

NEW ATOKAN PRODUCTOID BRACHIOPODS FROM THE UPPER
CARBONIFEROUS LADRONES LIMESTONE
OF SOUTHEASTERN ALASKA, WITH A PRELIMINARY NOTE ON THE
PHYLOGENY AND CLASSIFICATION OF
THE TRIBE RETARIINI

STANISLAV S. LAZAREV¹

JOHN L. CARTER

Curator, Section of Invertebrate Paleontology

ABSTRACT

One new genus and two new species of productoid brachiopods of the Subfamily Productininae are described from the Carboniferous Ladrone Limestone (Atokan, late Bashkirian or early Moscovian) of Prince of Wales Island, southeastern Alaska. The new genus *Caruthia*, type species *Caruthia borealis* n. sp., is assigned to the Tribe Productinini. A new species of the genus *Rugivestis* Muir-Wood and Cooper, 1960, of the Tribe Paramarginiferini, *R. girtyi*, is similar and probably closely related to *Rugivestis pristina* Carter and Poletaev, 1998, of approximately the same age, from Ellesmere Island, Canadian Arctic Archipelago.

Discovery of a shagreen texture within the ventral beak region of the genera *Keokukia* Carter, 1991, *Tesuquea* Sutherland and Harlow, 1973, and at least two species of *Spinocarinifera* Roberts, 1971, necessitates a new interpretation of the phylogenetic relationships and derivation of the Tribe Retariini (Subfamily Productinae). We suggest that Eurasian *Antiquatonia* Miloradovich, 1945, and North American *Tesuquea* Sutherland and Harlow, 1973, were sister genera, both derived from *Keokukia* Carter, 1991, common to both continents, and probably derived from the Tournaisian *Spinocarinifera nigra-arcuata* group.

KEY WORDS: brachiopods, productoids, Carboniferous, Atokan, Alaska, Ladrone Limestone, *Caruthia*

INTRODUCTION

The diverse brachiopod fauna of the Ladrone Limestone of southeastern Alaska is undescribed. G. H. Girty, of the U. S. Geological Survey, made sizable collections from this formation in 1918 and initiated identification of the fauna but did not publish on it although he apparently recognized its unusual nature; several of Girty's sorted taxa are labeled as new species. Several nonbrachiopod faunal elements of the Ladrone Limestone fauna have been described. Savage and Barkeley (1985) described the conodonts, Hahn and Hahn (1991, 1992) the trilobites, and Douglas (1971) the fusulinids.

The Ladrone Limestone was named by Eberlein and Churkin (1970:59) for about 300 m of thick or indistinctly bedded gray sublithographic limestone exposed on the Ladrone Islands in Trocadero Bay near Prince of Wales Island, southeastern Alaska. The fossils described here are from two very small islands composed entirely of Ladrone Limestone with no good indication of relative stratigraphic position.

The precise age of these collections is not certain. The age of the Ladrone

¹ Paleontological Institute, Russian Academy of Sciences, Profsoyuznaya 123, Moscow 117647, Russia.

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Limestone fusulinids is Middle Pennsylvanian according to Douglas (1971). According to Savage and Barkeley (1985) the Ladrone Limestone is Lower to Middle Pennsylvanian as based on several conodont samples. The brachiopods suggest an Atokan age. The generic composition of the brachiopod fauna is closely similar to that of the Hare Fiord Formation of Ellesmere Island which is known to be of Atokan age (Nassichuk, 1975).

This paper contains descriptions of two new productoid species in the Ladrone Limestone fauna and represents the first description of Alaskan Carboniferous brachiopods.

All of the specimens upon which these new species are based were collected by G. H. Girty of the U. S. Geological Survey in 1918 from small unnamed islands of the Ladrone group in Trocadero Bay, about six and one-half miles south-southeast of Craig (Craig Quadrangle), Prince of Wales Island, Alaska. In May 1997, the junior author collected more specimens from these localities, although none of the specimens described here was collected at that time. The three collections used here—USGS 3708-PC, 3762-PC, and 3763-PC—are from the south coast of a small island in the middle of the Ladrone Islands, near the mouth of Trocadero Bay, Prince of Wales Island, Alaska. Girty gave the coordinates of locality 3708-PC as latitude $55^{\circ}23'00''$ N, longitude $133^{\circ}04'52''$ W as based on an old coastal chart. Coordinates of latitude $55^{\circ}23.095'$ N, longitude $133^{\circ}05.136'$ W were obtained using a GPS device in 1997 for a locality probably slightly to the west of Girty's 3708-PC locality. USGS 3762-PC includes specimens from various localities on the south coast of this island. USGS 3763-PC is located just east of locality 3708-PC.

