Revision of latest Givetian–Frasnian Atrypida (Brachiopoda) from central North America

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The brachiopod fauna of the Middle–Late Devonian cratonic carbonate platform deposits of the Iowa Basin, central North America, contains twenty species of the order Atrypida, some of which are types for widespread genera common in Middle and Late Devonian faunas. The latest Givetian–early Frasnian deposits yield a diverse fauna consisting of ten species (two new) included in *Desquamatia (Independatrypa), D. (Seratrypa), Pseudoatrypa, Radiatrypa, Spinatrypa (Spinatrypa)* and *Spinatrypina (Exatrypa)*. Many of these forms occur in, or are closely similar to species known from, coeval faunas of central and western Canada. Middle Frasnian deposits of northern Iowa contain two species included in *Spinatrypa (S.)* and *Pseudoatrypa*, both of which are new. Late Frasnian strata of the Iowa Basin yield eight species included in *Costatrypa, Iowatrypa, Pseudoatrypa*, and *Spinatrypa (Spinatrypa)*, some of which are widespread in other subtropical and tropical faunas of the western US and western Canada. The taxa *Pseudoatrypa witzkei* sp. n., *Spinatrypa (S.) bunkeri* sp. n., *Spinatrypa (S.) thompsoni* sp. n., and *Spinatrypina (Exatrypa) johnsoni* sp. n. are proposed. *Pseudoatrypa*? sp. from the very late Frasnian of southern New Mexico is also illustrated.

K e y w o r d s : Brachiopoda, Atrypida, taxonomy, Givetian, Frasnian, Devonian, North America.

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Introduction

The most diverse and abundant latest Givetian and Frasnian atrypid brachiopod (order Atrypida, family Atrypidae) faunas known from subtropical settings in North America occur in carbonate platform facies in the Iowa Basin in Iowa, northwestern Illinois, and central Missouri (Figs 1, 2). The latest Givetian and Frasnian atrypid fauna of the Iowa Basin includes at least twenty species (four new). The ranges of nearly all known Devonian species of the order Atrypida in the Iowa Basin have been documented with respect to the conodont and brachiopod sequences by one of us (see Day 1989, 1990,

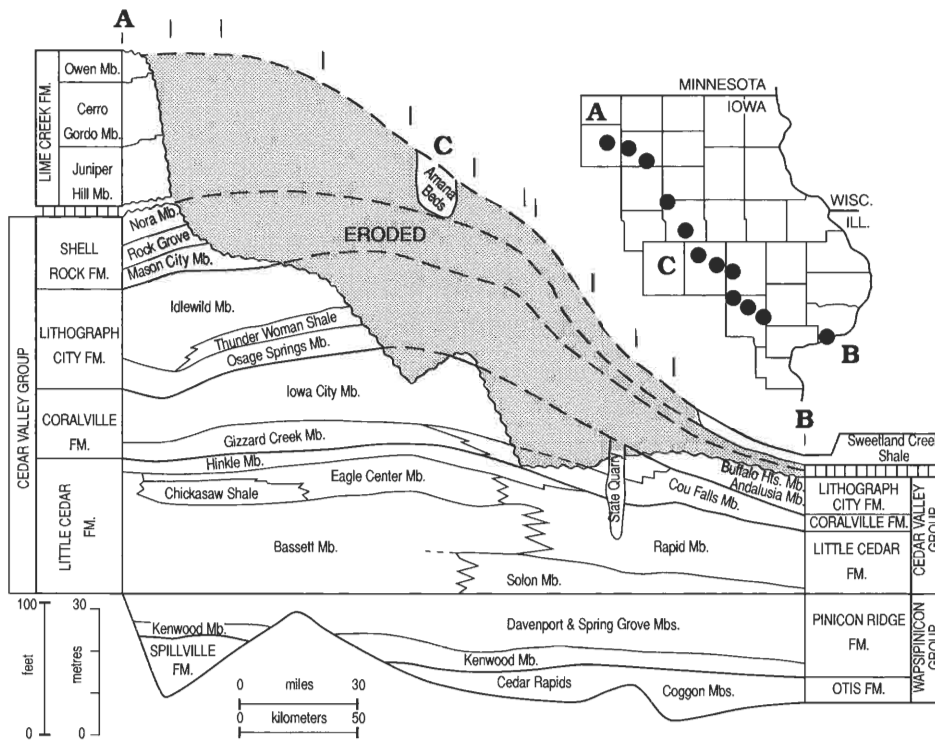


Fig. 1. Cross section of the late Eifelian–Frasnian strata of north-central and eastern Iowa. Modified from fig. 1 of Witzke *et al.* (1989), after fig. 1 of Day & Koch (1994), and Day (1994, 1996).

1992, 1994, 1995, 1996, 1997). Detailed discussions of geographic occurrences and biostratigraphic ranges of many of the Iowa Devonian (late Givetian–Frasnian) atrypids are also given in Day (1998).

A substantial number of widespread late Givetian and Frasnian Atrypida known across central and western North America were first described from the Devonian of Iowa and Missouri. Owing to the importance of this diverse and abundant fauna, we outline preliminary taxonomic revisions to selected Iowa Basin latest Givetian and Frasnian atrypids, including descriptions of four new species.

The material described in this paper is housed in University of Missouri, Columbia, Missouri (abbreviated UM) and University of Iowa, Iowa City, Iowa (abbreviated SUI).

Latest Givetian–Frasnian strata and atrypid brachiopod faunas of the Iowa Basin

The use of subage terms here including latest Givetian, early Frasnian, middle Frasnian and very late Frasnian follows Day (1998). Latest Givetian–early Frasnian rocks in the Iowa Basin (Figs 1, 2) are included in the Lithograph City Formation of Iowa and northeastern Missouri, and the upper Cedar Valley Formation and Snyder Creek Shale of central Missouri (Fig. 2). These rocks yield at least ten species of atrypids (Table 1). The

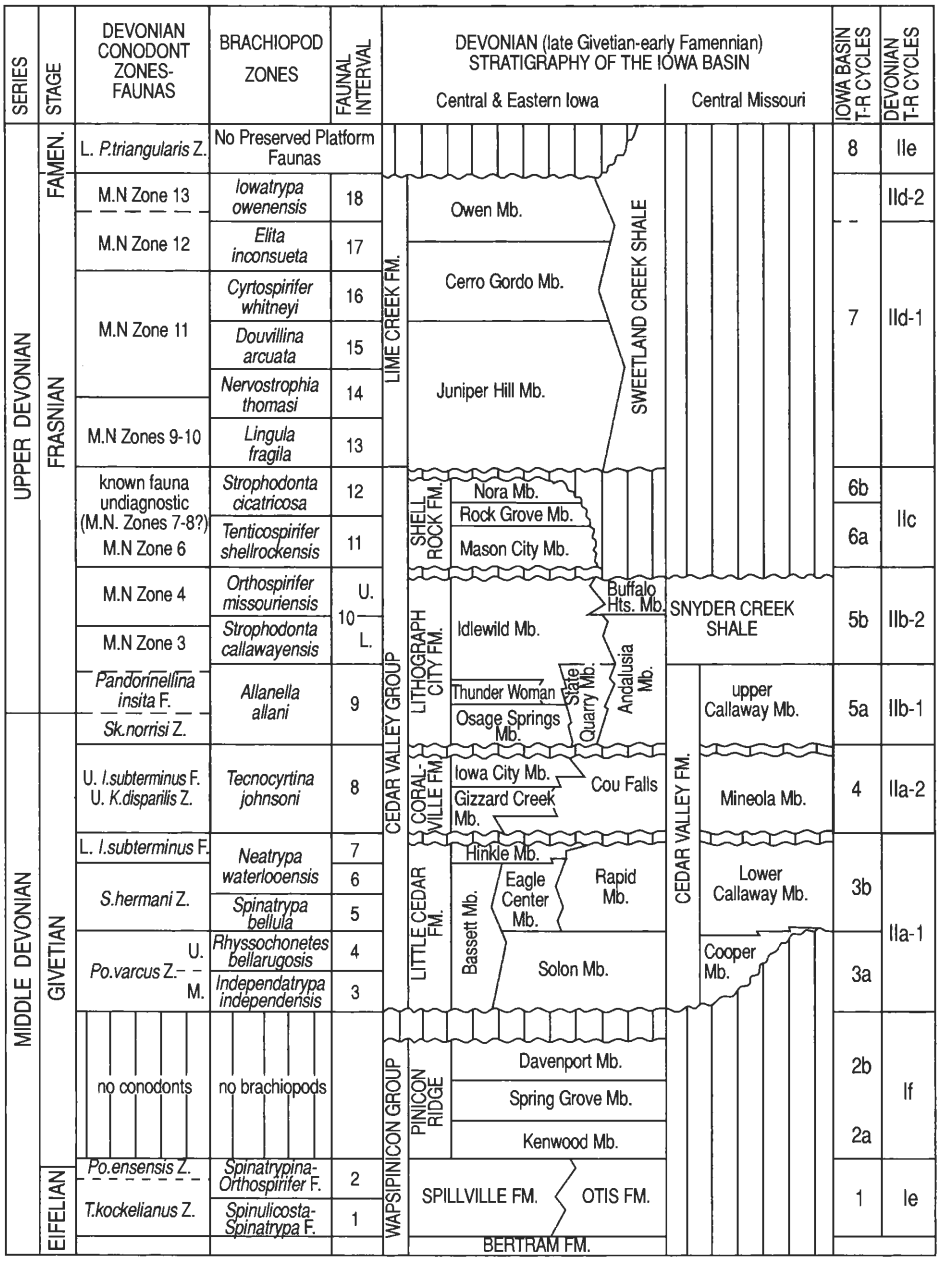


Fig. 2. Stratigraphic and biostratigraphic framework for the Middle–Late Devonian (late Eifelian–early Famennian) strata of the Iowa Basin showing relationships between: the eustatic Transgressive–Regressive (T-R) cycles of Johnson *et al.* (1985), Johnson & Klapper (1992), Day *et al.* (1996), and this study; and Iowa Basin Devonian T-R cycles of Witzke *et al.* (1989), Bunker & Witzke (1992), and Witzke & Bunker (1996). Conodont biostratigraphy follows Witzke *et al.* (1989), Klapper & Johnson in Johnson (1990), Day (1990), Klapper in Johnson & Klapper (1992). Brachiopod biostratigraphy from Day (1989, 1992, 1996, 1997). Iowa Devonian Faunal Intervals (I.D.F.I.) after Day (1996, 1997). Iowa Basin stratigraphy after Witzke *et al.* (1989) and Day (1997). Modified from Day (1997: fig. 4). Abbreviations: *I.* – *Icriodus, K.* – *Klapperina, P.* – *Palmatolepis, Po.* – *Polygnathus, S.* – *Schmidtognathus, Sk.* – *Skeletognathus, T.* – *Tortodus.*

Table 1. Latest Givetian–late Frasnian atrypid fauna from the Iowa Basin of the US midcontinent.

Fauna of the Lithograph City Formation (latest Givetian–early Frasnian) *Desquamatia (Independatrypa) scutiformis* (Stainbrook, 1938) *Pseudoatrypa lineata* (Webster, 1921) *P. rugatula* (Stainbrook & Ladd, 1924) *Radiatrypa clarkei* (Warren, 1944) *Spinatrypina (Exatrypa) johnsoni* sp. n.
Fauna of the Upper Callaway Member, Cedar Valley Formation (latest Givetian–early Frasnian) *D. (I.) scutiformis* (Stainbrook, 1938) *Pseudoatrypa missouriensis* (Miller, 1894)
Fauna of the Snyder Creek Shale (early Frasnian) *D. (Seratrypa) callawayensis* (Greger, 1936a) *D. (S) snyderensis* (Greger, 1936a). *P. missouriensis* (Miller, 1894) *R. gregeri* (Rowley, 1900) *Spinatrypa (Spinatrypa) thompsoni* sp. n.
Fauna of the Shell Rock Formation (middle Frasnian) *Pseudoatrypa witzkei* sp. n. *Spinatrypa (S.) bunkeri* sp. n.
Fauna of the Lime Creek Formation (late Frasnian) *Costatrypa varicostata* (Stainbrook, 1945) *Iowatrypa owenensis* (Webster, 1921) *I. minor* (Fenton & Fenton, 1924) *Pseudoatrypa devoniana* (Webster, 1921) *Spinatrypa (S.) rockfordensis* (Fenton & Fenton, 1924) *Spinatrypa (S.) planosulcata* (Webster, 1888)
Fauna of the Amana Beds (late Frasnian) *Costatrypa varicostata* (Stainbrook, 1945) *Pseudoatrypa devoniana* (Webster, 1921) *Spinatrypa (S.) planosulcata* (Webster, 1888) *Spinatrypa (S.) trulla* (Stainbrook, 1945)
Fauna of the Independence Shale (late Frasnian) *Costatrypa varicostata* (Stainbrook, 1945) *I. americana* (Stainbrook, 1945) *Pseudoatrypa devoniana* (Webster, 1921) *Spinatrypa (S.) trulla* (Stainbrook, 1945)

brachiopod sequence in these units is subdivided into three assemblage zones which are (in ascending order): the *Allanella allani, Strophodonta (S.) callawayensis*, and *Orthospirifer missouriensis* zones (Fig 2). Atrypids from these zones are associated with conodonts spanning the *Skeletognathus norrisi* Zone through Montagne Noire (M.N.) Zone 4 of Klapper (1989). Very late Givetian and early Frasnian faunas of the *Allanella allani* Zone (Fig. 2) feature *Desquamatia (Independatrypa) scutiformis* (Stainbrook, 1938), *Pseudoatrypa rugatula* (Stainbrook & Ladd, 1924), *P. missouriensis* (Miller, 1894), and *Spinatrypina (Exatrypa) johnsoni* sp. n. They occur in the lower Andalusia, State Quarry, Osage Springs, and lower Idlewild members of the Lithograph City Formation, and upper part of the Callaway member of the Cedar Valley Formation.

Atrypids from the early Frasnian *Strophodonta callawayensis* Zone (Fig. 2) include *Desquamatia (Independatrypa) scutiformis* (Stainbrook, 1938), *D. (Seratrypa) callawayensis* (Greger, 1936), *P. missouriensis* (Miller, 1894), *P. lineata* (Webster, 1921),

Radiatrypa clarkei (Warren, 1944), *R. gregeri* (Rowley, 1900), and *Spinatrypa (S.) thompsoni* sp. n. Atrypida of the early Frasnian *Orthospirifer missouriensis* Zone (upper Idlewild Member of the Lithograph City Formation and upper Snyder Creek Shale) include: *P. missouriensis* (Miller, 1894), *P. lineata* (Webster, 1921), *S. (D.) snyderensis* (Greger, 1936), and *Spinatrypa (S.) thompsoni* sp. n.

Middle Frasnian deposits of the Shell Rock Formation of Iowa (Table 1) feature two new species of *Pseudoatrypa* and *Spinatrypa*. The Shell Rock Formation is divided into the Mason City, Rock Grove, and Nora members (Figs 1, 2). The brachiopod sequence of the Shell Rock Formation (Day 1989) is divided into the basal *Tenticospirifer shellrockensis* and overlying *Strophodonta cicatricosa* zones (Fig. 2). Both of the Shell Rock species first occur at or near the base of the *T. shellrockensis* Zone and range into the latter zone in northern Iowa.

Late Frasnian deposits of Iowa are included in the Amana Beds, Independence Shale and Lime Creek Formation (Table 1). The Lime Creek Formation consists of mixed carbonate-clastic platform deposits yielding well preserved, abundant, and diverse brachiopods. The Lime Creek is divided into the Juniper Hill, Cerro Gordo, and Owen members (Fig. 2). Day (1989, 1996) subdivided the brachiopod sequence in the Lime Creek Formation into six zonal intervals (Fig. 2). Atrypids (*Pseudoatrypa devoniana*) first appear in the *Nervostrophia thomasi* Zone with conodonts correlated with M.N. Zone 11. Range inceptions of the remainder of the Lime Creek atrypid fauna (Table 1) are in the succeeding zonal intervals (see Day 1998: fig. 4).

The Amana Beds (formerly considered as part of the Independence Shale by Stainbrook 1945) are known to be an in-place succession of shales and limestones considered as a deeper water facies of most of the Cerro Gordo, and perhaps part of the Owen Member of the Lime Creek Formation (Bunker & Witzke 1992; Day 1995, 1996; Witzke & Bunker 1996). Three of the four species of Atrypida known from the Amana Beds (Fig. 2, Table 1) also occur in the Lime Creek Formation. The Independence Shale is a shale unit that fills karst cavities in older Cedar Valley Group platform carbonate rocks in eastern Iowa. Shelly fossils from the Independence Shale are only known from those cave-fillings in the vicinity of the town of Independence (type area). Other cave fillings discovered during construction on the University of Iowa campus in the Johnson County area have yielded abundant late Frasnian conodonts, but no brachiopods (W. Furnish personal communication 1990). The collective faunas of the late Frasnian units of Iowa include: *Pseudoatrypa devoniana* (Webster, 1921), *Spinatrypa (S.) planosulcata* (Webster, 1888), *S. (S.) rockfordensis* (Fenton & Fenton, 1924), *S. (S.) trulla* (Stainbrook, 1945), *Costatrypa varicostata* (Stainbrook, 1945), *Iowatrypa owenensis* (Webster, 1921), *I. minor* (Fenton & Fenton, 1924) and *I. americana* (Stainbrook, 1945).

Systematic paleontology

***Desquamatia (Independatrypa) scutiformis* (Stainbrook, 1938).** — [= *Atrypa reticularis* Hall 1858: p. 515, pl. 6: 4–5. = *Atrypa lineata* Webster, variant Fenton & Fenton 1935: p. 380, pl. 38: 8; pl. 43: 10, 11. = *Atrypa scutiformis* Stainbrook 1938: p. 234, pl. 31: 15, 16, 19, 20; Maurin & Raasch 1972: pl. 6: 1–4. = *Atrypa* n. sp. 'KAKWA' Maurin & Raasch 1972: pl. 6: 5–12].

Revised description. — Medium to large *D. (Independatrypa)* (Figs 3, 4); shell dorsibiconvex, shield-shaped outline; maximum length slightly less than or equal to width in large adult

specimens; maximum shell width normally just anterior of hinge line; moderately to highly inflated dorsal valve, much more so than its presumed ancestor *D. (I.) randalia* (Stainbrook, 1938); costae wider and higher than in *D. (I.) independensis* (Webster, 1921) from the Little Cedar Formation of Iowa, and *D. (I.)* sp. cf. *D. (I) independensis* (Webster, 1921) from the Souris River Formation of Manitoba (Norris: in Norris *et al.* 1982), and the Waterways Formation of Alberta (Norris 1983); growth lamellae/frill bases less regularly spaced than in *D. (I.). independensis* (Webster, 1921) and *D. (I.)* sp. cf. *D. (I.) independensis* (Webster, 1921), becoming crowded anteriorly in large adult specimens.

Discussion. — Large numbers of forms typical of Stainbrook's (1938) *Atrypa scutiformis* with the more inflated-elongate morphotypes typical of *A. lineata* Webster, variant of Fenton & Fenton (1935), and intergradational specimens occur in direct association in the Andalusia Member of the Lithograph City Formation in eastern Iowa (see Buffalo Quarry locality of Day 1992: p. 70, fig. 10, units 8, 9). The form illustrated and described by Fenton & Fenton (1935) from Andalusia, Illinois is identical to juvenile growth forms of Stainbrook's *Atrypa scutiformis*. Stainbrook (1938: p. 235) designated the type locality of *A. scutiformis* as Carpenters Quarry in Muscatine County (now inactive and flooded). A type stratum was never specified other than the *Stropheodonta* zonule of the *Waterlooensis* zone. This interval corresponds to the lower 1.39 metres (4.5 feet) of the Andalusia Member of the Lithograph City Formation (see Day 1992: fig. 10, units 8, 9) exposed at the Lafarge Corporation Quarry (=Buffalo Quarry of older reports) in the town of Buffalo, Scott County, Iowa.

Range and occurrence. — This species is restricted to most of the latest Givetian–early Frasnian T-R cycle IIb of Johnson *et al.* (1985), Johnson & Klapper (1992), or the entire interval of T-R cycle IIb-1 and lower part of T-R cycle IIb-2 of Day *et al.* (1994, 1996) in Iowa, Missouri, and western Canada. In Iowa, this species occurs in the State Quarry, Andalusia, Osage Springs, and lower half of the Idlewild Member of the Lithograph City Formation. In central Missouri, it occurs in the upper part of the Callaway Member (strata bearing the conodonts of the lower part of the *P. insita* conodont Fauna = *S. norrisi* Zone) of the Cedar Valley Formation in Callaway and Montgomery counties. In northeastern British Columbia, Maurin & Raasch (1972, pl. 6: 1–4) illustrate this species from the Flume Formation in the upper part of their Assemblage 3.

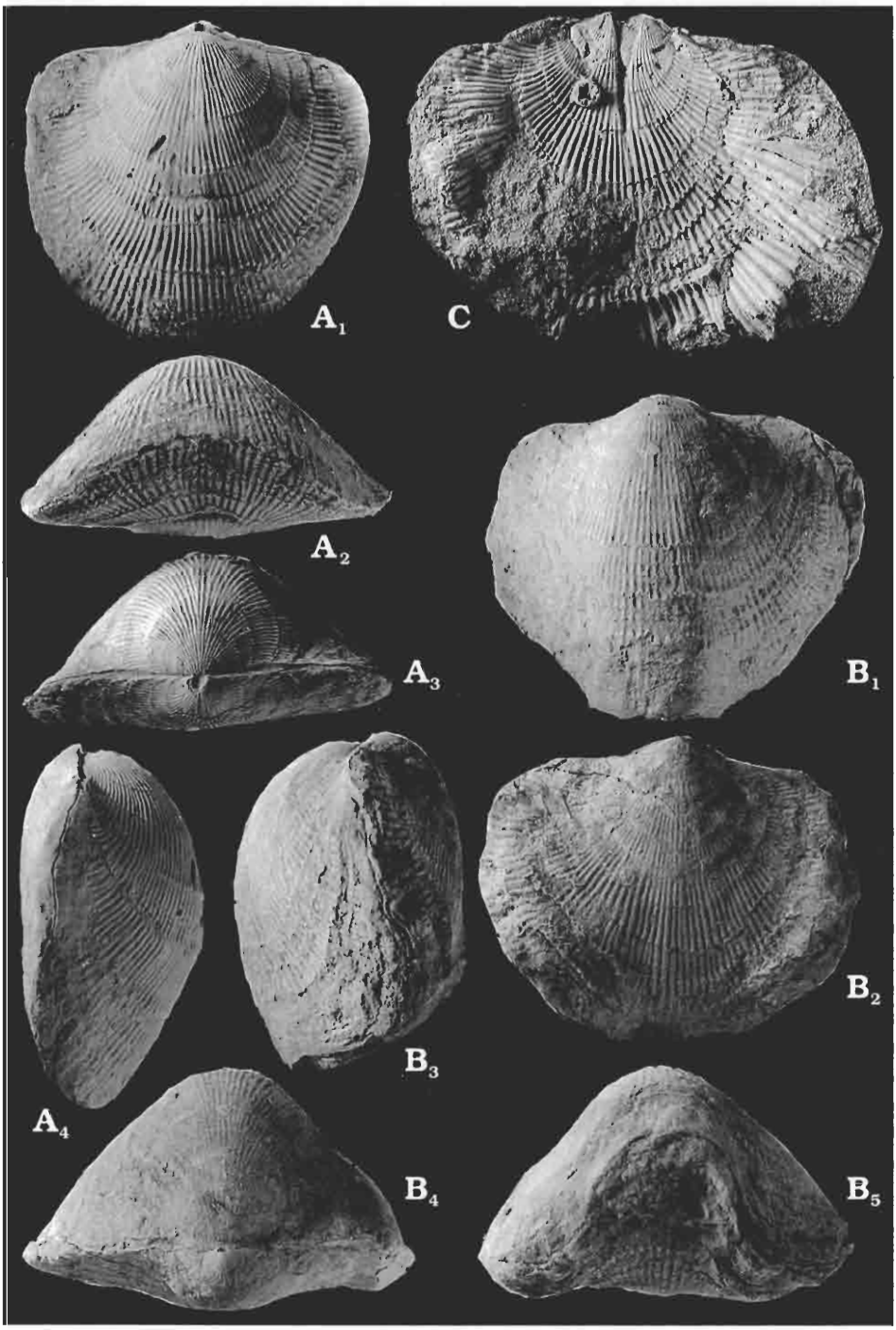
Its range in the Iowa Basin brachiopod sequence is from the base of the *Allanella allani* Zone through the *Strophodonta callawayensis* Zone (Fig. 2). Based on associated conodont faunas (Day 1992, 1996, 1997; Day *et al.* 1996), its range is from lower part of the *Skeletognathus norrisi* Zone to the upper part of M.N. Zone 3 of Klapper (1989).

