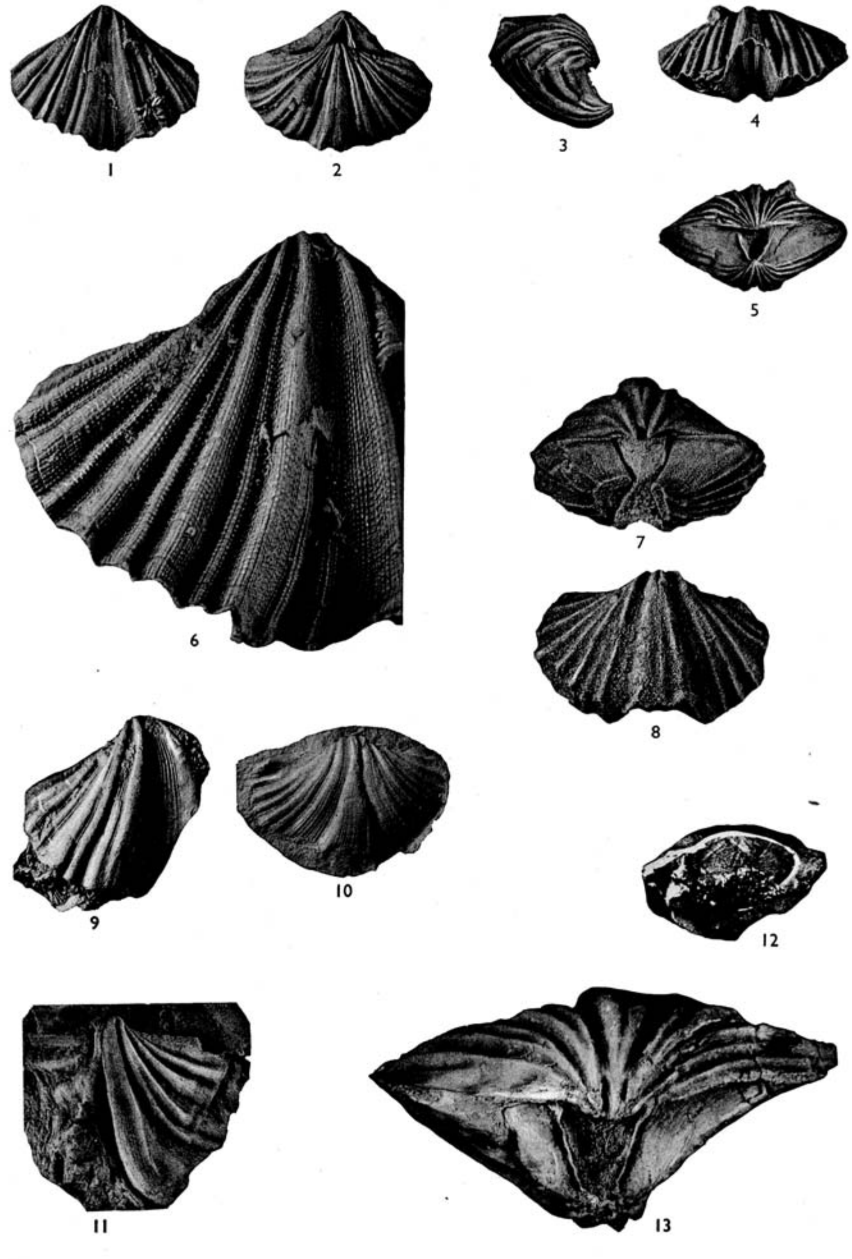

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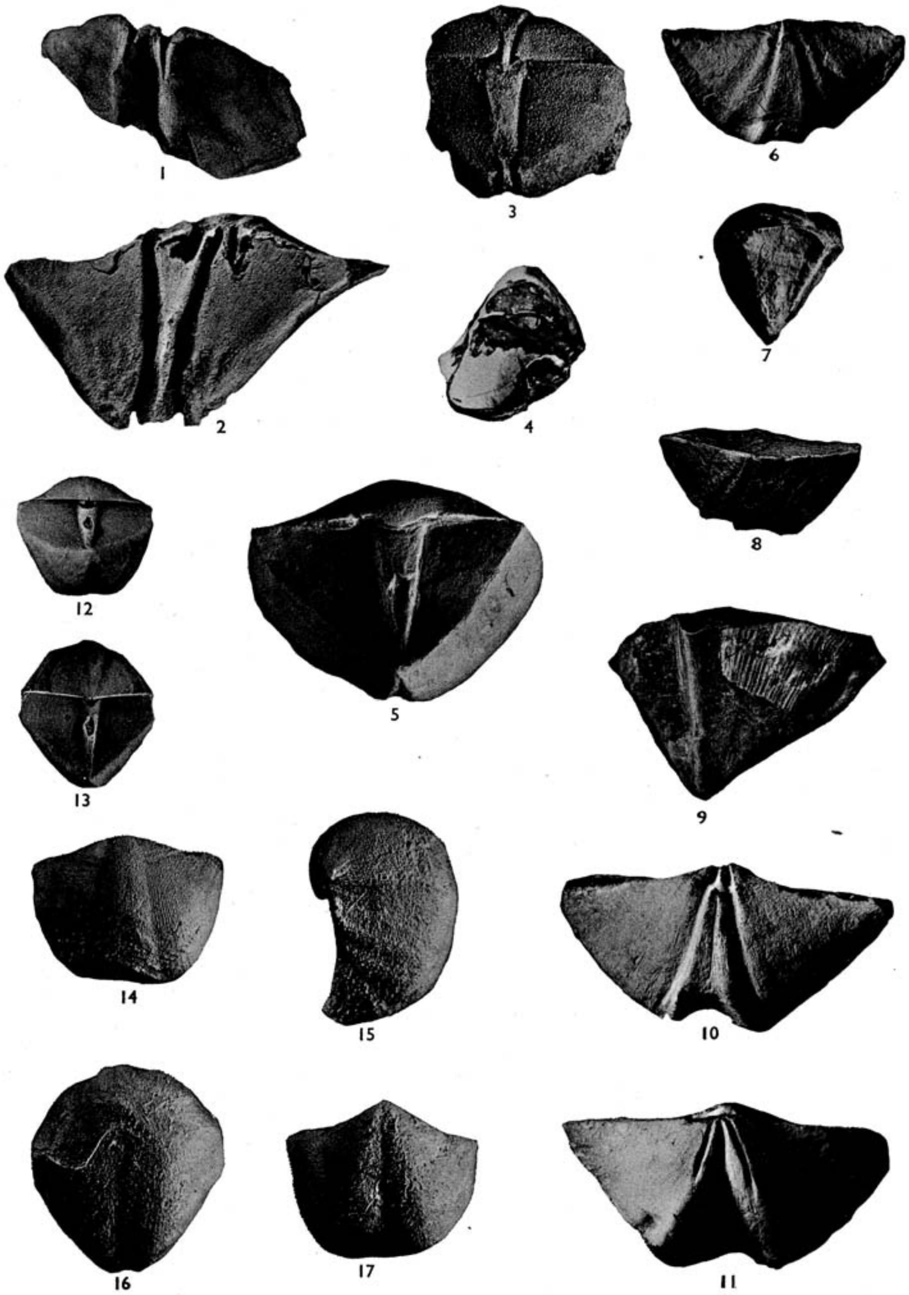

