Distribution of latest Givetian–Frasnian Atrypida (Brachiopoda) in central and western North America

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Diverse atrypid brachiopod faunas characterize very late Givetian–early Frasnian deposits of Devonian Transgressive–Regressive (T-R) cycle IIb in North America which feature species of *Desquamatia (Seratrypa), Desquamatia (Independatrypa), Pseudoatrypa, Radiatrypa, Spinatrypina (S.), S. (Exatrypa), Spinatrypa (S.), Davidsonia*, and possibly *Iowatrypa.* Middle Frasnian faunas are not well documented in much of North America. Middle Frasnian deposits of T-R cycle IIc in the Great Basin, Iowa, and the southern Northwest Territories and Mackenzie shelf feature species of *Neatrypa, Pseudoatrypa, Radiatrypa, D. (Seratrypa), Spinatrypa*, and possibly *Costatrypa. Radiatrypa* does not carry over into late Frasnian rocks of T-R cycle IId in North America. Genera common to late Frasnian deposits of T-R cycle IId-1 in central and western North America include widespread species of *Pseudoatrypa, Spinatrypa, Costatrypa, Iowatrypa. D. (Seratrypa)* and *Neatrypa* were restricted to the tropical platforms of western Canada at that time. Very late Frasnian brachiopod faunas of T-R cycle IId-2 yield species of *Pseudoatrypa, Spinatrypa, Iowatrypa*, and *Pseudoatrypa*? (southwest US only). Available data on Late Frasnian brachiopod records in North American subtropical platforms (New Mexico and Iowa) indicate that two successive stepped late Frasnian extinction events affected those faunas, coinciding with the Lower Kellwasser Event and the Frasnian-Famennian (F-F) Event. Over half of the atrypid genera represented in late Frasnian North American faunas survived the first wave of extinctions (Lower Kellwasser Event). The surviving species, recorded in very late Frasnian deposits of Devonian T-R cycle IId-2, became extinct during the final crisis associated with the F-F Event.

Key words: Brachiopoda, Atrypida, biostratigraphy, biogeography, mass-extinction, Kellwasser Crisis, Transgressive–Regressive cycles, Givetian, Frasnian, Devonian, North America.

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Introduction

This investigation summarizes the current state of knowledge of the paleogeographic and biostratigraphic distribution of Atrypida in latest Givetian–Frasnian tropical and

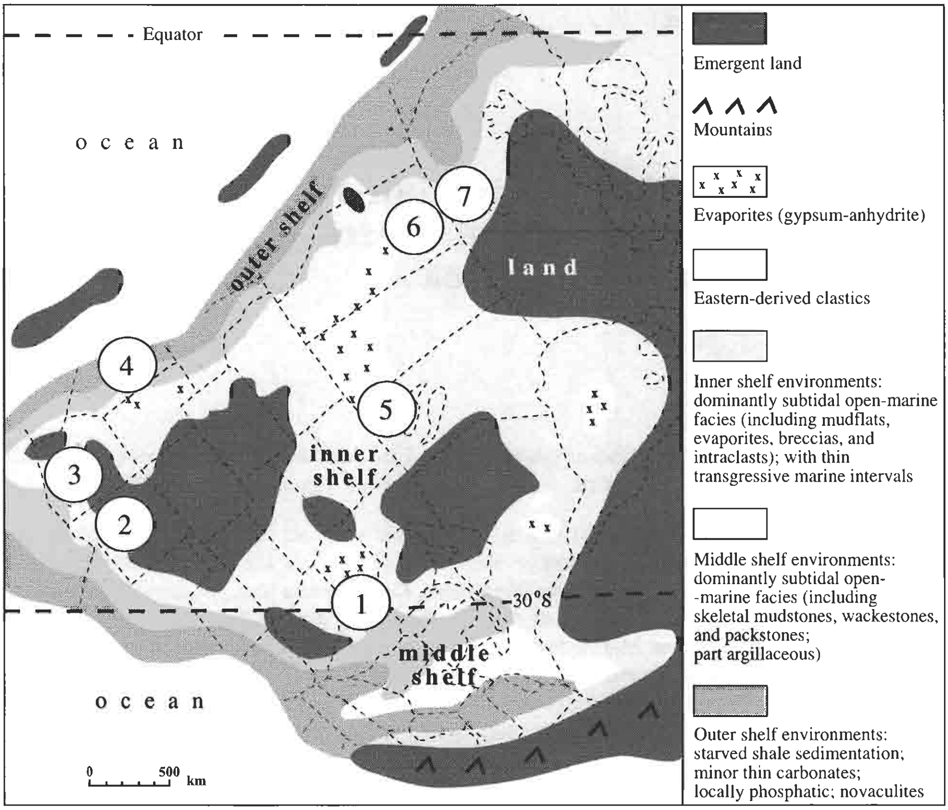

Fig. 1. Late Givetian–early Frasnian paleogeographic map of western and central Laurussia showing locations of important cratonic platform and continental margin successions with described latest Givetian and Frasnian atrypidan brachiopod faunas. Locality key: 1 – Iowa Basin (Iowa & central Missouri); 2 – San Andres and Sacramento Mountains, New Mexico; 3 – central and southeastern Arizona; 4 – Great Basin (Nevada and western Utah); 5 – southwestern Manitoba; 6 – northeastern Alberta; 7 – southern District of Mackenzie, Northwest Territories (NWT). Modified from fig. 1 of Day *et al.* (1996).

subtropical carbonate platform facies in North America (Fig. 1). Summaries of available data on the compositions of important faunas and ranges of various species from central and western North America are presented. Information on atrypid distribution are organized in terms of known occurrences in shelf facies of major sequence packages deposited during Devonian eustatic Transgressive–Regressive (T-R) cycles IIb–IId of Johnson *et al.* (1985, 1986), Johnson & Klapper (1992).

T-R cycles serve here as genetic subdivisions of the late Givetian–Frasnian interval of the Middle and Late Devonian of North America (Fig. 2). Durations of T-R cycles and ranges of atrypid taxa are discussed in terms of the Frasnian conodont Zonation established in the Montagne Noire (M.N.) sequence by Klapper (1989). The M.N. Frasnian zonation is tied directly to the Frasnian composite standard (CS) for graphic correlation (Klapper *et al.* 1995, 1996; Klapper 1997). Subdivisions of the Frasnian stage in this study (i.e. early, middle, late, very late) refer to the spans of T-R cycles IIb–IId and their subdivisions (Fig. 2) in terms of the Montagne Noire Frasnian conodont zonation of

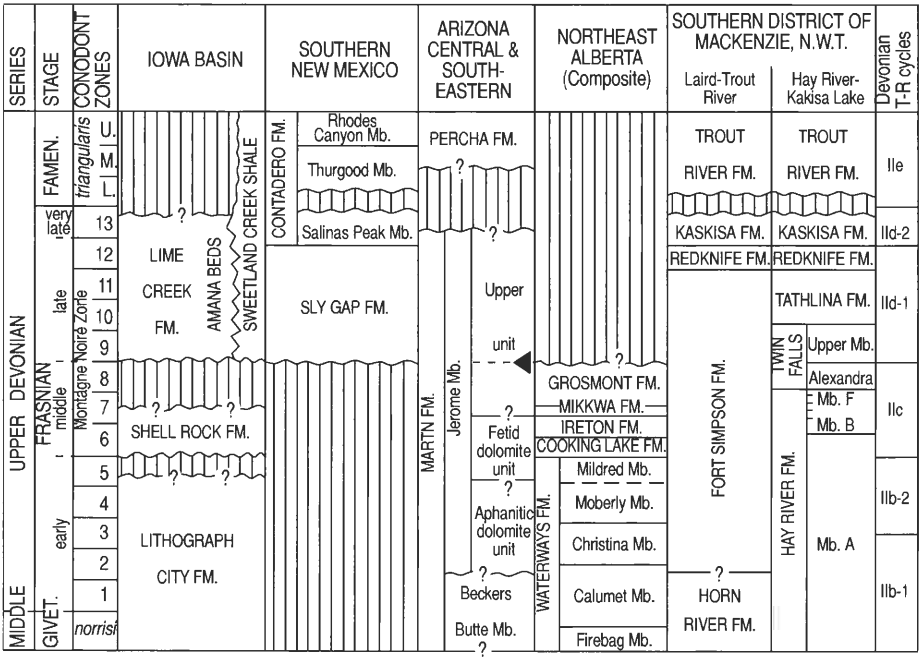

Fig. 2. Correlation chart of Middle and Late Devonian (latest Givetian–early Famennian) strata in six of the seven study sites shown in Fig. 1. Late Givetian conodont biostratigraphy (left column) follows Klapper & Johnson (1990), and Klapper's (1989) Frasnian Montagne Noire Frasnian zonation. Devonian Transgressive–Regressive (T-R) cycles IIb–IIe shown in right hand column are from Johnson *et al.* (1985), revised in Johnson & Klapper (1992), with subdivisions of T-R cycle IIb by Day *et al.* (1996). Provisional subdivisions of T-R cycle IId outlined in this study. Devonian stratigraphy of the Iowa Basin after Witzke *et al.* (1989), and Day (1997); stratigraphy for New Mexico follows Cooper & Dutro (1982) and Sorauf (1984). Arizona Devonian stratigraphy (Teichert 1964) and biostratigraphy of the Martin Formation of Arizona from Day & Beus (1982) and Day (1990). Black triangle marks the position of the lowest shelly faunas in the Jerome Member of the Martin Formation. Stratigraphy of northeast Alberta and the southern District of Mackenzie after Norris & Uyeno (1983), McLean *et al.* (1987), McLean & Sorauf (1989), and Norris (1998).

Klapper (1989). Current definitions of late Givetian and Frasnian T-R cycles are reviewed below (also see Johnson & Klapper 1992; Day *et al.* 1996; and Johnson *et al.* 1996).

Devonian T-R cycles, tied directly to conodont and brachiopod sequences in various well studied platform successions, provide a natural framework for the evaluation and study of paleobiogeographic and temporal distribution of atrypids in the Middle and Late Devonian of North America. The timing of major atrypid migrations, radiations, and extinctions correlates closely to the timing of sea level fluctuations that initiated or ended T-R cycles IIb–IId and their subdivisions (see Day *et al.* 1996). Distinctive suites of atrypid taxa characterize five major unconformity-bound stratigraphic packages (Figs 1, 2) corresponding to T-R cycles IIb through IId of Johnson *et al.* (1985), Johnson & Klapper (1992), subdivisions of T-R cycle IIb proposed by Day *et al.* (1994, 1996), and the two-fold subdivision of Frasnian T-R cycle IId (as revised in Johnson & Klapper 1992) proposed herein.

Very late Givetian–Frasnian atrypid brachiopod faunas in central and western North American carbonate platforms are dominated by species of widespread variatrypine and spinatrypid genera. The variatrypines *Desquamatia (Independatrypa), D. (Seratrypa), Neatrypa, Pseudoatrypa*, and *Radiatrypa)* are most diverse in western North American and US midcontinent faunas. A new very late Frasnian form recovered from New Mexico appears to represent a variatrypine of the genus *Pseudoatrypa*? The dominant spinatrypids in North American faunas include *Spinatrypa (Spinatrypa), Spinatrypina (Exatrypa)*, and *S. (Spinatrypina)*. The latter subgenus was restricted to western North America by the early Frasnian. Migrations and radiation of *Spinatrypina* and *Pseudoatrypa* in western Canadian and central North American platforms coincided with the initial transgression of the late Givetian sea level rise of T-R cycle IIb-1. *Spinatrypina* was extinct in the Iowa Basin high in the interval of the early Frasnian (Fig. 2), and apparently is extinct in North America by the middle Frasnian. Distinctive species of *Spinatrypa (S.)* were the dominant and most widespread spinatrypids in North America carbonate platforms and clastic shelf facies during the Frasnian. Species related to *S. (S.) planosulcata* (Fenton & Fenton, 1924), became widespread in early Frasnian rocks in central and western North America, and range into the very late Frasnian. Species similar to *S. (S.) trulla* (Stainbrook, 1945) were widespread across North America following the late Frasnian sea level rise of T-R cycle IId-1.

Davidsonidae (*Davidsonia*) range into early Frasnian deposits in the Great Basin, but are unknown in middle and late Frasnian rocks in North America (Johnson 1990). A possible carinatinid (*Carinatrypa*?) has been illustrated from early Frasnian rocks in western Canada, although Copper (in Copper & Gourvennec 1996: p. 84) suggested that reported latest Givetian and Frasnian carinitinids are most likely spinatrypinids or atrypids (Atrypinae). Migration of *Costatrypa* into North America during middle Frasnian is evidenced by the occurrence of an undescribed form in the Hay River Formation in the Northwest Territories of western Canada. Prior to that time, it is unknown in Devonian rocks of North America. Renewed sea level rise and transgression during the late Frasnian allowed *Costatrypa* to expand its geographic range by migration into the central and western US, presumably from western Canada.

Members of the Invertinae are not well known in North American faunas prior to the late Frasnian. An initial migration of invertinids from European source areas into western Canada may have occurred during the early Frasnian as evidenced by the illustration of *Pseudogruenewaldtia*? by Norris (1983) from the Waterways Formation. A late Frasnian migration of *Iowatrypa* into North American carbonate platforms is marked by the appearance of 3–5 closely related species in shelf facies of T-R cycle IId in western and central North America.

Eastern North American atrypid faunas are poorly documented. Recent study of late Frasnian brachiopod faunas from rocks in western New York (see Day in Wichtowski *et al.* 1997) and older data available from Stainbrook (1942) and Dutro (1981) indicate that Frasnian atrypid faunas in the Catskill Delta facies of New York consist of species of *Pseudoatrypa* and *Spinatrypa*. Day (in Wichtowski *et al.* 1997) reported *Spinatrypa* cf. *S. compacta* Cooper & Dutro (1982) associated with the conodonts *Polygnathus brevicarina* and *P. webbi* from the late Frasnian Wiscoy Member of the Java Formation from western New York. Late Givetian (Day 1994a) and early Frasnian (author's collections) atrypids recovered from the subsurface of the Michigan Basin are similar to those seen in eastern North American faunas in the Moose River Basin of Ontario described by Norris (in Norris *et al.* 1992).

Late Givetian–Frasnian Bioevents and Transgressive–Regressive (T-R) Cycles

There is a high degree of correlation between the distribution of late Givetian and Frasnian North American tropical and subtropical carbonate platform brachiopod faunas and eustatic sea level changes (Johnson 1970, 1990; Day 1992, 1996b). Major migrations and radiations in various atrypid lineages in North American faunas are correlated closely with the timing of major eustatic sea level rises and resultant transgressions that initiated Middle and Late Devonian Transgressive–Regressive (T-R) cycles first proposed by Johnson *et al.* (1985). Certain revisions to T-R cycles were introduced in studies by Johnson *et al.* (1986), Johnson & Sandberg (1989), Klapper & Johnson (1992), Johnson *et al.* (1996), or subdivided by Day *et al.* (1994, 1996). Proposed subdivisions of T-R cycles of Johnson et al. (1985) relevant to this study are new divisions of T-R cycle IIb designated as T-R cycles IIb-1 and IIb-2 (Fig. 2), and subdivisions of T-R cycle IId as outlined below.

A number of extinctions of global and regional significance affected North American carbonate platform shelly faunas during the late Givetian–Frasnian and the timing of these correlate closely with either sea level rises that initiated or low-stands that terminated certain T-R cycles. The timing of two extinctions correlate closely with regressions terminating deposition of T-R cycles IIa-2 (highest *Klapperina disparilis* Zone or very late Givetian) and IIc (upper part of M.N. Zone 8 or end of middle Frasnian as discussed below). The first of two stepped extinctions of shelly fossils in the late Frasnian correlate with the Lower Kellwasser Event of Becker (1993), referred to as the Late Frasnian Event of Walliser (1995), or the latest M.N. Zone 12 Extinction of (Day 1996a). The timing of this event coincided with the rapid sea level rise and platform drowning associated with onset of T-R cycle IId-2, and the second extinction is the F-F Boundary Event of Walliser (1995).

At this time, there is no direct evidence of a rapid sea level rise associated with the Frasnian-Famennian Boundary Event in platform facies of North America related to either tsunamis or eustatic sea level rise. As described in Johnson *et al.* (1985) and later studies (Johnson & Klapper 1992; Day 1996b; Lamaskin & Elrick 1997) regression terminated T-R cycle IId deposition across most shelf areas in North America. Emergence in the very early Famennian resulted in erosion of neritic records in platform successions that have been well documented in central and western North America as of this writing.