***Desquamatia (Seratrypa) callawayensis* (Greger, 1936).** — [= *Atrypa callawayensis* Greger 1936a: p. 51–52, pl. 3: 9–11; (*non* Branson 1944: pl. 23: 15)].

Discussion. — This rare species (Fig. 5) is restricted to the lower part (New Bloomfield Member) of the Snyder Creek Shale of central Missouri, and is the presumed ancestor of *D. (S.) snyderensis* (Greger, 1936). The later form occurs above *D. (S.) callawayensis* in the upper part of the Snyder Creek Shale (upper part of the Craghead Branch and Cow Creek members) in the Craghead Branch Quarry (Day 1997: fig. 6, section CCQ, table 3).

The close relationship of both species is reflected by similar external ornament including: the numerous, rounded tubular ribs; regularly spaced growth lamellae marking attachment sites of frills; and numerous very fine growth lamellae between major raised lamellae marking frill attachment sites. Frills on the valves of shells of both species are often well preserved and extend laterally and anteriorly beyond the shell margin to distances equal to half of the shell length.

Fig 3. **A–C.** *Desquamatia (Independatrypa) scutiformis* (Stainbrook, 1938), **A_1–A_4** dorsal, anterior, posterior, and lateral views of SUI 51740; **B_1–B_5** dorsal, ventral, lateral, posterior and anterior views of SUI 85775, both from latest Givetian–early Frasnian Andalusia Member of the Lithograph City Formation, unit 9 at the Buffalo Quarry section of Day (1992: figs 10, 11, sample 11). **C.** Ventral view of SUI 85776 showing



frill attached to ventral valve; from latest Givetian Andalusia Member of the Lithograph City Formation, unit 8 at the Buffalo Quarry section of Day (1992: figs 10, 11: sample 9), Scott County, Iowa. All × 1.25.

D. (S.) callawayensis differs from its descendent *D. (S.) snyderensis* in its smaller adult shell size (up to 32 mm wide, 27 mm long) versus the always larger adult shells of *D. (S.) snyderensis* (up to 49 mm wide, 44 mm long). The latter species is distinguished by its much more inflated dorsal valve. In both forms, adult shell width exceeds length (Figs 5–7). *D. (S.) callawayensis* is also distinguished from its descendent by its much coarser tubular ribs which average 4 ribs/5 mm on the ventral shell surface at a distance of 10 mm from the ventral beak, versus 8 ribs/5 mm at the same distance from the ventral beak on shells of *D. (S.) snyderensis*. The fine growth lamellae on the shell surface between frills of *D. (S.) snyderensis* differ from those of *D. (S.) callawayensis* in that they are lamellose (0.1 mm) and erect being deflected upward at a high angle away from the shell surface, especially where well preserved in the rounded grooves or interspaces between ribs. The two species also differ in development of the anterior fold. In anterior view (Fig. 5E–I) the folds of *D. (S.) callawayensis* are gently rounded and their depth ranges from 60 to 85% of the total shell thickness, whereas the depth of the sulcus is 50–70% of total shell thickness in *D. (S.) snyderensis* (Fig. 7, see anterior views).

D. (S.) callawayensis is restricted to the early Frasnian New Bloomfield Member of the Snyder Creek Shale in its type area in Callaway County in central Missouri. There, the range of this species is confined to *Strophodonta callawayensis* Zone (Fig. 2) as defined in Day (1992), and revised by Day (1997), corresponding to Iowa Devonian Faunal Interval (I.D.F.I.) 10L of Day (1997). Conodont faunas (Day 1997) from the interval in Missouri correlated with the *Strophodonta callawayensis* Zone (= I.D.F.I. 10L) are correlated with upper part of M.N. Zone 3 and lowermost M.N. Zone 4 of Klapper (1989).

The occurrence of these two forms in the Iowa early Frasnian provides evidence that this subgenus was reintroduced to the Iowa Basin from the western Canada during the transgression that initiated T-R cycle IIb-2 (Fig. 2). The older Iowa Basin species lineage is developed in late Givetian rocks of the Little Cedar and Coralville formations in the lower part of the Cedar Valley Group (Day 1992, Fig. 2), and consists of *D. (Seratrypa) rustica* (Stainbrook, 1938) and *D. (S.) rotunda* (Stainbrook, 1938). The last element of this older lineage, i.e. *D. (S.) rotunda*, was extinct in the US midcontinent within the upper part of the undifferentiated *disparilis* Zone (late Givetian).

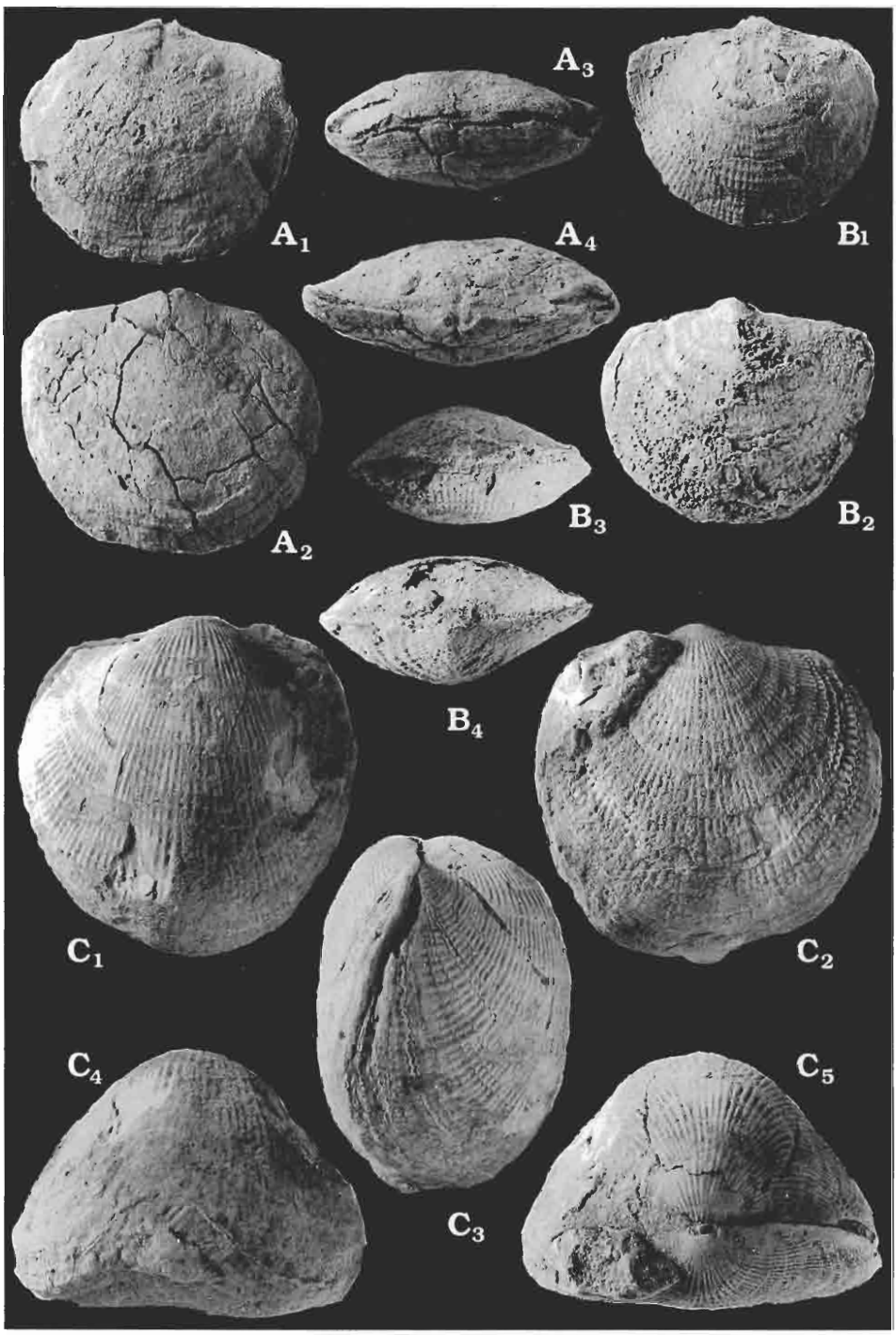
***Desquamatia (Seratrypa) snyderensis* (Greger, 1936).** — [= *Atrypa reticularis* (Linnaeus) Branson 1923: p. 97, pl. 21: 7 only, pl. 23: 13 only. = *Atrypa snyderensis* Greger 1936a: p. 52, pl. 4: 1–5. =*Atrypa callawayensis* Greger, Branson 1944: p. 150, pl. 23: 15].

Discussion. — This large and distinctive finer-ribbed species of *D. (Seratrypa)* (Figs 6, 7) is most common in the uppermost meter of the Craghead Branch Member and ranges into the lower half of the Cow Creek Member of the Snyder Creek Shale in exposures along Craghead and Aux Vasse creeks in eastern Callaway County, Missouri. Its lowest occurrence (SUI 85849) is in the lower metre of the Craghead Branch Shales at the New Bloomfield East locality of Day (1997) corresponding to the lower part of unit 4 of New Bloomfield section of the Snyder Creek Shale (Thompson 1993: p. 148, fig. 104).

This species is only known from central Missouri, where its range (Fig. 2) is restricted to the interval of the early Frasnian *Orthospirifer missouriensis* Zone, corresponding to I.D.F.I. 10U of Day (1997). Conodonts (Day 1997) from the interval of the *O. missouriensis* Zone are within M.N. Zone 4 of Klapper (1989).

Material and localities. — UM 5375 which is the same shell illustrated by Branson (1923: pl. 23: 13; 1944: pl. 23: 15). Measured specimens: SUI 65613, 65615, 65616, 65621–65627, 65629–65634, and SUI 65618 and SUI 65619 (Branson Collection). All from the uppermost part →

Fig. 4. **A–B**. *Pseudoatrypa*? sp. $\mathbf{A_1}$–$\mathbf{A_4}$ dorsal, ventral, anterior and posterior views respectively of SUI 85752; $\mathbf{B_1}$–$\mathbf{B_4}$ dorsal, ventral, anterior and posterior views respectively of SUI 85753; both from latest Frasnian Salinas Peak Member of the Contadero Formation, sample 27 at Salinas Peak Section, locality 5; all × 2. **C**. *Desquamatia (Independatrypa) scutiformis* (Stainbrook 1938). $\mathbf{C_1}$–$\mathbf{C_5}$ dorsal, ventral, lateral, anterior and posterior views of SUI 85774; × 1.25, from latest Givetian–early Frasnian Andalusia Member



of the Lithograph City Formation, unit 9 at the Buffalo Quarry section of Day (1992: figs 10, 11, sample 11), Scott County, Iowa.

of the Craghead and Cow Creek members from exposures on Craghead Creek (erroneous Snyder Creek Shale type section reported by Branson 1923: p. 38), and the Craghead Creek Quarry (see Thompson 1993: p. 152, fig. 109) east of the aforementioned section on Craghead Creek (= Craghead Creek Quarry Section of Day 1997).

***Pseudoatrypa*? sp.** — Specimens recovered by Day (1988) from late Frasnian in the San Andres Mountains of southern New Mexico (Fig. 4) have dorso-ventrally compressed biconvex shells, shield-like outline, fine radial costae, concentric growth lamellae, and planar apsacline ventral interareas. These external features are similar to those of certain species of *Pseudoatrypa* Copper (1973). The state of preservation of the four specimens on hand does not permit a positive identification and assignment to *Psuedoatrypa* or species description at this time. The New Mexico material assigned to *Pseudoatrypa*? sp. was recovered from the upper part of the Salinas Peak Member of the Contadero Formation in the northern San Andres Mountains. The best preserved specimens come from sample 27 in the Salinas Peak Member of the Contadero Formation at Salinas Peak (Day 1998: figs 9–11). Two additional occur in sample 35 from the Salinas Peak Member at Rhodes Canyon (Day 1998: figs 10, 11). The interior remains unknown. The stratigraphic range of the *Pseudoatrypa*? sp. is very high Frasnian (M.N. Zone 13).

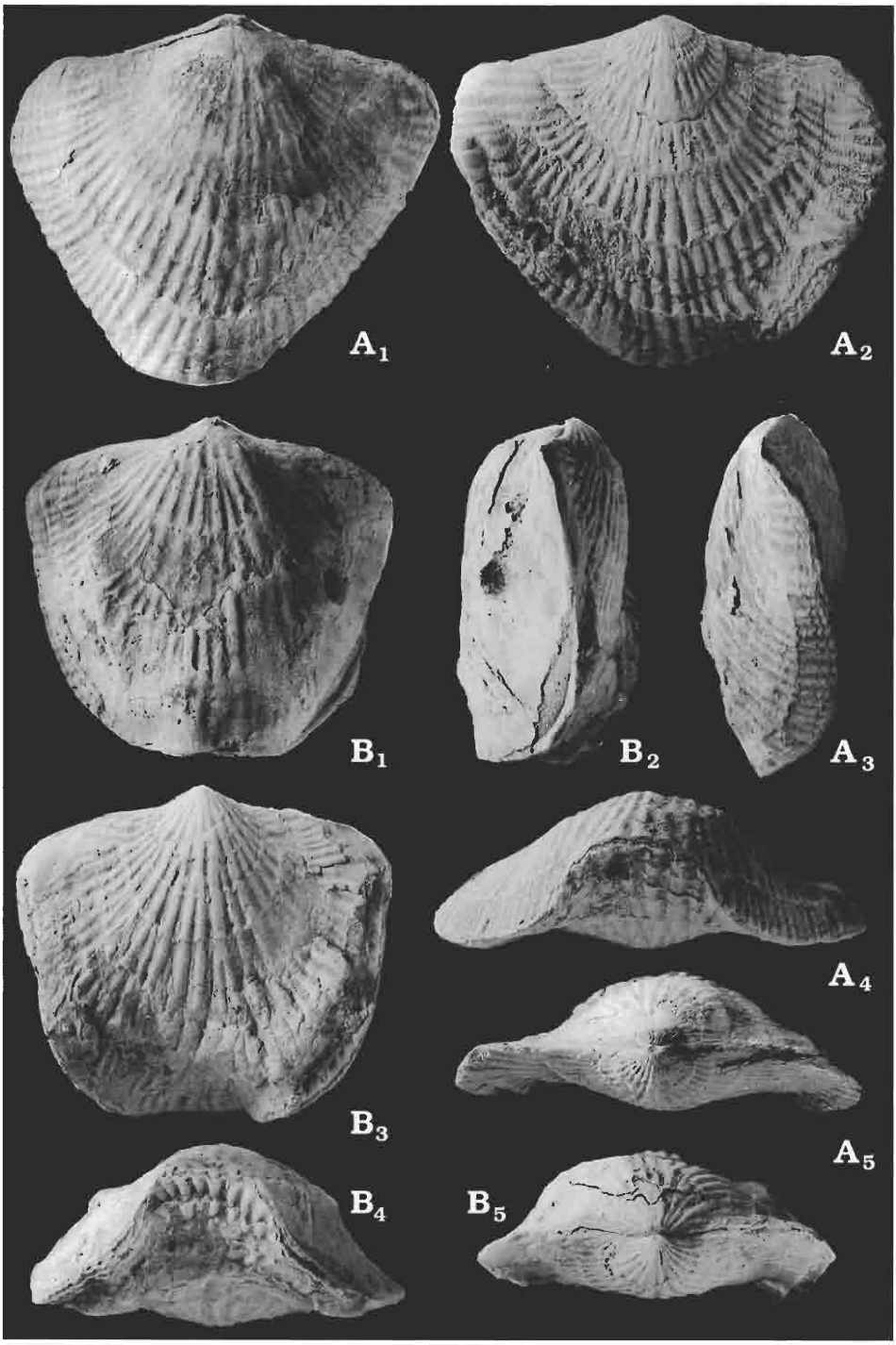
***Pseudoatrypa devoniana* (Webster, 1921).** — [= *Atrypa devoniana* Webster, 1921; Fenton & Fenton 1924: pp. 134–136, pl. 26: 16–24; Fenton & Fenton 1932: pl. 21: 5; Fenton & Fenton 1935: (forms A–C) p. 382–383, pl. 37: 1–8, pl. 39: 12; Stainbrook 1935: p. 711, pl. 2: 1–2; Stainbrook 1945: p. 47, pl. 5: 24–26, 29–32, fig. 1: 1; Stainbrook 1948: p. 776, pl. 2: 23, 24, 48; Wallace 1978: fig. 4H. = *Atrypa devoniana alta* Fenton & Fenton 1924: pp. 136–137, pl. 26: 25, 26. = *Atrypa devoniana decrescens* Fenton & Fenton 1935: p. 383, pl. 38: 4–6. = *Atrypa hackberryensis* Fenton & Fenton 1924: p. 137–138, pl. 26: 12–15. = *Atrypa* cf. *devoniana* Webster, Warren & Stelck 1956: pl. 18: 1–3. = *Atrypa* cf. *hackberryensis* Fenton & Fenton, Warren & Stelck 1956: pl. 18: 4–6, pl. 20: 20–27. = *Atrypa* sp. J, McLaren, Norris, McGregor 1962: p. 30, pl. 14: 16–18. = *Pseudoatrypa devoniana* (Webster) Copper 1973: p. 493–494, pl. 1: 3–6; Beus 1978: pp. 49–50, pl. 1: 35, 39–42, fig. 1; Cooper & Dutro 1982: p. 87, pl. 22: 1–16, pl. 23: 32–38].

Discussion. — A variety of Givetian forms in the United States have erroneously been assigned to *P. devoniana* (Webster, 1921). The species is restricted to the late Frasnian, but is closely related to the middle Frasnian *P. witzkei* sp. n. described below. *P. devoniana* (Fig. 8) is a eurytopic species that occurs in a wide variety of late Frasnian carbonate and clastic shelf deposits throughout western Canada, the western US (Arizona, New Mexico), the US midcontinent, and possibly eastern North America.

Study of shells from the type section of the Cerro Gordo Member of the Lime Creek Formation and the Amana Beds (Fig. 9) indicate that *P. devoniana* displays a wide range of phenotypic variation that encompasses: compressed convexoplane morphotypes with alate cardinal margins such as *Atrypa hackberryensis* Fenton & Fenton, 1924 (Figs 8B_1–B_5); elongate and more inflated dorsibiconvex forms typical of material illustrated under *Atrypa devoniana* Webster, 1921, by Fenton & Fenton (1924: p. 231, pl. 26); and other varieties illustrated in Fenton & Fenton (1932, 1935).

This species is known from Iowa, Arizona, New Mexico, Alberta (Warren & Stelck 1956; McLaren *et al.* 1962), the Northwest Territories (NWT), and from the Guilmette Formation of the Great Basin (Drewes 1967). The oldest occurrence of *P. devoniana* in the Iowa Devonian is within late Frasnian M.N. Zone 11 of Klapper (1989) as documented in Day (1989, 1990). The first occurrence of this species is in the *Douvillina arcuata* Zone in the Juniper Hill Member of the Lime Creek Formation in the subsurface of southeastern Cerro Gordo County (Day 1989a, 1995a). The highest known occurrences in the Lime Creek Formation are within the *Iowatrypa owenensis* Zone

Fig. 5. **A–B.** *Desquamatia (Seratrypa) callawayensis* (Greger, 1936). **A_1–A_5** dorsal, ventral, lateral, anterior, and posterior views of UM 1283b; **B_1–B_5** dorsal, lateral, ventral, anterior, and posterior views of UM 1283a. Both from the type section the Snyder Creek Shale, Callaway County, Missouri (location in Thompson 1993; location of type section given in Branson 1923: p. 38 is erroneous). All × 2.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(Fig. 2, M.N. Zone 12-M.N. Zone 13?). Occurrences in the Upper Mount Hawk Formation (Warren & Stelck 1956) also are late Frasnian, within the M.N. Zone 12 based on Mount Hawk conodont faunas yielding *Palmatolepis foliacea* (Klapper & Lane 1989).

***Pseudoatrypa lineata* (Webster, 1921).** — [= *Atrypa lineata* Webster 1921: p. 17; Fenton & Fenton 1932: p. 207, fig. 2B; Fenton & Fenton 1935: p. 379–380, pl. 38: 1–3, 7, pl. 43: 8, 9. (non *Atrypa lineata* Webster, variant Fenton & Fenton 1935: p. 380, pl. 38: 8, pl. 43: 10, 11). = *Atrypa lineata* var. *inflata* Webster 1921: p. 19; *Atrypa inflata* Webster, Fenton & Fenton 1935: p. 381, pl. 43: 1–7. = *Atrypa* sp. nov. 473, var. A of Maurin & Raasch 1972: pl. 7: 1–8].

Emended description. — A large (up to 37 mm in length, 35 mm in width) species of *Pseudoatrypa* (Fig. 10) with a globose dorsibiconvex-convexoplane shell with an inflated hemispherical dome-like dorsal valve; shell length exceeds width in all growth stages (Fig. 11); broad to angular fold developed posterior of mid-valve, becoming more pronounced towards anterior margin in large adult shells (30 mm), depth of the fold is 1/4–1/3 shell thickness in large adult shells; exterior of both valves with fine radial tubular ribs (9–10/5 mm at anterior margin); regularly spaced concentric lamellae marking attachment sites of frills in early growth stages (shells up to 20 mm in length), lamellae becoming crowded towards anterior and lateral margins in larger adults (20 mm length); short frills rarely preserved.

Discussion. — The presumed ancestor of this species is *Pseudoatrypa missouriensis* (Miller, 1894). *P. missouriensis* evolved during the very late Givetian in shallow carbonate platform habitats along the southern margin of the Iowa Basin, perhaps from an older late Givetian stock with fine tubular ribs such as *P. minor* (Stainbrook, 1938). *Pseudoatrypa lineata* probably evolved in the early Frasnian as one of a number of geographic species of *Pseudoatrypa* during migration and rapid dispersal of populations into new habitats in the main part of the Iowa Basin (north-central Iowa) and from there into western North America (British Columbia).