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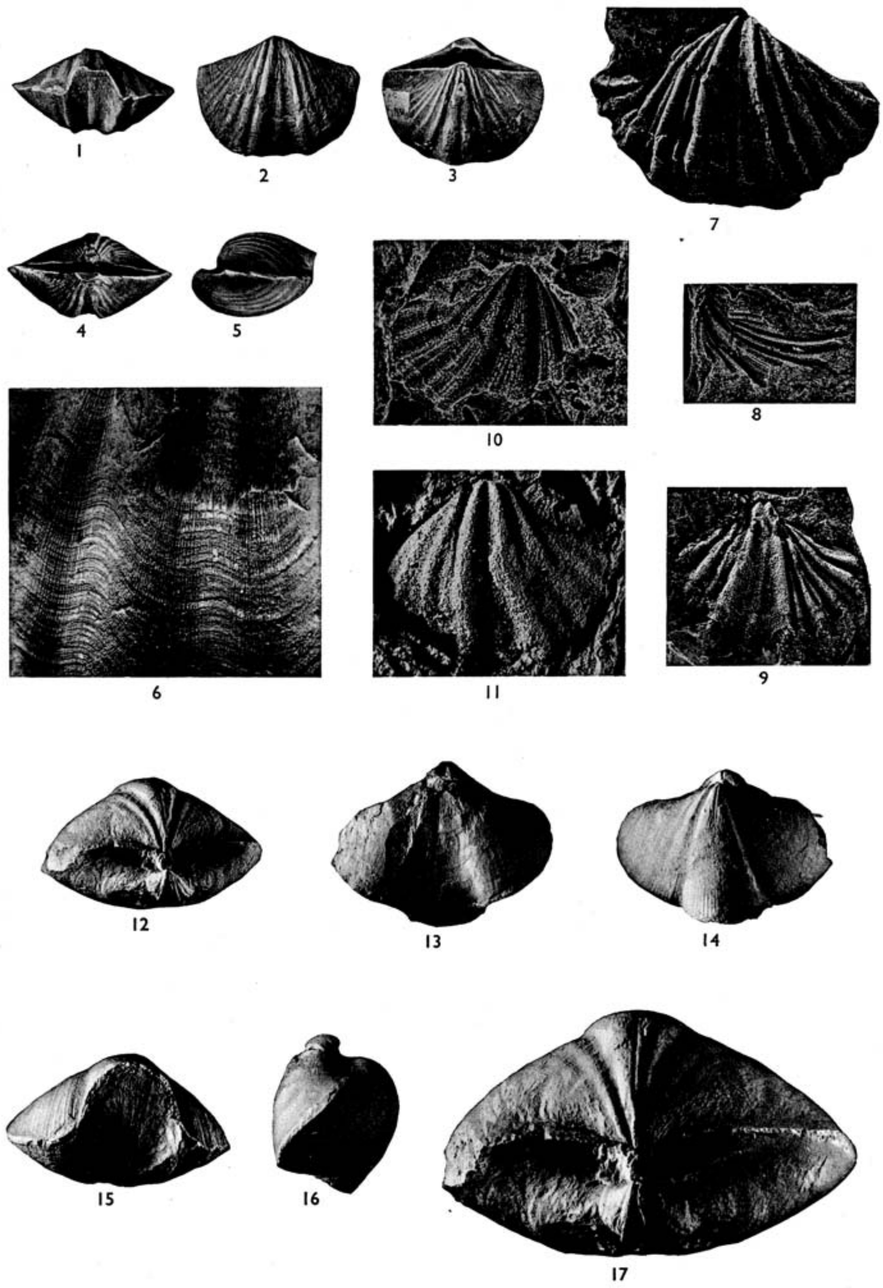