SYSTEMATIC PALEONTOLOGY

A revised classification of the Order Productida was recently published by Brunton et al. (1995). In general, that classification is followed here.

All primary types are deposited in the National Museum of Natural History, Washington, D.C. (acronym USNM). The specimens in Figure 3 are in the collections of the Carnegie Museum of Natural History (CM), Pittsburgh, Pennsylvania.

Suborder Productidina Waagen, 1883
Superfamily Productoidea Gray, 1840
Family Productellidae Schuchert, 1929
Subfamily Productininae Schuchert, 1929
Tribe Productinini Muir-Wood and Cooper, 1960
[= Chonetellini Likharev, 1960]
Caruthia, **new genus**

Type Species.—*Caruthia borealis*, n. sp.

Derivation of Name.—This genus is named in honor of Ruth C. Carter and is derived from her surname and first name.

Diagnosis.—Small, outline subtriangular but not nasute; disc concavoconvex with shallow corpus; lateral profile nearly semicircular or moderately asymmetrical but without clear geniculation; venter near midlength weakly convex, flattened or with weak sulcus, dorsum occasionally with low fold; ornament consisting of fine weak ribs on both valves, excluding posterior part of visceral disc,

and weak rugae on dorsal valve; rare thick spines only on ventral valve, including row of spines at base of flanks; interiors of both valves with strong lateral ridges bordering ears and extending anteriorly as weak marginal ridges; muscle scars weakly impressed in both valves.

Comments.—The discovery of this genus permits us to suggest a new phylogeny and systematic composition for the Subfamily Productininae, as submitted for the forthcoming revised edition of the Treatise on Invertebrate Paleontology (see also the revised classification proposed by Brunton et al., 1995). The latter was based on the assumption that the Tribe Chonetellini appeared in the Permian, being derived from the Paramarginiferini by the loss of ribbing. Now we have evidence to suggest two parallel lineages during the Carboniferous and Permian. One of them, the Productinini [= Chonetellini] was more conservative, that is, without pronounced ribbing, always with a shallow corpus cavity, lacking a cincture, and with a row of spines on the flanks. The second lineage consisted of the Tribe Paramarginiferini, forms with a shallow or moderately deep corpus cavity, stronger ribbing, sometimes with a cincture, and lacking a row of spines on the flanks. Both lineages are comprised in the Subfamily Productininae, characterized by a subtriangular outline (sometimes nasute anteriorly), a few coarse spines on the ventral valve only, the development of marginal structures inside both valves, and the peculiar orientation of the brachial ridges (with the anterior lobe axes directed anteromediad).

Comparisons.—*Caruthia* differs from all other members of the Tribe Productinini in its weak, obscure ribbing and strong lateral ridges inside each valve. In addition, it differs from *Productina* Sutton, 1938, in its costate nonlamellose dorsal valve. *Argentiproductus* Cooper and Muir-Wood, 1951, is much more transverse and less convex and has a lamellose dorsal exterior. Similarly, *Dorsirugatia* Lazarev, 1992, from the Late Devonian of Mongolia, is more transverse in outline and has a lamellose, more weakly costate dorsal exterior. *Productellina* Reed, 1943, from the very early Carboniferous of England, is similar in outline to *Caruthia* but differs in having a strongly lamellose, noncostate dorsal exterior, in addition to the general differences noted above.

Age and Distribution.—Atokan (late Bashkirian or early Moscovian) of southeastern Alaska.

Species Assigned.—Type species only.