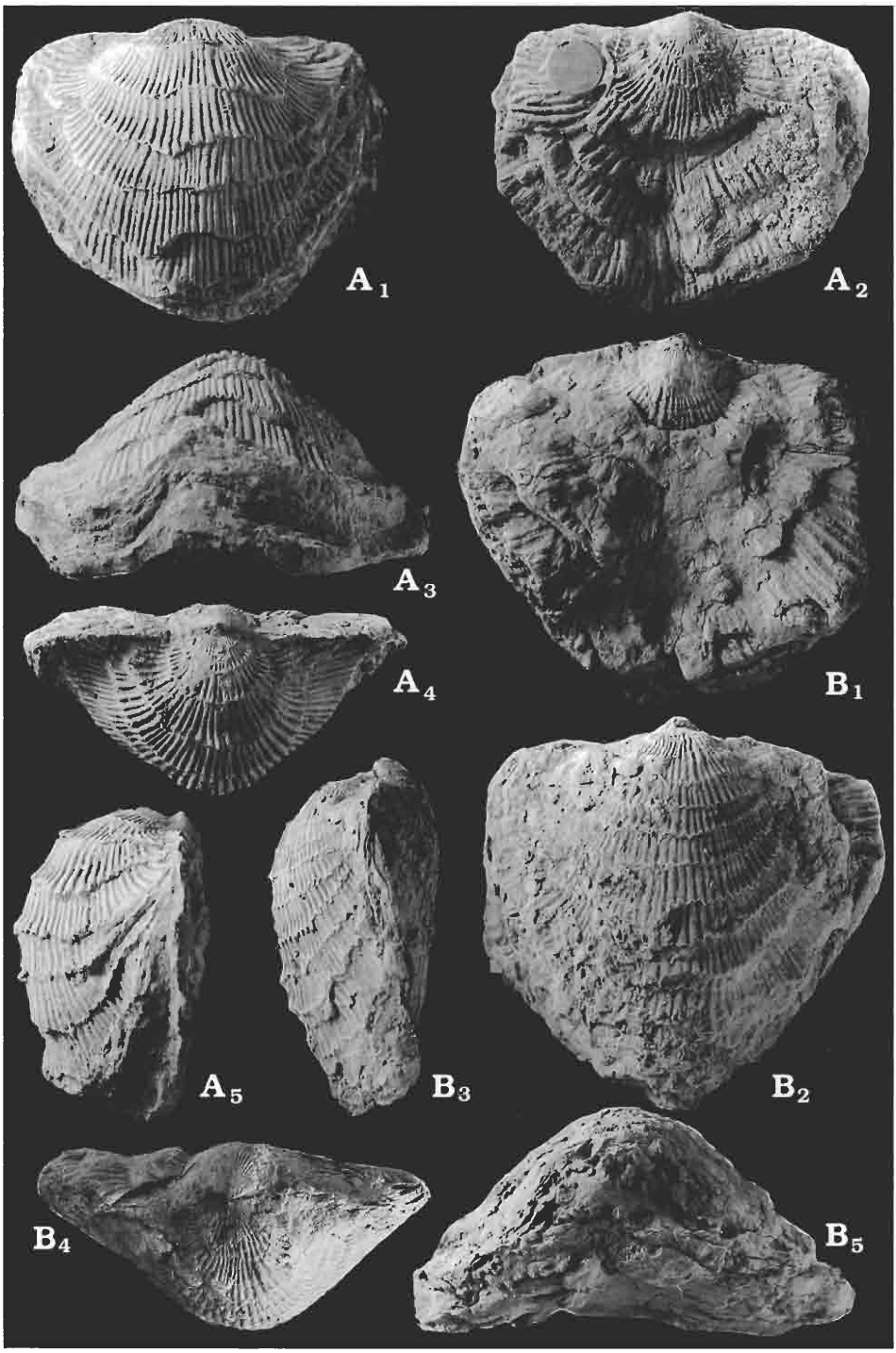
Pseudoatrypa lineata (Webster, 1921) differs from *P. missouriensis* (Miller, 1894) in the development of more numerous fine tubular radial ribs, smaller adult size, and broader angular fold. It lacks the strong elevated and prominent dorsal fold developed anterior of mid-valve as seen on large adult shells of *P. missouriensis*, and does not develop a tongue at the anterior margin by the dorsal deflection of the margin of the ventral valve in the sulcus as seen in larger (40 mm) adult shells of *P. missouriensis*.

The holotype of *Atrypa lineata* (Webster, 1921) came from the upper Osage Springs Member of the Lithograph City Formation in the vicinity of Charles City, Iowa. Websters type and additional new specimens were illustrated in Fenton & Fenton (1935). Numerous additional specimens (Figs 7, 8) are from the upper Idlewild Member at the Hanneman Quarry in western Floyd County (Day 1992, 1996).

Occurrence and range. — In Iowa *P. lineata* occurs in the upper Osage Springs and Idlewild members of the Lithograph City Formation. Maurin & Raasch (1972) illustrated this form from British Columbia from the middle part of the Flume Formation.

***Pseudoatrypa missouriensis* (Miller, 1894).** — [=*Atrypa missouriensis* Miller 1892: p. 61, pl. 9: 19–21; Miller 1894: p. 315, pl. 9: 19–21. = *Atrypa missouriensis* Miller, Fenton & Fenton 1930: p. 15–17, pl. 2: 5–9; Greger 1936: pl. 1: 1–16, pl. 2: 1–6; Fraunfelter 1974: p. 58, pl. 21: 4; Kottlowski 1950: pl. 2: 1–12; (*non*: Girty 1899: p. 29, pl. LXVI: 2a–2c; Laird 1947: p. 457, pl. 64: 19–22). = *Atrypa reticularis* (Linnaeus) Branson 1923: p. 97, pl. 23: 12 only. = *Atrypa devoniana* Fenton & Fenton, Greger 1936: p. 48, pl. 3: 1–5].

Fig. 6. **A–B.** *Desquamatia (Seratrypa) snyderensis* (Greger, 1936). $\mathbf{A_1}$–$\mathbf{A_5}$ dorsal, ventral, anterior, posterior, and lateral views of UM 5373; $\mathbf{B_1}$–$\mathbf{B_5}$ ventral, dorsal, lateral, posterior, and anterior views SUI 65617. Specimens UM 5373 (Branson collection) from the early Frasnian Cow Creek Member of the Snyder Creek Shale, eastern Callaway County, Missouri (exact locality unknown). SUI 65617 from the New Bloomfield Member of the Snyder Creek Shale at the New Bloomfield East locality of Day (1997: fig. 6, locality NBE, table 4, sample from unit 3) from southern Callaway County, Missouri. All × 1.25.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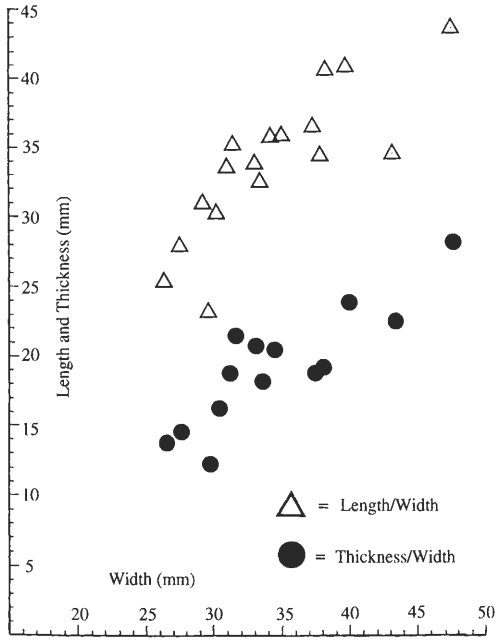


Fig 7. Plots of shell measurements of *Desquamatia (Seratrypa) snyderensis* (Greger, 1936). All specimens early Frasnian, from the uppermost Craghead Branch and Cow Creek members of the Snyder Creek Shale, Callaway County, Missouri.

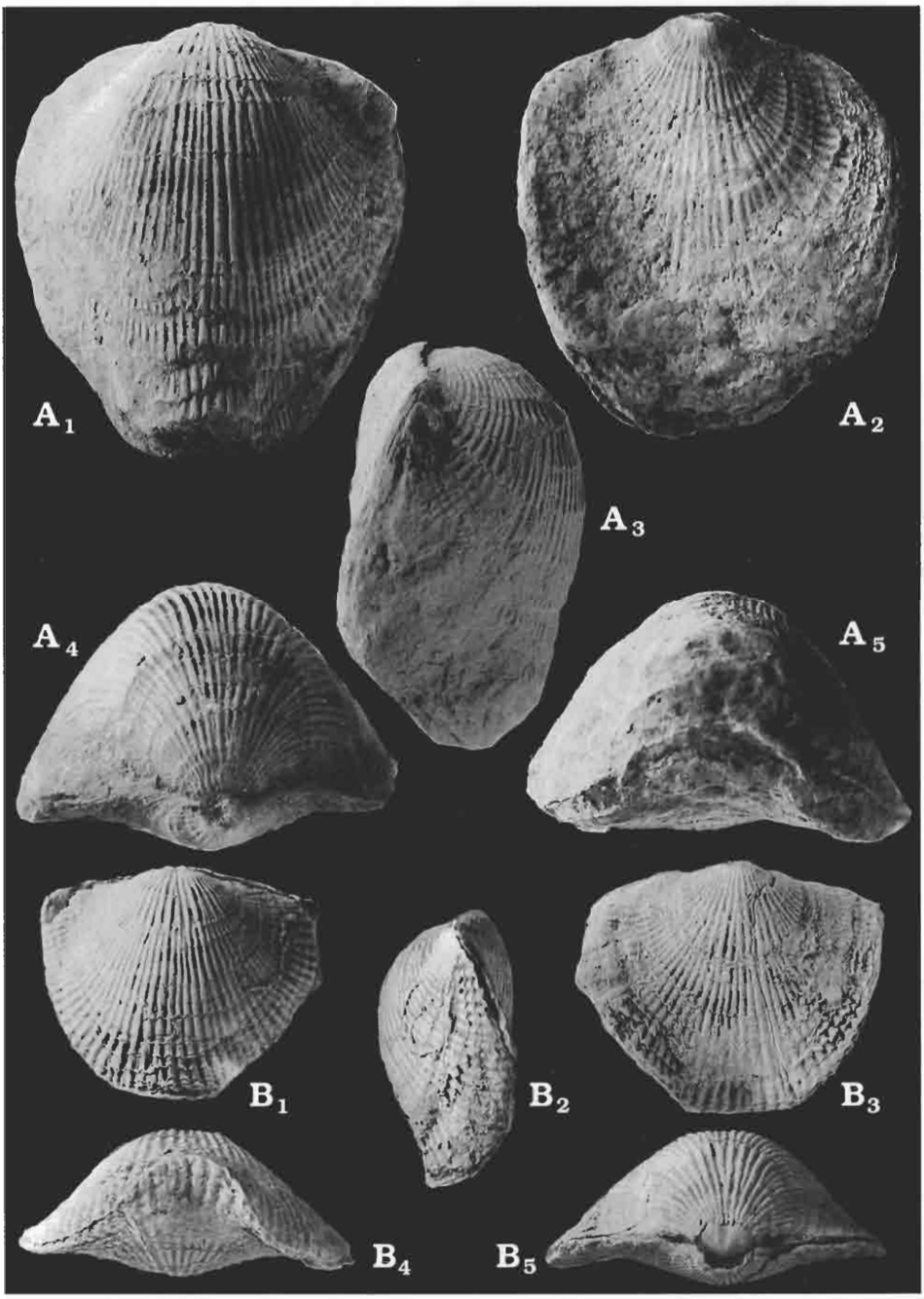
C o m m e n t s . — The diagnosis of *Pseudoatrypa missouriensis* (Miller, 1894) is emended here to recognize and include the wide range of phenotypic variation and large adult shell size (Figs 12, 13) achieved by specimens in large collections from the latest Givetian and early Frasnian Cedar Valley Formation and Snyder Creek Shale. The type specimens of Miller (1894), redescribed in Fenton & Fenton (1930), are juvenile shells. Large adult specimens (Fig. 12) are up to three times the size of the type specimens described in Miller (1892, 1894) and Fenton & Fenton (1930). This species is restricted to the latest Givetian and early Frasnian upper part of the Cedar Valley Limestone (upper Callaway Member) and Snyder Creek Shale as discussed in Miller (1892), and Day (1997).

R e v i s e d d i a g n o s i s . — A large (up to 44 mm in length, 47 mm in width) species of *Pseudoatrypa* with a globose dorsibiconvex shell with an inflated dome-like dorsal/brachial valve; shell width slightly exceeds length in nearly all juvenile and adult shells (elongate shells occur but are rare); pronounced-elevated and rounded fold develop at mid-valve becoming very pronounced towards anterior margin in large adult shells (20–25 mm); exterior of both valves with rounded tubular ribs with (6–8 ribs/5 mm at anterior margin); regularly spaced concentric lamellae marking attachment sites of frills (every 5–6 mm) in shells up to 40 mm in length, becoming crowded towards valve margins in larger adults (35–40 mm length), short frills or extended lamellae up to 4 mm in length observed on juvenile shells, not preserved on large shells. Anterior edge of shell of ventral valve strongly deflected dorsally opposite the fold to form tongue at anterior commissure in shells with strong-rounded to angular folds (Fig. 12).

***Pseudoatrypa rugatula* (Stainbrook & Ladd, 1924).** — [*Atrypa reticularis* var. *rugatula* Stainbrook & Ladd 1924: p. 358, pl. 1: 8 only].

C o m m e n t s . — The two specimens illustrated by Stainbrook & Ladd (1924) under the name *Atrypa reticularis* var. *rugatula* are assignable to both *Pseudoatrypa* and *Spinatrypina*. Illustrated

Fig. 8. **A, B.** *Pseudoatrypa devoniana* (Webster, 1921). A_1–A_5 dorsal, ventral, lateral, posterior, and lateral views of SUI 65042, from the Late Frasnian Cerro Gordo Member of the Lime Creek Formation at



Hackberry Grove, Cerro Gordo County, Iowa (Day 1998: fig. 6: locality 5); **B1–B5** dorsal, ventral, lateral, anterior, and posterior views of UMMP 7373 (= holotype of *Atrypa hackberryensis* of Fenton & Fenton 1924); from the late Frasnian Cerro Gordo Member of the Lime Creek Formation, Rockford Quarry, Floyd

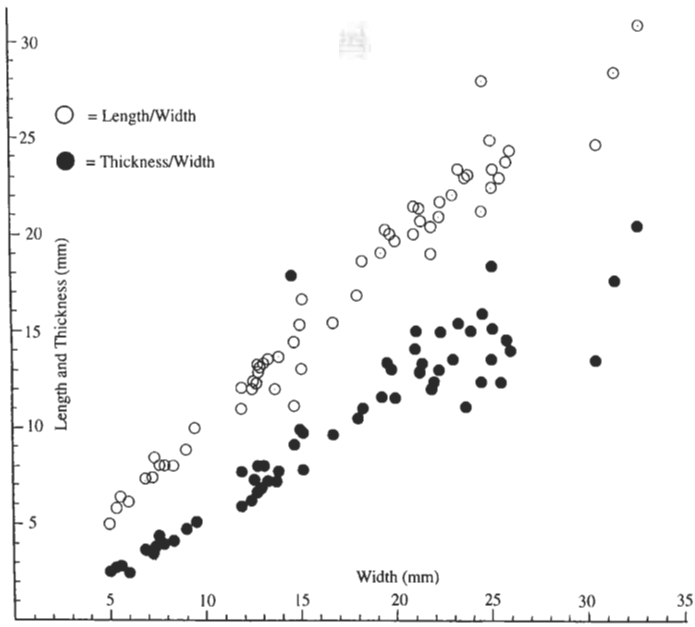


Fig. 9. Plot of shell measurements of *Pseudoatrypa devoniana* (Webster, 1921). Based on specimens from the type section of the Amana Beds (Belanski Collection, University of Iowa) (Day 1998: fig. 5, locality 1) and from the type section of the Cerro Gordo Member at the Hackberry Grove locality of the Lime Creek Formation, Cerro Gordo County, Iowa (Day 1998: fig. 6, locality 4 = Belanski loc. 1 in Strimple & Leverson 1969).

holotype (Stainbrook & Ladd 1924: p. 358, pl. 1: 8 only) is clearly a *Pseudoatrypa*. Consequently a new diagnosis of *Atrypa reticularis* var. *rugatula* (as restricted here) is provided below, and additional specimens of *Pseudoatrypa rugatula* (Stainbrook & Ladd, 1924) are illustrated in Fig. 14. The illustrated paratype of *Atrypa reticularis* var. *rugatula* Stainbrook & Ladd, 1924 (p. 358 pl. 1: 9 only) is a poorly preserved specimen of *Spinatrypina (Exatrypa)*.

Revised diagnosis. — Medium sized (largest brachial valve 26 mm in width, 25 mm in length); nearly biconvex to ventribiconvex *Pseudoatrypa*, convexity of dorsal and ventral valves nearly equal; dorsal valve nearly circular in outline; juvenile shells slightly elongate with shell length equal to or normally exceeding width, large adults are wider than long; very broad and shallow anterior fold; numerous tubular ribs ranging from 7–10, averaging 8 ribs/5 mm as counted 15 mm anterior of posterior margin of dorsal valve, angular in cross-section; numerous closely spaced concentric growth lamellae between more prominent lamellae marking attachment sites of frills (with spacing averaging 2.1 mm along plane of symmetry), often not visible on abraded shell surfaces, frills not observed, pronounced lamellae marking apparent frill attachment sites best preserved on anterior 1/3 of dorsal and ventral valves. Most shells in the Stainbrook, Belanski, and University of Iowa collections are disarticulated.

Discussion. — This species is by far the most abundant brachiopod in the Coralville Lake area of Johnson County, where it is extremely abundant in the main tidal channel fill complex of the State Quarry Member (Day 1992). It is associated with a moderately diverse brachiopod fauna that includes: *Allanella annae, Eleutherokomma* sp. (very large form), *Cyrtina* sp. A of Norris (1981), *Tecnocyrtina curvilineata, Spinatrypina johnsoni* sp. n., *Cranaena depressa, Strophodonta iowensis, Hadrorhynchia solon,* and rare *Schizophoria lata.* They are characteristic of the latest Givetian–early Frasnian *Allanella allani* Zone (Day 1992, 1996), and of I.D.F.I. 9 of Day (1996). The State Quarry

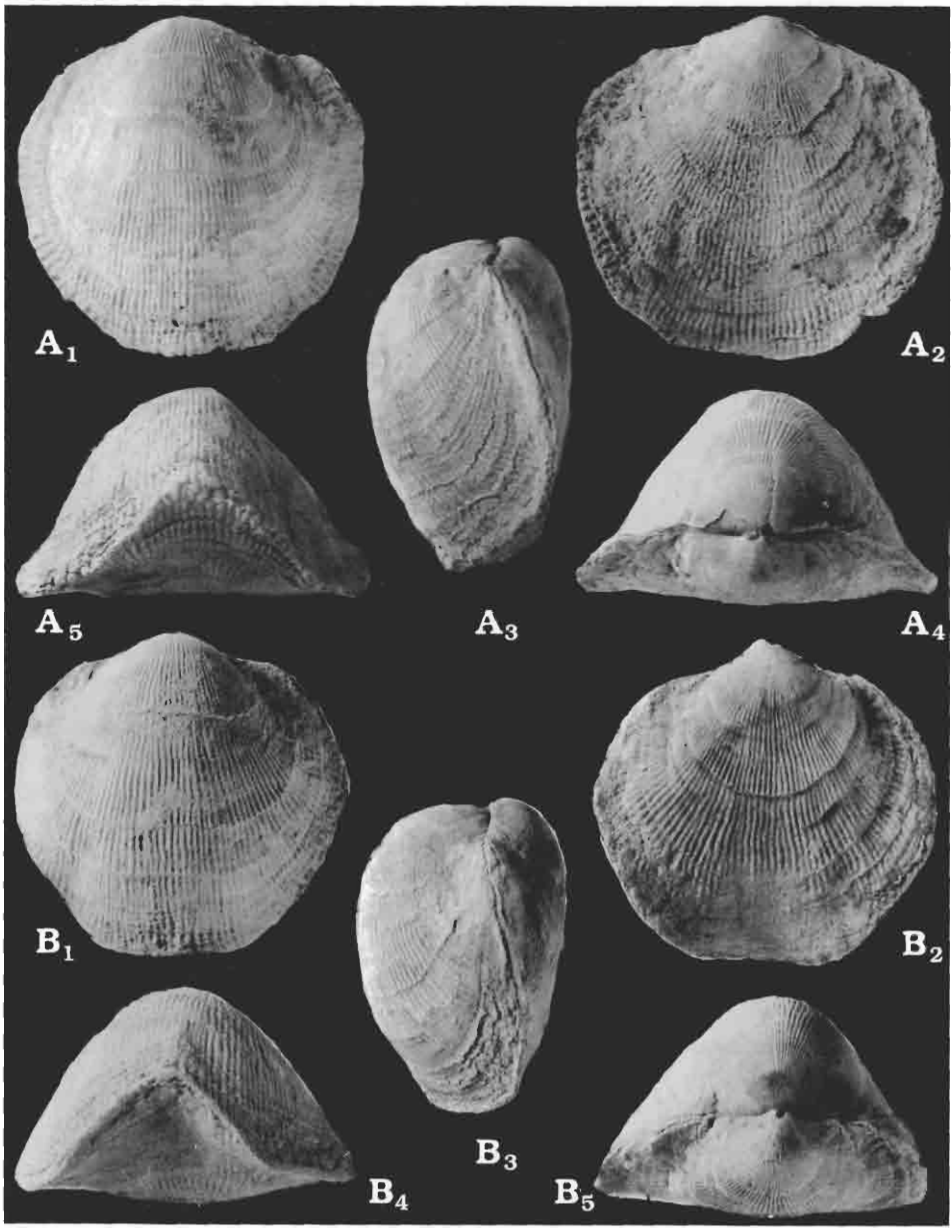


Fig. 10. **A–B**. Adult specimens of *Pseudoatrypa lineata* (Webster, 1921). **A1–A5** dorsal, ventral, lateral, posterior and anterior views of SUI 65338; **B1–B5** dorsal, ventral, lateral, posterior and anterior views of SUI 65330; both from unit 19 of the upper Idlewild Member of the Lithograph City Formation at Day's (1992: figs 13, 14) Hanneman Quarry locality in southeastern Floyd County, Iowa. All × 1.25.

Member yields conodonts of the *S. norrisi* Zone at on the west side of Coralville Lake (Metzger 1993), and fossils of the older part of the *P. insita* Fauna (Witzke *et al.* 1989; Bunker & Witzke 1992; Day, Bunker & Witzke in Day *et al.* 1996).