Givetian–Frasnian Event/Upper *disparilis* Zone extinction. — The Givetian–Frasnian Boundary Event of Walliser (1995) or Upper *disparilis* Zone extinction of Day (1996a, 1996b) immediately preceded the initial sea level rise of T-R cycle IIb in the very late Givetian. Most major North American cratonic carbonate platforms appear to have been emergent during the terminal part of the Upper *K. disparilis* Zone. This extinction (see discussion of Middle-Upper Devonian boundary in McLaren 1970 and Braun *et al.* 1989) of North American platform brachiopod faunas precedes the Givetian-Frasnian boundary as it is currently defined (now at the base of the former Lower *Polygnathaus symmetrica* Zone = base of Frasnian Montagne Noire Zone 1 of Klapper 1989, or first entry of the early form of *Ancryodella rotundiloba*).

Platform emergence in the late Givetian coincided with the culmination of extinctions of North American carbonate platform shelly faunas that marked the close of T-R cycle IIa. In the US midcontinent, typical atrypids that characterized late Givetian faunas of the Little Cedar and Coralville formations (Figs 2, 3) became extinct in central North America at that time (Day 1996b), including *Neatrypa*, *Desquamatia* (*Seratrypa*), and *Spinatrypa*. These survived in other platform habitats in western Canada and eastern Laurussia (western and eastern Europe) which served as source populations for later migrations into central North America at different times in the Frasnian. The latter two were reintroduced (joined also by *Radiatrypa*) to the central US Iowa Basin by migrations coinciding with the early Frasnian sea level rise of T-R cycle IIb-2 (Fig. 2).

T-R cycle IIb-1 (late Givetian–early Frasnian). — The initial T-R cycle IIb transgression immediately followed the period of pronounced emergence of cratonic carbonate platforms across central and western North America coinciding with the late Givetian extinction discussed above. One of the more significant eustatic sea level rises of the later part of the Devonian occurred in the very late Givetian at or near the base of the *Skeletognathus norrisi* Zone (see: Johnson 1990; Johnson & Klapper 1992; Day *et al.* 1996; Johnson *et al.* 1996). North American atrypid faunas at this time are cosmopolitan (at generic level) in character, and remain so for the duration of the Frasnian Stage. Emergence of inner shelf facies tracts in cratonic basins in the central US (Day, Witzke & Bunker, in Day *et al.* 1996) and central Canada (Uyeno, Norris & Day in Day *et al.* 1996) immediately preceded the onset of a second sea level rise that initiated T-R cycle IIb-2.

T-R cycle IIb-2 (early Frasnian). — A second marked rapid sea level rise in the early Frasnian within the interval of Montagne Noire (M.N.) Zone 3 of Klapper (1989) led to resumption of open marine sedimentation across North American cratonic platforms in central and western North America (Fig. 2). Atrypid migrations associated with the sea level rise of T-R cycle IIb-2 include the immigration of *Radiatrypa* into northern Iowa and central Missouri areas of the Iowa Basin. *Spinatrypa* (*S.*) and *Desquamatia* (*Seratrypa*) were also reintroduced through migrations into central North America. All of the aforementioned forms appear to have immigrated from platform habitats in central and western Canada into the central US at that time. Platform aggradation and emergence of inner shelf facies tracts is evident in the US midcontinent, and marked the end of T-R cycle IIb-2 in that area (Figs 1, 2). This appears to have occurred in the interval of the upper part of M.N. Zone 5 of Klapper (see Johnson & Klapper 1992).

T-R cycle IIc (middle Frasnian). — Renewed sea level rise marking the initiation of T-R cycle IIc (Fig. 2) began in the upper part of M.N. Zone 5 or lower part of Zone 6 (Johnson & Klapper 1992; see discussion of age of Cooking Lake-Majeau Lake interval in western Canada in McLean & Klapper 1997). Records of atrypid faunas in deposits included in this interval are only known from parts of western North America and now from the US Midcontinent (see Day & Copper 1998). Thus far, the most diverse atrypid fauna known at this time is from the Hay River Formation of the southern NWT (Fig. 2) that yields at least seven species of *Desquamatia* (*Seratrypa*), *Neatrypa*, *Pseudoatrypa*, *Radiatrypa*, and *Spinatrypa*.

T-R cycle IIc deposition was terminated across the U.S. midcontinent by major regional regression, and evidence from western Canada suggests emergence of platforms occurred in the NWT and perhaps affected platforms in western Alberta (see Whalen *et al.* 1997). The timing of this regression was during the interval of M.N. Zone 8. In the Iowa Basin, Devonian karst features developed to a depth of nearly 80 metres (262 feet) into the older Cedar Valley Group platform carbonates in the central and eastern parts of the Iowa Basin (Figs 1–3). At that time IIc deposits of the Shell Rock Formation (Figs 2, 3) were removed by erosion across much of eastern Iowa. The Independence Shale (Lime Creek Formation equivalents) of eastern Iowa is a stratigraphic leak of late Frasnian deposits that in-filled karst cavities that developed during the sea level low-stand and resultant terminal T-R cycle IIc regression. In the Northwest Territories, the reefal platform margin (Alexandra Member-Twin Falls Formation) in the Mackenzie Shelf aggraded to sea level and is capped by peritidal mudflat facies at Alexadra Falls on Hay River. Development of the disconformity at the contact of the Alexandra and Upper members of the Twin Falls indicate emergence at the close of the middle Frasnian in the southern NWT.

Middle Frasnian extinction? — Analysis of the temporal changes in brachiopod diversity in Middle–Late Devonian of the Iowa Basin by Day (1996b: text-fig. 9) show that no middle Frasnian brachiopod species of the Shell Rock Formation characterizing Iowa Devonian Faunal Intervals (F.I.) 11 and 12 carry over into late Frasnian faunas of F.I. 13–18 (Fig. 3). Important genera that became extinct at that time include the mucrospiriferid *Eluetherokomma* and the rhynchonellid *Lorangerella*. The abundance of athyrids also declined sharply in all North American platform faunas in the late Frasnian. On the other hand, 19 of 21 genera represented in the Shell Rock fauna carry over (including *Pseudoatrypa* and *Spinatrypa*) and are represented by species in the rich late Frasnian faunas of the Lime Creek Formation, Amana Beds and Independence Shale of Iowa and its equivalents elsewhere in North America (Figs 2, 3). The significance of the apparent middle Frasnian extinction of US midcontinent faunas is still poorly understood. The actual significance of this apparent extinction will

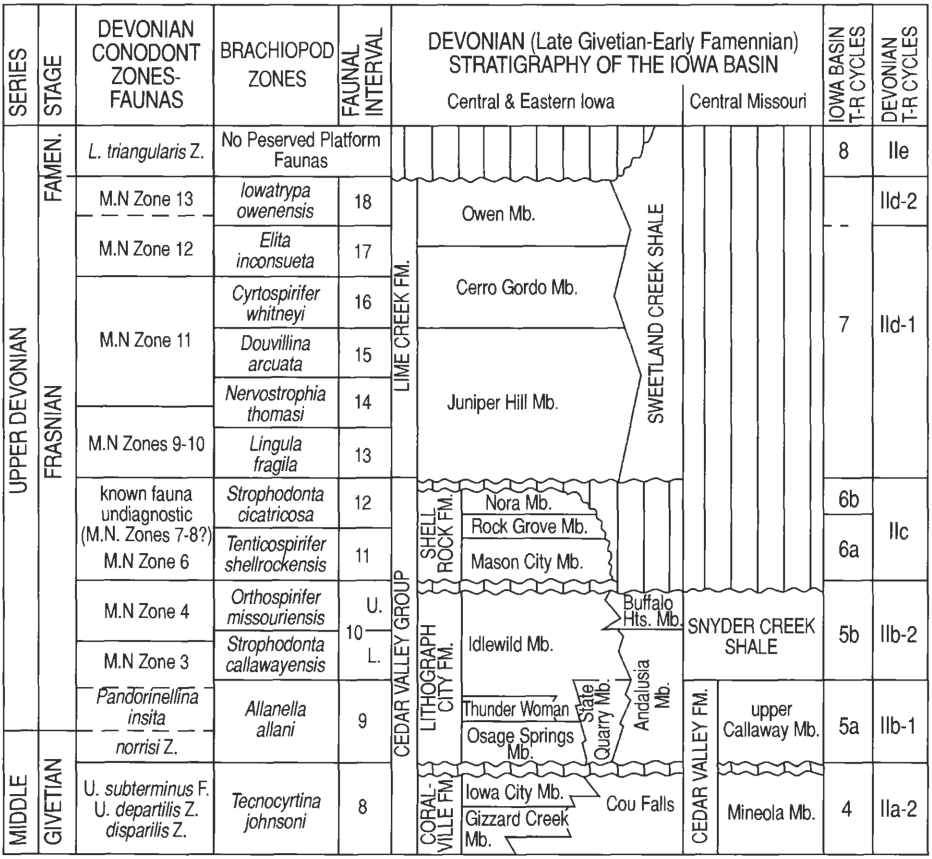

Fig. 3. Stratigraphic and biostratigraphic framework for the upper Middle–Late Devonian (late Givetian–early Famennian) strata of the Iowa Basin showing relationships between: the qualitative eustatic T-R cycles of Johnson *et al.* 1985, Johnson & Klapper 1992, Day *et al.* 1996, and this study; and Iowa Basin Devonian T-R cycles of Witzke *et al.* (1989), Bunker & Witzke (1992), and Witzke & Bunker (1996). Iowa Devonian conodont biostratigraphy follows Witzke *et al.* (1989), Klapper & Johnson in Johnson (1990), Day (1990), Klapper in Johnson & Klapper (1992), Bunker & Witzke (1992), Witzke & Bunker (1996). Devonian brachiopod biostratigraphy from Day (1989a, 1992, 1996b, 1997). Iowa Devonian Faunal Intervals after Day (1996b, 1997). Iowa Basin Devonian stratigraphy after Witzke *et al.* (1989) and Day (1997). Modified from Day (1997: fig. 4).

only be understood after other middle-late Frasnian brachiopod faunas and sequences are better documented from other regions of North America and elswhere.

T-R cycle IId-1 (late Frasnian). — The two sea level rises within the interval of late Frasnian T-R cycle IId shown on the original qualitative eustatic sea curve of Johnson *et al.* (1985: fig. 12) provide a basis for its two-fold subdivision provisionally designated here as T-R cycles IId-1 and IId-2 (Fig. 2). The initial sea level rise of T-R cycle IId (T-R cycle IId-1) began during M. N. Zone 9 (see revision to T-R cycle IId in Johnson & Klapper 1992). The base of T-R cycle IId as originally defined in Johnson *et al.* (1985: see discussions by Sandberg & Johnson) was placed at the position of the incoming of *Palmatolepis semichatovae* in Frasnian carbonate platforms facies in various areas of western North America. The widely reported first occurrences of this species in cratonic platform sections of Montana (Sandberg *et al.* 1989), Nevada-Utah (Sandberg in Johnson *et al.* 1991, see discussion of early *Palmatolepis rhenana* Zone), and in the Belgian sections (Sandberg *et al.* 1992) may mark the level in those areas of the maximum flooding of the IId-1 sea level rise. In Montagne Noire Frasnian zonation of Klapper (1989), the lowest occurrence of *P. semichatovae* lies near the base of M. N. Zone 11, well above the lower boundary of T-R cycle IId which is currently aligned with the base of M.N. Zone 9 (Fig. 2).

T-R cycle IId-1 was not terminated by regression in most carbonate platforms. Late Frasnian IId-2 deposition ended as a consequence of rapid sea level rise that initiated T-R cycle IId-2 and drowned shelf areas resulting in platform back-stepping in central and western North America (Fig. 2). The first of two late Frasnian extinctions (discussed below) is closely associated with the sea level rise that initiated T-R cycle IId-2.

Late Frasnian Event or Lower Kellwasser Event. — The timing of the extinction of the late Frasnian brachiopod fauna of the Sly Gap Formation in the subtropical shelf succession in southern New Mexico (Copper & Dutro 1982; Dutro 1986; Day 1987a, 1988) coincides with the timing of the Lower Kellwasser Event of Becker (1993) or Late Frasnian (LFr) Event of Walliser (1996). Available conodont evidence (Day 1988, 1990) permits correlation of the upper part Sly Gap with a position in M.N. Zone 12 (Fig. 2). There, nearly 85% of all Sly Gap brachiopod species became extinct. Eight to nine surviving Sly Gap brachiopod taxa are joined by other forms closely allied to Appalachian Basin forms in the very late Frasnian age fauna of the upper part of the Salinas Peak Member of the Contadero Formation (see discussion in Day 1988).

T-R cycle IId-2 (very late Frasnian). — Published data from North American sections establish the timing of a second sea level rise within the interval of T-R cycle IId of Johnson *et al.* (1985) that appears to coincide with the position of base of the Kellwasser interval in European sections. As shown in Fig. 2, the timing of this sea level rise appears to have begun within the uppermost part of M.N. Zone 12 or at the base of M.N. Zone 13 and spans the remainder of late Frasnian M.N. Zone 13. The latest Frasnian *Palmatolepis linguiformis* Zone of Ziegler & Sandberg (1990) coincides with the upper part of M.N. Zone 13 as currently defined, and includes the upper part of in the interval of T-R cycle IId-2.

The IId-2 deepening event coincided with the deposition of the Pipe Creek Shale in western New York in the Appalachian foreland Basin (Johnson *et al.* 1985: fig. 8), recently correlated with M.N. Zone 13 by Over (1997: figs 3, 7) and Over *et al.* (1997). In Iowa, deposits spanning part of this interval have recently been recognized in platform facies included in the upper half of the Owen Member of the Lime Creek Formation. These deposits do yield low diversity brachiopod faunas (up to seven genera) that feature *Spinatrypa* and possibly *Iowatrypa.* Very latest Frasnian platform deposits spanning the Frasnian-Famennian boundary are not preserved owing to emergence of the Lime Creek platform for much of the early Famennian (Bunker & Witzke 1992; Witzke & Bunker 1996). In New Mexico, this event coincided with onset of deposition of turbidites of the lower part of the Salinas Peak Member of the Contadero Formation, which overlay middle shelf deposits of the older late Frasnian Sly Gap Formation (Fig. 2, T-R cycle IId-1). In western Canada, the Blue Ridge, Ronde-Simla, and Kakisa equivalents (Fig. 2) were deposited during the interval of M.N. Zone 13 (McLean & Klapper 1997).

Deep water records spanning the Frasnian Famennian boundary are known from different parts of North America. Thus far, it appears that most North American platforms became emergent in the latest Frasnian–earliest Famennian. This sea level low-stand resulted in erosion of latest Frasnian neritic deposits in most cratonic and continental margin platforms in many areas of North America. Conodont evidence from the western US and western Canada indicates that early Famennian onlap of the older shallow-water Frasnian platforms and resumption of deposition of platform facies in those areas did not occur until the Middle–Upper *P. triangularis* Zones.

Michigan Basin fauna

Prior to initial reports of Day (1994a), latest Givetian and Frasnian (T-R cycle IIb) atrypids were poorly known or unknown from the Michigan Basin. The somewhat older late Givetian (T-R cycle

IIa-2) fauna of the lower part of the Squaw Bay Formation (subsurface only) and Whiskey Creek Formation of western Michigan does include an undescribed species of *Pseudoatrypa*.

A low diversity atrypid fauna was recovered from very late Givetian and Frasnian rocks in the upper part of the Traverse Group (upper two thirds of the Squaw Bay Formation) and the lower Norwood Member of the Antrim Formation in the subsurface of the Michigan Basin (Day 1994a). The Squaw Bay and Norwood faunas are still under study. The atrypid fauna from the middle-upper part of the Squaw Bay (T-R cycle IIb) consists of *Spinatrypa* cf. *S. tribulosa* Norris, 1992 with *Pseudoatrypa* sp. The latter is close to a form described as *Desquamatia* (*Independatrypa*) sp. A in Norris *et al.* (1992: pl. 6: 1–19). The middle Frasnian fauna from the subsurface Norwood Member (author's collections) of the Antrim Shale (see stratigraphy in Gutschick & Sandberg 1991) yields a low diversity fauna dominated by rhynchonellids, with *Spinatrypa* cf. *S. tribulosa* Norris, 1992, associated with species of *Retichonetes*, *Schizophoria*, *Tylothyris* and lingulate brachiopods. Conodont faunas from the Norwood (in Gutschick & Sandberg 1991) indicate that those rocks were deposited during mid-Frasnian T-R cycle IIc.