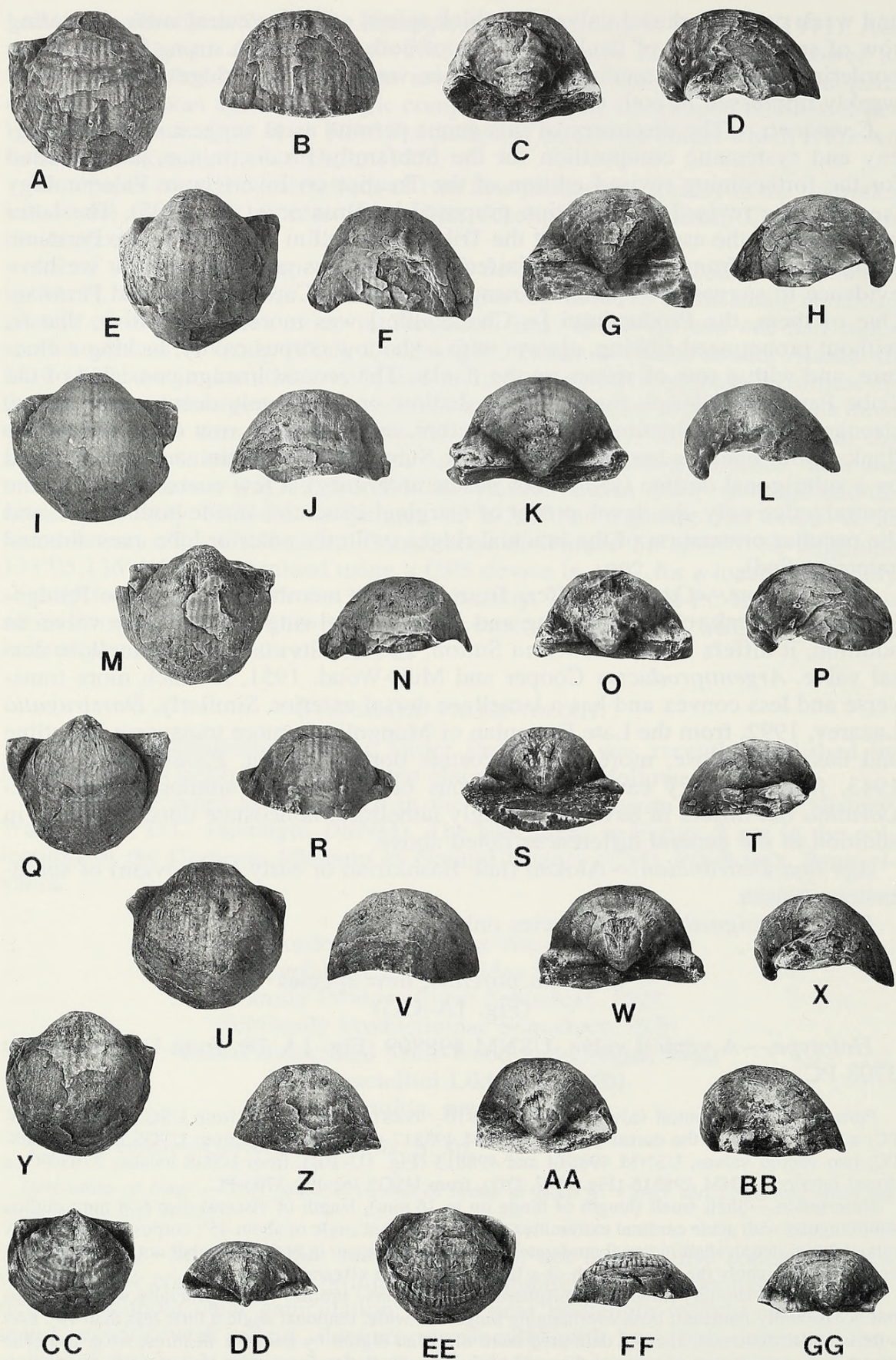
Caruthia borealis, new species
(Fig. 1A–GG)

Holotype.—A ventral valve, USNM 498809 (Fig. 1A–D), from USGS locality 3708-PC.

Paratypes.—Four ventral valves, USNM 498810–498813 (Fig. 1E–T), from USGS locality 3708-PC; a natural mold of the dorsal exterior, USNM 498817 (Fig. 1EE–GG), from USGS locality 3708-PC; two ventral valves, USNM 498814 and 498815 (Fig. 1U–BB), from USGS locality 3763-PC; a dorsal interior, USNM 498816 (Fig. 1CC, DD), from USGS locality 3763-PC.

Description.—Shell small (length of hinge up to 16 mm), length of visceral disc 6–8 mm; outline subtriangular with acute cardinal extremities forming cardinal angle of about 45°; corpus cavity shallow (about 2 mm deep); shell material moderately thick; trails present in both valves but not well separated, being approximately the same length or a little longer than visceral disc.

Ventral valve strongly inflated, hemispherical in transverse profile; venter generally without sulcus but occasionally flattened; beak overhanging hingeline, wide; umbonal angle a little less than 90°; ears subtriangular, flattened, sharply delimited from umbonal region by concave flexures; weak costellae present on anterior part of visceral disc and trail; irregular fluting present on trail of some specimens;



rare thick spines (diameter 0.6–0.8 mm, sometimes up to 1 mm) scattered on trail; hinge spines absent; rare spines scattered on venter and trail; curving row of up to four spines wraps around ears and down flanks.