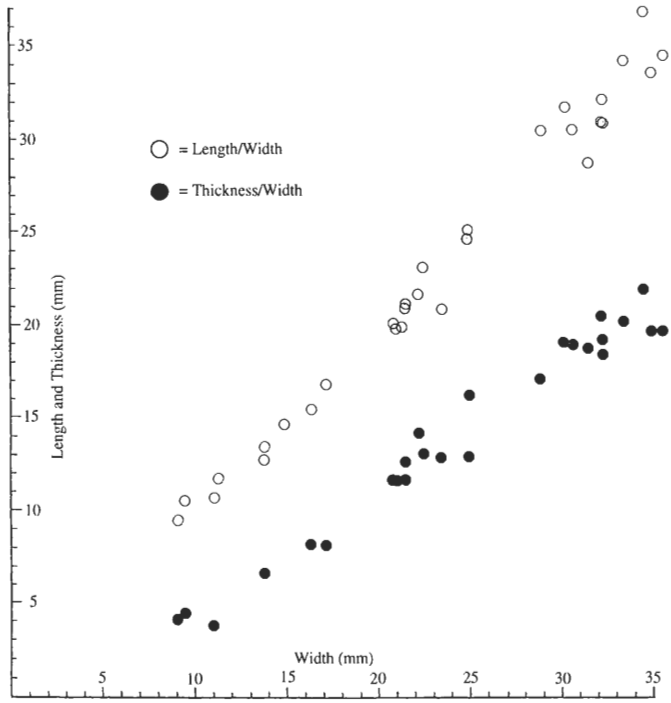


Fig. 11. Plot of shell measurements of *Pseudoatrypa lineata* (Webster, 1921) from the early Frasnian Idlewild Member of the Lithograph City Formation at the Hanneman Quarry locality of Day (1992: p. 77, fig. 14).

A similar specimen designated here as *P.* sp. aff. *P. rugatula*, was illustrated by Maurin & Raasch (1972: pl. 7: 9–12, 17–20) from the assemblage 4 from the Flume Formation in British Columbia, although its shell appears to have a deeper anterior fold. The Flume species occurs in association with *Tecnocyrtina billingsi* that is known to have its lowest occurrence with conodonts of the *S. norrisi* Zone across western Canada (see discussion of range of *T. billingsi* in Day 1997). Consequently, the Flume atrypid would be of comparable age as *P. rugatula* in the State Quarry Member in Iowa. Recognition of *P. rugatula* outside of the Iowa Basin can not be confirmed with certainty pending restudy of material illustrated by Maurin & Raasch (1972).

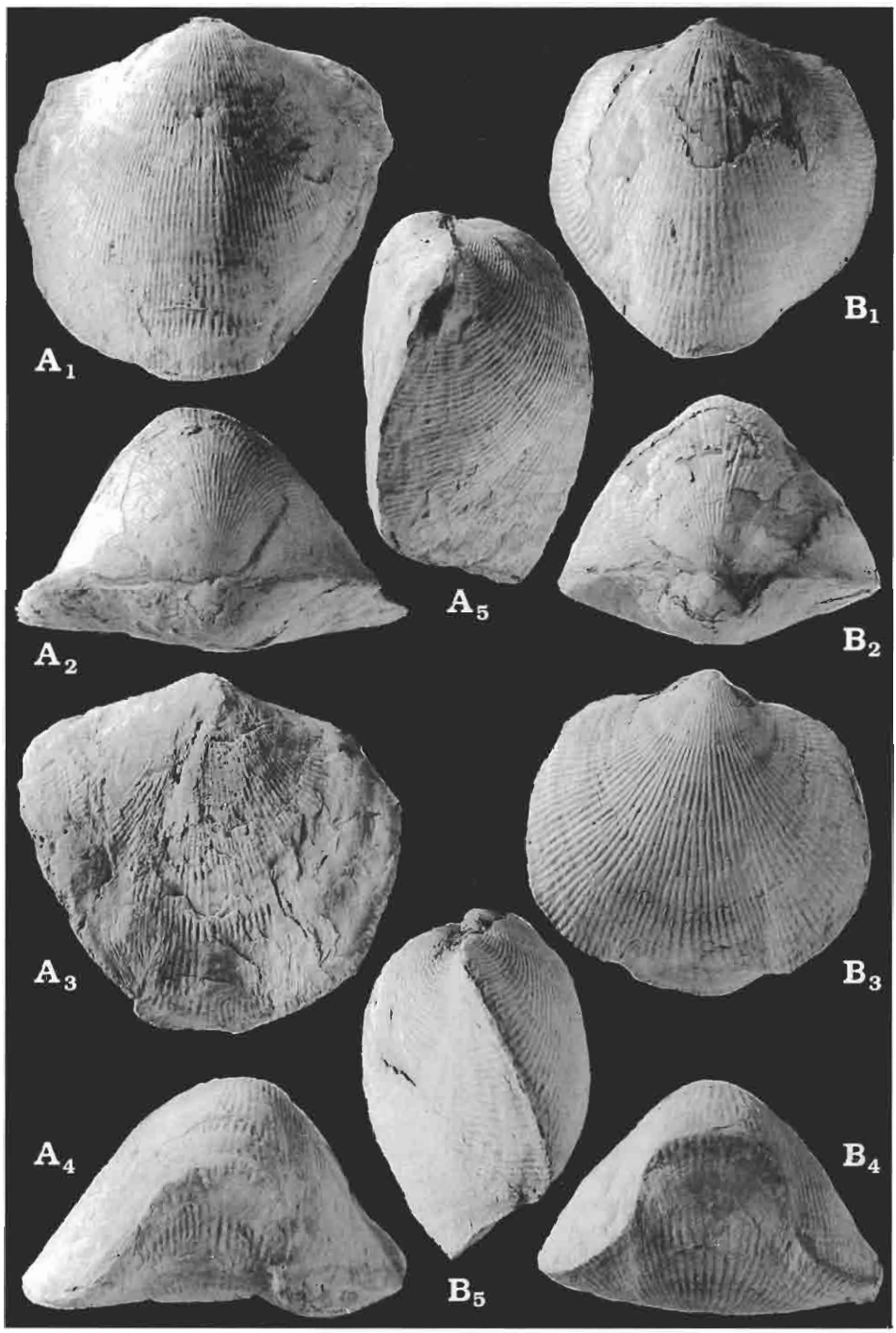
***Pseudoatrypa witzkei* sp. n.**
Figs 15–17.

Type material: Specimen SUI 65517 is the holotype (Fig. 15A), another specimen SUI 65507 is designated as paratype.

Type locality: The Mason City Member of the Shell Rock Formation (Belanski locality 64). Location given in Strimple & Leverson (1969).

Type horizon: Bed number 6 in Belanski's measured section at his locality 64 (= *Cladopora* Zonule of Belanski 1972 = uppermost bed of the Mason City Member) at Copper Bens on the Shell Rock River, in west-central Cerro Gordo County, Iowa.

Fig. 12. **A–B**. *Pseudoatrypa missouriensis* (Miller, 1894). $\mathbf{A_1}$–$\mathbf{A_5}$ dorsal, ventral, lateral, posterior and anterior views of SUI 65967; $\mathbf{B_1}$–$\mathbf{B_5}$ dorsal, ventral, lateral, posterior and anterior views of SUI 65964; both from the New Bloomfield Member of the Snyder Creek Shale (Day 1997: fig. 6, locality NBE, unit 3), New Bloomfield East Locality, southern Callaway County, Missouri. All × 1.25.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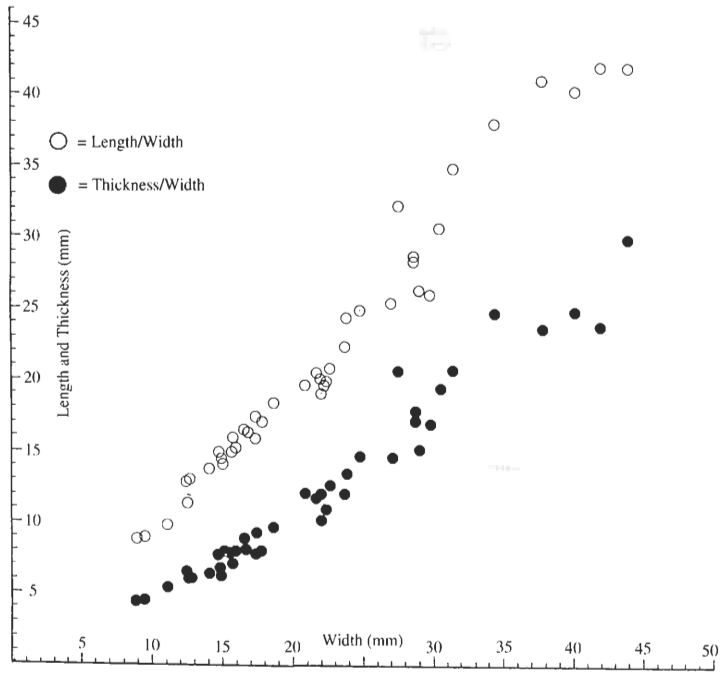


Fig. 13. Plot of shell measurements of *Pseudoatrypa missouriensis* (Miller, 1894). All early Frasnian, from the New Bloomfield Member of the Snyder Creek Shale at the New Bloomfield East Locality of Day (1997: fig. 3, locality NBE, unit 3).

Derivation of the name: In honor of Dr. Brian Witzke of the Iowa Department of Natural Resources, who has made major contributions to the understanding of the Middle and Late Devonian of central North America.

Diagnosis. — Medium to large species of *Pseudoatrypa* with dorsibiconvex shell, length slightly greater than width in adult shells, outline variable although shells tend to be shield-like with subparallel lateral margins along posterior one half to two thirds of length in adult shells, with broad well developed anterior fold.

Description. — Medium-large size shells for genus (holotype shell 32 mm in width, and 33 mm in length; largest unnumbered topotype specimen with width of 34 mm, length of 37.6 mm); juvenile shells (7–20 mm width) are nearly equally biconvex with convexity of dorsal valve slightly greater than ventral valve, large adult shells (15–34 mm) dorsibiconvex as dorsal valve becomes more inflated, ventral valve is initially convex becoming convexo-plane (only in largest shells), shell width equal to or normally exceeding length in juvenile shells (up to 20 mm in width), shells become slightly elongated with length exceeding width in large adult shells (width 30 mm); juvenile shells (up to 20 mm width) with rounded ovate outlines developing shield-shaped-subrectangular outlines with extended hinge lines along posterior margin; lateral margins in large shells variable but most develop nearly parallel lateral margins from the hinge line to just anterior of mid-valve in large adult growth stages; cardinal extensions of overlapping frill lamellae along posterior margin in large adult specimens; tubular costae rounded in cross-section; lamellae marking attachment sites of frills irregularly spaced, best preserved along anterior and lateral commissural margins of dorsal and ventral valves; development of anterior fold is variable, broad and shallow in wide thin shells, more narrow and deeper (up to 50–60% of total shell thickness) in elongate adult shells.

Comparison and discussion. — This middle Frasnian age species is closely related to and is a possible ancestor of the late Frasnian *Pseudoatrypa devoniana* (Webster, 1921). Both species

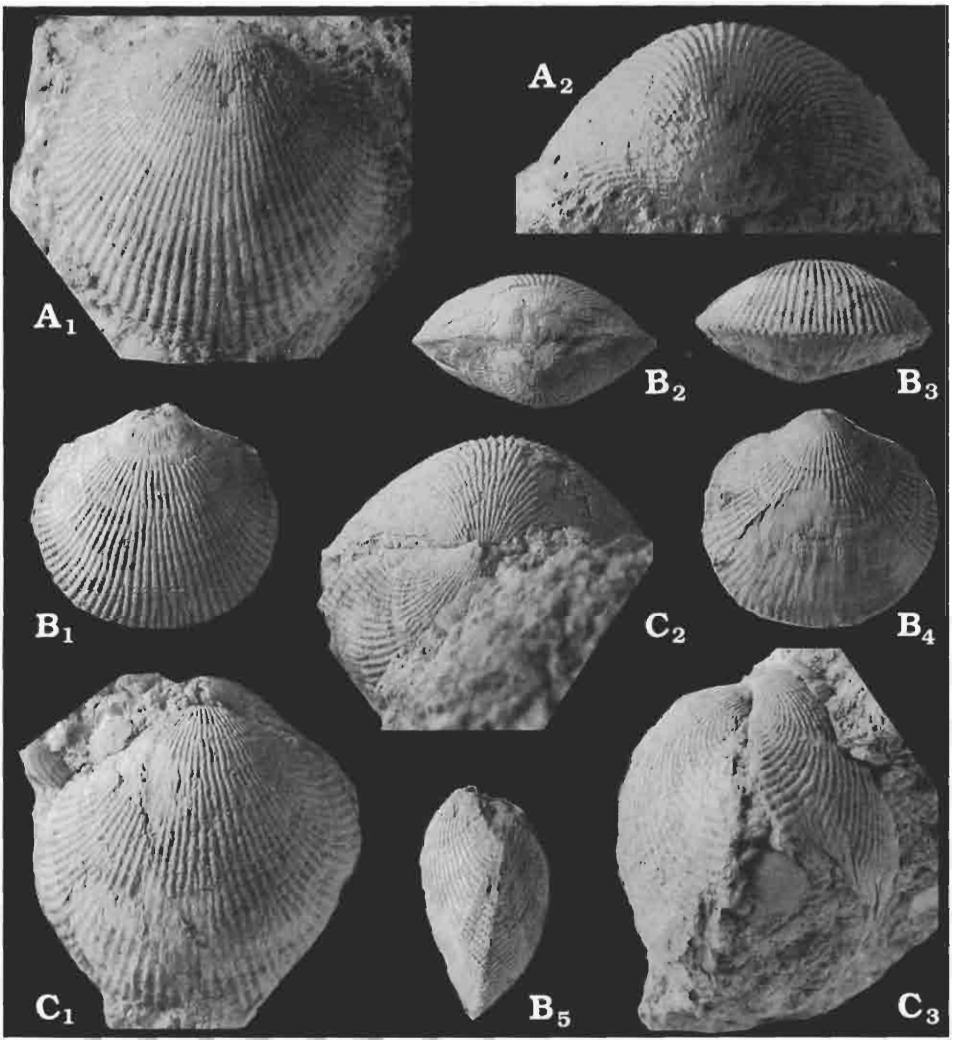


Fig. 14. **A–C.** *Pseudoatrypa rugatula* (Stainbrook & Ladd, 1924). **A1** and **A2** are dorsal and posterior views of SUI 85780; **B1–B5** are dorsal, posterior, anterior, ventral and lateral views of SUI 85799; **C1–C3** are dorsal, posterior and lateral views of SUI 85781. All from the latest Givetian–early Frasnian State Quarry Member of the Lithograph City Formation, from unit 3 at the Indian Cave section locality of Day (1992: figs 15, 18, location on pp. 102–103 of appendix) on east shore of Coralville Lake, Johnson County, Iowa. All at × 2.

display the similar ranges of phenotypic variation in morphology (ranging from wide thin alate-shield-shaped shells with broad folds, to thick rounded elongate shells with narrower and deeper folds). *P. witzkei* sp. n. from the Shell Rock Formation does achieve a larger maximum adult shell size than *P. devoniana* from the Lime Creek Formation or Amana Beds in Iowa (compare Figs 9 and 17). Large adult shells of *Pseudoatrypa witzkei* sp. n. display elongate straight hinge lines with roughly parallel lateral margins, versus the rounded hinge line and ovate-rounded outlines of most *P. devoniana.*

Pseudoatrypa witzkei sp. n. is very close to forms from the Hay River Formation in the southern NWT identified as *Atrypa devoniana* by Warren & Stelck (1956), Jones (in McLean *et al.* 1987), and in sample HR-5A of the Amoco-Canada collections (University of Alberta-Emondton). This large *Psuedoatrypa* (*P.* sp. cf. *P. witzkei*, see discussion in Day 1998) from the Hay River Formation is probably conspecific with *P. witzkei* sp. n. from the Iowa Basin. The Hay River form differs only in that it achieves a slightly larger maximum shell size (up to 38 mm wide, and 39 mm long; single shell from the Amoco-Canada locality HR-5A) than the middle Frasnian shells from Iowa.

Material and localities. — Besides of the holotype there are three measured specimens and paratype from Belanski locality 2-7, and 20 additional from diverse Belanski localities (Mason City Member: 25-5, 38-5, 43-11, 56-5, 80-2; Nora Member: 78-6; see Strimple & Leverson 1969 for locations).

***Radiatrypa clarkei* (Warren, 1944).** — [= *Atrypa clarkei* Warren 1944: p. 122–123, pl. 3: 10–12; Warren & Stelck 1956: pl. 7: 5–7. = *Atrypa clarkei* Warren (var.) Warren & Stelck 1956: pl. 8: 13–15. = *Atrypa gregeri* Rowley, Warren & Stelck 1956: pl. 13: 1–3. = *Variatrypa (Radiatrypa) clarkei* (Warren, 1944), Copper 1978: p. 326, pl. 5: 7–11; Norris in Norris & Uyeno 1981: p. 17, pl. 7: 13–20; Norris in Norris & Uyeno 1983: p. 26, pl. 5: 34–48, pl. 6: 1–6].

Discussion. — All material representing *R. clarkei* (Warren, 1944) from Iowa was recovered from the Idlewild Member of the Lithograph City Formation at the Hanneman Quarry locality of Day (1992: fig. 14, unit 19). There it occurs in the Upper *Strophodonta* fauna of Day (1992) in assemblages dominated by *Pseudoatrypa lineata, Athyris vittata, Allanella* sp., *Floweria* sp. *Gypidulina* sp., and *Strophodonta* sp. cf. *S. callawayensis*. The occurrence of *R. clarkei* in Iowa is within the lower part of I.D.F.I. 10L of Day (1996,1997), or within the *Strophodonta callawayensis* Zone of Day (1992, 1996, 1997).

In western Canada, this species is common in latest Givetian–early Frasnian deposits of the Waterways Formation in northeastern Alberta (Warren 1944; Warren & Stelck 1956; Norris 1963; Copper 1978). In the Birch River area of northeastern Alberta, the lowest occurrence of *R. clarkei* is in the *Ladogioides asmenista–Eleutherokomma jasperensis* fauna in units 1–4 of the Waterways Formation (Norris & Uyeno 1981). There, it first occurs in association with conodonts of the latest Givetian *norrisi* Zone, and ranges into rocks yielding conodonts of M.N. Zone 1 (Uyeno in Norris & Uyeno 1981; Klapper 1989). Norris (in Norris & Uyeno 1983) also illustrated *R. clarkei* from the Peace Point Member of the Waterways Formation, where it occurs with conodonts of the oldest part of the *Pandorinellina insita* Fauna (= *Skeletognathus norrisi* Zone). In Alberta, it has its highest occurrence in the Moberly Member of the Waterways Formation, which is now aligned with parts of M.N. Zones 3–4 (Uyeno in Day *et al.* 1996).

***Radiatrypa gregeri* (Rowley, 1900).** — [= *Atrypa gregeri* Rowley 1900: p. 264, pl. 5: 9–11. = *Atrypa gregeri* Rowley, Greger 1909: p. 376; Branson 1923: p. 97, pl. 18: 7–9. = *Gruenewaldtia gregeri* (Rowley), Greger 1936b: p. 94–95, pl. 1: 1–13].

Discussion. — This species is not illustrated here and will be redescribed in a later study. It probably evolved from a peripheral population of *R. clarkei* (Warren, 1944) or *R. multicostellata* (Kottlowski, 1950) that became isolated in the southern Iowa Basin. From Rowley's (1900) and Greger's (1936b) discussions, *R. gregeri* occurs in a single bed in the lower part of the Snyder Creek Shale. Based on its very restricted stratigraphic occurrence, it appears that this form evolved quickly, and was extinct shortly after is brief appearance in the early Frasnian of Missouri.

Adult shells of *Radiatrypa clarkei* (Warren, 1944) from northern Iowa and elsewhere in central and western Canada are much larger that those of *R. gregeri*. In *R. clarkei*, shell width always exceeds length, (Fig. 25B, SUI 65328 with width of 28.7 mm and length 26.6 mm), whereas length exceeds width in all adult shells (12 mm length) of *R. gregeri*. The average shell size of five specimens measured by Greger (1936b) were: length 19 mm, width 17 mm, thickness 12 mm. The largest shell of *Radiatrypa gregeri* examined by us has a width of 19.6 mm and length of 20.7 mm. Fine tubular radial ribs, lack of pronounced growth lamellae and frills are characteristic features of both species. The smaller species (*R. gregeri*) averages 15 ribs/5 mm counted on the ventral valve at a distance

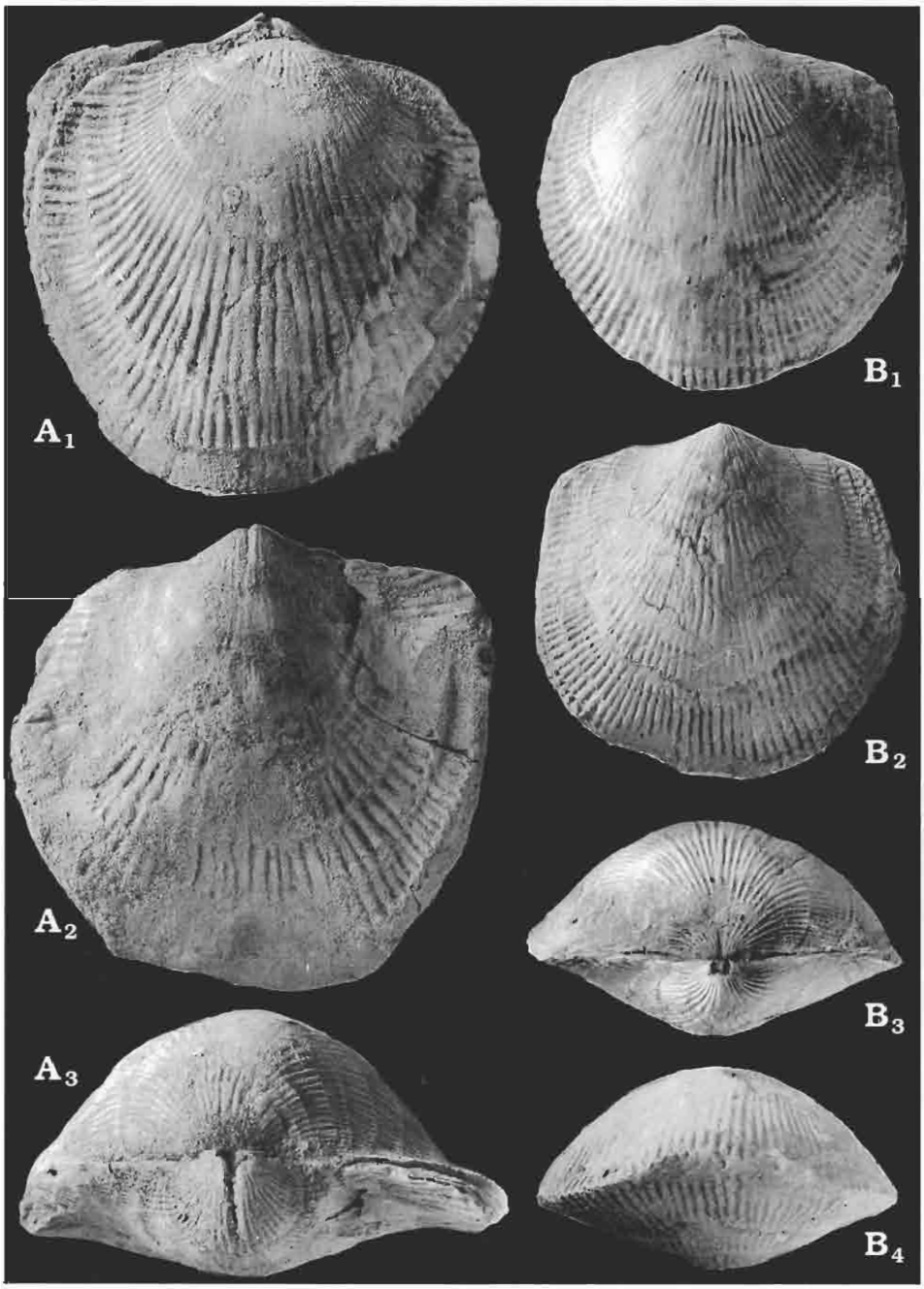


Fig. 15. **A, B.** *Pseudoatrypa witzkei* sp. n. **A1–A3** dorsal, ventral and posterior of holotype SUI 65517. **B1–B4** dorsal, ventral, posterior, and anterior views of SUI 65497. Both from middle Frasnian Mason City Member of the Shell Rock Formation. All × 2.