Iowa Basin faunas

The most diverse and abundant latest Givetian and Frasnian atrypid brachiopod faunas known from central North America occur in carbonate platform facies in the Iowa Basin in Iowa, northwestern Illinois, and central Missouri (Figs 3, 4). Species of atrypids from the Iowa Basin Devonian have been described or illustrated in numerous studies including: Hall (1858), Webster (1888, 1921), Miller (1892, 1894), Branson (1923, 1944), Fenton & Fenton (1924, 1930, 1932, 1935), Stainbrook & Ladd (1924), Greger (1936a, 1936b), Stainbrook (1935, 1938, 1945, 1948), Fraunfelter (1974), Copper (1973, 1978), Cooper & Dutro (1982), and Copper & Chen (1995).

The Iowa Basin latest Givetian and Frasnian atrypid brachiopod fauna includes at least twenty species. Day & Copper (1998) illustrate most of these forms including four new species. The ranges of nearly all known Devonian atrypid species in the Iowa Basin have been documented in terms of the Iowa Devonian conodont sequence and brachiopod zonation (Fig. 4) in a series of studies by Day (1989a, 1990, 1992, 1994b, 1995a, 1996b, 1997). Additional new data necessitating revisions to ranges of certain species are outlined below.

Latest Givetian–early Frasnian rocks of T-R cycles IIb-1 and IIb-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. 3). These rocks yield 10 species of atrypid brachiopods (Fig. 4), including the new species *Spinatrypina (Exatrypa) johnsoni* Day & Copper, 1998 and *Spinatrypa (S.) thompsoni* Day & Copper, 1998. This fauna is similar to coeval western Canadian faunas, especially those from the Waterways Formation of Alberta and the upper part of Flume Formation in northeastern British Columbia.

Middle Frasnian deposits of T-R cycle IIc in Iowa are included in the Shell Rock Formation which yield two species (described in Day & Copper 1998) of atrypids assigned here to *Pseudoatrypa* and *Spinatrypa*. The new species of *Pseudoatrypa* from the Shell Rock is similar to certain middle Frasnian forms identified as *P. devoniana* from the middle Frasnian Hay River Formation in the southern District of Mackenzie, southern NWT (Fig. 1, locality 7).

In Iowa, Late Frasnian deposits of T-R cycle IId-1 yielding shelly fossils are included in the Amana Beds, Independence Shale and most of the Lime Creek Formation. These deposits yield an abundant fauna that includes eight species of *Costatrypa, Iowatrypa, Pseudoatrypa*, and *Spinatrypa.* Unpublished stratigraphic and conodont data indicate that very late Frasnian shelf facies (probable equivalents of the lower part of the Kellwasser interval, i.e. M.N. Zone 13) are preserved in the northern part of the Iowa Basin. These rocks consist of the upper part of the Owen Member of the Lime Creek Formation. Brachiopod and conodont sequences from the upper Owen Member interval are still under study. Initial sampling from the upper Owen Member in 1996 yielded *Spinatrypa* (*S.*) sp. cf. *S. (S.) planosulcata* (Webster, 1888). Offshore basinal facies (black-brown shales of the Sweetland Creek Shale) span the F-F boundary in southeastern Iowa (Fig. 3), but only yield lingulate brachiopods.

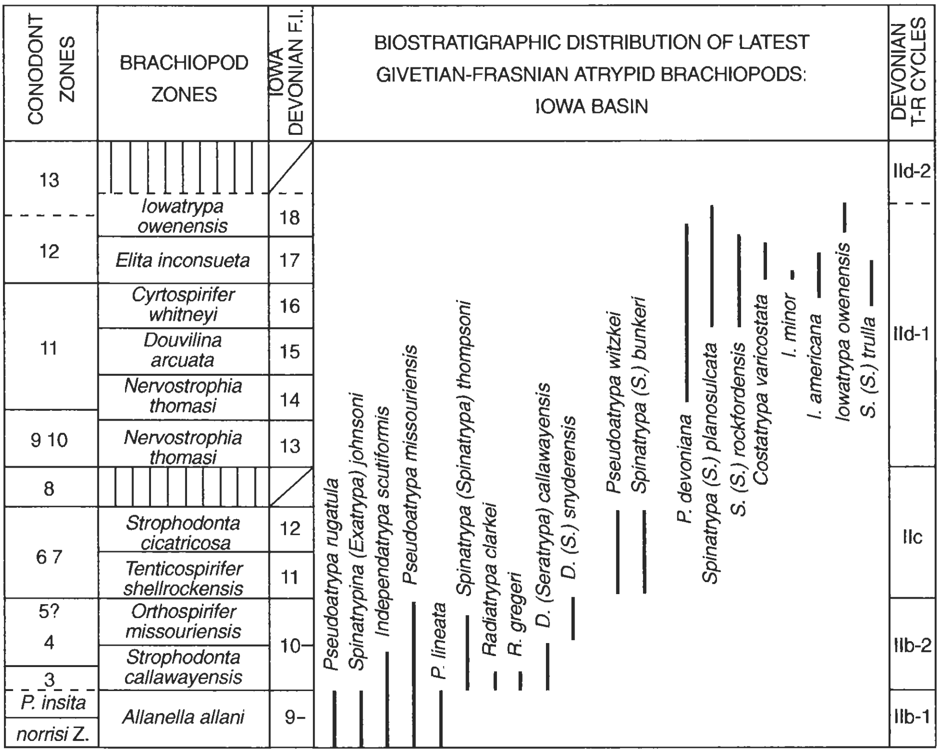

Fig. 4. Chart showing ranges of atrypid brachiopods in the latest Givetian and Frasnian in the U.S. midcontinent Iowa Basin (Fig. 1, Locality 1). Conodont and brachiopod biostratigraphy and Iowa Devonian composite faunal intervals after Fig. 3.

Latest Givetian–early Frasnian (T-R cycle IIb) fauna. — The atrypid fauna of Iowa Basin deposits included in T-R cycle IIb (Figs 2, 3) are known from strata yielding brachiopods of the *Allanella allani, Strophodonta callawayensis,* and *Orthospirifer missouriensis* Zones of Day (1989a, 1992, 1996b, 1997) associated with conodont faunas spanning the *Skeletognathus norrisi* Zone through M.N. Zone 4 of Klapper (1989). The T-R cycle IIb-1 brachiopod fauna occurs in the interval of the *Allanella allani* Zone (Figs 3, 4). Atrypida from deposits of T-R cycle IIb-2 (Fig. 4) are elements of faunas of the *Strophodonta callawayensis* and *Orthospirifer missouriensis* zones (see Day 1992, 1996a, 1997).

T-R cycle IIb-1 fauna. — A widespread atrypid found in T-R cycle IIb-1 deposits in the Iowa Basin is *Desquamatia* (*Independatrypa*) *scutiformis* (Stainbrook, 1938). This species occurs in the Osage Springs, State Quarry and Andalusia members of the Lithograph City of central and eastern Iowa, and coeval rocks of the Callaway Member of the Cedar Valley Formation of central Missouri (Fig. 3). *Pseudoatrypa missouriensis* (Miller, 1894) is the most abundant atrypid in T-R cycle IIb-1 deposits in Missouri where its lowest occurrence is in shallow inner platform rocks of the basal part of the Upper Callaway Member of the Cedar Valley Formation.

The holotype of *Atrypa reticularis* var. *rugatula* Stainbrook & Ladd, 1924 (pl. 1: 8 of their paper) was assigned to *Pseudoatrypa* by Day (1989a). In Iowa, this species is restricted to the State Quarry Member of the Lithograph City Formation in eastern Iowa. Shells similar to *P. rugatula* are illustrated from the fauna of the upper part of the Flume Formation in British Columbia (Assemblage Zone 4 of Maurin & Raasch 1972). The other illustrated specimen of *A. r. rugatula* in Stainbrook & Ladd (1924: pl. 1: 9) serves as a paratype of *Spinatrypina* (*Exatrypa*) *johnsoni* Day & Copper,

1998. This new form from the State Quarry Member is closely related to *S.* (*E.*) *albertensis* (Warren, 1944) from western Canada.

T-R cycle IIb-2 fauna. — A diverse atrypid fauna occurs in the upper half of the Idlewild, upper Andalusia, and Buffalo Heights members of the Lithograph City Formation of Iowa, and the Snyder Creek Shale of Missouri (Figs 3, 4). In the Iowa Devonian, *Desquamatia* (*Independatrypa*) *scutiformis* (Stainbrook, 1938) has its highest occurrence in the upper part of the Andalusia Member in the section at the Buffalo Quarry in southeastern Iowa (Day 1992: figs 4, 6, sample 22; Day 1997: fig. 5, table 1, sample 22). *Pseudoatrypa lineata* (Webster, 1921) was first illustrated from northern Iowa by Fenton & Fenton (1935) and occurs in rocks included in the upper Osage Springs and Idlewild members of the Lithograph City Formation. *Radiatrypa clarkei* (Warren, 1944) was recovered from a single horizon in the upper part of the Idlewild Member of the Lithograph City Formation at the Hanneman Quarry in Floyd County in north-central Iowa (Day 1986, 1992: p. 77, fig. 14, unit 19). There it is associated directly with abundant *P. lineata* (Webster, 1921).

The range of *Pseudoatrypa missouriensis* (Miller, 1894) in Missouri begins in the Cedar Valley Formation at a position just above the base of the *Allanella allani* Zone, and ranges into the upper part of the Snyder Creek Shale correlated with the upper part of the *Orthospirifer missouriensis* Zone (Fig. 4). Additional early Frasnian atrypids known from the Snyder Creek Shale include *Desquamatia* (*Seratrypa*) *callawayensis* (Greger, 1936), *D.* (*S.*) *snyderensis* (Greger, 1936), *Spinatrypa* (*S.*) *thompsoni* Day & Copper, 1998, and rare *Radiatrypa gregeri* (Rowley, 1900).

The ranges of most of the aforementioned forms begin in the lower 4.6 metres of the Snyder Creek Shale (New Bloomfield Member of Day 1997: fig. 6). The lower Snyder Creek yields *Pseudoatrypa missouriensis* (Miller, 1894), *Radiatrypa gregeri* (Rowley, 1900), *Desquamatia* (*Seratrypa*) *callawayensis* (Greger, 1936), and *Spinatrypa thompsoni* Day & Copper, 1998. These are directly associated with conodonts spanning parts of Frasnian Montagne Noire Zones 3–lower part of Zone 4 of Klapper (1989) as discussed in Day (1993, 1997).

Radiatrypa gregeri is restricted to the lower part of the New Bloomfield Member and has only been recovered at localities along Craghead Creek in eastern Callaway County, Missouri. This form is most likely a geographic species that evolved from a small population of *R. clarkei* (Warren, 1944) that became isolated in the southern Iowa Basin during the early Frasnian. Its presumed ancestor, *R. clarkei* (Warren, 1944), first occurs in older latest Givetian and early Frasnian deposits of T-R cycle IIb-1 in western Canada, and migrated into the Iowa Basin during the T-R cycle IIb-2 transgression.

The upper two thirds of the Snyder Creek Shale are included in the Craghead Branch and Cow Creek members. *Spinatrypa (S.) thompsoni* Day & Copper, 1998 ranges into the middle part of the Craghead Branch Member (see Greger 1936a: p. 48). *Desquamatia (Seratrypa) snyderensis* (Greger, 1936) is restricted to the interval of the Craghead Branch and Cow Creek members. *Pseudoatrypa missouriensis* (Miller, 1894) has its highest occurrence in the lower part of the Cow Creek Member (Day 1997: fig. 6, table 3). The latter species was reported by Greger (1936a) from rocks now included in the Cow Creek Member and identified as *Atrypa devoniana* Webster in that study.

Middle Frasnian (T-R cycle IIc) fauna. — Shelf carbonates of the Shell Rock Formation are the only rocks preserved in the Iowa Basin deposited during part of the middle Frasnian T-R cycle IIc of Johnson *et al.* (1985) and Johnson & Klapper (1992). The Shell Rock consists of three members including the basal Mason City, Rock Grove, and Nora, and all yield atrypids. Based on data on Shell Rock conodont faunas (Anderson 1966; Klapper & Johnson 1992; Day 1996a), and position below the Lime Creek Formation (T-R cycle IId), the Shell Rock is correlated with M.N. zones 6–8? of Klapper (1989).

Belanski (1928) described brachiopods from the Shell Rock Formation, although Atrypida were not described in that study. Day (1989a) listed the Shell Rock atrypids as species of *Pseudoatrypa* and *Spinatrypina*. The form assigned to *Spinatrypina* in Day (1989a, 1996a) is assigned to *Spinatrypa* (*S.*) based on well preserved juvenile shells with preserved spines. *Pseudoatrypa witzkei* Day & Copper, 1998 and *Spinatrypa* (*S.*) *bunkeri* Day & Copper, 1998 come from the Shell Rock. The latter form may be restricted to the Iowa Basin region. *Pseudoatrypa witzkei* Day & Copper, 1998 is similar to the form identified as *Atrypa devoniana* by Warren & Stelck (1956) from the middle Frasnian Hay River

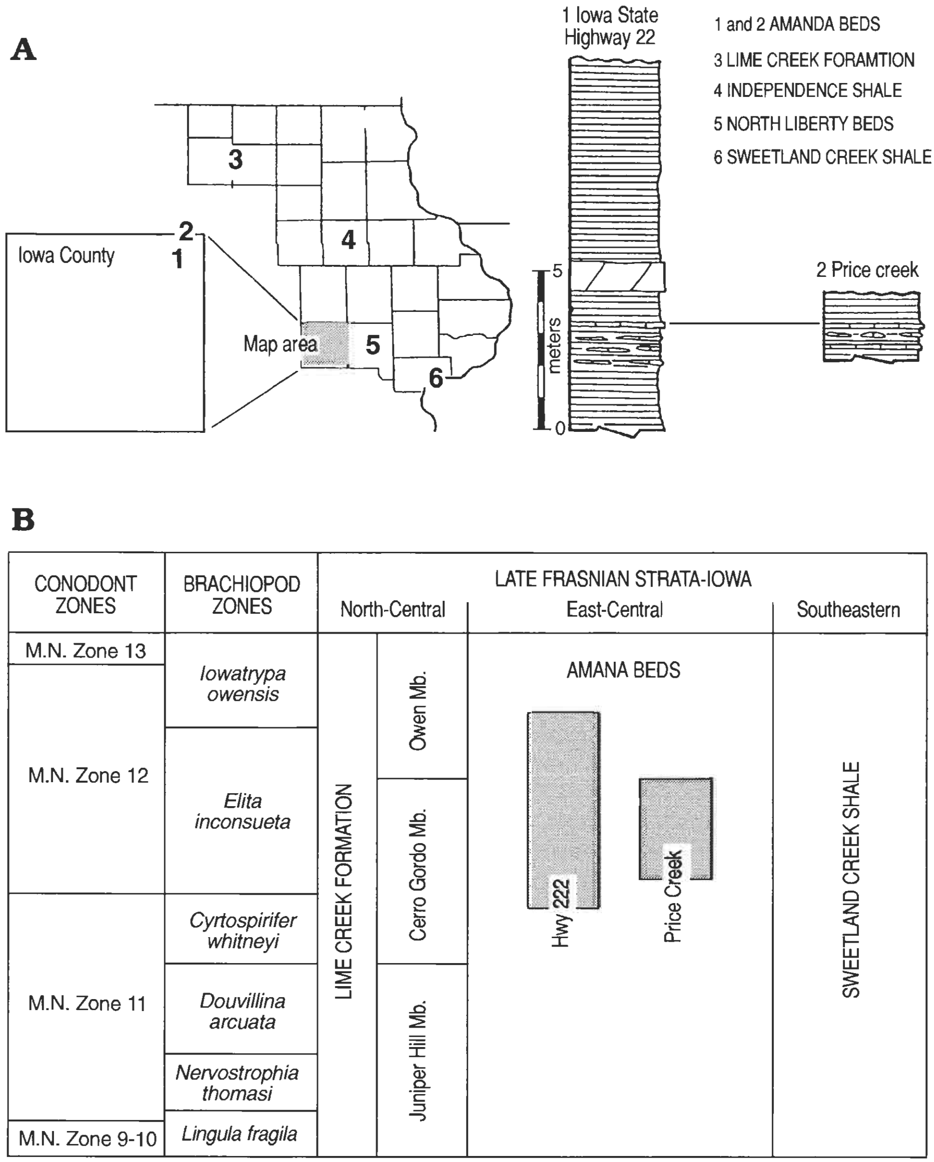

Fig. 5. **A**. Map on left-side shows locations of known late Frasnian rocks in central and eastern Iowa. Names applied to Late Frasnian units are given on right-side, with correlated columns of the Amana Beds at its type section (locality 1 after Müller & Müller 1957) and new exposures of the Amana Beds at Price Creek (locality 2). Adapted from Day (1995a: fig. 4). **B**. From right to left, conodont and brachiopod zonations and current correlations of shelf facies of the Lime Creek Formation, outer shelf facies of the Amana Beds, and anoxic-dysoxic basinal shales of the Sweetland Creek Shale of southeastern Iowa. Conodont biostratigraphy of the Sweetland Creek Shale after Klapper in Johnson & Klapper (1992), and for Lime Creek Formation modified from Day (1990). Modified from Day (1995a: fig. 5).