Dorsal valve moderately concave; dorsum commonly arched as low fold; ornament consisting of weak concentric rugae, weak ribs, and rounded pits complementary to ventral spines.

Ventral interior with strong, but not crenulated, lateral ridges becoming weaker anteriorly; muscle scars generally not seen, or more rarely, short adductor scars situated medially near posterior ends of larger diductor impressions.

Dorsal interior with lateral and marginal ridges bordering corpus and peripheral cavities as in ventral valve, with ridges following closely those of ventral valve but being placed slightly outside those of opposite valve; cardinal process wide, quadrilobed internally; dorsal muscle scars almost indistinguishable; brachial ridges not impressed; surface finely tuberculate excepting posteromedianly in both valves.

Measurements.—See Table 1.

Distribution.—USGS Locality 3708-PC (more than 60 specimens) and USGS locality 3763-PC (about 30 specimens).

Tribe Paramarginiferini Lazarev, 1986
Genus *Rugivestis* Muir-Wood and Cooper, 1960
Rugivestis girtyi, new species
(Fig. 2A–R)

Holotype.—A ventral valve, USNM 498817 (Fig. 2E–H), from USGS locality 3708-PC.

Paratypes.—Three partial ventral valves missing the ventral visceral disks, USNM 498818, 498821, and 498822 (Fig. 2A–D, M–R); a ventral valve, USNM 498820 (Fig. 2I–L); all from USGS locality 3708-PC.

Diagnosis.—This species is characterized by relatively weak concentric rugae on the visceral disc and coarse costae on the trail.

Description.—Shell small (width up to 2 cm), length of visceral disc about 7–9 mm; outline transversely subtriangular, variably nasute anteriorly but commonly with well-defined, incomplete siphon; both valves geniculate, angle between visceral disc and trail 90°; corpus cavity shallow (about 2 mm).

Ventral visceral disc weakly convex, without sulcus but medially flattened or with very weak depression; beak small, obtuse, slightly overhanging hingeline; ears subtriangular, flattened, well delineated from flanks and trail; cardinal angle about 60°; trail approximately twice as long as visceral disc, almost straight in longitudinal profile but with small concave flexure posterior to nasute extension; posterior part of trail flat in transverse profile or with weak sinus; lateral portions of trail sloping steeply to commissures near ears; outline of nasute extension variable in ventral view but sharply delimited from remainder of trail; radial ribs covering most of surface, excluding beak and ears; weak rugae present on visceral disc, where ribs are better developed than rugae, 6–9 ribs per 5 mm (commonly 7–9) near point of geniculation; width of ribs increases anteriorly but becoming more variable (3–7 per 5 mm); nasute region generally with weaker ribbing; rugae variably developed but commonly with less relief than ribs, or when well developed they can cover the point of geniculation; spines rare and of moderate diameter (0.3–0.4 mm), often difficult to detect; interior with strong lateral ridges

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Fig. 1.—*Caruthia borealis*, n. gen. n. sp. A–D. Ventral, anterior, posterior, and lateral views of the holotype from USGS locality 3708-PC, USNM 498809. E–T. Ventral, anterior, posterior, and lateral views of four ventral valve paratypes from USGS locality 3708-PC, USNM 498810–498813. U–BB. Ventral, anterior, posterior, and lateral views of two ventral valve paratypes from USGS locality 3763-PC, USNM 498821, 498822. CC, DD. Dorsal and posterior views of a dorsal valve interior paratype with cardinal process from USGS locality 3763-PC, USNM 498816. EE–GG. Dorsal, anterior, and posterior views of a natural mold of a dorsal valve exterior paratype from USGS locality 3708-PC, USNM 498817. All $\times 2$.

Table 1.—Measurements in mm of the type specimens of *Caruthia borealis*, n. gen. n. sp. DV = dorsal valve.