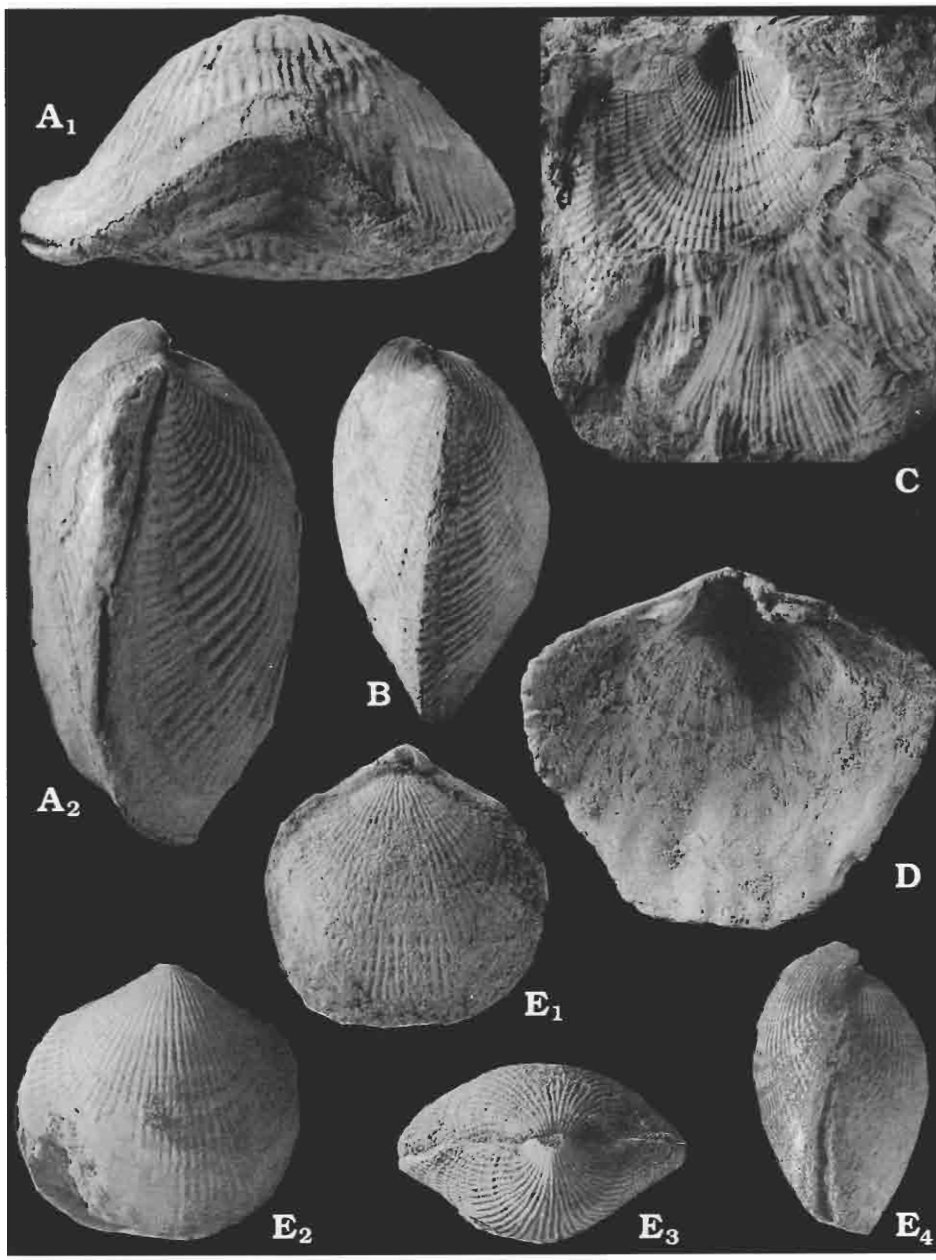


Fig. 16. **A–E.** *Pseudoatrypa witzkei* sp. n. **A1** and **A2** anterior and lateral views of holotype SUI 65517; **B** lateral view of SUI 65497; **C** decorticated ventral valve in matrix with preserved marginal frill, SUI 85782; **D** internal view of isolated ventral valve with dental ridges and teeth; **E1–E4** dorsal, ventral, posterior, and lateral views of paratype SUI 65507. All × 2.

10 mm anterior of the ventral beak. The ribs on this form are crowded and increase by bifurcation and have with very narrow interspaces or grooves between ribs approximately 1/4–1/3 the rib width.

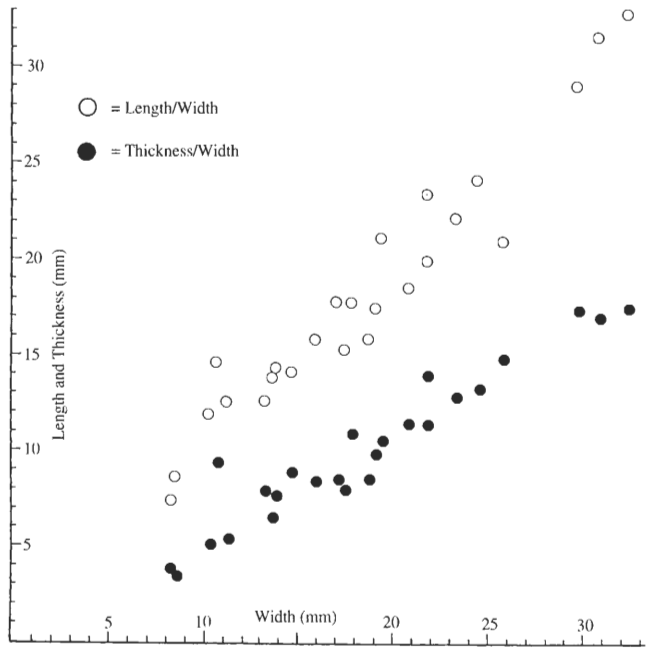


Fig. 17. Plots of shell measurements of shells of *Pseudoatrypa witzkei* sp. n. All are middle Frasnian, from the Mason City and Nora members the Shell Rock Formation, north-central Iowa. Measured specimens numbered SUI 65493–65517 from Belanski Collection (University of Iowa).

The larger species (*R. clarkei*) averages 10 ribs/5 mm (counted on shells from Iowa) at the same distance from the ventral beak, with interspaces or grooves approximately 1/2 the rib width. The ovate to circular outline, biconvex lateral and longitudinal profiles, and gentle anterior fold of adult shells of *R. gregeri* are similar to juveniles of *R. clarkei*, but the latter species has a deeper fold and tends to develop larger dorsibiconvex shells with deeper dorsal valves at maturity.

This rare early Frasnian species is only known from the middle part of the New Bloomfield Member of the Snyder Creek Shale, southern Iowa Basin. Its occurrence in the New Bloomfield Member is just above the position where Day (1997) recovered the lowest conodonts of M.N. Zone 4. *Radiatrypa gregeri* is associated with a diverse brachiopod fauna correlated directly with the *Strophodonta callawayensis* Zone (Fig. 2) as defined by Day (1992) and restricted in Day (1997). Rowely's (1900) type material, specimens illustrated in Branson (1923), Greger (1936a), and specimens from the Branson Collection (University of Missouri) come from exposures of the lower Snyder Creek along Craghead Creek (see Thompson 1993: p. 145 for description of the Craghead Creek locality = Branson's 1923: p. 38, location of type section of the Snyder Creek Shale). Float specimens (SUI 85777) in Day's collections are from 1/4 mile west of the aforementioned locality at the Craghead Creek Quarry locality of Day (1997: fig. 6).

***Costatrypa varicostata* (Stainbrook, 1945)**. — [= *Atrypa varicostata* Stainbrook 1945: p. 47, pl. 5: 13–17; Stainbrook 1948: p. 776, pl. 2: 44–47. = *Atrypa* sp. K, McLaren, Norris, & McGregor 1962: p. 31, pl. 14: 19–21. = *Atryparia (Costatrypa) varicostata* Stainbrook & Copper 1973: p. 494, pl. 2: 9–15. = *Costatrypa varicostata* (Stainbrook) Cooper & Dutro 1982: p. 88–89, pl. 23: 7–31. = *Costatrypa extensa* Cooper & Dutro 1982: p. 87, pl. 23: 39–56, pl. 24: 1–12].

R e m a r k s . — The description of the type species by Stainbrook (1945) was based on specimens from late Frasnian cave-fillings of the Independence Shale from central Iowa, with additional material from the Sly Gap Formation of southern New Mexico (Stainbrook 1935).

Specimens also are from the lower half of the Amana Beds at the type section (Müller & Müller 1957) in Iowa County (Belanski and Stainbrook collections, University of Iowa), and a single specimen in Day's collections from the middle part of the Cerro Gordo Member of the Lime Creek Formation (Fig. 19).

C. varicostata also occurs in the late Frasnian Sly Gap Formation of southern New Mexico (Stainbrook 1935, 1948; Cooper & Dutro 1982). It was reported by Day (1989) from the upper unit of the Jerome Member of the Martin Formation taken at the Pinal Creek section north of the town of Globe, south-central Arizona (Stainbrook Collection, University of Iowa). The occurrence in the Martin is at or above the lowest occurrence of the conodont *Palmatolepis foliacea*, based on restudy of conodonts by Klapper. Consequently, the known Martin occurrences of *C. varicostata* are within the upper Frasnian M.N. Zone 12 of Klapper (1989).

Cooper & Dutro (1982) described *C. extensa* from the Sly Gap Formation of New Mexico. It occurs there with *C. varicostata*. Specimens of *Costatrypa* in large collections from the Sly Gap display a range of morphologies grading from *C. varicostata* and *C. extensa* as end member phenotypes in highly variable populations. The pronounced variations in these collections with intermediate morphotypes strongly suggest that *C. extensa* is conspecific with *C. varicostata*. Typical specimens of *C. extensa* illustrated by Cooper & Dutro (1982) have more rectilinear alate posterior margins and are flatter than most forms of *C. varicostata*. The inflated shell of the large adult shell shown in Fig. 19 has a straight posterior margin.

***Iowatrypa owenensis* (Webster, 1921).** — [*Atrypa owenensis* Webster 1921: p. 14–15; Fenton & Fenton 1924: p. 141, pl. 26: 9–11. = *Atrypa owensis* Webster [misspelling] Fenton & Fenton 1935: [includes forms A, B] p. 383–384, pl. 42: 1–6. = *Iowatrypa owenensis* (Webster, 1921) Copper 1973: pl. 2: 5–8; Copper & Chen 1995: p. 256, figs. 2.21–2.25, figs. 3, 4; Savage & Baxter 1995: p. 1039–1040, figs. 2.22–2.26, and fig. 19.

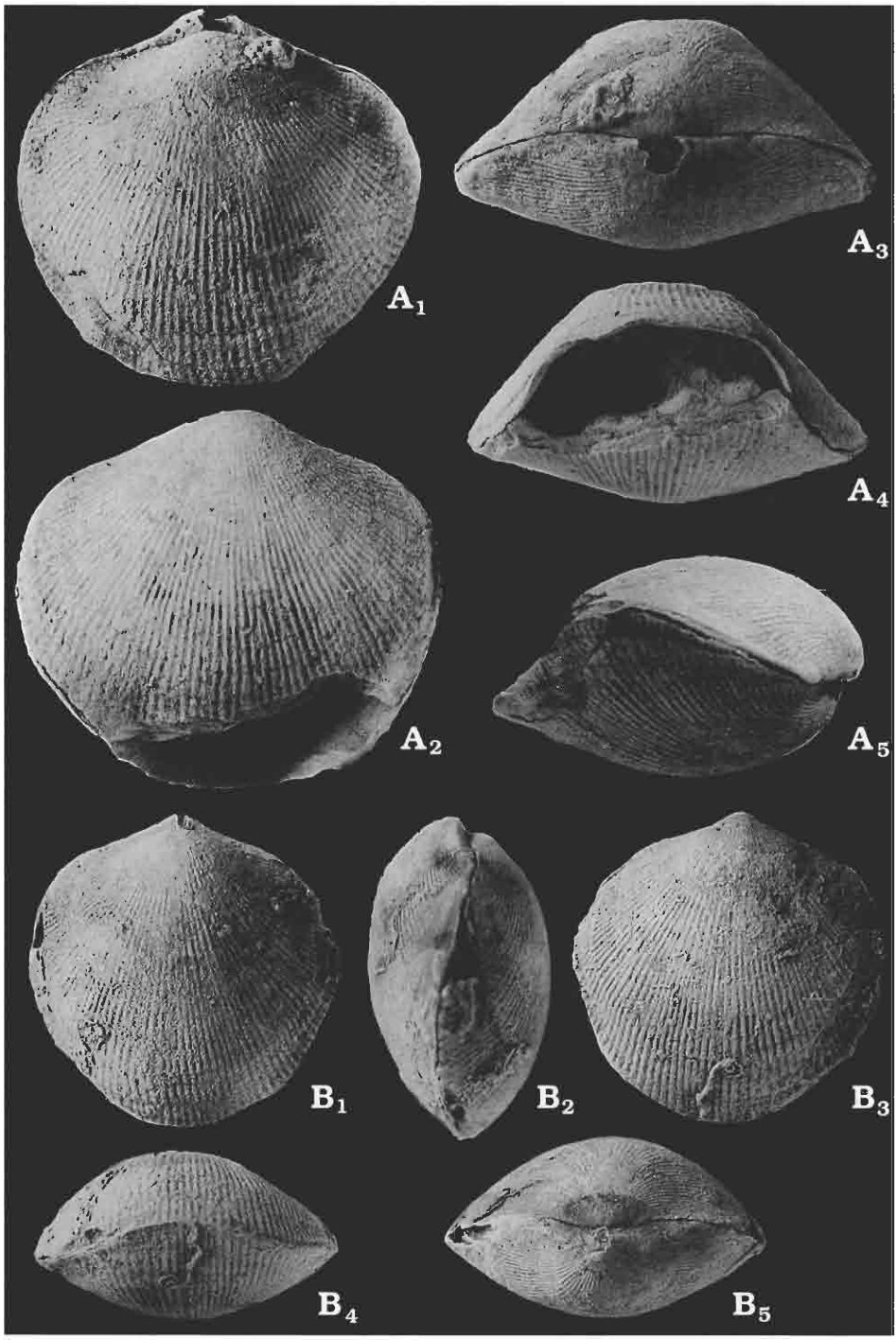
Discussion. — Copper (1973: pp. 495–496) established the genus *Iowatrypa* with the upper Frasnian *Atrypa owenensis* (Webster, 1921) as the type species (Fig. 20A, B). Copper (1973: p. 495) and Copper & Chen (1995: p. 256) have suggested that *I. americana* (Stainbrook, 1945) and *I. owenensis* may be conspecific. We are not prepared to resolve this problem here pending study of the interior of *I. americana*. The paratypes (Stainbrook 1945: pl. 5: 21–23, 27, 28) of *Grunewaldtia americana* Stainbrook, 1945 are similar externally to young shells of *I. owenensis* (Belanski Collection, University of Iowa) from the middle part of the Owen Member of the Lime Creek Formation at its type locality, and other localities in southern Cerro Gordo County, northern Iowa. *G. americana* was erected on specimens from the Independence Shale, Buchanan County, Iowa.

Day (1989: p. 319) defined the base of the *Iowatrypa owenensis* Zone in Iowa at its lowest occurrence in the middle part of the Owen Member in bed 8 at Belanskis Owen Member section locality 17 on Beaver Creek in southern Cerro Gordo County. In terms of conodonts, the range of *I. owenensis* begins high in the M.N. Zone 12, and may extend into the M.N. 13 (Fig 2, see fig. 4 of Day 1998). Its range in the Iowa Frasnian characterizes I.D.F.I. 18 of Day (1996).

***Iowatrypa minor* (Fenton & Fenton, 1924).** — [= *Atrypa planosulcata minor* Fenton & Fenton 1924: p. 140, pl. 27: 17–18].

Discussion.—This is a small form (Fig. 20C) described from the Cerro Gordo Member of the Lime Creek Formation by Fenton & Fenton (1924: p. 40, pl. 27: 17 & 18). Thus far it is known only from the two type specimens from the lower part of the Cerro Gordo Member at the Rockford Quarry. The position of the type stratum (see Day 1998) is at or just above the lowest occurrence of the conodont *Palmatolepis foliacea* (Anderson 1966; Day 1990) and thus would correlate with a position low in M.N. Zone 12 of Klapper (1989).

Fig. 18. **A–B.** *Radiatrypa clarkei* (Warren, 1944). $\mathbf{A_1}$–$\mathbf{A_5}$ dorsal, lateral, ventral, posterior, and anterior views of SUI 65328. $\mathbf{B_1}$–$\mathbf{B_5}$ dorsal, ventral, posterior, anterior, and lateral views of SUI 65327. Both from unit 19 of the early Frasnian Idlewild Member of the Lithograph City Formation at the Hanneman Quarry locality of Day (1992: fig. 14), Floyd County, Iowa. All × 2.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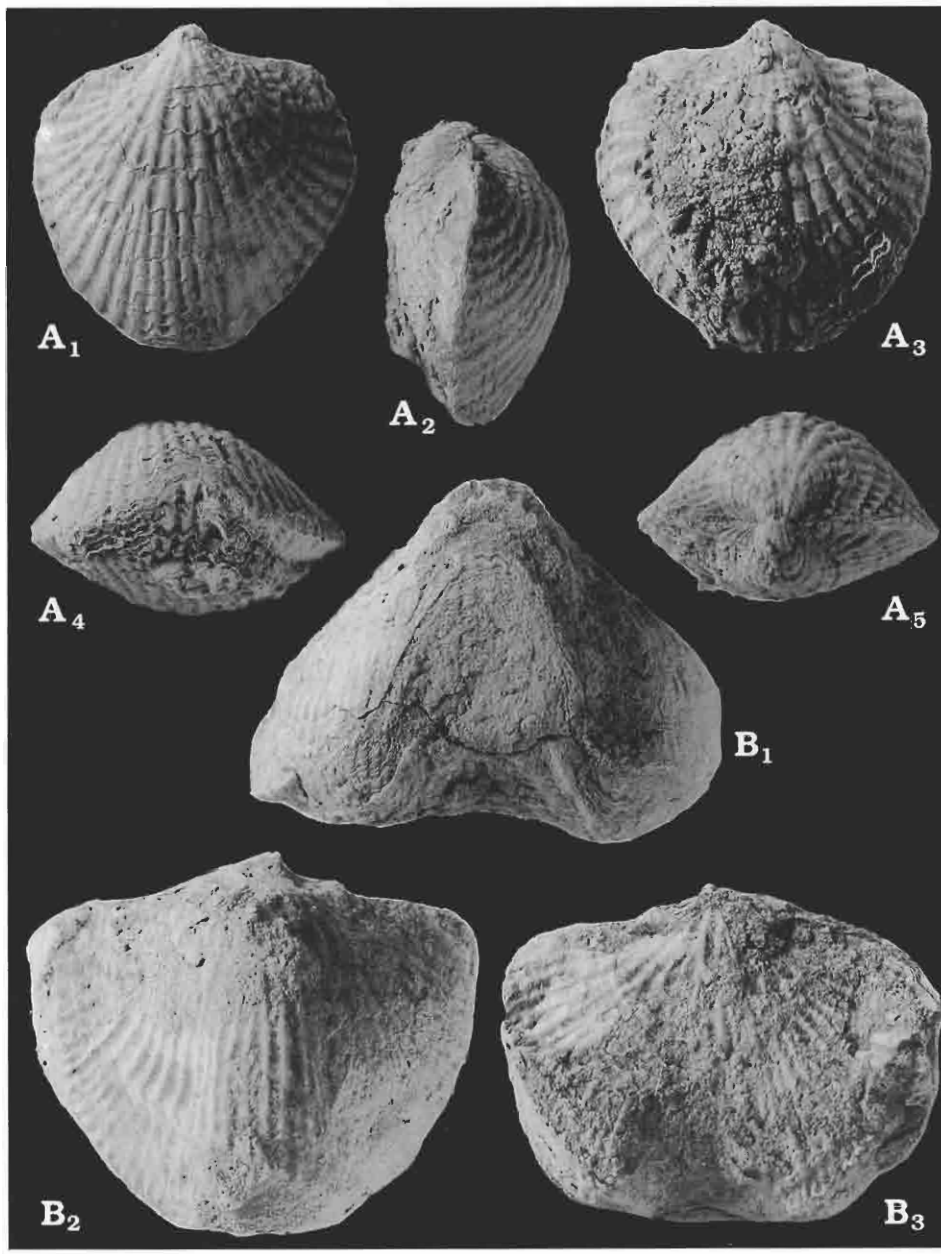


Fig. 19. **A–B**. *Costatrypa varicostata* (Stainbrook, 1945). **A1–A5** dorsal, lateral, ventral, anterior, and posterior views of SUI 85750; **B1–B3** anterior, dorsal, and ventral views of SUI 85778. Specimen SUI 85750 is from the Cerro Gordo Member of the Lime Creek Formation, sample position 24 at the Rockford Quarry locality of Day (1998: fig. 6, locality 3, fig. 7), Floyd County, Iowa. Specimen SUI 85778 is from the type section of the Amana Beds (Day 1998: fig. 5, locality 1, Belanski Collection). Views of SUI 85750 × 3, views of SUI 85778 × 2.