Formation of the southern NWT. *P. witzkei* Day & Copper, 1998 may be ancestral to *P. devoniana* (Webster, 1921) that is a widespread late Frasnian deposits of central and western north America.

T-R cycle IId-1 fauna. — Late Frasnian age Atrypida are well known from the Lime Creek Formation, the Amana Beds, and the Independence Shale (Fig. 3). The combined atrypid fauna from these units includes: *Pseudoatrypa devoniana* (Webster, 1921), *Spinatrypa* (*S.*) *planosulcata* (Webster, 1888), *S. (S.) rockfordensis* (Fenton & Fenton, 1924), *S.* (*S.*) *trulla* (Stainbrook, 1945), *Costatrypa varicostata* (Stainbrook, 1945), *I. americana* (Stainbrook, 1945), *I. owenensis* (Webster, 1921), and *I. minor* (Fenton & Fenton, 1924).

Amana Beds. — The late Frasnian Amana Beds of Iowa County, Iowa, are now considered as an informal member of the Lime Creek Formation, and correlate with part of the Cerro Gordo and Owen members in the type area of the Lime Creek (Day 1995a, 1995b; Witzke & Bunker 1996). The Amana Beds represent an offshore facies that accumulated along the deeper water ramp seaward of the Lime Creek shelf break (see Lime Creek depositional model in Witzke 1987 and Day 1990).

Stainbrook (1945) considered the Amana Beds to be an exposure of the Independence Shale based on close similarities of their brachiopod faunas. The Amana Beds are known to be an in-place succession above rocks of the Lithograph City Formation (T-R cycle IIb) of the Cedar Valley Group. They are at least 12 metres thick at the type section at the road cuts on the north side of Iowa Highway 220 west of the town of Middle Amana (see Müller & Müller 1957) and reach a thickness of nearly 15 metres in the nearby subsurface (Amana Golf Course Core).

The bulk of Amana Beds brachiopods available in the Belanski and Stainbrook collections (University of Iowa) came from the lower 5.0–5.3 metres of the roadcut exposure at the type locality (Fig. 5, locality 1). Additional large collections have been made at new exposures recently discovered along Price Creek two miles (3.2 km) northeast of the type section (Fig. 5, locality 2). The Amana Beds atrypid fauna illustrated by Stainbrook (1945) included *Pseudoatrypa devoniana* (Webster, 1921) and *Spinatrypa* (*S.*) *trulla* (Stainbrook, 1945). New collections made in 1995 at the Price Creek localities yield both of those forms as well as *S.* (*S.*) *planosulcata* (Webster, 1888).

Independence Shale. — The Independence Shale occurs as stratigraphic leaks of Late Frasnian sediments that filled karst cavities developed in older Cedar Valley Group carbonates that formed during the regression and emergence of the Cedar Valley Group carbonate platform in the middle Frasnian. Its fauna was described by Stainbrook (1945) and consists of *Iowatrypa americana* (Stainbrook, 1945), *Pseudoatrypa devoniana* (Webster, 1921), and *Spinatrypa* (*S.*) *trulla* (Stainbrook, 1945).

Lime Creek Formation. — The Lime Creek Formation consists of three members which are (in ascending order): the Juniper Hill, Cerro Gordo and Owen (Figs 3, 5, 6). All three yield atrypids and nearly all species have been described or illustrated in a series of studies including Webster (1888, 1921), Fenton & Fenton (1924), and Stainbrook (1945). The Lime Creek brachiopod sequence and zonation (Figs 3, 5, 6) has been outlined in a recent papers by Day (1989a, 1995a, 1996a).

Pseudoatrypa devoniana (Webster, 1921) and is the most abundant atrypid found in the Lime Creek Formation. Webster (1921) first named this highly variable species based on specimens from the Rockford Quarry in Floyd County in northern Iowa. Fenton & Fenton (1924) later erected *Atrypa hackberryensis* and *A. devoniana alta* based on material from the Lime Creek. These latter two forms are considered as variants of *P. devoniana* Webster (1921) by Day & Copper (1998). *P. devoniana* first occurs 5.05 metres above the base of the Juniper Hill Member in the subsurface Lime Creek in the Cerro Gordo Project Hole 1 (Fig. 6, locality 1, sample 11; Fig. 7) and ranges into the lower part of the Owen Member in surface sections at the Bird Hill and Owens Grove localities (Fig. 6, localities 2, 5; Fig. 7). Its range in the US midcontinent relative to the Frasnian conodont sequence begins in the lower part of M.N. Zone 11 and apparently terminates at a position in the upper part of M.N. Zone 12. Its range in the Iowa Devonian brachiopod sequence begins in the upper *Nervostrophia thomasi* Zone, and ranges into the lower part of the *Iowatrypa owenensis* Zone of Day (1989a).

The lectotype and paratype material of *Atrypa hystrix var. planosulcata* Webster, 1888 illustrated in Fenton & Fenton (1924) and juvenile specimens in my collections display preserved spine bases indicating assignment to *Spinatrypa* Stainbrook, 1951. Juvenile shells of this species lacking preserved spines were identified as *Spinatrypina* in earlier studies by Day (1989a, 1995a, 1996b). The range of *S. planosulcata* (Webster, 1888) in the Cerro Gordo Member is shown in Fig. 7. In the Amana Beds at the Price Creek Locality, Day (1995a, b) this species occurs in association with conodonts of M.N.

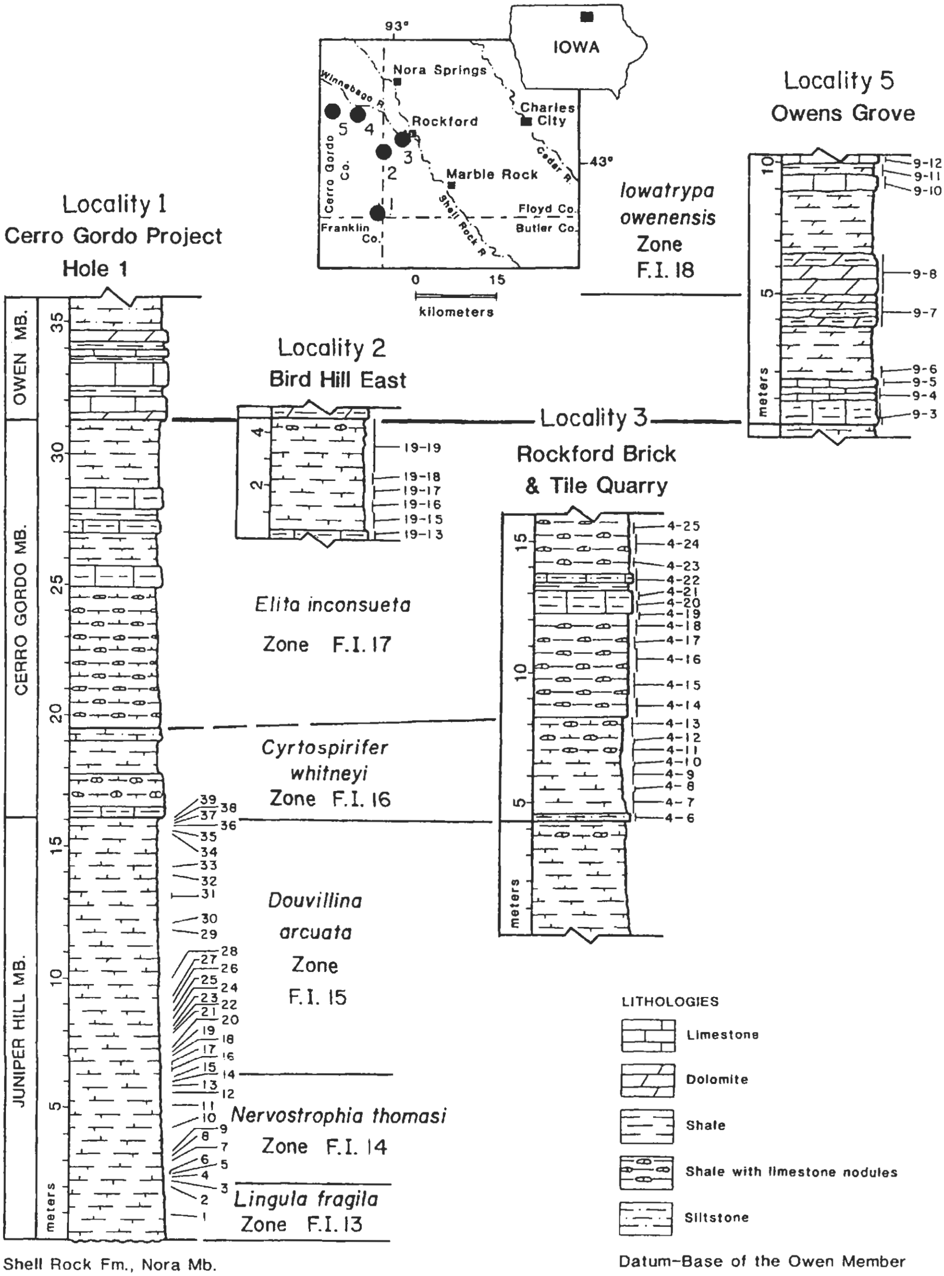

Fig. 6. Map at top shows locations of important reference and type sections of various members of the Lime Creek Formation in north-central Iowa. Stratigraphic columns of measured sections show positions and numbers of sample intervals at sections localities 1–4 and the positions of brachiopod zonal boundaries defined by Day (1989a, 1996b). Modified from fig. 6 of Day (1995a). Locality 4 is the type section of the Cerro Gordo Member at Hackberry Grove (= Cerro Gordo County Clay Banks Natural Area = Belanski locality 1 in Strimple & Leverson 1969).

Cerro Gordo Project Hole 1

SAMPLE NUMBER	*P. devoniana*
39	●
37	●
36	●
35	●
33	●
26	●
16	●
11	●

Rockeford Quarry Bird Hill East Owens Grove

SAMPLE NUMBER	*P. devoniana*	*S. rockfordensis*	*S. planosuleata*	*C. varicostata*	*I. owenensis*
9-12	●				?
9-11					
9-10					●
9-8					●
19-19	●	●			
19-18	●	●	●		
4-25 19-17	●	●	●		
4-24 19-16	●	●	●	●	▲
4-23 19-15	●				
4-22 19-13	●		●		
4-21			●		
4-20		●	●		
4-19					
4-18		●			
4-17					
4-16	●	●			
4-15	●	●			
4-14		●	●		
4-12	●				
4-10	●				
4-6	●				

Fig. 7. Charts showing ranges of atrypid brachiopod species in the Lime Creek Formation at sampled surface and subsurface localities shown in Fig. 6. Chart on left shows the range of *Pseudoatrypa devoniana* (Webster, 1921) in the Juniper Hill Member in the Cerro Gordo Project Hole 1 core (Fig. 6, locality 1). Chart on right shows the ranges of atrypidan species in the Cerro Gordo and Owen members in samples at section localities 3 and 4. Sample positions and numbers at all section localities as in Fig. 6. Black dots and question mark in the right hand column of the right hand chart denotes occurrences of *Iowatrypa owenensis* (Webster, 1921); triangle in the same column indicates the position of *I. minor* (Fenton & Fenton, 1924). Abbreviations of generic names: *C* – *Costatrypa, I. – Iowatrypa, P. – Pseudoatrypa, S. – Spinatrypa.*

Zone 12 of Klapper (1989). Data from recent collections from the Owen Member indicate that it probably ranges to a level correlated with a position in the upper part of the *Iowatrypa owenensis* Zone (Day 1989a; Fig. 3). This species also occurs in the upper part of the Sly Gap Formation in southern New Mexico and has been reported from the Martin Formation of southern Arizona.

Spinatrypa (S.) rockfordensis (Fenton & Fenton, 1924), occurs in association with *Pseudoatrypa devoniana* (Webster, 1921), *S. (S.) planosulcata* (Webster, 1888), and *Costatrypa varicostata* (Stainbrook, 1945) in the Cerro Gordo Member, and ranges into the lower part of the Owen Member in outcrops in northern Iowa (Figs 4, 6, 7). Additional forms described from the Lime Creek attributed to *Spinatrypa (S.)* include *Atrypa rockfordensis elongata* Webster, 1888, and *A. subhannibalensis* Webster, 1921. These both are interpreted as variants of *S. (S.) rockfordensis* (Fenton & Fenton, 1924). *S. (S.) rockfordensis* is closely related to *S (S.) trulla* (Stainbrook, 1945) but is distinguished from the latter species by its greater number of low-rounded radial costae and a more inflated ventral valve. The former species characterizes middle shelf facies of the Cerro Gordo and lower part of the Owen members. *Spinatrypa (S.) trulla* (Stainbrook, 1945) is found in slightly deeper-water deposits of the Amana Beds and the Independence Shale in eastern Iowa.

Costatrypa varicostata (Stainbrook, 1945) was recovered from the middle part of Cerro Gordo Member of the Lime Creek Formation at the Rockford Quarry in the interval of Belanski sample

4-24 (Fig. 6, locality 3; Fig. 7). Although rare in the Lime Creek Formation of north-central Iowa, this species is more abundant in deeper water facies of the Amana Beds at its type locality in Iowa County (see specimens illustrated in Day & Copper 1998), and at the type locality of the Independence Shale in Buchanan County, Iowa (Fig. 5, locality 4; Stainbrook 1945).

The illustrated paratypes of *Grunewaldtia americana* Stainbrook, 1945 (p. 66, pl. 5: 21–23) from the Independence Shale are similar to specimens of *Iowatrypa owenensis* (Webster, 1921). This form was considered as a possible junior synonym of *I. owenensis* by Copper (1973) and Copper & Chen (1995). The type specimens of *Atrypa planosulcata* var. *minor* Fenton & Fenton, 1924 (p. 140, pl. 27: 17, 18) appear to represent a small species of *Iowatrypa* similar to *Iowatrypa deflecta* (Warren 1944). The latter species is common in parts of the Mount Hawk Formation in the Alberta Rocky Mountains. *Iowatrypa minor* (Fenton & Fenton, 1924) is only known from the type stratum in the lower half of the Cerro Gordo Member. The lowest occurrence of *I. owenensis* is well above that level in the middle part of the overlying Owen Member (Fig. 4). According to the discussion by the Fentons (1924: p. 140), the cotypes of *Atrypa planosulcata minor* came from the interval of their *Gypidula* faunule (see Fenton & Fenton 1924: p. 12). Their description places the type stratum or horizon at 14.0–14.5 feet (4.26–4.41 metres) above the base of the Cerro Gordo Member, corresponding to the position of Belanski sample 4-14 (Figs 6, 7). This horizon is at or near the base of the *Elita inconsueta* Zone of Day (1989a), at or above the lowest occurrence of the conodont *Palmatolepis foliacea* (Anderson 1966; Day 1990). Consequently, this occurrence would be low in the interval of M.N. Zone 12 of Klapper (1989).

The range of *Iowatrypa owenensis* (Webster, 1921) begins in the upper half to two thirds of the Owen Member in north-central Iowa at a position in the upper part of M.N. Zone 12 (see discussions by Day 1995a, 1996b). The upper part of the range of this species could be within part of M.N. Zone 13 (Fig. 4), but has to be confirmed by additional study of the conodont sequence in the upper part of the Owen Member.

Elk Point Basin fauna

Latest Givetian and early Frasnian atrypids are known from the upper part of the Point Wilkins Member and Sagmace Member of the Souris River Formation of the Manitoba Group of southwestern Manitoba (McCammon 1960; Norris in Norris *et al.* 1982; Braun *et al.* 1989; Day & Norris in Day *et al.* 1996). According to correlations outlined by Witzke *et al.* (1989) and Day *et al.* (1996: fig. 2), the Micritic Limestone Beds of the Point Wilkins Member of the Souris River Formation were deposited during T-R cycle IIb-1. The Dolomitic Limestone Beds of the upper Point Wilkins Member, and perhaps the Sagemace Member, were probably deposited during T-R cycle IIb-2.