USNM #	Locality	Length	Width	Height	Surface measure
498809	3708-PC	11.7	+11.8	7.2	21.0
498810	3708-PC	11.7	12.2	7.1	19.5
498811	3708-PC	11.2	12.6	6.9	20.2
498812	3708-PC	10.0	11.4	7.8	17.1
498813	3708-PC	10.1	12.1	6.0	14.8
498817 (DV)	3708-PC	8.6	+10.2	4.3	11.3
498814	3763-PC	11.2	+11.5	7.2	19.1
498815	3763-PC	10.1	+11.0	6.7	18.0
498816 (DV)	3763-PC	7.9	9.7	3.3	10.5

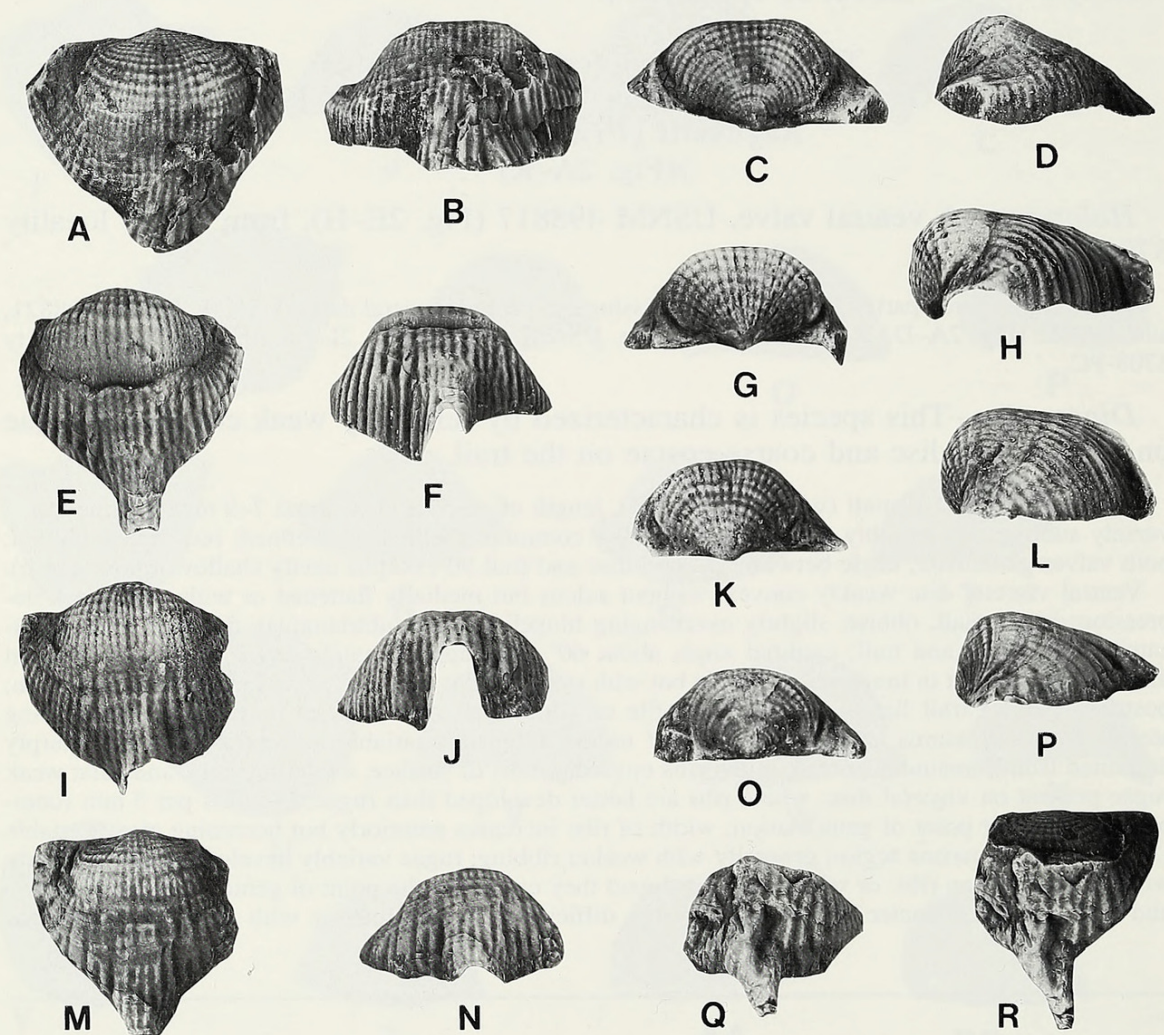


Fig. 2.—*Rugivestis girtyi*, n. sp. A–D. Ventral, anterior, posterior, and lateral views of a large paratype with the visceral disc removed leaving the ventral trail and mold of the dorsal exterior, USNM 498818. E–H. Ventral, anterior, posterior, and lateral views of the nearly complete ventral valve holotype, USNM 498819. I–L. Ventral, anterior, posterior, and lateral views of a ventral valve paratype, USNM 498820. M–P. Ventral, anterior, posterior, and lateral views of a paratype with the visceral disc removed leaving the ventral trail and mold of the dorsal exterior, USNM 498821. Q, R. Anterior and ventral views of a partial specimen with the corpus missing of an unusually elongated nasute paratype, USNM 498822. All $\times 1.5$; all from USGS locality 3708-PC.