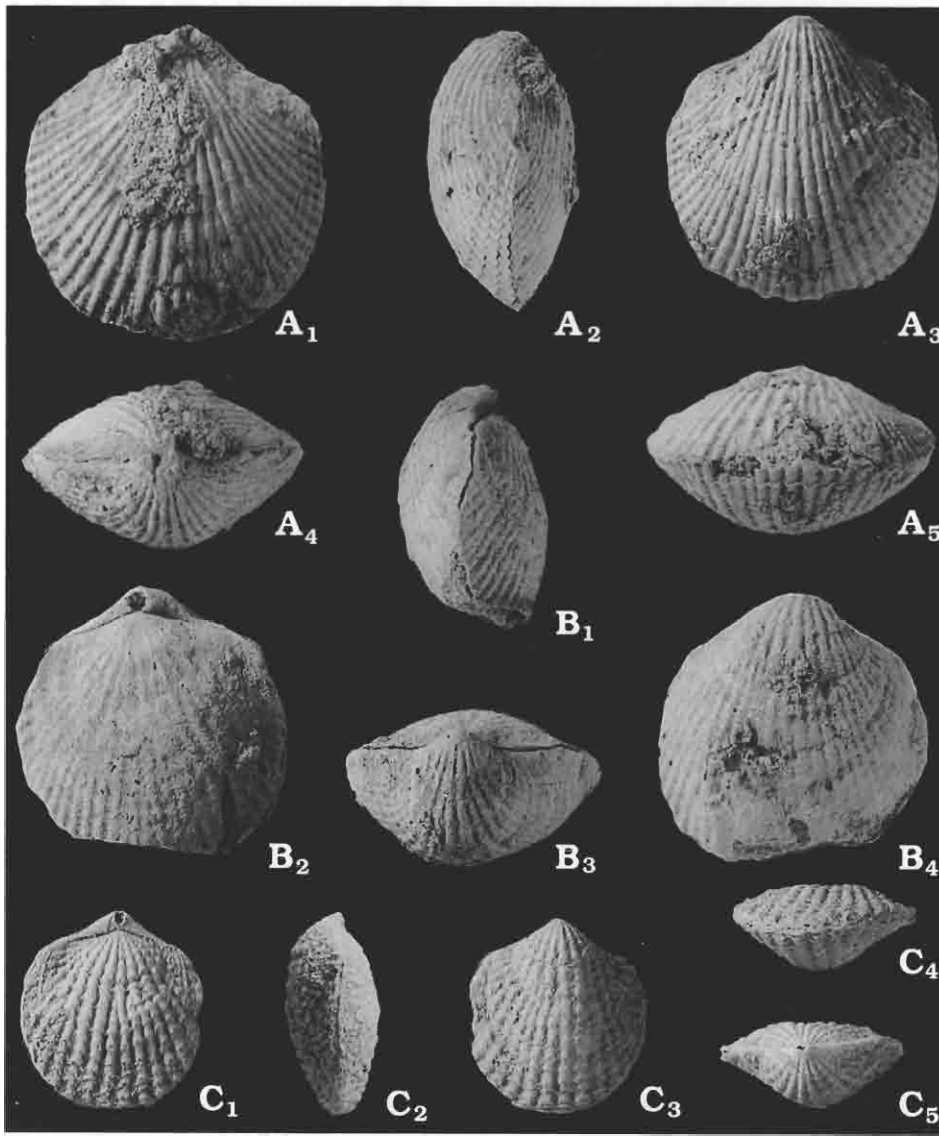


Fig. 20. **A–B**. *Iowatrypa owenensis* (Webster, 1921). **A1–A5** dorsal, lateral, ventral, posterior and anterior views of SUI 85745; **B1–B4** lateral, dorsal, posterior, and ventral views of SUI 85746; late Frasnian, both from type section of the Owen Member of the Lime Creek Formation at Owens Grove (Day 1998: fig. 6: locality 5, sample 9–8; Belanski Locality 9, in Strimple & Leverson 1969). **C**. *Iowatrypa minor* (Fenton & Fenton, 1924). **C1–C5** dorsal, lateral, ventral, anterior, and posterior views of UMMP 8001A (one of two cotypes of Fenton & Fenton, 1924), late Frasnian, from Cerro Gordo Member of the Lime Creek Formation at the Rockford Quarry (Day 1998: fig. 6, locality 3, sample 4-24; fig. 7). All × 3.

***Iowatrypa americana* (Stainbrook, 1945)**. — [= *Gruenewaldtia americana* Stainbrook 1945: p. 52, pl. 5: 18–23, 27, 28, fig. 1: 6). = *Iowatrypa americana* (Stainbrook, 1945), Copper 1973: pl. 2: 1–4; Cooper & Dutro 1982: p. 89, pl. 24: 13, 14].

Discussion.—As mentioned above, this form has been proposed as a possible synonym of the type *Iowatrypa owenensis* (Webster, 1921). The interior is still under study by the authors and will be illustrated later. Readers are referred to the illustrations in Stainbrook (1945), Copper (1973), and Cooper & Dutro (1982). *I. americana* is only known from the Independence Shale of Buchanan County in eastern Iowa. The associated brachiopod fauna (Stainbrook 1945) includes species of *Calvinaria, Coeloterorhynchus, Hypothyridina, Elita, Rigauxia, Thomasaria, Acutatheca.*

***Spinatrypa (S.) bunkeri* sp. n.**

Figs 21, 22.

[= *Spinatrypina* n. sp. Day 1989: p. 309–310, table 3, fig. 7. = *Spinatrypina* sp. n. aff *S. planosulcata* Day 1996: p. 285, fig. 7].

Type material: Holotype is SUI 65446 (Fig. 21B). Four paratypes include SUI 65443, 65427, 65539, 65439.

Type locality: The holotype and paratype SUI 65443 are from Belanski locality 158-17; paratype SUI 65427 from Belanski locality 2-7; paratype SUI 65539 from Belanski locality 89-4; paratype SUI 65439 from Belanski locality 79-10. Locations and section descriptions of the Shell Rock at Belanski localities are given in the Belanski Register (University of Iowa) (see also Strimple & Leverson 1969).

Type horizon: Bed/unit 17 (Rock Grove Member) at the measured section of the Shell Rock Formation at Belanski Locality 158 (*Strobilocystites* Zonule, *Schizophoria* Zone, see Belanski, 1927).

Derivation of the name: In honor of William (Billy) Bunker of the Iowa Department of Natural Resources, for his contributions to the knowledge of the Paleozoic stratigraphy of central North America.

Diagnosis. — Adults shells of medium size (maximum observed is 25.5 mm wide), flattened shells wider than long in juvenile growth stages (up to 15 mm in width) developing globose dorsibiconvex shell with rounded outlines in adult shells (15 mm wide), with numerous rounded lamellose ribs.

Description. — A small-medium sized *Spinatrypa* (Fig. 22, largest shells up to 25.5 mm in width, 23 mm in length, 15 mm in thickness); globose dorsibiconvex adult shells with rounded outline; rounded lamellose ribs (7–10 ribs/10 mm, averaging 8 ribs/10 mm counted at 15 mm anterior of beak of ventral valve), with imbricated spinose lamellae spaced 1.0–2.0 mm on juvenile shells, increasing to 2.0–3.0 mm on larger shells (15 mm) where well preserved; interspaces between ribs up to 1.5 rib width near margins of adults shells; short spines (2–3 mm) arise from concentric lamellae normal to shell surface, rarely preserved on large adult shells, more frequently seen on small juveniles shells; dorsal valve inflated, 1.5–2.0 times as deep as ventral valve; anterior fold usually absent in juveniles less than 10 mm in width, develops anterior to midvalve in large adult shells, depth of fold ranges from 20–30% of shell thickness.

Comparisons. — In terms of rib size and density this species is most similar to *Atrypa* cf. *deflecta* (Warren) of Warren & Stelck (1956: pl. 21: 18–20, 27–29) from the Hay River Formation of the NWT. Day (1998) refers to that form as *S. (S.)* sp. 2. *Spinatrypa (S.) bunkeri* sp. n. differs from that form in achieving a much larger adult shell, with a deeper dorsal valve (dorsibiconvex) versus the more equally biconvex shell of *S. (S.)* sp. 2, its greater spacing between spinose lamellae in both juvenile and adult shells. It is easily distinguished from the younger Frasnian species *S. (S.) planosulcata* (Webster, 1888) on the basis of its larger adult shell size, thicker shell, more inflated dorsal valve in adult shells, and more numerous ribs with 11 ribs/10 mm versus 6–8 ribs/10 mm in *S. (S.) planosulcata.*

Distribution and range. — Middle Frasnian of the Iowa Basin, occurs in the Mason City, Rock Grove, and Nora members of Shell Rock Formation (Figs 1, 2). Its local range in Iowa is from the base of the *Tenticospirifer shellrockensis* Zone, into the upper part of the *Strophodonta cicatricosa* Zone of Day (1989).

Material and localities. — Besides of the type material there are 18 measured specimens from locality labeled as 2.5 miles (4 kilometers) SW of the town of Marble Rock, Floyd

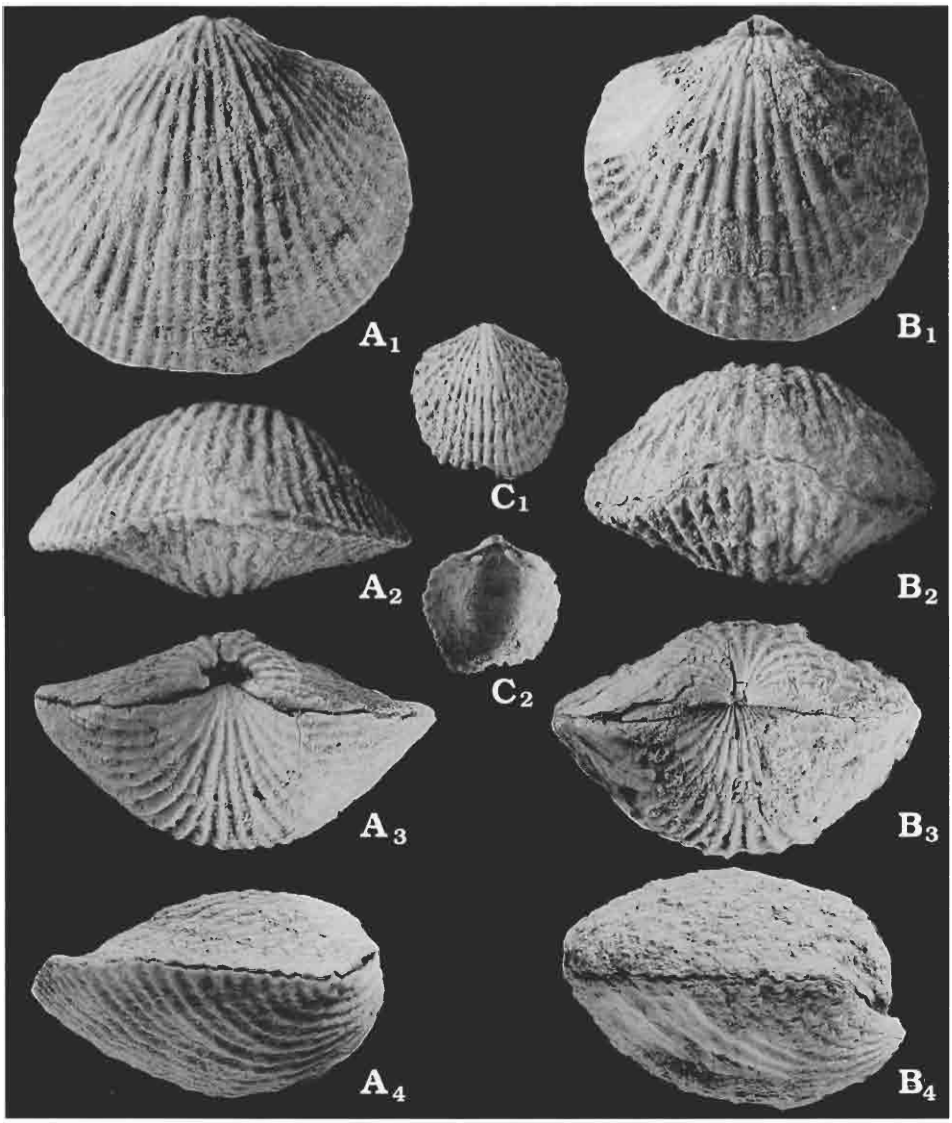


Fig. 21. **A–C**. *Spinatrypa (Spinatrypa) bunkeri* sp. n. **A1–A4** dorsal, anterior, posterior, and lateral views of the holotype SUI 65446; **B1–B4** dorsal, anterior, posterior, and lateral views of SUI 65443; **C1** and **C2** internal and external views of ventral valve of SUI 65427. Middle Frasnian, Rock Grove Member, Shell Rock Formation. Specimens **A**, **B** from Belanski locality 158-17; **C** from Belanski locality 2-7. All × 2.

County, Iowa (Mason City Member), and 40 others from diverse Belanski localities (Mason City Member: 2-7, 56-5, 159-9; Nora Member: 93-9; see Strimple & Leverson 1969 for location).

***Spinatrypa (S.) planosulcata* (Webster, 1888)**. — [= *Atrypa hystrix* var. *planosulcata* Webster 1888: p. 1104. = *Atrypa spinosa* (?) Fenton 1919: p. 372. = *Atrypa planosulcata* Webster, Fenton & Fenton 1924: p. 139, pl. 27: 13–16; (*non* Fenton & Fenton 1932: pl. 23: 3–6)].

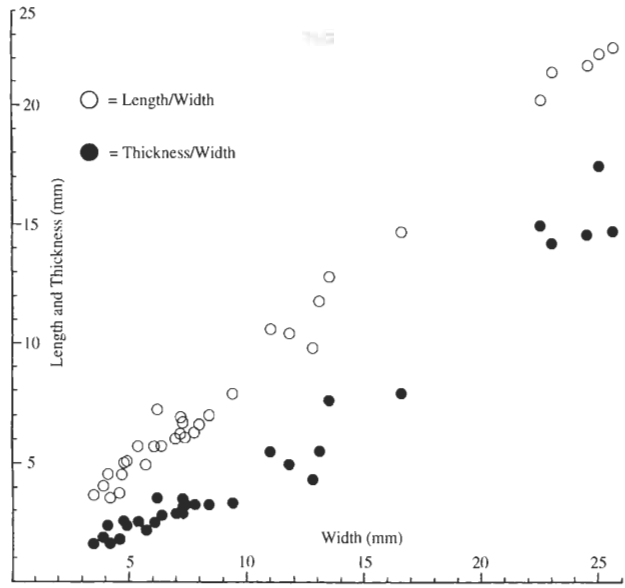


Fig. 22. Plots of shell measurements of *Spinatrypa (Spinatrypa) bunkeri* sp. n. All are middle Frasnian, from the Mason City Member of the Shell Rock Formation of northern Iowa.

D i s c u s s i o n . — This distinctive spinatrypid (Fig. 23) is found in subtropical carbonate platform faunas in the central US midcontinent and the southwestern US. Closely related species first occur in middle Frasnian rocks in central and western North America. *S. (S.) planosulcata* is characterized by transverse nearly biconvex to somewhat dorsibiconvex shells (Figs 23, 24) with pronounced-crowded concentric spinose lamellae (1.0–1.7 mm spacing between lamellae, averaging 1.2 mm along plane of symmetry from posterior to anterior margins); and numerous, elevated-rounded (cross-section) radial ribs (6–8 ribs/ 10 mm, at 15 mm from beak of ventral valve).

This species probably evolved from the closely related middle Frasnian form known from the Hay River Formation designated as *S. (S.)* sp. 1 by Day (1998) which has been illustrated as *Atrypa planosulcata* by Fenton & Fenton (1932), and later as *Atrypa* cf. *albertensis* Warren in Warren & Stelck (1956). Externally, *S. (S.) planosulcata* is most similar to the Hay River form in nearly identical shell size and shape (Fig. 24), and number and types of ribs. The main difference between shells of the two forms is the average distance between the concentric-spinose lamellae, which average 2.0 mm in *S. (S.)* sp. 1 versus 1.2 mm in *S. (S.) planosulcata*. The evolution of *S. (S.) planosulcata* from *S. (S.)* sp. 1 could have proceeded through a reduction in the spacing between the lamellose spinose growth lamellae.

It is easily distinguished from the older Iowa Frasnian species *S. (S.) bunkeri* sp. n. from the Shell Rock Formation on the basis of its the smaller maximum adult size (up to 23 mm wide), thinner shell, less inflated dorsal valve in adult shells, and fewer radial spinose ribs (6–8 ribs/10 mm) in *S. (S.) planosulcata*, versus an average of 11 ribs/10 mm in *S. (S.) bunkeri* sp. n. It is readily distinguished from species such as *S. trulla* and *S. rockfordensis*, owing to its more numerous and more rounded-elevated radial ribs (as above), versus the average of 3 very low-rounded ribs/10 mm on shells of *S. (S.) trulla*, and 4 ribs/10 mm in *S. (S). rockfordensis.*

D i s t r i b u t i o n a n d r a n g e . — In Iowa and elsewhere in the western US, the range of *S. (S.) planosulcata* is restricted to upper Frasnian. In Iowa, its documented range begins in the middle part of the *Cyrtospirifer whitneyi* Zone (Day 1998: fig. 6, Rockford Quarry Section, sample 4–10) and ranges through most of the remainder of the Cerro Gordo Member at the Rockford Quarry and

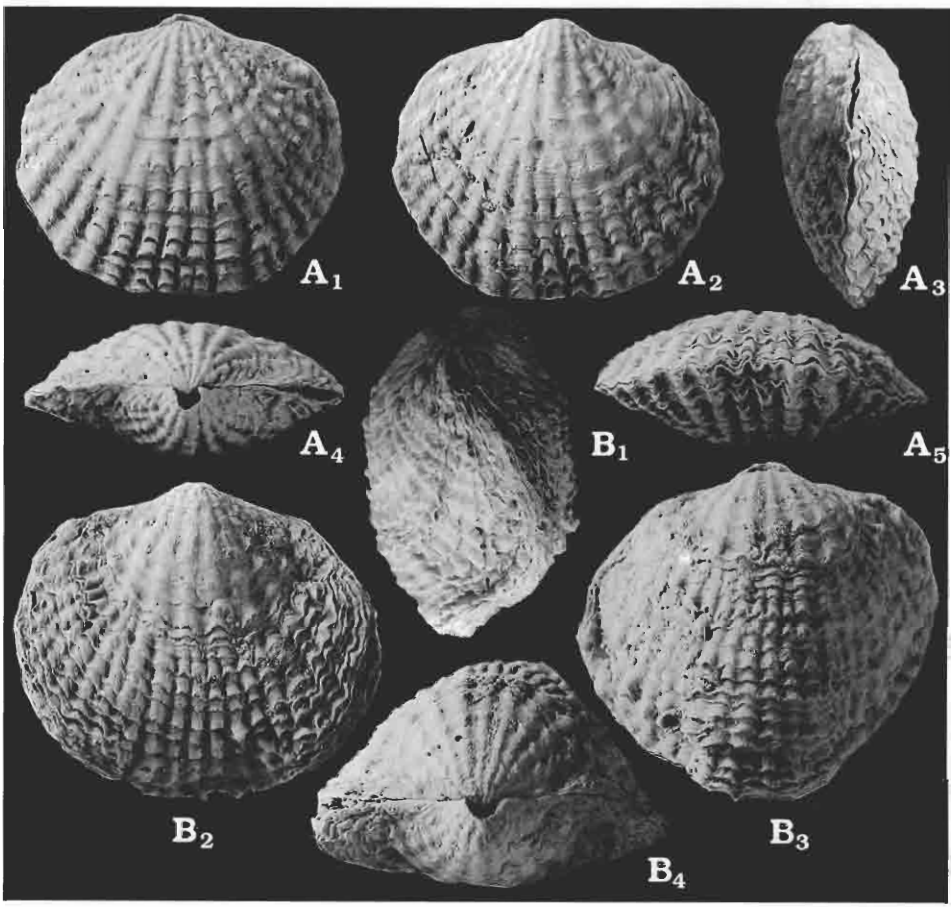


Fig. 23. **A–B**. *Spinatrypa (Spinatrypa) planosulcata* (Webster, 1888). **A1–A5** dorsal, ventral, lateral, posterior, and anterior views of paratype UMMP 7997; **B1–B5** lateral, ventral, dorsal, posterior, and anterior views of holotype UMMP 7996. Both from the late Frasnian Cerro Gordo Member of the Lime Creek Formation, Floyd County, from the Rockford Quarry (Day 1998: fig. 6, locality 3). All × 2.

at Bird Hill (Day 1998: figs 4, 6, 7), and apparently into very late Frasnian rocks as represented by a single specimen from the upper part of the Owen Member at the Buseman Quarry (see Baker *et al.* 1986: locality 4) in Butler County, Iowa (unpublished data of J.D.). In Iowa, the lowest specimens occur in association with conodonts correlated with the upper part of M.N. Zone 11, and ranges into the upper part of the Owen (part of M.N. Zone 13; see Figs 1, 2).

The single specimen from the Sly Gap Formation in the northern San Andres Mountains of New Mexico (Day 1998: figs 9, 10) occurs within the interval yielding conodonts of M.N. Zone 12 of Klapper (1989). It was also reported by Meader (1976) from the upper unit of the Jerome Member of the Martin Formation, Gila County, Arizona.

***Spinatrypa (S.) rockfordensis* (Fenton & Fenton, 1924)**. — [= *Atrypa asper* var. *hystrix* Calvin 1897: p. 167. = *Atrypa subhannibalensis* Webster 1921: p. 18. = *Atrypa hystrix* Hall, Branson 1923: p. 99, pl. 23: 7. = *Atrypa rockfordensis* Fenton & Fenton 1924: p. 142–144, pl. 27: 4–12. = *Atrypa rockfordensis elongata* Webster, Fenton & Fenton 1924: p. 144–145, pl. 32: 5–7].

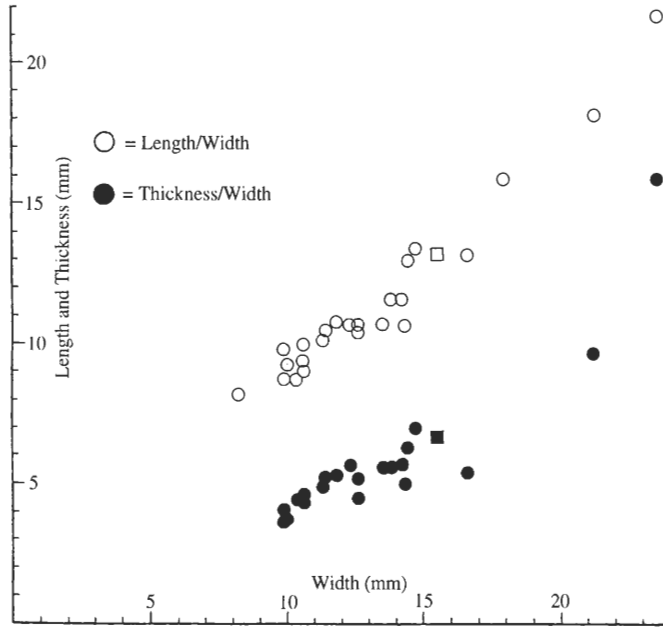


Fig. 24. Plots of shell measurements of *Spinatrypa (Spinatrypa) planosulcata* (Webster, 1888). All specimens are late Frasnian, from the middle and upper Cerro Gordo Member of the Lime Creek Formation.

Discussion. — In Iowa, *Spinatrypa* (*S.*) *rockfordensis* (Fig. 25) is restricted to the Lime Creek Formation. The type locality for *S. (S.) rockfordensis* is the Rockford Quarry, and no precise type stratum other than the *Spirifer* Zone (= upper 20 feet or 6 metres of the Cerro Gordo Member) was designated by Fenton & Fenton (1924: p. 142–144). The closely related species, *S. (S.) trulla* (Stainbrook, 1945) (Figs 26, 29, 30), is restricted to deeper water facies of the Amana Beds and Independence Shale in east-central Iowa. *S. (S.) rockfordensis* (Fenton & Fenton, 1924) is known in upper Frasnian Jerome Member of the Martin Formation in south-central Arizona (Meader 1976), and is a common component of middle shelf biofacies of the Jerome Member (*Cyrtospirifer–Pseudoatrypa* paleocommunity of Day 1984 and Day & Beus 1987) in the Canyon Creek area of Gila County in east-central Arizona.