A low diversity atrypid fauna consisting of *Desquamatia (Independatrypa)* cf. *I. independensis* (Webster, 1921) occurs in association with conodonts of the *Skeletognathus norrisi* Zone and the upper part of the *Pandorinellina insita* Fauna in the Micritic Limestone Beds of the Point Wilkins Member in the Mafeking Quarry section near Mafeking, Manitoba (see discussion of conodont faunas by Uyeno in Norris *et al.* 1982; Uyeno & Day in Day *et al.* 1996: figs 3–5). Day and Norris (in Day *et al.* 1996) reported *Radiatrypa clarkei* (Warren, 1944) from the overlying the Dolomitic limestone beds of the upper Point Wilkins Member at that same locality. Restudy of that material indicates that their initial identification was in error, and that the form in the Dolomitic Limestone Beds has closely spaced growth lamellae with frills representing a medium sized species of *Pseudoatrypa* similar to *P. lineata* (Webster, 1921)

Atrypids have not been illustrated from the early Frasnian Sagemace Member, although Norris (in Norris *et al.* 1982: p. 68, chart 4) listed *Desquamatia (Variatrypa) clarkei* (Warren, 1944) (= *Radiatrypa* of this report), *D. (Independatrypa)* cf. *D.* (*I.*) *independensis* (Webster, 1921) and *Spinatrypa* sp. cf. *S. albertensis* (Warren, 1944) from the Sagemace based on subsurface collections. *Atrypa albertensis* Warren, 1944, from the early Frasnian of Alberta was reassigned by Copper (1978: p. 301) to *Spinatrypina (Exatrypa)* Copper, 1967a. The occurrence of this form in the Sagemace is correlated with a position in the Moberly Member of the Waterways Formation of Alberta by Norris (in Norris *et al.* 1982: p. 68; in Day *et al.* 1996).

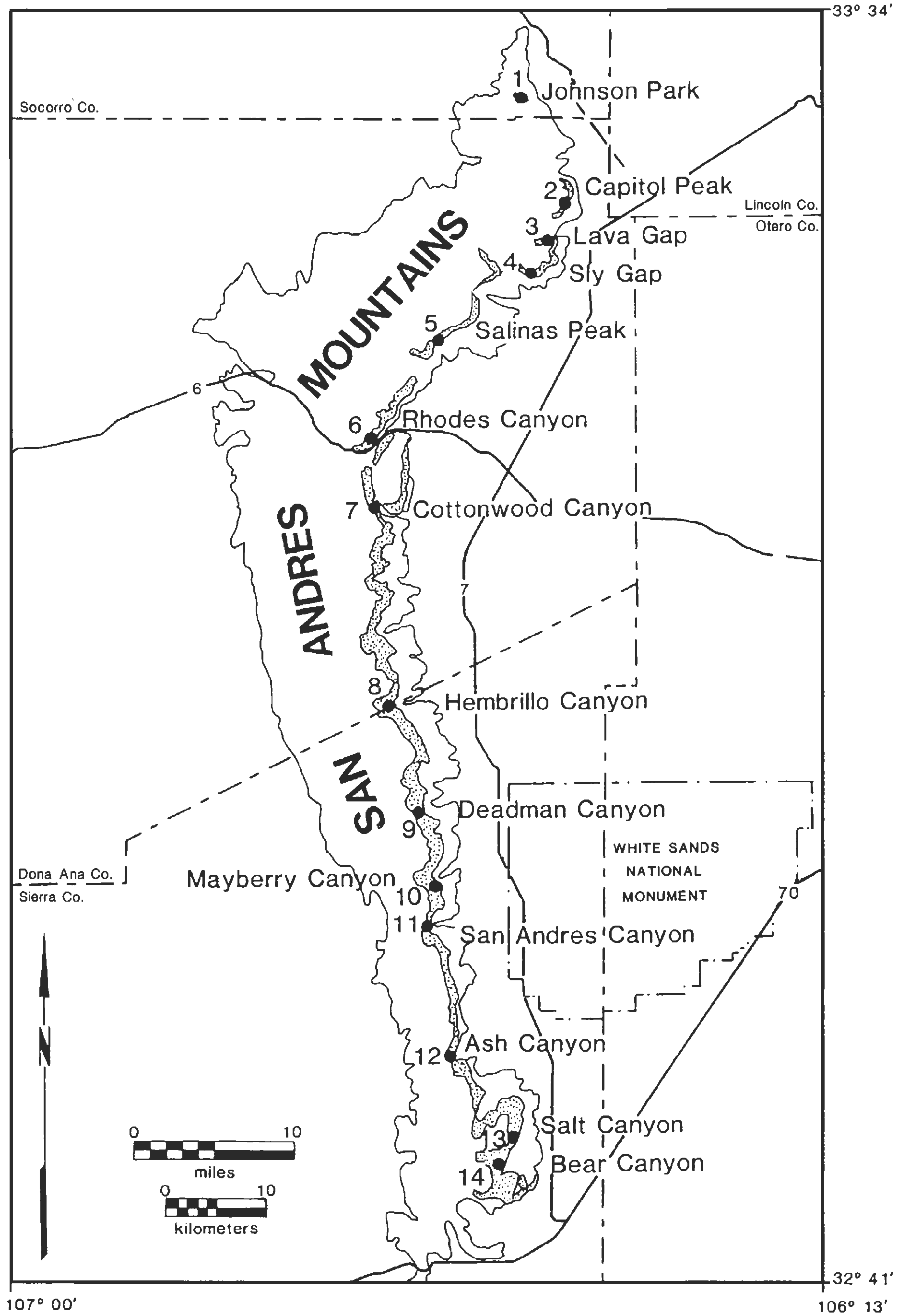

Fig. 8. Locations of Day's (1988) measured sections of Middle and Late Devonian rocks in the San Andres Mountains in south-central New Mexico (modified from fig. 3b of Day 1988). Detailed locations and descriptions of measured sections are given in appendix I of Day (1988). Stipled areas are Devonian–Lower Carboniferous outcrops.

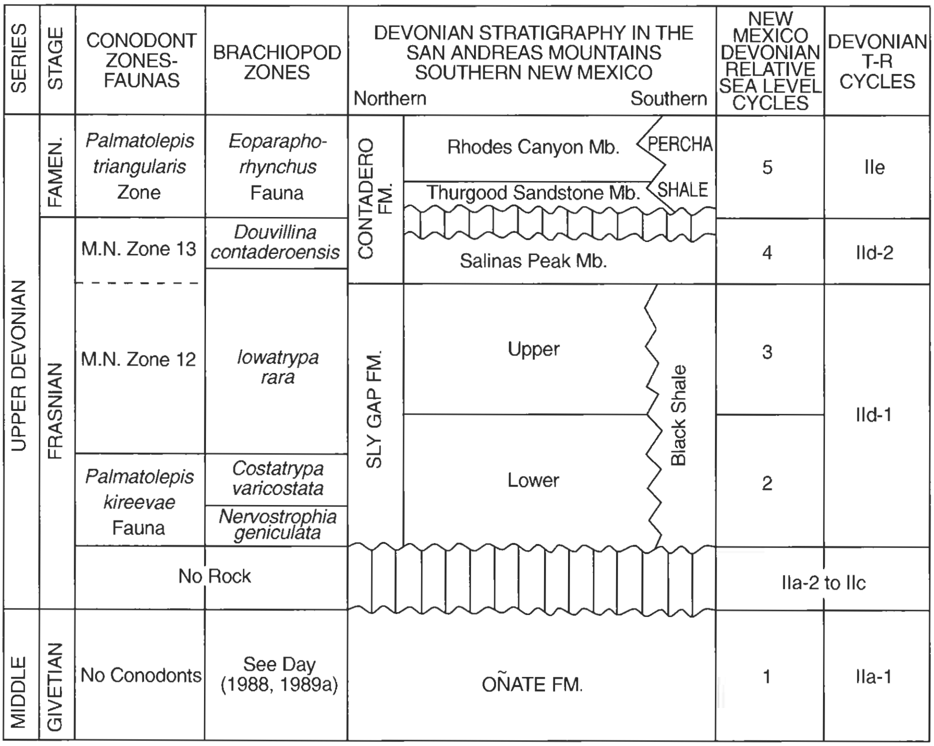

Fig. 9. Current lithostratigraphic and biostratigraphic frameworks for the Devonian (Givetian–Famennian) rocks in the San Andres and adjacent Sacramento Mountains of southern New Mexico. Brachiopod biostratigraphy after Day (1988, 1989b); conodont biostratigraphy based on Day (1988, 1990), Sorauf (1984), and Sandberg (1976). Relationships between New Mexico Givetian and Frasnian sea level events 1–4 of Day (1988) and T-R cycles of Johnson *et al.* (1985), Johnson & Klapper (1992), and Day *et al.* (1996) are shown in the two left-hand columns.

Southwestern U.S. faunas

Species of late Frasnian atrypids are known from the Martin Formation of central and southeastern Arizona, and the Sly Gap and lower part of the Contadero formations of southern New Mexico.

Martin Formation – Central and Southeastern Arizona. — The Martin Formation of central Arizona yields species of late Frasnian *Costatrypa*, *Pseudoatrypa*, and *Spinatrypa*. These also occur in the faunas of the Sly Gap Formation of New Mexico and Lime Creek Formation of Iowa as well as Great Basin and western Canadian faunas. Available conodont and brachiopod evidence indicate correlation of the fossiliferous part of the Upper unit of the Jerome Member with the interval of T-R cycle IId-1 (Fig. 2). Conodont faunas recovered by Witter (1976) from the Upper unit of the Jerome Member were correlated with parts of M.N. Zones 9–12 by Day (1990a). Very late Frasnian (M.N. Zone 13) strata have yet to be identified in Arizona. Most of the Martin fauna has never been illustrated, although Beus (1978) illustrated about 25% of the brachiopod species known to occur in the Martin in central and eastern Arizona.

The late Frasnian rocks of the Upper unit of the Jerome Member in east-central Arizona feature *Pseudoatrypa devoniana* (Webster, 1921), *Spinatrypa rockfordensis* (Fenton & Fenton, 1924), and *Costatrypa varicostata* (Stainbrook, 1945). In central Arizona, *Pseudoatrypa devoniana* (Webster, 1921) occurs with *Cyrtospirifer whitneyi* (Hall, 1858) in the lowest fossiliferous beds of the Jerome

Member of the Martin at the Cliff House Canyon section (Day 1984: pl. 3). At that same locality, *Spinatrypa rockfordensis* (Fenton & Fenton, 1924) first occurs well above the first entry of *P. devoniana* in samples above the biostromal units of the Upper unit of the Jerome (Day 1984). At that locality it is associated with *Elita* cf. *E. inconsueta* (Fenton & Fenton, 1924) and the large palaeotrochid archaeogastropod *Turbonopsis apachiensis* Day & Beus, 1982. In Iowa, *E. inconsueta* and *T. hackberryensis* (Webster, 1906) are found together (Day 1987b) in the interval of the *Elita inconsueta* Zone of Day (1989a). There both of those forms make their first appearances at or above the lowest conodont faunas correlated with M.N. Zone 12 (Day 1990a, 1995a).

Merril Stainbrook (Stainbrook Collection, University of Iowa) collected *Costatrypa varicostata* (Stainbrook, 1945) from the Martin Formation in the Pinal Creek area three miles (4.83 km) north of the town of Globe, Gila County, Arizona (Day 1988, 1989a, 1990a). Meader (1977) apparently recovered *C. varicostata* in beds yielding brachiopods assigned to his *Atrypa–Cyrtospirifer* assemblage in unit 25 of his section of the Martin at Pinal Creek (see Meader 1977: p. 91 of appendix). This coincides to a position at or above the level where Witter (1976) recovered *Palmatolepis foliacea* (= M.N. Zone 12 of Klapper 1989). There, Meader (1977: p. 28) lists *C. varicostata* in association with *Cyrtospirifer whitneyi, Atrypa devoniana, A. planosulcata* [= *Spinatrypa planosulcata*], *A. owenensis* (= *Iowatrypa owenensis*?), with species of *Tenticospirifer, Nervostrophia, Strophonelloides, Devonoproductus*, and *Schizophoria*. This collection is similar to Stainbrook's collection from the Pinal Creek area, which contains *Costatrypa varicostata* and *Pseudoatrypa devoniana* associated with the same stropheodontids spiriferids, and orthids.

Sly Gap and Contadero formations – New Mexico. — Late and latest Frasnian atrypids are known from the Sly Gap and Contadero formations in the central and southern San Andres and Sacramento Mountains of southern New Mexico (Figs 2, 9–11). Most of these were described in studies by Stainbrook (1935, 1945, 1948) and Cooper & Dutro (1982). Ranges of most species were not precisely documented in those studies that were based on specimens from float collections made by earlier investigators. The late and very late Frasnian brachiopod sequence of southern New Mexico preserves a record of platform shelly faunas. Sorauf (1988) noted that all Frasnian colonial rugosan taxa became extinct in New Mexico in the upper part of the Sly Gap Formation, and only solitary rugosan taxa (such as *Tabulophyllum*) range into very late Frasnian deposits of the Salinas Peak Member of the Contadero Formation (Figs 9, 10).

Day (1988) established ranges of most brachiopod taxa in the New Mexico Givetian and Frasnian relative to Devonian conodont faunas. Additional atrypids, not reported in older studies were also reported by Day (1988). These include *Spinatrypa planosulcata* (Webster, 1888) from the Sly Gap Formation (sample 10, Sly Gap Section of Figs 8–11); and four specimens provisionally assigned to *Pseudoatrypa* Copper (1973) from the upper part of the Salinas Peak Member of the Contadero Formation.

Dutro (1986) noted significant decline in articulate brachiopod diversity in the New Frasnian prior to the Frasnian Famennian boundary. Day (1987a) noted a stepped pattern of extinction consisting of two late Frasnian extinction events. The first and most significant extinctions resulted in the loss of up to 66 of the 72 brachiopod species known from the brachiopod fauna of the Sly Gap Formation, the second corresponds to the F-F Boundary Event which involved extinction of most species known from the very late Frasnian fauna of the Salinas Peak Member. Day (1996a) referred to these as the late Frasnian (M.N. Zone 12) and terminal Frasnian extinction events coinciding with the Late Frasnian (LFr) and F-F bioevents of Walliser (1995).

Conodont faunas recovered from the Sly Gap Formation (Day 1988, 1990a) are correlated with parts of M.N. zones 9–12 of Klapper (1989). Day (1990a) reported a very late Frasnian conodont fauna containing *Ancyrognathus calvini* with *Palmatolepis bogartensis* from the Salinas Peak Member of the Contadero Formation (Figs 2, 10, 11). That fauna correlates with the lower part of M.N. Zone 13 of Klapper (1989). Brachiopod (Day 1988, 1989c) and conodont-based correlations (Fig. 9) indicate that the Sly Gap was deposited during T-R cycle IId-1 (Fig. 9), and the Salinas Peak Member of the Contadero Formation comprises a younger very late Frasnian sequence package deposited during T-R cycle IId-2 of this report. As such, the latter package was deposited during the Kellwasser interval of

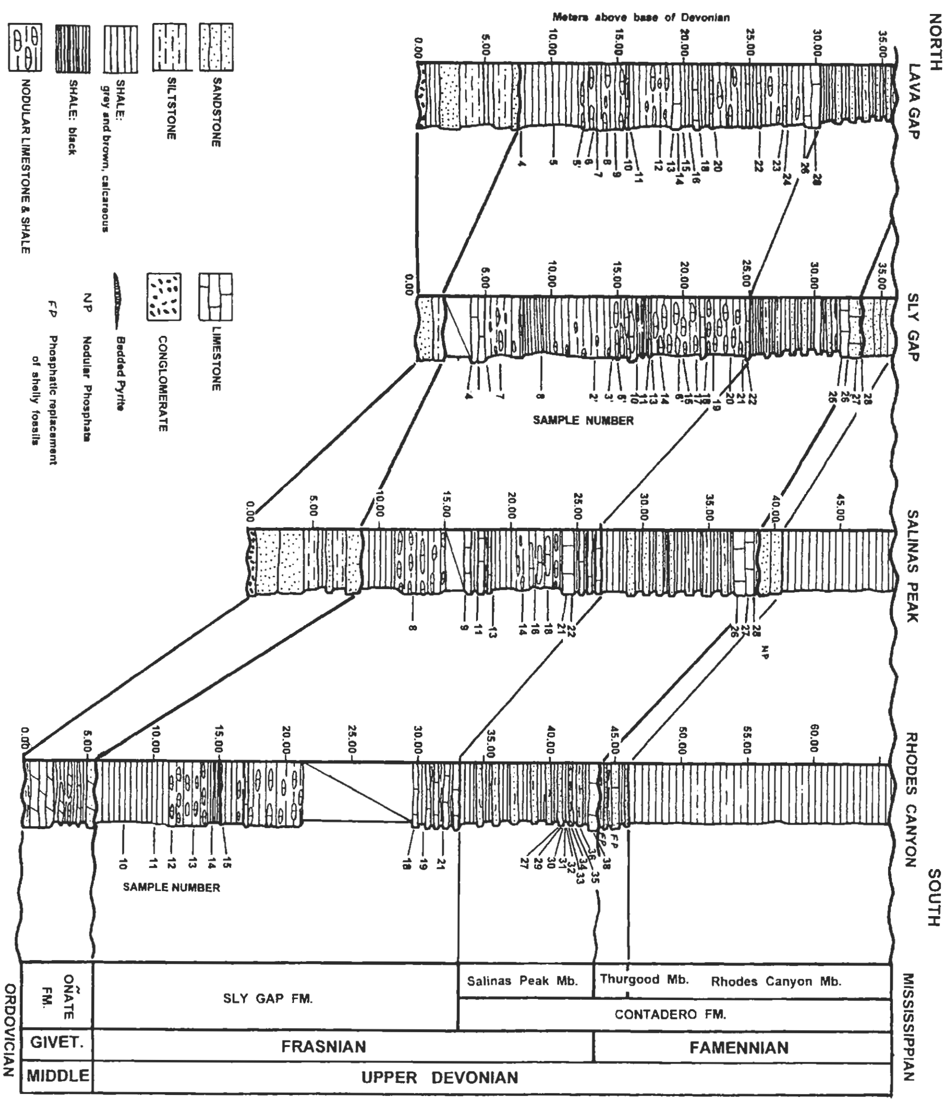

Fig. 10. Stratigraphy of the Middle and Upper Devonian rocks in the central and northern San Andres Mountains at localities 3–6 of Fig 9: Lava Gap Section – locality 3, Sly Gap Section – locality 4; Salinas Peak – locality 5; and Rhodes Canyon Section – locality 6. Lines and numbers to the right of stratigraphic section columns denote elevations and numbers of fossil samples of Day (1988).