Table 2.—Measurements in mm of the type specimens of *Rugivestis girtyi*, n. sp. from USGS locality 3708-PC.

USNM #	Length	Width	Height	Surface measure
498818	17.0	+19.7	6.8	23.4
498819	18.5	16.7	8.3	26.7
498820	16.1	+17.2	8.6	27.0
498821	15.8	+15.9	6.7	21.2
498822	16.4	+14.0	6.1	—

which merge into thick marginal ridge anteriorly; cincture sometimes formed externally, marking internal thickened marginal ridge and producing weakly concave resupination in longitudinal profile; muscle scars not impressed.

Visceral disk of dorsal valve flatter and more sharply geniculate than opposite valve; ears delimited from flanks by narrow ridges; trail slightly longer than visceral disc but anterior portion of trail not forming nasute extension; ribs weaker than those of ventral valve; concentric rugae dominate over ribs in visceral disk, unlike ventral valve; spines and pits lacking; internally with vague, short, lateral ridges which delimit ears in juvenile stages; cardinal process short and wide; adductor muscle scars forming obscure triangular thickening.

- Measurements.*—See Table 2.
- Comparisons.*—This new species differs from *R. pristina* Carter and Poletaev, 1998, from similar-aged strata of Ellesmere Island in having broader ribs, much weaker rugae and a narrower, better defined anterior nasute extension. The weak ornamentation of the visceral disc also differentiates *R. girtyi* from other species of the genus *Rugivestis*.
- Comments.*—A well-preserved dorsal interior of this distinctive genus is still not known.
- Distribution.*—USGS Locality 3708-PC (more than 60 specimens); USGS locality 3763-PC (about 25 specimens); USGS locality 3762-PC (3 specimens).

A PRELIMINARY NOTE ON THE PHYLOGENY AND
CLASSIFICATION OF THE TRIBE RETARIINI

During the past several years, ideas about the phylogeny and systematics of the group of productoids with a deep corpus cavity, commonly referred to the productoid Family Dictyoclostidae of Muir-Wood and Cooper (1960), have changed fundamentally. This is due to reevaluation of the systematic importance of the internal characters of productidines as a whole. This reevaluation is based on the sequence of the appearance of these morphological characters during ontogeny (Brunton et al., 1995). In particular, the appearance of the deep corpus cavity (formerly termed the body cavity) and the marginal or peripheral cavities separated from this deep corpus, which functioned as a defense against penetration of the mantle cavity by undesirable particulate matter, are of great evolutionary significance (Lazarev, 1985). This note is a preliminary report on the ongoing investigation of the nature of the ventral portion of the corpus cavity.

Here we emphasize the systematic importance of a relatively recently appreciated morphological character, the presence of a shagreen (rough or pitted) texture on the inner umbonal surface of the ventral valve beak. Lazarev (1985, 1990) discussed the nature of the coelomic cavity of productoids at some length.

The ventral beak region posterior to the muscle scars within most productoids is smooth, indicating that a normal visceral or coelomic cavity was present. How-

ever, some productoids have fine pits or irregular grooves posterior to the muscle scars that may indicate gonadal attachment. Small tubercles (or endospines) that are the sites of papillae may be present. This rough shagreen texture indicates the extension of mantle cavity posterior to the ventral muscle field. In other words we infer that the mantle cavity, with concomitant gonads and papillae, has occupied the ventral beak region. Thus, the visceral or coelomic cavity hung suspended freely between the dorsal valve cardinal process and the adductor field, except for the distal portion of the ventral beak. The position and size of the suspended portion of the visceral cavity was associated with migration of the dorsal adductor field anteriorly from the hingeline during ontogeny. For example, in the early Viséan genus *Keokukia* Carter, 1991, the distance between the cardinal process and the adductor scars is relatively great (Carter, 1991:fig. 6.1, 6.2). This anterior position of the adductor scars is additional, indirect evidence of a penetration by the mantle cavity of the middle portion of the ventral valve beak region.