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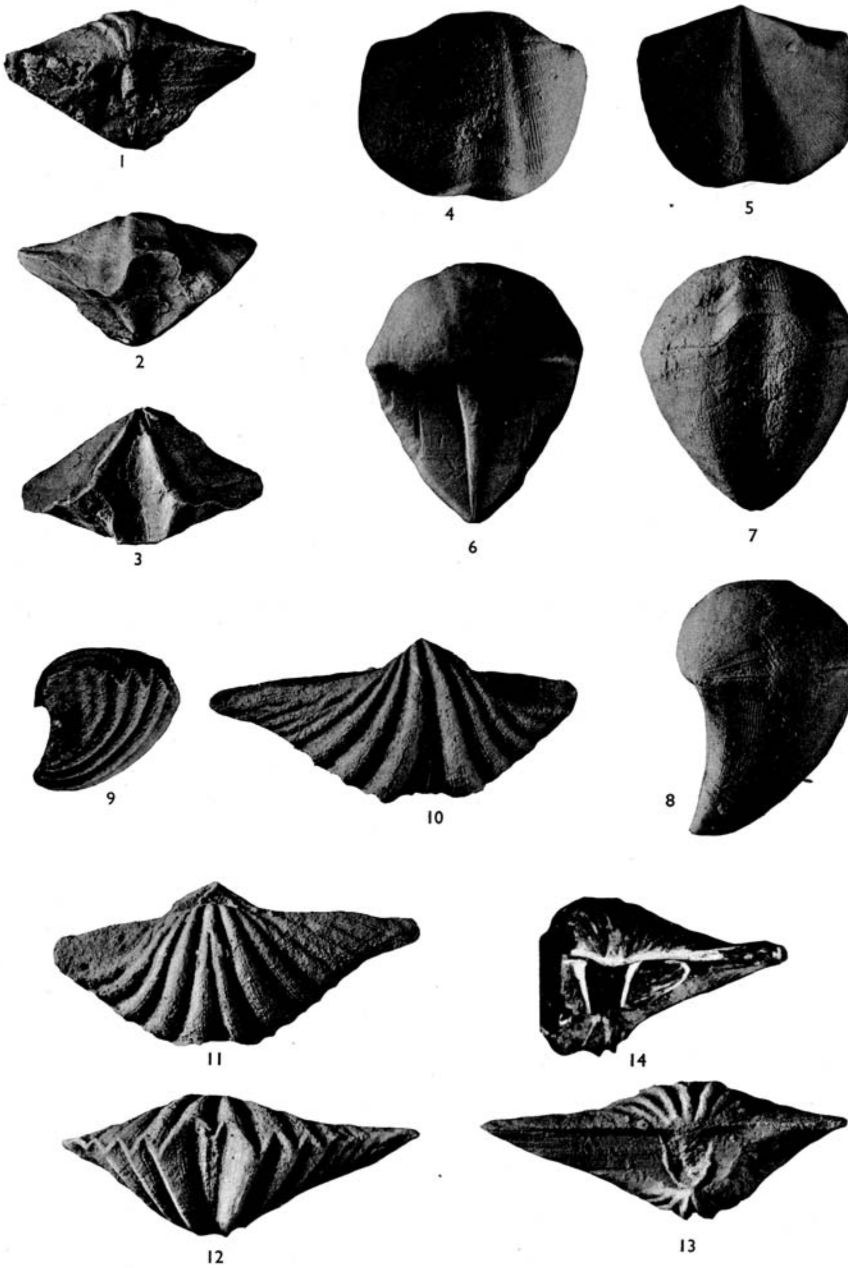

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