Schindler (1990) and Walliser (1995). The Salinas Peak Member is overlain by early Famennian strata of the Thurgood Sandstone Member of the Contadero Formation (Figs 2, 10, 11). At Rhodes Canyon (Figs 9, 10), Sorauf indicates (1988: pp. 156–157, fig. 5) that the basal beds of the Thurgood yield early Famennian conodonts of the Middle *Palmatolepis triangularis* Zone, based on study of conodonts from that unit by Sandberg (personal communication to Sorauf 1984: p. 156).

An unconformity is developed at the F-F Boundary in the shelf sections in the central and northern San Andres Mountains. Very late Frasnian and some early Famennian rocks were removed by erosion in the Sacramento Mountains to the east. The hiatus in the eroded platform facies in the

Lava Gap

SAMPLE NUMBER	*Costatrypa varicostata*	*Pseudoatrypa devoniana*	*Spinatrypa trulla decorticata*	*Iowatrypa rara*
28				
26	●	●		
24	●	●		
23				
22	●	●	●	
20				
18	●	●	●	
16	●		●	
15	●		●	
14	●	●	●	●
13				
12	●			
11	●		●	
10	●			
9	●	●		
8	●			
7	●	●		
6	●	●	●	
5'	●			
5	●		●	
4	●	●		

Sly Gap

SAMPLE NUMBER	*Costatrypa varicostata*	*Pseudoatrypa devoniana*	*Spinatrypa planosulcata*	*Iowatrypa rara*	*Spinatrypa trulla decorticata*	*Spinatrypa compacta*
28						
27						●
26						●
25	?					
22						
21	●					
20	●				●	
19		●			●	
18						
17	●	●			●	
15		●				
6'	●	●				
14	●				●	
13	●	●		●	●	
11	●	●				
10	●	●	●			
5'	●					
3'	●					
2'	●					
8						
7						
4	●					

Salinas Peak

SAMPLE NUMBER	*Costatrypa varicostata*	*Pseudoatrypa devoniana*	*Spinatrypa trulla decorticata*	*Spinatrypa compacta*	*Pseudoatrypa? sp.*
28				●	
27				●	●
26					
22	●	●			
21	●				
18	●	●			
16		●			
14	●	●			
13	●	●	●		
11	●	●	●		
9	●		●		
8	●				

Rhodes Canyon

SAMPLE NUMBER	*Costatrypa varicostata*	*Pseudoatrypa devoniana*	*Spinatrypa trulla decorticata*	*Spinatrypa compacta*	*Pseudoatrypa? sp.*
38					
36				●	
35				●	●
34				●	
33				●	
32				●	
31				●	
30				●	
29					
27				●	
21					
19	●	●			
18	●	●	●		
15	●		●		
14					
13	●	●	●		
12	●		●		
11	●	●			
10	●				

Fig. 11. Atrypid brachiopod sequence in the late Frasnian Sly Gap Formation and Salinas Peak Member of the Contadero Formation in sampled intervals at section localities 3–6 (Figs 9, 10).

central and northern San Andres Mountains spans the upper part of M.N. Zone 13 through the Lower–Middle *triangularis* Zone.

Sly Gap Fauna (late Frasnian). — The Sly Gap Formation atrypid fauna includes *Costatrypa varicostata* (Stainbrook, 1945); *C. extensa* Cooper & Dutro, 1982; *Iowatrypa rara* Cooper & Dutro, 1982; *Pseudoatrypa devoniana* (Webster, 1921); *Spinatrypa (S.) trulla decorticata* Cooper & Dutro, 1982; and *Spinatrypa (S.) planosulcata* (Webster, 1888). Forms assignable to *C. varicostata* (Stainbrook, 1945) and *C. extensa* Cooper & Dutro, 1982, occur in the same samples and display a wide range of variation with respect to development of alate posterior margins, and shell thickness. The flattened-alate forms typical of *C. extensa* Cooper & Dutro 1982, may be phenotypic variants of *C. varicostata* (Stainbrook, 1945). Ranges of Sly Gap atrypids in Devonian sections in the San Andres Mountains are shown in Figs 10 and 11.

Salinas Peak Fauna (very late Frasnian). — Cooper & Dutro (1982) described *Spinatrypa (S.) compacta* and *S. (S.) obsolescens* from the upper Salinas Peak Member of the Contadero Formation. The first species mentioned above is the most abundant and long ranging form in the Salinas Peak and occurs in beds just below the Frasnian-Famennian boundary at Rhodes Canyon (Figs 10, 11, sample 36). I did not recover specimens of *S. (S.) obsolescens* in my collections.

Pseudoatrypa? sp. occurs at two levels in the upper Salinas Peak Member. The lowest occurrence is in sample 27 of Salinas Peak section (Day 1988; Figs 10, 11) in the bedded carbonate unit of the upper part of the Salinas Peak Member. Additional specimens were recovered in the upper Salinas

Peak 50 centimeters below the Frasnian-Famennian (F-F) boundary in sample 35 at Day's Rhodes Canyon section (Figs 10, 11).

Great Basin and US Rocky Mountain faunas

A relatively complete Givetian–Frasnian succession is preserved in the Great Basin in eastern and central Nevada and western and northern Utah (Fig. 1), southern Idaho, and adjacent areas of the Rocky Mountains in western Montana. Unfortunately the majority of the middle–late Frasnian brachiopod faunas and sequences in this immense region remains undocumented. Relevant studies featuring illustrations of atrypids from the Great Basin or the western US Cordillera (Montana, Idaho) include: Merriam (1940), Laird (1947), Kottlowski (1950), Beus (1965), Johnson (1977), Johnson *et al.* (1980), and Johnson & Trojan (1982).

Biostratigraphic ranges of most Givetian and early Frasnian forms from the Great Basin are summarized in Johnson (1990: fig. 50). Latest Givetian and Frasnian strata in Nevada and Utah are included in the Upper Denay Limestone, the Devils Gate Limestone, the Guilmette Formation, and part of the Pilot Shale (Johnson 1990; Johnson & Sandberg 1991; Johnson *et al.* 1996). Brachiopod faunas with atrypids from the Upper Denay and parts of the Devils Gate have been described or discussed in various studies including Kindle (1908), Merriam (1940), Drewes (1967), Johnson (1977), Johnson *et al.* (1980), Johnson & Trojan (1982), and Johnson (1990). The works by Johnson and his coworkers have documented the latest Givetian and early Frasnian brachiopod and conodont sequences in the Denay and Devils Gate, with some limited discussion of late Frasnian faunas (Johnson *et al.* 1980). Faunal lists in Drewes (1967) indicate the presence of late Frasnian faunas in the Guilmette Formation in the Schell Creek Range in eastern Nevada, although those collections need to be restudied. Sequence stratigraphic and conodont studies by Lamaskin & Elrick (1997) led to refinement of correlations of the inner shelf and cratonic platform facies of the Guilmette Formation with the offshore slope facies of the Denay and Devils Gate (T-R cycles IIa–IId). Unfortunately no new data on brachiopod faunas was presented in that study.

Deposits of T-R cycle IIb are included in the Upper Denay Limestone in the Antelope Range in central Nevada (Johnson *et al.* 1996). Brachiopods from these rocks characterize Great Basin Devonian Faunal Intervals (F.I.) 28–29 (Johnson *et al.* 1980; Johnson & Trojan 1982; Johnson 1990; Johnson *et al.* 1996). The Upper Denay faunas of F.I. 28–29 feature *Davidsonia antelopensis* Johnson & Trojan, 1982, *Radiatrypa klukasi* Norris, 1981, *R.* sp. (small), and *Spinatrypina angusticostata* Johnson & Trojan, 1982.

Middle Frasnian rocks of the Upper Denay Limestone deposited during the lower part of T-R cycle IIc yield brachiopod faunas of F.I. 30 of Johnson (1977, 1990). Johnson (1977, 1990) and Johnson *et al.* (1980) indicate that *Radiatrypa multicostellata* (Kottlowski, 1950) is the typical atrypid known as of this writing from that interval in the Great Basin (see this form illustrated as *Atrypa* cf. *missouriensis* Miller in Merriam 1940: pl. 7: 15, 16). *Spinatrypa* sp. cf. *S. montanensis* (Kindle, 1908) appears to occur in the interval of the *Allanella* Fauna (= *Spirifer argentarius* Fauna of Merriam 1940: pl. 8: 12–17) in the Devils Gate Limestone at Devils Gate in central Nevada. Conodonts associated with brachiopods from the interval of the *Allanella* Fauna in the Devils Gate Limestone at the Devils Gate section of Sandberg (in Sandberg *et al.* 1989: fig. 9) indicate a correlation within T-R cycle IIc of Johnson *et al.* (1985).

The Jefferson Limestone of Montana and Idaho yields a similar early-middle Frasnian atrypid fauna illustrated in studies by Kindle (1908), Laird (1947), Kottlowski (1950), and Beus (1965). Laird (1947) illustrated *Spinatrypa montanensis* (Kindle, 1908) and a *Radiatrypa* identified as *Atrypa missouriensis* Miller from the Jefferson of northwestern Montana. Kottlowski (1950) placed the form Laird (1947: p. 457, pl. 64: 19–22) identified as *Atrypa missouriensis* in synonomy with his new species *Atrypa* (now *Radiatrypa*) *multicostellata* from the Jefferson Limestone. Beus (1965), apparently unaware of Kottlowksis work, erected *Atrypa oneidensis*, based on specimens from the Jefferson in northern Utah and southern Idaho. That form may well be a synonym of *R. multicostellata* (Kottlowski, 1950). The ranges of both *Spinatrypa montanensis* and *Radiatrypa multicostellata* are not precisely established in terms of the Frasnian conodont sequence. Sandberg (in Sandberg *et al.* 1989) aligned most of Jefferson at its type section near Logan, Montana, in the middle Frasnian Upper *Mesotaxis asymmetrica–Ancyrognathus triangularis* zonal interval. This is comparable to its range in Nevada Johnson's (1980) Great Basin F.I. 30, placing it in the middle Frasnian interval of T-R cycle IIc.

Faunas from Eastern British Columbia and Alberta

Atrypids from the Flume Formation in northeastern British Columbia are illustrated in Maurin & Raasch (1972). Late Givetian–middle? Frasnian species are elements of their faunal assemblages 3, 4, and 5 from the Flume. Substantial atrypid faunas are known from a variety of late Givetian and Frasnian units in western and northern Alberta, the best documented of these is from the Waterways Formation (late Givetian–early Frasnian) in northeastern Alberta (see Warren & Stelck 1956; recent reports by Norris 1963; Norris & Uyeno 1981, 1983). Many elements of the late Frasnian atrypid fauna of the Mount Hawk Formation of western Alberta are illustrated in Warren & Stelck (1956) and McLaren *et al.* (1962). In both studies the stratigraphic ranges of illustrated species are not carefully documented. The brachiopod faunas from rocks in the Alberta Rocky Mountains included in the Flume, Maligne, Cairn, Perdrix, Arcs, Ronde and Simla formations remain largely undocumented.

Flume Formation – Northeastern British Columbia. — The lower Flume Formation yielding the fauna of assemblage zone 2 and lower part of zone 3 with *Tecnocyrtina missouriensis raaschi* Johnson & Trojan, 1982, is correlated directly with the *T. johnsoni* Zone of the Iowa Basin Devonian brachiopod sequence of Day (1997). The base of the *T. johnsoni* Zone in Iowa is at or near the base of the Upper *disparilis* Zone (see Day 1997). The lower Flume strata with *T. m. raaschi* were deposited during the late Givetian T-R cycle IIa-2 of Day *et al.* (1996).

The occurrence of typical Waterways brachiopods such as *Tecnocyrtina billingsi* (Meek) in the part of the Flume yielding faunas of Maurin & Raasch's (1972) assemblage zones 3 (upper part only) and 4 are correlated with other deposits of T-R cycle IIb (undivided) in western Canada and the US midcontinent. That species has its lowest occurrence in Northeastern Alberta (Norris & Uyeno 1981, 1983) and elsewhere in western Canada no lower than the *Skeletognathus norrisi* Zone (Day 1997). The Flume fauna of the upper part of assemblage zone 3 and zone 4 of Maurin & Raasch (1972) features many species of atrypids, spiriferids, stropheodontids, and orthids common to the Lithograph City Formation of the Iowa Basin and the Waterways Formation of northeastern Alberta.

Precise correlation of the upper Flume Formation yielding the brachiopod fauna of assemblage zone 5 of Maurin & Raasch (1972) is uncertain. A position above zone 4 faunas and the occurrence of *Radiatrypa* cf. *R. multicostellata* (Kottlowski, 1950) suggest correlation with Johnson's (1990) Great Basin Devonian F.I. 30. This is also equivalent to part of the Cooking Lake Formation in northern Alberta; the upper Hay River Formation (uppermost Member A and younger) in the southern NWT; and the lower Shell Rock Formation of Iowa (Fig. 2). If new conodont data from the Flume Formation substantiate this hypothesis, then the assemblage zone 5 fauna would allow recognition of middle Frasnian T-R cycle IIc deposits at the Cecilia Lake region in British Columbia. Systematic assignments made here of atrypid specimens illustrated from T-R cycle IIb deposits of the middle and upper Flume are provisional pending restudy of specimens collected by Maurin & Raasch (1972).

Upper Assemblage 3: late Givetian. — Assemblage 3 deposits contain species of *Spinatrypina, Carinatrypa*?, *Desquamatia (Independatrypa)* [*I. scutiformis* (Stainbrook, 1938)], *D. (Seratrypa)*, and *Pseudoatrypa*. These include: *Carinatrypa*? sp. = *Atrypa* sp. nov. 496 of Maurin & Raasch (1972: pl. 6: 21–24); *Desquamatia (Independatrypa) scutiformis* (Stainbrook, 1938) = *Atrypa scutiformis* Stainbrook (1938) of Maurin & Raasch (1972: pl. 6: 1–4); *Desquamatia (Seratrypa)* sp. = *Atrypa* sp. n. 'KAKWA' and *A.* sp. n. 'KAKWA' var. of Maurin & Raasch 1972: pl. 6: 5–12, 17–20. Possibly = *Atrypa* n. sp. 'KAKWA' var. 497 (Maurin & Raasch 1972: pl. 6: 13–16); and *Spinatrypina* sp. = 'Atrypide genus undet.' of Maurin & Raasch (1972: pl. 5: 10–20).