The Tribe Retariini of the Subfamily Productinae, as perceived in this paper, consists of genera now known to bear a shagreen texture in the ventral beak. It would include most of the genera assigned by Lazarev (1990) to his Subfamily Retariinae, namely *Retaria* Muir-Wood and Cooper, 1960, *Kutorginella* Ivanova, 1951, *Antiquatonia* Miloradovich, 1945, *Tesuquea* Sutherland and Harlow, 1973, *Thamnusia* Cooper and Grant, 1969, *Thuleproductus* Sarycheva and Waterhouse, 1972, and *Tubaria* Muir-Wood and Cooper, 1960. A shagreen texture has been observed in the ventral umbo in all of the preceding genera by the senior author. Until recently we have not known of true retariins older than the Upper Viséan, but it is now clear that the Lower Viséan genus *Keokukia* belongs in the Tribe Retariini because the inner beak of its ventral valve has the shagreen texture (see Fig. 3A of *Keokukia rotunda* Carter) discussed above. This suggests that *Keokukia* might be the ancestor of the Upper Viséan retariin genus *Antiquatonia* and the later retariins. In *Keokukia sulcata* Carter there is a short row of spines on the flanks anterior to the point of geniculation, a feature that is also suggestive of the genus *Antiquatonia*.

The ancestor of the earliest retariin *Keokukia* probably most closely resembled some species of the genus *Spinocarinifera* Roberts, 1971. We have detected the shagreen texture inside the ventral beak, characteristic of the retariins, in *Spinocarinifera nigra* (Gosselet, 1888) from northeastern France (Fig. 3D) and *S. arcuata* (Hall, 1858) from northeastern Missouri (Fig. 3B). These *Spinocarinifera* species differ from typical *Keokukia* in their smaller size, more posteriorly positioned dorsal adductor scars, and the usual absence of a row of spines on the flanks in front of the ears.

Therefore, we regard the *Spinocarinifera nigra-arcuata* group to be the probable ancestor for all of the deep corpus productoids with the shagreen-textured inner surface of the ventral beak. These include the genus *Dictyoclostus* Muir-Wood, 1930 (in the strict sense) which belongs in the Subfamily Dictyoclostinae (the senior author has observed a shagreen texture in the ventral beak of this entire subfamily). It seems likely that the genus *Keokukia*, which occurs in both North America and Eurasia, was the ancestor of the Eurasian genus *Antiquatonia* Miloradovich, 1945, because of its morphology and stratigraphic age.

No authentic species of the genus *Antiquatonia* (species with shagreen texture in the ventral beak) is known from North America. We have examined the inner surfaces of the ventral umbones of several North American species formerly assigned to *Antiquatonia* such as "*A.*" *hermosana* (Girty, 1903), "*A.*" *colora-*