Its stratigraphic range in the Lime Creek Formation is from the middle part of the *Cyrtospirifer whitneyi* Zone (Fig. 2) to the upper part of *Elita inconsueta* Zone. In conodont terms it begins in the upper part of M.N. Zone 11 and ranges into the upper part of M.N. Zone 12 (Fig. 2).

***Spinatrypa* (*S.*?) *thompsoni* sp. n.**

Figs 27, 28.

[= *Atrypa spinosa* Hall, Branson 1923: p. 98, pl. 20: 8–11, pl. 23: 8–9; Branson 1944: p. 150, pl. 23: 16–17. = *Atrypa planosulcata* Webster, Greger 1936a: p. 47, pl. 2: 7–12. = *Atrypa rockfordensis* Fenton & Fenton, Greger 1936a: p. 48, 50, pl. 3: 6–8].

Type material: Holotype is SUI 85754 (Fig. 27A). Additional three paratypes are SUI 85756-85758.

Type locality: The Missouri Highway 29 roadcut locality in Montgomery Count, Missouri (see location in Thompson 1993: p. 124, fig. 87).

Type horizon: Type specimens from the lower 1.5 m of the New Bloomfield Member of the Snyder Creek Shale, early Frasnian, at the Missouri Highway 29 roadcut locality in Montgomery County, Missouri (see Thompson 1993: p. 124, fig. 87).

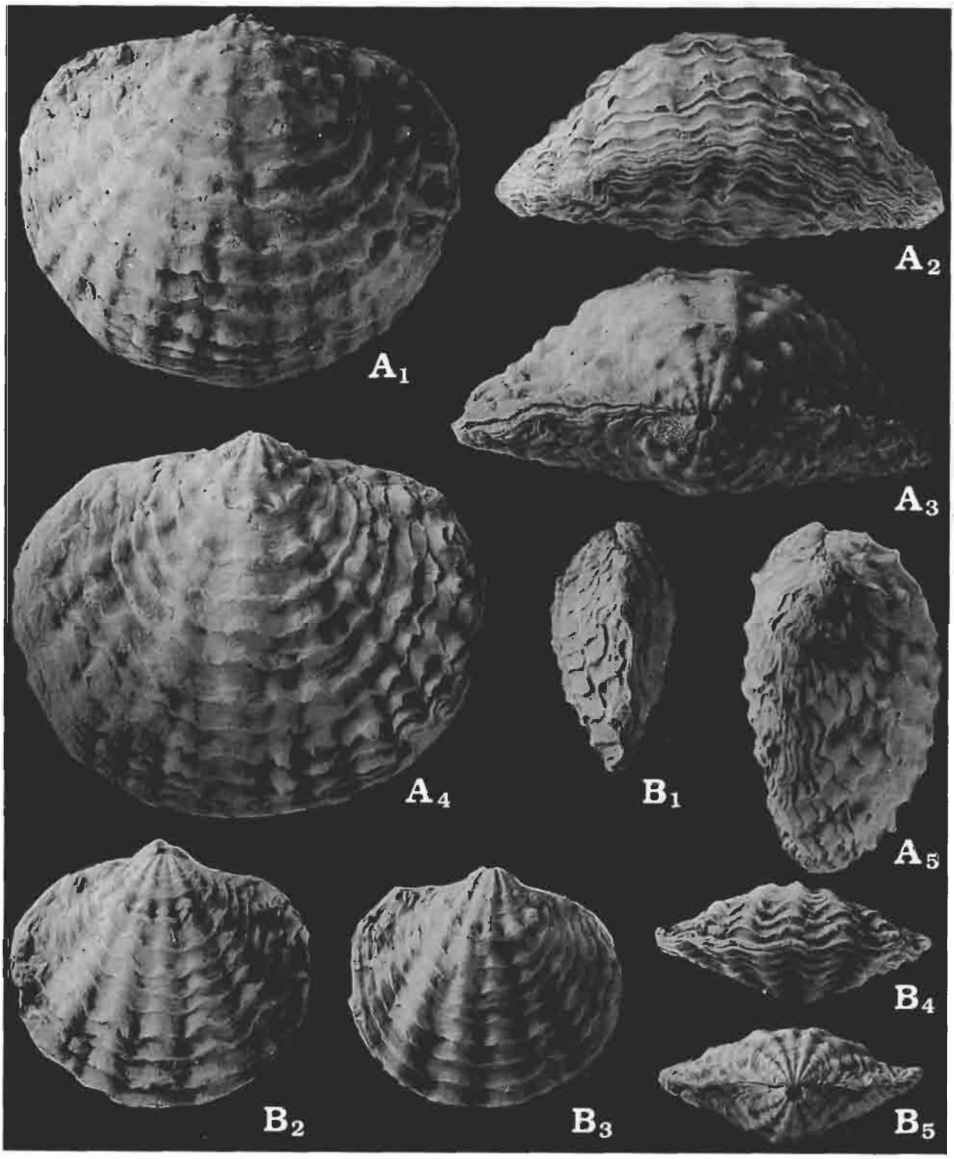


Fig. 25. **A–B**. *Spinatrypa (Spinatrypa) rockfordensis* (Fenton & Fenton, 1924). **A1–A5** dorsal, anterior, posterior, ventral, and lateral views of holotype UM 7985; **B1–B2** lateral, dorsal, ventral, anterior and posterior views of SUI 85763. Both from Late Frasnian Cerro Gordo Member of the Lime Creek Formation, Rockford Quarry (Day 1998: fig. 6, locality 3). All × 2.

Derivation of the name: In honor of Dr. Thomas L. Thompson, Missouri Deprtment of Natural Resources, for his contributions for knowledge of the Paleozoic stratigraphy and conodonts of Missouri.

Diagnosis. — A medium to large *Spinatrypa* with biconvex to slightly dorsibiconvex shells; wider than long with rounded outlines, elongate forms rare; maximum width at midvalve; broad shallow anterior fold; undulating ribs with 4–7 ribs (average of 5/10 mm) at anterior margin.

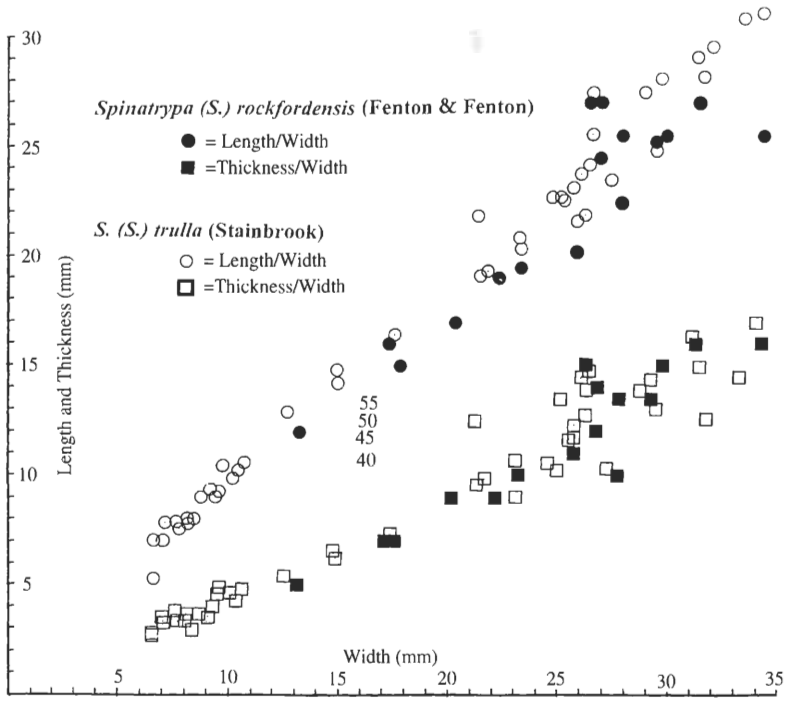


Fig. 26. Plot of shell measurements of specimens of *Spinatrypa (Spinatrypa) rockfordensis* (Fenton & Fenton, 1924) and *S. (S.) trulla* (Stainbrook, 1945).

D e s c r i p t i o n . — A medium to large species of *Spinatrypa (Spinatrypa)* with shells up to 36 mm in width (see Table 2), biconvex to dorsibiconvex; adult shells wider than long, shell width usually up to twice the thickness; outline is rounded; concentric spinose lamellae with average spacing of 2 mm in juvenile shells, spacing more irregular and becoming crowded towards margins in larger shells; numerous fine growth lamellae on shell surface between spinose lamella; well developed rounded ribs, ranging from 4–7 in number (average of 5/10 mm at anterior shell margin); ribs increase mainly by splitting, with less common increase by insertion; broad-shallow anterior fold in most shells. The ventral valve is somewhat inflated near the umbo, sloping gently anteriorly into a broad sulcus opposite the fold; area orthocline; beak erect; with small ovate foramen just below beak, interior unknown. Dorsal valve with gently concave profile, rarely inflated posterior of midvalve, interior of dorsal valve unknown.

C o m p a r i s o n s . — The only North American Frasnian spinatrypids comparable to *Spinatrypa (S.) thompsoni* sp. n. are *S. (S.) planosulcata* (Webster, 1888) and *S. (S.)* sp. 1. Both of these younger species have more numerous ribs, smaller adult shell sizes, with more inflated dorsal valves (dorsibiconvex shells), versus the proportionally thinner biconvex shells with compressed dorsal valves in *S. (S.) thompsoni* sp. n. Externally this species is closest to *S. aspera meridiana* Copper, 1967, from the late Eifelian of Germany, and the Frasnian form *S. semilukiana* (Lyashenko, 1959) from the Russian Platform. *S. (S.) thompsoni* differs from both of these species in much larger adult shell size (up to 36 mm wide), its rounded shell outline and proportionally longer shell. The European and Russian spinatrypids are much smaller (up to 24 mm wide) and their shells are proportionally much wider that those of the Missouri form.

D i s t r i b u t i o n a n d r a n g e . — This species is restricted to the central Missouri region of the central US midcontinent, where it occurs the New Bloomfield Member and lower part of the overlying Craghead Branch Member of the Snyder Creek Shale. It is most abundant in the lower

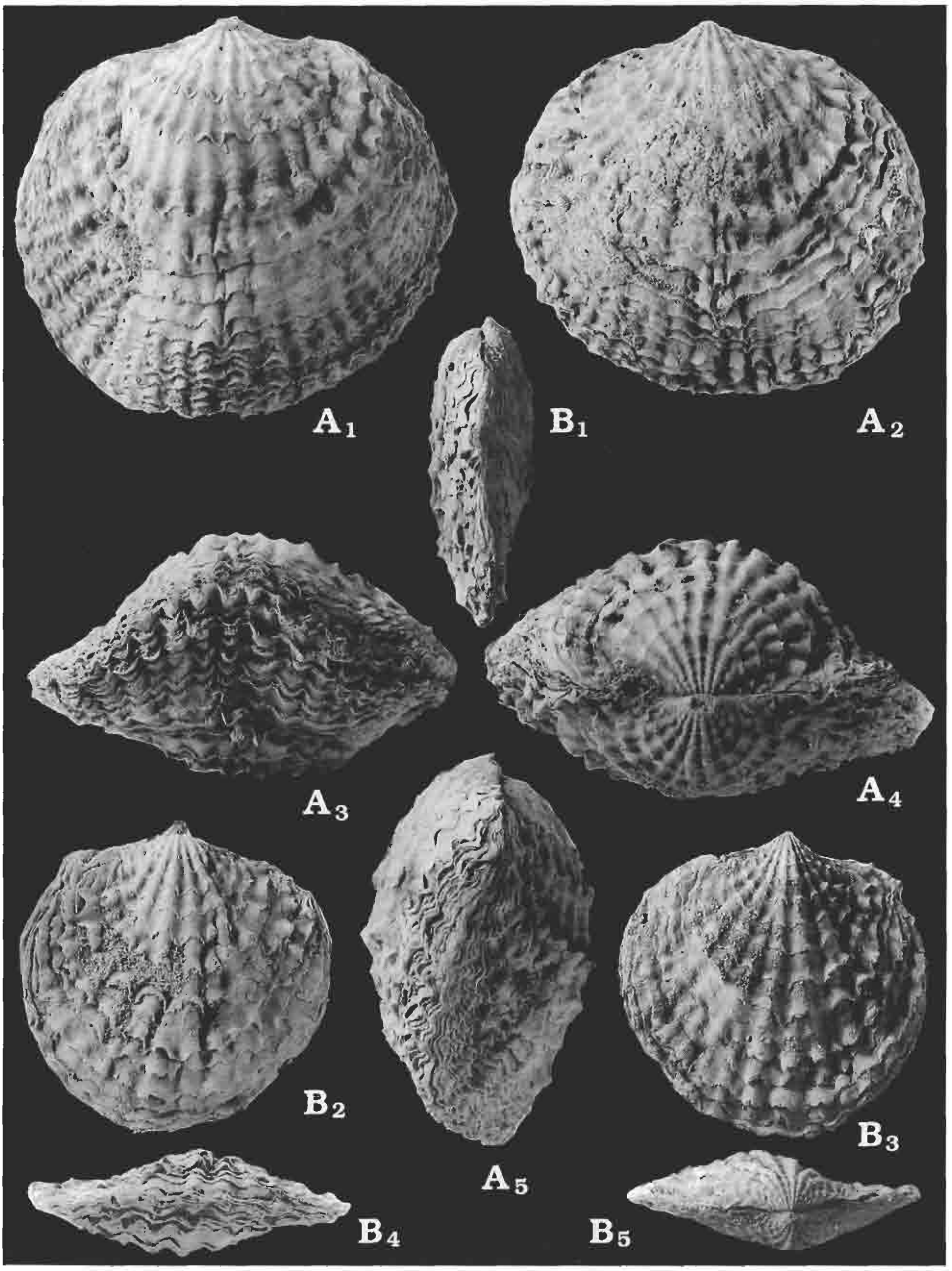


Fig. 27. **A–B**. *Spinatrypa (Spinatrypa) thompsoni* sp. n. **A1–A5** dorsal, ventral, anterior, posterior, and lateral views of holotype SUI 85754; **B1–B5** lateral, dorsal, ventral, anterior, and posterior views of paratype SUI 85758. Both from the early Frasnian New Bloomfield Member of the Snyder Creek Shale, at the Missouri Highway 19-Big Spring locality (Thompson 1993: p. 124, fig. 87, lower part of unit 7), Montgomery County, Missouri. All × 2.

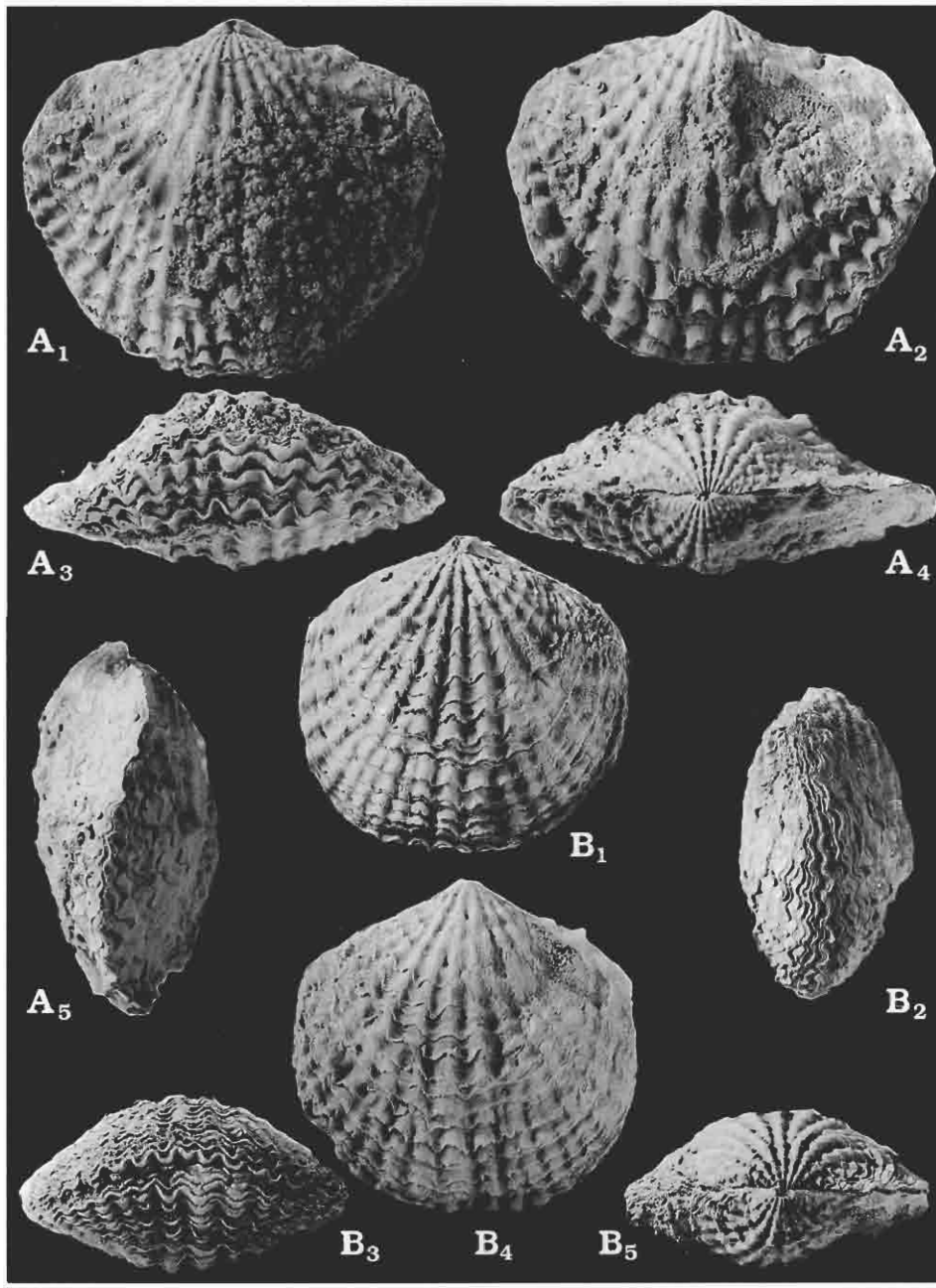


Fig. 28. **A–B**. *Spinatrypa (Spinatrypa) thompsoni* sp. n. **A1–A5** anterior, posterior, and lateral views of paratype SUI 85757; **B1–B5** dorsal, lateral, ventral, anterior, and posterior views of paratype SUI 85756. Early Frasnian, from the lower 2 metres of the New Bloomfield Member of the Snyder Creek Shale, at the Highway 19-Big Spring locality (see Thompson 1993: p. 124, fig. 87, lower part of unit 7), Montgomery County, Missouri. All × 2.

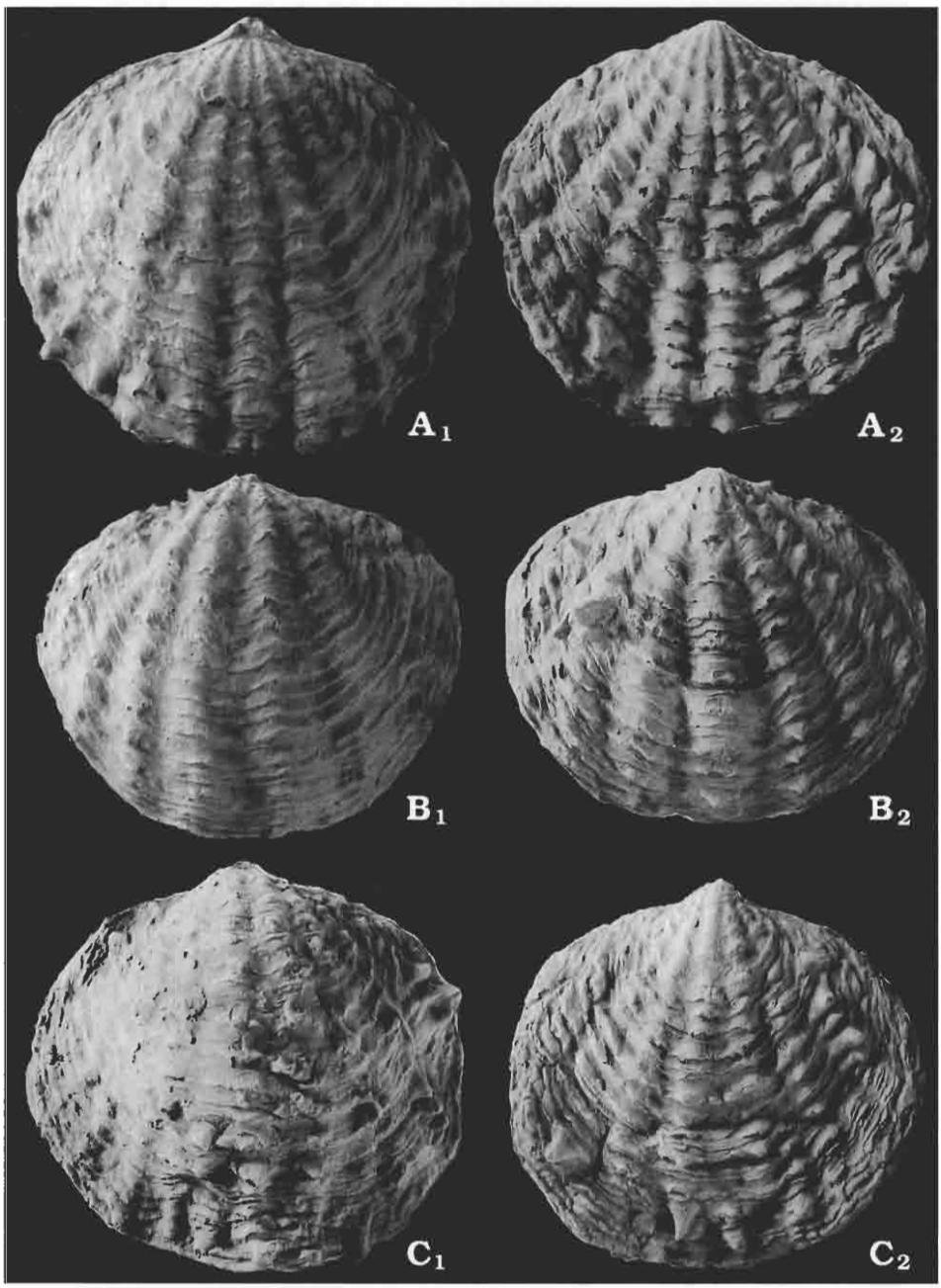


Fig. 29. **A–C**. *Spinatrypa (Spinatrypa) trulla* (Stainbrook, 1945). **A1**, **A2** dorsal and ventral views of SUI 85610; **B1**, **B2** dorsal and ventral views of SUI 85614; **C1**, **C2** dorsal and ventral views of SUI 85611. All from the Belanski Collection (University of Iowa), late Frasnian, Amana Beds at the type section (Day 1998: fig. 5A, locality 1), Iowa County, Iowa. All × 2.