Assemblage 4: early Frasnian. — The fauna of assemblage 4 features many species common to the faunas of the Lithograph City Formation of the Iowa Basin, and the Waterways

Formation of northern Alberta. The fauna appears to include the following: *Pseudoatrypa lineata* (Webster, 1921) = *Atrypa* sp. nov. 473 var. A and *Atrypa devoniana* var. *minor* Stainbrook, 1938, of Maurin & Raasch (1972: pl. 7: 1–8, pl. 8: 24–27); *Pseudoatrypa* sp. aff. *P. rugatula* (Stainbrook & Ladd, 1924) = *Atrypa* sp. nov. 473 var. B of Maurin & Raasch (1972: pl. 7: 9–20); *Pseudoatrypa* sp. = *Atrypa* sp. nov. 473 var. C of Maurin & Raasch (1972: pl. 7: 21–24); *Radiatrypa* cf. *R. multicostellata* = *Atrypa gregeri* Rowley of Maurin & Raasch (1972: pl. 8: 5–11); *Pseudoatrypa* sp. aff. *P. witzkei* Day & Copper, 1998 = *Atrypa blackhawkensis* Stainbrook of Maurin & Raasch (1972: pl. 12: 16–19); *Spinatrypina (Exatrypa)* sp. cf. *S. (E.) angusticostata* Johnson & Trojan, 1982 = Atrypid genus undet. (548) of Maurin & Raasch (1972: pl. 8: 12–15); and *S. (E.) albertensis* (Warren) = *Spinatrypa albertensis* (Warren), and *Spinatrypa* sp. 548 of Maurin & Raasch (1972: pl. 8: 16–23, pl. 12: 20–22).

Assemblage 5: Middle Frasnian? — Assemblage 5 probably represents a Middle Frasnian fauna consisting of species of *Radiatrypa* and *Neatrypa.* These include: *Radiatrypa* sp. cf. *R. multicostellata* (Kottlowski, 1950) = *Atrypa* sp. 544 of Maurin & Raasch (1972: pl. 12: 8–11); and *Neatrypa* sp. = *Atrypa pronis* Fenton & Fenton of Maurin & Raasch (1972: pl. 12: 12–15).

Waterways Formation – Northeastern Alberta. — A significant latest Givetian and early Frasnian atrypid fauna is known from the Waterways Formation of northern Alberta. The Waterways is widely correlated with latest Givetian and early Frasnian units deposited during T-R cycle IIb (undifferentiated) across North America (Day *et al.* 1996: fig. 2). Waterways conodont faunas (see discussion by Uyeno in Day *et al.* 1996; Uyeno 1998) span the interval of the *Skeletognathus norrisi* Zone through M.N. Zone 4, and perhaps include faunas spanning part of M.N. Zone 5 (Mildred Member). The Waterways fauna includes species common to other faunas in British Columbia and the Iowa Basin.

The first atrypids illustrated from the Waterways were in studies by Warren (1944) and Warren & Stelck (1956), although ranges of forms were never documented in those works. Waterways atrypids first described by Warren (1944) include *Radiatrypa clarkei* (Warren, 1944) and *Spinatrypina (Exatrypa) albertensis* (Warren, 1944). Warren & Stelck (1956) later illustrated these species and additional forms that include: *Desquamatia (Independatrypa)* cf. *I. independensis* (Webster, 1921) as shown in Warren & Stelck (1956: pl. 10: 11–13, 17–19, pl. 12: 1–4), *Pseudoatrypa* cf. *P. gigantea* (Webster, 1921) as in Warren & Stelck (1956: pl. 11: 16–18); the coarse ribbed species of *Pseudoatrypa* designated as *Atrypa* cf. *bremerensis* Stainbrook (Warren & Stelck 1956: pl. 13: 8–9). The form identified as *Atrypa* cf. *owenensis* Webster (1921: pl. 13: 23–25) can not be attributed to *Iowatrypa* on the basis of their illustrations. The form identified as *Atrypa scutiformis* Stainbrook (1938: pl. 12: 27–29) is closest to *Pseudoatrypa lineata* (Webster, 1921) illustrated by Day & Copper 1998.

More recent studies of the Waterways fauna by Norris (1963, 1983; in Norris & Uyeno 1981, 1983) have documented brachiopod faunas from various members of the Waterways defined by Crickmay (1957). The lower four members of the Waterways Formation (Firebag, Calumet, Christina, and Moberly) crop out in the Athabasca-Clearwater rivers area of northeastern Alberta, and the uppermost Mildred Member is known only in the subsurface (Norris 1983). Norris illustrated species of *Desquamatia (Independatrypa), Pseudoatrypa, Radiatrypa*, *Spinatrypina*, and possibly *Neatrypa* and *Iowatrypa*, including most forms first illustrated in works by Warren (1944) and Warren & Stelck (1956). The species of *Spinatrypa* mentioned in Norris (1963: p. 27) has not yet been described from the Waterways.

Parts of the Calumet and Christina members yield atrypids in Waterways outcrops on Birch River (Norris & Uyeno 1981) that include: include *Radiatrypa clarkei* (Warren, 1944), *Pseudoatrypa* cf. *P. blackhawkensis* (Stainbrook, 1938), *Pseudoatrypa* cf. *P. gigantea* (Webster, 1921), and *Spinatrypina (Exatrypa)* sp. A. Norris (in Norris & Uyeno 1983) described atrypids from the Peace Point Member of the Waterways in the Gypsum Cliffs area of northeastern Alberta, including the following: *Pseudoatrypa devoniana boyeri* Norris; *Desquamatia (Independatrypa)) independensis* (Webster, 1921); *D. (I.)* sp. cf. *D. (I.) independensis* (Webster, 1921); *D. (Variatrypa) clarkei* (Warren, 1944); *D. (V.) klukasi* Norris, 1983; and *Pseudogruenewaldtia*? sp. The latter form may be the same species illustrated as *Atrypa* cf. *owenensis* Webster by Warren & Stelck (1956). It is difficult to assign that form to *Iowatrypa* or other genera of the Invertinae based on Norris's illustrations. *Pseudoatrypa devoniana boyeri* desribed in Norris & Uyeno (1981) appears to be an older element of the lineage including the forms *P. witzkei* Day & Copper, 1998 and *P. devoniana* (Webster, 1921).

Atrypids identified as *Desquamatia (Independatrypa) independensis* (Webster, 1921) and *D.* (*I.*) cf. *D.* (*I.*) *independensis* (Webster, 1921) from the Waterways and the Point Wilkins Member of the Souris River Formation in southwestern Manitoba (see Norris & Uyeno 1983; and Norris & Day in Day *et al.* 1996), are approximately half the adult size of typical *D.* (*I.*) *independensis* (Webster, 1921) from Iowa. The older late Givetian form occurs in the Little Cedar Formation of the Iowa Basin and the Dawson Bay Formation of southwestern Manitoba. This suggests that the latest Givetian and early Frasnian forms probably are a younger smaller descendent that evolved as a geographic species of the *independensis* stock in western Canada following its migration after the late Givetian transgression of T-R cycle IIa-1. *Desquamatia (Variatrypa) clarkei* and *D. (V.) klukasi* are both considered here as species of *Radiatrypa* following Copper (1978) and Johnson & Trojan (1982).

Mikkwa and Grosmont formations – Peace River Area – Northern Alberta. — Norris (1963) reported the occurrence of Frasnian atrypids from the Mikkwa and Grosmont formations (Fig. 2) which crop out on Peace River in the vicinity of Vermillion Chutes in northern Alberta. Provisional correlations outlined in Norris (1963) and in McLean & Sorauf (1989) indicate that the Mikkwa and Grossmont are equivalents of the upper part of the Hay River Formation in the southern NWT. Consequently these units were most likely deposited during T-R cycle IIc (Fig. 2). The Mikkwa is divided into a basal Lower Limestone Member and an upper Mottled Limestone Member. The latter unit yields a fauna similar to that seen in Members A (upper part), B, C, and D of the Hay River Formation. Norris (1963: p. 72) listed a number of atrypids from the Mottled Limestone Member, that include *Atrypa* sp., *A.* cf. *canadensis* Webster, *A. canadensis* Webster, *Spinatrypa* sp., *Spinatrypa* sp. n., and *Spinatrypa* sp. N. The forms attributed to Webster's 1921 species are now assigned to *Neatrypa*. The overlying Grosmont is badly dolomitized, although Norris (1963: p. 74) did note the occurrence of forms assigned at that time to *Atrypa* and *Spinatrypa*. Further discussion of the Mikkwa and Grosmont brachiopods must await future stratigraphic and systematic study of those faunas.

Alberta Rocky Mountains – Western Alberta. — A variety of atrypid brachiopods have been illustrated from late Frasnian deposits in the Canadian Rocky Mountain of western Alberta included in the Mount Hawk Formation. Atrypids apparently recovered from the Mount Hawk illustrated by Warren & Stelck(1956), McLaren *et al.* (1962), or discussed in Copper (1973), are similar to well known late Frasnian faunas in New Mexico and Iowa (Figs 1, 2). From specimens illustrated in these earlier studies, and recent new collections from the Mt. Hawk along the southern margin of the Miette Reef platform of the author, it is clear that the Mount Hawk fauna includes elements of widespread lineages of *Costatrypa, Pseudoatrypa, Spinatrypa*, and *Iowatrypa.* The conodont sequence from the upper Perdrix and Mount Hawk formations in the Nikanassin Range and Ancient Wall areas of the Alberta Rocky Mountains was documented in Klapper & Lane (1989: figs 1, 2). They correlated the upper Perdrix and Mount Hawk sequence with Frasnian M. N. zones 9–12. These rocks were deposited during part of T-R cycle IId (IId-1 of this report).

Atrypids from the Mount Hawk Formation were first illustrated as elements of Warren & Stelcks (1956) *Macgeea* and *Tenticospirifer cyrtiniformis* faunas. Additional late Frasnian atrypids were illustrated as elements of their *Manticoceras sinusosum* fauna from the Imperial Formation from the Norman Wells area of the lower Mackenzie River Valley of the NWT. Mount Hawk forms include: *Iowatrypa*? sp. named *Gruenwaldtia* sp. in Warren & Stelck (1956: pl. 17: 19–24), *Pseudoatrypa* sp. cf. *P. devoniana* (Webster, 1921) illustrated as *Atrypa* cf. *hackberryensis* Fenton & Fenton, 1924, by Warren & Stelck (1956: pl. 20: 2–4, 20–27); and *P.* sp. cf. *P. bentonensis* (Stainbrook, 1938) illustrated as *Atrypa* cf. *bentonensis* Stainbrook (1938: pl. 20: 5–7). Additional Mount Hawk atrypids were later illustrated in McLaren *et al.* (1962) which include *Iowatrypa owenensis* (Webster, 1921) (= *Grunewaldtia americana* Stainbrook, McLaren *et al.* 1962: pl. 13: 1, 2); *Costatrypa* sp. cf. *C. varicostata* (Stainbrook, 1945) (= *Atrypa* sp. K of McLaren *et al.* 1962: pl. 14: 19–21). The remaining forms in their study (i.e. *Atrypa* sp. J, L, and M; pl. 14) appear to be *Pseudoatrypa* close to *P. devoniana* (Webster, 1921).

Southern Northwest Territories faunas

Conodont studies (Klapper & Lane 1985, 1989; Geldsetzer *et al.* 1993) and recent conodont-based graphic correlations (Klapper *et al.* 1995; Klapper 1997) indicate that a relatively complete middle-late Frasnian platform succession is developed in the southern NWT (see Figs 1, 2, 12). This thick Late Devonian succession accumulated inboard of the continental margin on the Mackenzie Shelf (Morrow & Geldsetzer 1989: fig. 3). Ranges of atrypid brachiopod taxa in the Frasnian rocks in the Hay River region (Fig. 12) are approximated, and were compiled using data on atrypid brachiopod occurrences in faunal lists in McLean *et al.* (1987).

The latest Givetian–middle Frasnian Hay River Formation was deposited during several sea level fluctuations corresponding to T-R cycles IIb-1 to IIc (lower part), although sequence boundaries within the Hay River Formation have not yet been positively identified and characterized. The lower part of Member A in the subsurface is correlated with the Waterways Formation of northeastern Alberta (McLean & Sorauf 1989; Day *et al.* 1996; Fig. 2). The upper part of Member A yields the nominal species of Frasnian M.N. Zone 6 (*Ancyrognathus ancyrognathoideus*) and represents the lower part of T-R cycle IIc in this area of western Canada (Figs 2, 12). The remainder of the Hay River (members B-F) and overlying Alexandra Member of the Twin Falls Formation represent a cratonic middle shelf succession deposited during the remainder of the middle Frasnian T-R cycle IIc. The base of T-R cycle IId (Figs 2, 12) is positioned at the unconformity at the base of the Upper Member of the Twin Falls Formation. The overlying Tathlina and Redknife formations represent the remainder of T-R cycle IId-1. The Kakisa Formation is a discrete very late Frasnian depositional sequence deposited during the later part of T-R cycle IId (IId-2 of Figs 2, 12). The upper contact of the Kakisa is characterized by development of a disconformity with microkarst features, and is overlain by early Famennian rocks of the Trout River Formation. The Trout River yields conodonts of the *P. crepida* Zone (Klapper & Lane 1985), or possibly the Lower–Middle *Palmatolepis triangularis* Zone as discussed by Orchard (1989) and Geldsetzer *et al.* (1993).

The southern NWT Frasnian succession (Fig. 12) yields a diverse Frasnian brachiopod fauna. Atrypids from this succession have been illustrated and described in studies by Kindle (1908), Webster (1921), Fenton & Fenton (1932, 1935), Warren (1944), Warren & Stelck (1956), and Crickmay (1952, 1957, 1967). These include: *Atryparia* sp. (= *Costatrypa*?); *Iowatrypa deflecta* (Warren) (Imperial Formation only); *Atrypa canadensis* Webster [= *Neatrypa canadensis* (Webster)]; *Neatrypa rubromitra* (Crickmay) (a probable synonym of *N. canadensis*); *Pseudoatrypa devoniana* (Webster); *P.* sp. cf. *P. bentonensis* (Stainbrook), '*Variatrypa cosmeta* (Crickmay)' [= *Radiatrypa cosmeta* (Crickmay)]; *Desquamatia (Seratrypa) ciliipes* (Crickmay); '*Spinatrypa albertensis* (Warren)' [= *Spinatrypa (S.)* sp. 1]; *Spinatrypa (S.) montanensis* (Kindle); and '*S.* sp. cf. *S. deflecta* (Warren)' (= *S.* sp. 2).

Pseudoatrypa is common in middle and late Frasnian units in the region. Warren & Stelck (1956: pl. 21: 1–4) illustrated *Atrypa* cf. *bentonensis* Stainbrook, which was later referred to as *P. bentonensis* (Stainbrook) in lists of brachiopod faunas of the Hay River, Twin Falls, Tathlina, Redknife and Kakisa formations in McLean *et al.* (1987). *Pseudoatrypa devoniana* (Webster, 1921) was listed from the Redknife Formation by McLean *et al.* (1987). Specimens on loan to the author from the lower Hay River Formation (Amoco Canada Ltd collections, Amoco Locality HR5) are close to *P. witzkei* Day & Copper, 1998, indicating that older elements of the *devoniana* stock were present in western Canada during the middle Frasnian.

Radiatrypa cosmeta (Crickmay, 1952) occurs in the upper part of Member A of the Hay River Formation, at a position low in the interval of T-R cycle IIc. The occurrences of *R. multicostellata* (Kottlowski, 1950) in the Great Basin and US Rocky Mountains are of similar age. Thus far no late Frasnian species of *Radiatrypa* have been illustrated from North America. The highest North American occurrence of *Desquamatia (Seratrypa)* is represented by *S. ciliipes* (Crickmay, 1957) in the late Frasnian part of the Late Devonian succession in the southern NWT as discussed by Copper (1978).