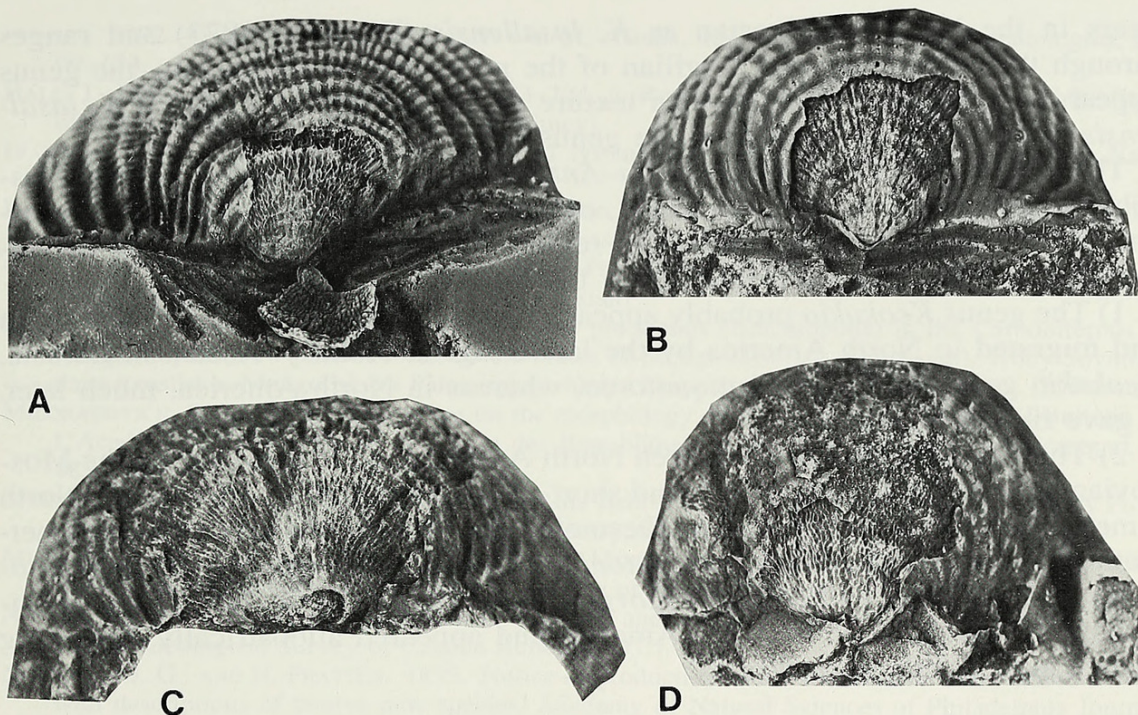


Fig. 3.—Posterior views of four taxa showing the shagreen texture within the ventral beak. A. *Keokukia rotunda* Carter, 1991, from the Keokuk Limestone of eastern Missouri (SL468), CM 45656. B. *Spinocarinifera arcuata* (Hall, 1858) from the Chouteau Limestone of northeastern Missouri (SL610), CM 45657. C. *Tesuquea formosa* Sutherland and Harlow, 1973, from the lower Gobbler Formation of southwestern New Mexico (SL4758), CM 45658. D. *Spinocarinifera nigra* (Gosselet, 1888) from the Calcaire d'Avesnelles Formation (lower Hastarian?) of northeastern France (M. Legrand-Blain Collection, SL 1244), CM 45659. All $\times 3$.

doensis (Girty, 1915), “A.” *crassicostata* (Dunbar and Condra, 1932), and “A.” *portlockiana* (Norwood and Pratten, 1855). None of these species has the shagreen texture inside the ventral umbones, nor do any of the Permian species assigned to the genus *Antiquatonia* by Cooper and Grant (1975). The North American species assigned to *Antiquatonia* may represent an undescribed homeomorph of considerably later origin than true Eurasian *Antiquatonia* of Viséan and Serpukhovian age. This unnamed North American genus is closely related to the genus *Reticulatia* Muir-Wood and Cooper, 1960, of Upper Carboniferous and Lower Permian age, which lacks the shagreen texture characteristic of the retariins. In fact, *Reticulatia* has a row of spines delimiting the ears and essentially differs externally from the so-called North American *Antiquatonia* only in lacking the ear ridge bearing the row of spines.

Following the Lower Viséan *Keokukia*, there are no other retariins in North America until the appearance of the Morrowan genus *Tesuquea* Sutherland and Harlow, 1973, which also bears a shagreen texture in the ventral beak (Fig. 3C). Sutherland and Harlow (1973) suggested close affinity of their new genus with *Antiquatonia* and noted the lack of an external ridge delimiting the ears and supporting the row of spines. However, a dorsal internal ridge delimiting the ears is absent in *Antiquatonia* but appears in the retariin genus *Kutorginella* Ivanova, 1951. Thus, similar morphologies and stratigraphic distributions suggest to us that *Tesuquea* and *Kutorginella* are sister genera, not *Tesuquea* and *Antiquatonia* as suggested by Sutherland and Harlow (1973). In North America, *Kutorginella* ap-

pears in the late Desmoinesian as *K. lasallensis* (Worthen, 1873) and ranges through the Missourian and Virgilian of the midcontinent; in Eurasia, the genus appears much earlier. The shagreen texture within the ventral umbo of *K. lasallensis* attests to its assignment to the genus *Kutorginella*.

The genera of the lineage *Keokukia*–*Antiquatonia*–*Kutorginella* are widely distributed in Eurasia. In North America, only *Keokukia* and *Kutorginella* are present, but the endemic genus *Tesuquea* replaces *Antiquatonia*. If this line of reasoning is correct, it permits us to draw the following conclusions:

1) The genus *Keokukia* probably appeared first in Eurasia in the late Tournaisian and migrated to North America by the late Osagean or early Viséan. In Eurasia, *Keokukia* gave rise to true *Antiquatonia*, whereas in North America, much later, it gave rise to *Tesuquea*.

2) The marine connection between North America and Eurasia during the Moscovian may have been temporary and short-lived. *Kutorginella* appeared in North America only near the end of the Desmoinesian (Moscovian). The North American sister genus of Eurasian *Antiquatonia*, *Tesuquea*, also was derived from *Keokukia* and appeared earlier than *Kutorginella*, sometime in the Morrowan (Bashkirian). It was endemic to North America and appeared allopatrically, becoming extinct later in the Morrowan.

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