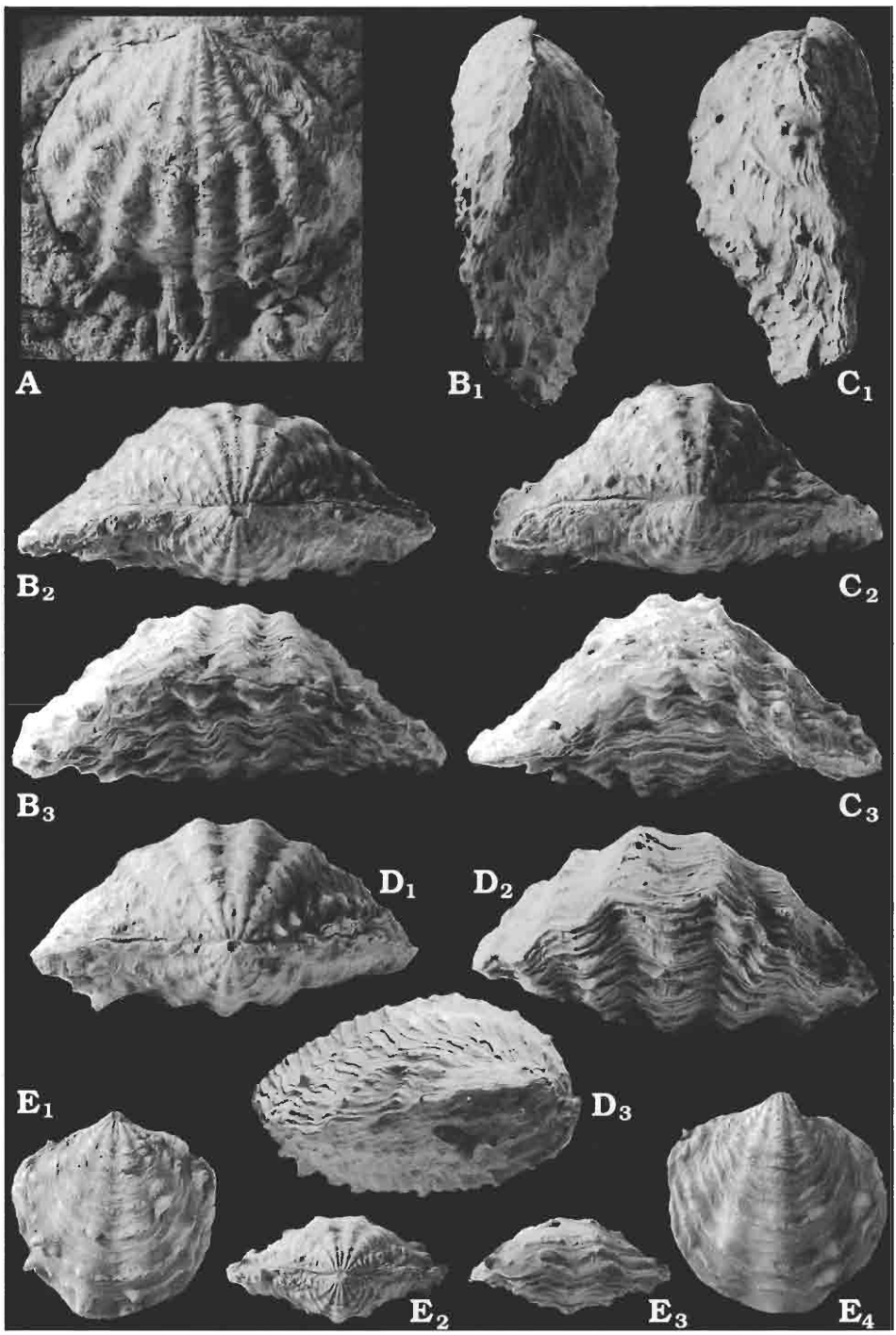
Table 2. Shell dimensions (in mm) and features of *Spinatrypa (Spinatrypa) thompsoni* sp. n. from the early Frasnian Snyder Creek Shale of central Missouri, southern Iowa Basin, US midcontinent. Abbreviations: T – shell thickness; W – maximum shell width; L – shell length; WF – width of fold; and C – number of ribs counted in 10 mm at anterior shell margin. Specimens designated A–D are unnumbered specimens from the Harner Collection, University of Iowa.

Specimen	W	L	T	WF	C
SUI 85754 (holotype)	30.1	27.3	16.8	22.3	5
SUI 85755 (topotype)	34.4	30.9	14.2	29.2	6
SUI 85756 (paratype)	21.9	21.0	11.9	19.5	6
SUI 85757 (paratype)	28.3	23.7	11.8	25.6	5
SUI 85758 (paratype)	21.2	20.5	–	–	5
SUI 85759 (paratype)	30.9	27.4	–	–	6
SUI 85760 (paratype)	33.6	30.3	15.3	30.0	5
SUI 85761 (paratype)	28.2	–	17.0	25.4	5
UM 1285a	20.5	18.4	–	17.6	5
UM 1285b	21.3	18.7	10.4	17.3	4
UM 3257a	18.5	17.8	10.2	15.3	4
UM 3257b	21.5	20.0	–	17.9	4
UM 3257c	16.2	15.0	7.5	14.3	5
UM 3257d	18.1	15.3	–	15.3	5
UM 3258	20.3	19.0	–	18.4	5
UM 9591a	23.4	21.7	10.8	21.3	4
UM9591b	31.3	29.4	11.3	23.9	5
A	16.0	15.9	8.7	13.2	7
B	18.9	19.6	11.7	15.4	6
C	22.0	22.0	10.6	20.1	4
D	18.7	17.8	10.2	16.9	4

2 metres of the New Bloomfield Member where it occurs in association with *Schizophoria athabaskensis* (Warren, 1944), *Strophodonta (S.) callawayensis* (Swallow, 1860), *S. (S.) navalis* (Swallow, 1860), and *Eostrophalosia callawayensis* (Swallow, 1960). This form was collected in the lower metre of the Snyder Creek at the Aux Vasse Quarry section in northern Callaway County, Missouri (see Day 1997: fig. 6, sample 19). Its biostratigraphic range (Fig. 2) begins just above the base of the *Strophodonta callawayensis* Zone (I.D.F.I. 10L) and ranges into the lower part of the *Orthospirifer missouriensis* Zone (Day 1997). Its range is from the upper part of M.N. Zone 3 to the lower part of M.N. Zone 4 of Klapper (1989).

Material and localities. — Besides of the type material, additional material includes nine specimens from the Branson Collection (University of Missouri), two of which were illustrated by Branson (1923: pl. 20: 8–11) under the name *Atrypa spinosa* Hall. They were collected from New

Fig. 30. **A–E.** *Spinatrypa (Spinatrypa) trulla* (Stainbrook, 1945). **A** ventral valve of SUI 84918; **B_1–B_3** lateral, posterior and anterior views of SUI 85610; **C_1–C_3** lateral, posterior and anterior views of SUI 85611; **D_1–D_3** posterior, anterior, and lateral views of SUI 85614; **E_1–E_4** dorsal, posterior, anterior, and ventral views of SUI 85641. All, except for SUI 84918, from the Belanski Collection (University of Iowa), late Frasnian Amana Beds at the type section (Fig. 5A, locality 1); SUI 84918 from Price Creek locality of the Amana Beds (Day 1998: fig. 5A, locality 2), Iowa County, Iowa. All × 2.


A
B1
C1
B2
C2
B3
C3
D1
D2
D3
E1
E2
E3
E4

Bloomfield and Craghead Branch members at the Craghead Creek streamcut, eastern Callaway County (see Thompson 1993: p. 151, fig. 108).

***Spinatrypa (S.) trulla* (Stainbrook, 1945).** — [= *Hystricina trulla* Stainbrook 1945: p. 50, pl., 5: 2–10, 12; Stainbrook 1948: p. 776, pl. 2: 28 only. =*Spinatrypa trulla* (Stainbrook), Cooper & Dutro 1982: p. 90, pl. 25: 1, 2].

Discussion. — *S. (S.) trulla* is an element of a distinctive and widespread group of late Frasnian *Spinatrypa* characterized by a marked reduction in the number and height of their radial costae (Figs 29, 30). Other closely related North American late Frasnian species are *S. (S.) rockfordensis* (Fenton & Fenton, 1924), *S. (S.) trulla decorticata* Cooper & Dutro, 1982, *S. (S.) compacta* Cooper & Dutro, 1982, and *S. (S.) obsolescens* Cooper & Dutro, 1982. Stainbrook (1942) illustrated of *Spinatrypa (S.* sp.) included in this group from the 'High Point Sandstone' of western New York. Recent study of conodonts and brachiopods from roadcut exposure near Stainbrook's High Point (Witchowski *et al.* 1997) indicates assignment of those beds to the late-latest Frasnian Wiscoy Member of the Java Formation (Kirchgasser *et al.* 1995: fig. 5). Spinatrypids recovered in the Wiscoy near Stainbrook's locality (collected by J. Over, State University of New York-Geneseo) are most similar to *S. (S.) compacta* Cooper & Dutro, 1982.

Shells of *Spinatrypa (S.) trulla* and *S. (S.) rockfordensis* have similar overall shell dimensions (Figs 26, 29, 30) but are readily distinguished on the basis of development of an average of three very low-rounded radial ribs/10 mm and less inflated ventral valve of *S. (S.) trulla*, versus the slightly greater spacing of spinose lamellae and average of four ribs/10 mm and more inflated ventral valve of shells of *S. (S). rockfordensis*. Both species show the same pattern of increase in numbers of costae by marginal insertion and branching. In Iowa, the latter species occurs in Cerro Gordo and Owen members of Lime Creek Formation. *S. (S.) trulla* is restricted to offshore facies of the Amana Beds (Fig. 2) and cave-filling deposits of the Independence Shale. *Spinatrypa (S.) trulla decorticata* Cooper & Dutro, 1982, is restricted to the late Frasnian Sly Gap Formation of New Mexico.

***Spinatrypina (Exatrypa) johnsoni* sp. n.**

Figs 31, 32.

[= *Atrypa reticulata* var. *rugatula* Stainbrook & Ladd 1924: pl. 1: 9 only].

Type material: The holotype is SUI 85766 (Fig. 31H). Ten paratypes, SUI 85767–85773, and SUI 65352.

Type locality: The holotype, paratype, and topotype specimens, except for paratype SUI 65352, from the State Quarry Member of the Lithograph City Formation at section locality 9/91-B on the wet shore of Coralville Lake, Johnson County, Iowa. Location of type locality is given in Day (1992: p. 105, fig. 15).

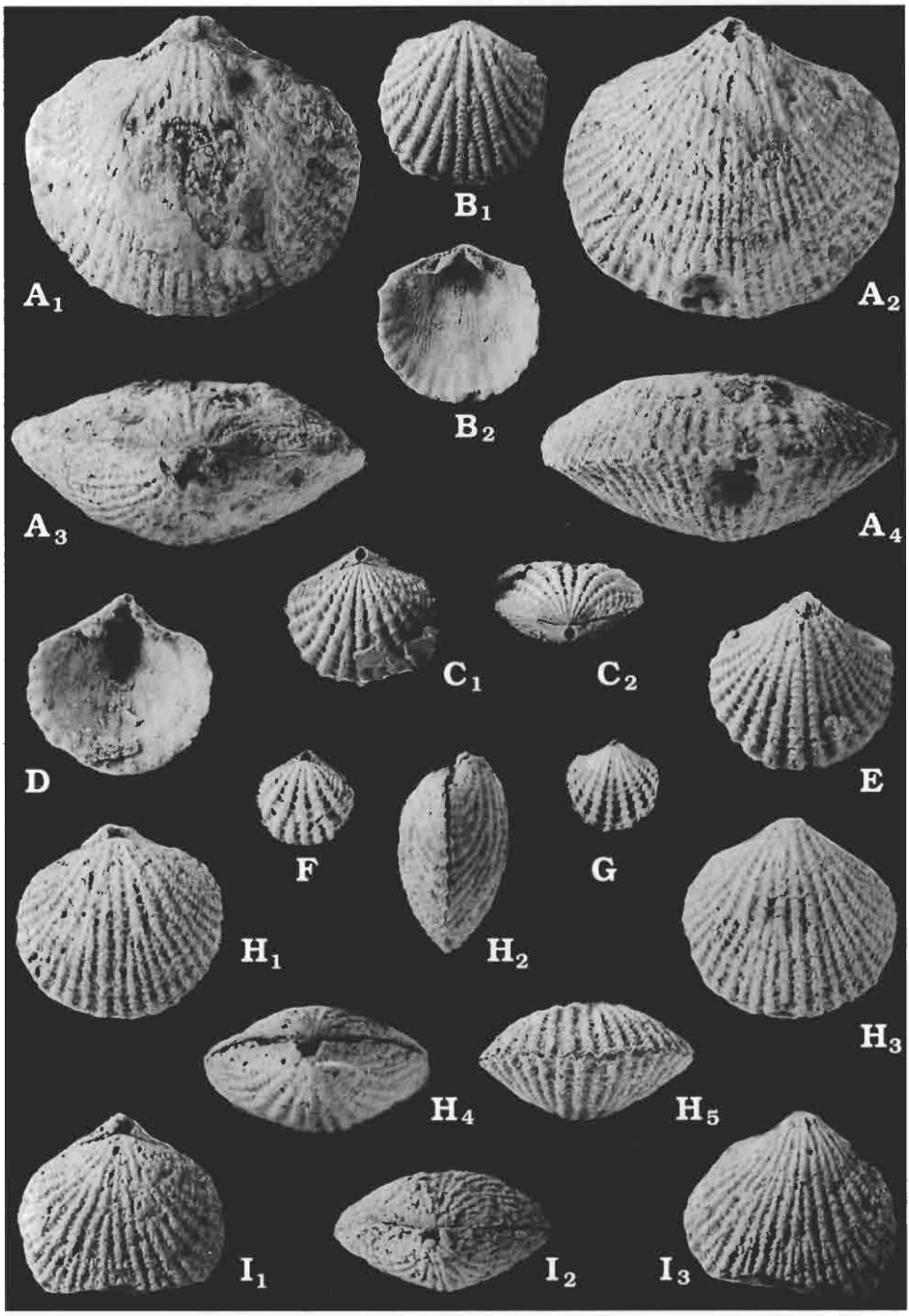
Type horizon: The type specimens were recovered in conodont sample interval 2 of Metzger (1993) in the State Quarry Member of the Lithograph City Formation.

Derivation of the name: In honor of John Granville Johnson (deceased), Oregon State University, for his major contributions to understanding of Devonian brachiopods, biostratigraphy, paleobiogeography, and eustasy.

Diagnosis. — A biconvex-ventribiconvex, transverse, compressed, lamellose species of *Spinatrypina (Exatrypa)* (Fig. 31).

Description. — Shells small (less than 20 mm wide); planar shells wider than long; nearly biconvex to slightly ventribiconvex (Fig. 32); anterior fold extremely shallow to obsolescent;

Fig. 31. **A–I.** *Spinatrypina (Exatrypa) johnsoni* sp. n. $\mathbf{A_1}$–$\mathbf{A_4}$ dorsal, ventral, posterior and anterior views of paratype SUI 65352; $\mathbf{B_1}$, $\mathbf{B_2}$ external and internal views of the dorsal valve, paratype SUI 85768; $\mathbf{C_1}$, $\mathbf{C_2}$ are dorsal and oblique posterior views of paratype SUI 85770; **D** and **E** internal and external views of a ventral valve, paratype SUI 85771; **F**, **G** are dorsal views of two juvenile shells numbered SUI 85773a and 85773b respectively; $\mathbf{H_1}$–$\mathbf{H_5}$ dorsal, lateral, ventral, posterior, and anterior views of holotype SUI 85766; $\mathbf{I_1}$–$\mathbf{I_3}$ dorsal, posterior, and ventral views of paratype SUI 85767. Latest Givetian–very early Frasnian, all



from the State Quarry Member of the Lithograph City Formation; all specimens, except SUI 65352, from section locality 9/91-B of (Day 1992: fig. 15), Johnson County, Iowa. Specimen SUI 65352 is from Belanski locality 165 (see Witzke & Bunker 1994). All × 3.

numerous tubular ribs (10–13 ribs/10 mm at anterior margin) with numerous imbricate lamella, exterior of dorsal valve with prominent medial rib in smallest juvenile shells that remains recognizable in large adult shells, ribs increase by insertion and branching-splitting; deltidial plates small, closing most of delthyrium early in ontogeny except for small-minute subhypothyrid foramen just below and posterior of orthocline beak in adult shells (12 mm wide), ventral area modestly developed in early growth stages, obscured in larger shells by as curvature of ventral area increases.

Teeth simple, oval-slightly elongate and parallel hinge line, nearly vertical, supported by small dental plates close to shell wall; lateral cavities minute to absent; muscle field elongate, not well defined.

Dorsal interior with moderately impressed adductor scars on floor of posterior third of valve separated by low undivided medial myophragm on posterior third of shell interior (in large adult shells only 12 mm wide), does not merge near cardinal margin with socket ridges; outer socket ridges modestly-strongly developed, erect along margins of sockets projecting ventrally where they join bases of crura, sockets elongate and appear to be corrugated; bases of crura project ventrally, jugal processes and spiralia not observed.

Discussion and comparison. — A poorly preserved specimen of *Spinatrypina (E.) johnsoni* sp. n. served as a cotype of *Atrypa rugatula* Stainbrook & Ladd (1924). The original description of *Atrypa rugatula* (Stainbrook & Ladd 1924: p. 358) undoubtedly refers to the species redescribed above as *P. rugatula* (Stainbrook & Ladd, 1924).

Spinatrypina (E.) johnsoni sp. n. is closest to *S. lamellosa* Johnson & Trojan, 1982 (Johnson & Trojan 1982: pl. 5: 1–17) from the late Givetian (Upper *K. disparilis* Zone) upper member of the Denay Limestone of Nevada. This older form is a likely ancestor of the younger latest Givetian and early Frasnian forms of *S. (E.) albertensis* group. The latter include: *S. lamellosa* Johnson & Trojan, 1982, *S.* cf. *comitata* Copper, 1967a as described in Johnson & Trojan (1982), *S. (E.) albertensis* (Warren, 1944), *S.(E.) johnsoni* sp. n., and *S. (E.)* sp. A of Norris (1981). The latter three species occur in T-R cycle IIb in carbonate platform facies in the US midcontinent and western Canada. Another closely related species is *S. (E.) explanata* (Schlotheim, 1820) from early Frasnian of the Refrath beds of the Steinbreche horizon in the Paffrath Syncline in Bergisches Land, Germany (Copper 1967a: p. 125–127, fig. 7, pl. 20: 1–4). This German species differs from *S. (E.) johnsoni* sp. n. in its proportionally wider and dorsibiconvex shell (versus the narrower biconvex shell of the Iowa form), presence of a well developed anterior fold, and larger more pronounced ventral interarea.

Externally *S. (E.) johnsoni* sp. n. is closest to *S. (E.) lamellosa* Johnson & Trojan, 1982, although it differs in that its radial ribs increase by both splitting and insertion, versus increase by splitting only in *S (E.) lamellosa.* Internally the dorsal valves of *S. (E.) johnsoni* sp. n. and *S. (E.) lamellosa* differ in that the latter has a split myophragm dividing the adductor muscle field, whereas the former is characterized by the presence of a simple undivided myophragm. The Nevada species could be ancestral to *S. (E.) johnsoni* sp. n. by fusion of the ridges of the myophragm on the floor of the dorsal valve, and modification to the method of increase in ribs by the mantle margin by development of rib insertion. *S. (E.) johnsoni* sp. n. is similar to *S. (E.) albertensis* (Warren, 1944) (Warren 1944: p. 118–119, pl. 3: 13–15) in terms of shell size, numbers of imbricate ribs (both with 10–13 ribs/10 mm counted at margins of adult shells), and both have incurved beaks. The latter species occurs in similar age deposits in the Waterways Formation of northeastern Alberta, and the Flume Formation in northeastern British Columbia (see discussion of Flume Fauna in Day 1998). *S. (E.) johnsoni* sp. n. differs from the latter in its thinner shell, more transverse shell outline, and more closely spaced imbricate lamellae, versus the more rounded outline, globose shell, and greater spacing of lamellae of shells of *S. (E.) albertensis* (Warren, 1944). *S. (E.) johnsoni* sp. n. differs from *S. (E.)* sp. A of Norris (in Norris & Uyeno 1981: p. 19, pl. 8: 1–6) in its proportionally wider shell at maturity, more pronounced-incurved beak, nearly planar anterior commissure, more numerous and finer tubular imbricate ribs (10–12 ribs/10 mm of *S. johnsoni* sp. n., versus 6–8 ribs/10 mm of *S.* sp. A).

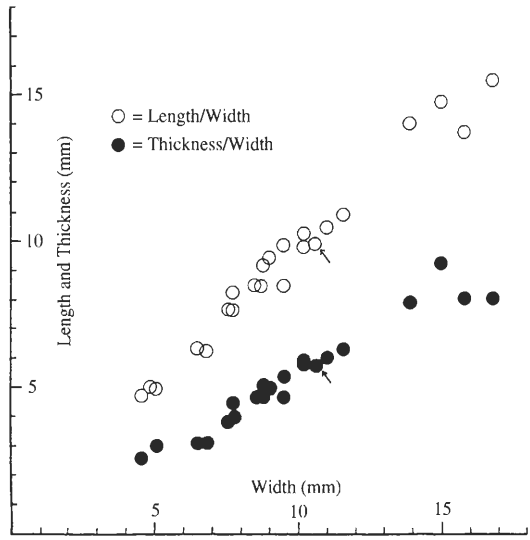


Fig. 32. Plot of shell measurement of specimens of *Spinatrypina (Exatrypa) johnsoni* sp. n. All specimens from the latest Givetian and early Frasnian State Quarry Member of the Lithograph City Formation, Johnson County, Iowa.

The Iowa form is easily distinguished from the other coeval species of *Spinatrypina (S.)*, such as *S. angusticostata* Johnson & Trojan, 1982, from the upper member of the Denay Limestone of central Nevada and *S. (S.)* sp. cf. *S. (S.) angusticostata* Johnson & Trojan, 1982, from the Flume Formation of northeastern British Columbia. Species of *Spinatrypina (S.)* have dorsibiconvex shells, are more globose with rounded outlines, and have finer and more numerous imbricate ribs as in *S. (S.) angusticostata* Johnson & Trojan, 1982 (Johnson & Trojan 1982: pl. 5: 18–28), or the older late Eifelian form *S. (S.) edmundsi* Copper, 1978 (Copper 1978: pl. 1: 15–19) from the late Eifelian-early Givetian of the NWT.

Distribution and range. — Latest Givetian–early Frasnian of east-central Iowa, occurs in the *Allanella allani* Zone (Day 1992) associated with conodonts of the *Skeletognathus norrisi* Zone and early Frasnian *Pandorinellina insita* Fauna. This interval corresponds to the lower part of I.D.F.I. 9 of Day (1996).

Material and localities. — Besides of the type specimens there are 66 silicified single valves from the type locality and type stratum, and 15 specimens (Fig. 32) from Belanski locality 169-2 (= type locality of the State Quarry Member of the Lithograph City Formation, see Witzke & Bunker 1994: fig. 18, pp. 54–58).

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Missouri-Columbia) provided loans of collections and types from the Middle and Late Devonian of Missouri. Dr. Brian Jones (University of Alberta-Edmonton) exchanged Frasnian atrypids from the Hay River area (NWT), and allowed access to Amoco-Canada LTD collections from the Hay River region during Days visit to his lab in 1991. Steven Travers and Cheryl Brokering assisted in measurement of specimens of Devonian atrypids as parts of geology undergraduate independent study projects supervised by J. Day at Illinois State University.

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