Two closely related forms of *Neatrypa* have been described from the Frasnian succession in the southern NWT (see discussion in Copper 1978: p. 295). *Neatrypa canadensis* was described by Webster (1921) and later illustrated in Fenton & Fenton (1935). This is presumably the form from

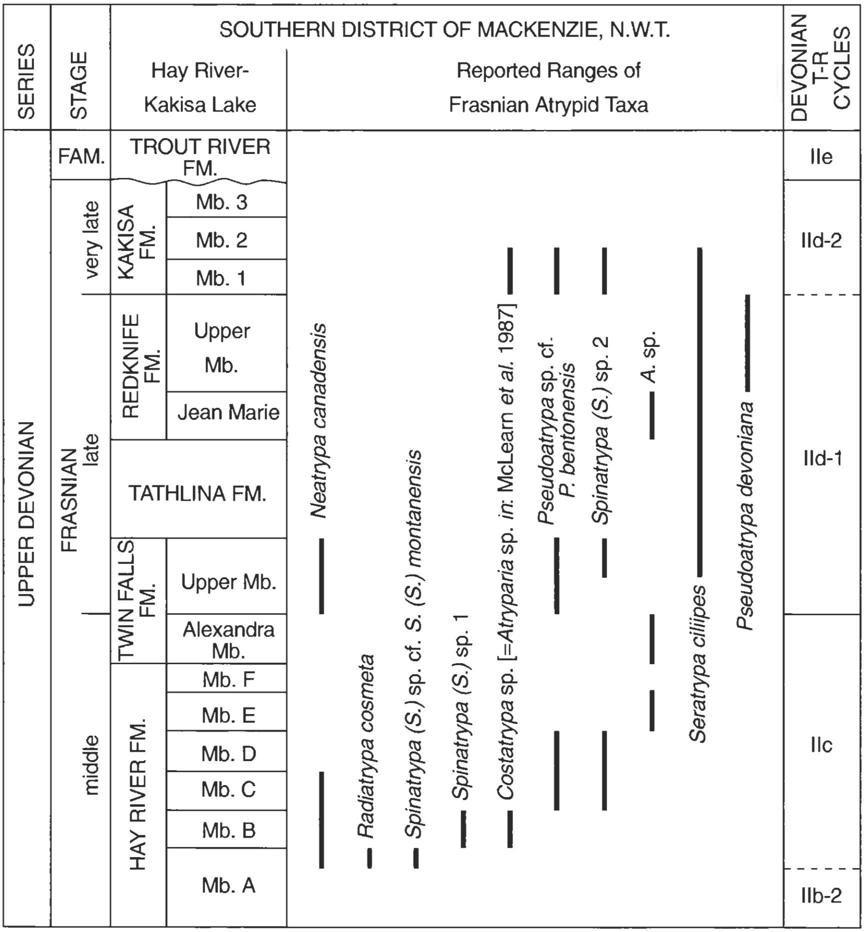

Fig. 12. Reported stratigraphic ranges of Frasnian Atrypida in the southern District of Mackenzie of the NWT of southern Canada. Stratigraphy as in Fig. 2, and alignment of lithostratigraphic units with T-R cycles from this study. Atrypid ranges based on identifications by Jones (in McLean *et al.* 1987), some of which are revised in this study.

the Hay River region identified as *Atrypa* cf. *gigantea* Webster in Warren & Stelck (1956: pl. 21: 24–26). McLean *et al.* (1987) indicate that this form ranges from the upper part of Member A through Member E of the Hay River. Crickmay (1957: p. 13, pl. 1: 9–11) described *Neatrypa rubromitra* (Crickmay) from the Grumbler Formation (= part of Upper Member of the Twin Falls Formation). The occurrence of these two forms is evidence that *Neatrypa* persisted into the middle and late Frasnian in the western Canadian faunas after becoming extinct in US midcontinent faunas during the late Givetian.

Specimens identified and listed as *Spinatrypa* cf. *S. albertensis* (Warren) in McLean *et al.* (1987) presumably correspond to form illustrated under the same name in Warren & Stelck (1956: pl. 18: 7–13). This apparently is the form illustrated as *Atrypa planosulcata* Webster var. by Fenton & Fenton (1932: p. 220, pl. 23, figs 4–6). This form appears to be an undescribed species closely related to and probably ancestral to *Spinatrypa (S.) planosulcata* (Webster). This form is left in open nomenclature and is referred to here and above as *S. (S.)* sp. 1 (Fig. 12). *Atrypa albertensis* Warren (1944) was placed in *Spinatrypina* (*Exatrypa*) by Copper (1978), and consequently the species referred to as *Spinatrypa* cf. *S. albertensis* (Warren) in McLean *et al.* (1987) and the Amoco-Canada LTD collections from the Hay River area should not be compared to Warren's *Atrypa albertensis.* Shells of *Spinatrypa* sp. cf. *S. montanensis* (Kindle) from the Hay River are more coarsely costate and more lamellose than *S. (S.)* sp. 1, and is similar to Kindles (1908) middle Frasnian species from the Jefferson Limestone of Montana. McLean *et al.* (1987: p. 37) also *Spinatrypa deflecta* (Warren) from the Kakisa Formation. This same form was identified as *Atrypa* cf. *deflecta* (Warren) by Warren & Stelck (1956: pl. 21: 18–20, 27–29). This form is a small species of *Spinatrypa* listed in open nomenclature as *S. (S.)* sp. 2.

T-R cycle IIb fauna (latest Givetian–early Frasnian). — Latest Givetian and early Frasnian atrypids from rocks included in the lower part of Member A of the Hay River Formation are discussed by Norris (in Day *et al.* 1996), and include *Radiatrypa* sp. cf. *R. clarkei* (Warren, 1944) and *Desquamatia (Independatrypa)* sp. cf. *I. independensis* (Webster, 1921). These forms occur in coeval faunas of the Peace Point and Firebag members of the Waterways Formation in northern Alberta (Fig. 2; Norris in Day *et al.* 1996).

T-R cycle IIc fauna (middle Frasnian). — The upper part of Member A, overlying members B-F of the Hay River Formation (Figs 2, 14), and the Alexandra Member of the Twin Falls Formation are exposed along Hay River. This middle Frasnian succession, deposited during T-R cycle IIc yields a distinctive atrypid brachiopod assemblage shown in Fig. 12.

T-R cycle IId Fauna (late-very late Frasnian). — Upper Frasnian deposits are included in the Twin Falls, Tathlina, Redknife and Kakisa formations (Fig. 12). These deposits are exposed in the upper part of the Late Devonian outcrops on Hay River and in the Laird River-Kakisa Lake region. Those rocks accumulated during sea level fluctuations corresponding to T-R cycles IId-1 and IId-2 (Fig. 12). The late Frasnian assemblage in T-R cycle IId-1 deposits includes: *Neatrypa canadensis* (Webster, 1921), *Pseudoatrypa devoniana* (Webster, 1921), *P.* sp. cf. *P. bentonensis* (Stainbrook, 1938), *Desquamatia (Seratrypa) ciliipes* (Crickmay, 1957), *Spinatrypa* sp., *S. (S.)* sp. n. 2, and *Atryparia* (= *Costatrypa*?). A specimen of *Costatrypa* sp. aff. C. *varicostata* (Stainbrook, 1945) was illustrated from the Bosworth sandstone member of Imperial Formation from the lower Mackenzie River Valley by Warren & Stelck (1956: = *Atrypa* sp. nov., pl. 24: 5–8). Whether this is the same form identified as *Atryparia* sp. from the late Frasnian of the Hay River region by McLean *et al.* (1987) is unclear. Specimens from locality TR1 from the Redknife Formation in the Amoco Canada Ltd. collections (see fig. 4 in Klapper & Lane 1985) are close to *Costatrypa varicostata* (Stainbrook, 1945). The occurrence of *Iowatrypa* has not been confirmed in the aforementioned units in the NWT.

The highest Frasnian rocks in this region (T-R cycle IId-2, Figs 2, 12) are included in the Kakisa Formation. The Kakisa is divided into members 1–3 by McLean *et al.* (1987) and McLean & Sorauf (1989). All three members yield brachiopods, although no atrypids are listed or discussed from members 2 and 3 in McLean *et al.* (1987). The Member 1 fauna listed in McLean *et al.* (1987) includes *Spinatrypa (S.)* sp., *Pseudoatrypa* sp. cf. *P. bentonensis*, *Atryparia* sp. (= *Costatrypa* sp.), and *Desquamatia (Seratrypa) ciliipes.* The F-F boundary in this region lies at the contact of the Kakisa (Mb. 3) and Trout River formations (Geldsetzer *et al.* 1993; Figs 2, 12).

North American late Givetian–Frasnian atrypid assemblages

Latest Givetian–early Frasnian. — The IIb transgression in the interval of the *Polygnathus norrisi* Zone followed a pronounced late Givetian eustatic sea level fall that terminated T-R cycle IIa-2 deposition (Johnson *et al.* 1996; Day 1996a, 1996b; Day *et al.* 1996). The timing of the post T-R cycle IIa-2 lowstand corresponds to a major species extinction event (McLaren 1970; Day 1996a, 1996b) which affected North American shelf faunas in the upper part of the *disparalis* Zone. *Neatrypa, Desquamatia (Seratrypa),* and *Spinatrypa* became extinct in the Iowa Basin platform during the Upper *Klapperina disparilis* Zone extinction (Day in Day *et al.* 1996; Day 1996a, 1996b).

Neatrypa is not known in subsequent late Frasnian Iowa Basin faunas of T-R cycles IIb–IId, but persisted in northwestern Canadian shelf faunas until the late Frasnian (Webster 1921; Fenton & Fenton 1935; Warren & Stelck 1956; McLean *et al.* 1987).

Most atrypid genera found in late Givetian or upper Taghanic age T-R cycle IIa-2 rocks carryover into latest Givetian and early Frasnian deposits of T-R cycle IIb-1 (*Skeletognathus norrisi* Zone–upper part M.N. Zone 3). North American latest Givetian–early Frasnian tropical and carbonate shelf rocks of T–R cycle IIb-1 contain a distinctive cosmopolitan atrypid fauna dominated by: *Neatrypa* (western North America only), *Desquamatia* (*Indepedendatrypa*), *D. (Seratrypa), Pseudoatrypa, Radiatrypa,* possibly *Iowatrypa*; the spinatrypids *Spinatrypa (S.), Spinatrypina* (*Exatrypa*), and *S.* (*Spinatrypina*); possibly rare davidsonids (*Davidsonia*); and possibly carinatinids (*Carinatrypa*?). The upper limits of the ranges of the latter two taxa in North America appear to be in the early Frasnian and both were restricted to western North America at that time. In the latest Givetian and earliest Frasnian *Neatrypa, Radiatrypa, Desquamatia (Seratrypa),* and *Spinatrypa* were geographically restricted to western Canada or the Great Basin. All but the first of these were reintroduced to central North America during migrations later in the early Frasnian (interval of T-R cycle IIb-2). Species of *Pseudoatrypa* also became widespread in deposits of T-R cycle IIb-1 in central and western North America.

A second early Frasnian migration of atrypids from western North America into central and eastern North America occurred during the transgression of T-R cycle IIb-2. *Spinatrypa* (*S.*) and *Desquamatia (Seratrypa)* were reintroduced into the Iowa Basin, and *Radiatrypa* also migrated into central North America carbonate platforms at that time. These new migrants joined species of the variatrypines *Desquamatia (Independatrypa)* and *Pseudoatrypa* to characterize deposits of T-R cycle IIb-2 in the Iowa Basin as well as in western Canadian platforms.

Illustration of possible davidsoniids by Maurin & Raasch (1972) from early Frasnian T-R cycle IIb deposits of the upper Flume Formation in the Canadian Rockies in northeastern British Columbia are questionably assigned to the carinatinid genus *Carinatrypa*? If that form from British Columbia is a davidsonid, then a second migration of carinitinids into North America followed their initial migrations during the Eifelian (*Tortodus australis* and upper *T. kockelianus* zones). Typical *Carinatina* and *Carinatrypa* (see Copper 1978) are not known from late Givetian deposits of T-R cycle IIa of Johnson *et al.* (1985, 1996) and Johnson & Klapper (1992). If the shells illustrated by Maurin & Raasch (1972) are *Carinatrypa*, this would necessitate extension of the range of the genus into the early Frasnian. Copper (1996: fig. 2; in Copper & Gourvennec 1996: fig. 2) shows *Carinatrypa* as restricted to the interval of the late Eifelian–Givetian. Resolution of the ranges of those forms awaits systematic restudy of the late Givetian and early Frasnian faunas of the Flume Formation in British Columbia. *Davidsonia antelopensis* Johnson & Trojan, 1982, was illustrated from the Upper Denay Limestone (late Givetian) in the Antelope Range of central Nevada. There, this form ranges into the early Frasnian where it occurs in assemblages of Great Basin Devonian Faunal Intervals 28–29 (Johnson 1990: fig. 50).

Middle Frasnian. — North American middle Frasnian brachiopod faunas from many areas of North America are not well documented. The US midcontinent brachiopod fauna of the Shell Rock Formation in Iowa (described in Day & Copper 1998) includes species of *Spinatrypa (S.)* and *Pseudoatrypa*. Middle Frasnian brachiopod faunas known from the interval of Great Basin Devonian faunal interval 30 (lower part T-R cycle IIc) yield species of *Radiatrypa* (Johnson *et al.* 1980; Johnson & Trojan 1982; Johnson 1990), and *Spinatrypa (S.)* (Kindle 1908; Merriam 1940; Laird 1947). Rocks in the Hay River–Upper Mackenzie River Valley region of the southern District of Mackenzie yield species of *Neatrypa, Pseudoatrypa, Radiatrypa, Spinatrypa*, and *Atryparia*? (= *Costatrypa*) based on identification of material in Amoco Canada Ltd collections by Jones (in McLean *et al.* 1987). The occurrence of a possible *Costatrypa* in the middle Frasnian in the Hay River region indicates that elements of the genus may have migrated into North America prior to the late Frasnian. *Radiatrypa* apparently was extinct in North America by the close of the middle Frasnian.

Late Frasnian. — Central and western North America subtropical faunas are characterized by the occurrence of widespread species of *Pseudoatrypa* (i.e. *P. devoniana*), *Spinatrypa* (*S*). *Iowatrypa*, and *Costatrypa*. Tropical faunas from western Canadian carbonate platforms feature species of these genera, but also feature species of *Neatrypa* and *Desquamatia (Seratrypa)*. Low diversity faunas characterize subtropical-temperate shelf areas of the Appalachian Basin in eastern North American, which yield species of *Pseudoatrypa* and *Spinatrypa.*

Deposits of T-R cycle IId-1 (Fig. 2) in central (Lime Creek Formation, Amana Beds, Independence Shale) and the southwestern US (Sly Gap and upper Martin formations) yield species of *Costatrypa, Iowatrypa, Pseudoatrypa*, and *Spinatrypa.* In western Canada, *Costatrypa, Neatrypa, Iowatrypa, Pseudoatrypa, Desquamatia (Seratrypa)*, and *Spinatrypa* occur in upper Frasnian deposits (Fig. 12) in the Hay River and upper Mackenzie River Valley region of the southern NWT (McLean *et al.* 1987). Most North American species of *Costatrypa*, are restricted to upper Frasnian age deposits of T-R cycle IId-1. Available range data from New Mexico indicates that the first occurrences of *Costatrypa* appear to be near the base of T-R cycle IId-1 (M.N. zones 9–10?). In Iowa, the occurrence of *C. varicostata* (Stainbrook, 1945) in the Lime Creek Formation and Amana Beds of northern and eastern Iowa is in the interval of M.N. Zone 12 (Fig. 4). In Iowa (Fig. 4) and New Mexico (Figs 12, 13), range inceptions of species of *Iowatrypa* (*I. minor* and *I. rara*) are in the lower part of M.N. Zone 12, or very high in Zone 12 and likely range into the interval of M.N. Zone 13 (*I. owenensis* in Iowa).

Very late Frasnian brachiopod faunas and sequences in North America are well documented in the US midcontinent (Iowa Basin), the southwest US, and in a provisional fashion in the southern NWT. Most species of late Frasnian atrypids in the Iowa Basin (Fig. 4) became extinct before the close of the Frasnian during the interval of M.N. Zone 12 of Klapper (1989). Recent investigations of the brachiopod fauna of the upper part of the Lime Creek Formation indicate that at least two atrypids range into very late Frasnian deposits (upper part of the Owen Member yielding the ammonoid *Manticoceras lindneri*) including *Iowatrypa* aff. *I. owenensis* (Webster, 1921) and *Spinatrypa (S.)* sp. cf. *S. (S.) planosulcata* (Webster, 1888). These new occurrences permit the upward extension of the ranges of these forms.

In the late Frasnian of New Mexico (Figs 9–11), atrypids and other groups of articulate brachiopods were affected by two waves of extinctions. The first, and most significant extinction episode occurred at position high in M.N. Zone 12 or near the base of Zone 13, and coincided with a rapid transgression and drowning of the older Sly Gap platform (Dutro 1986; Day 1987b). There, *Costatrypa*, and *Iowatrypa* became extinct in the interval of the upper part of Frasnian M.N. Zone 12. Two related species of *Spinatrypa* occur in very late Frasnian rocks (Salinas Peak Member of the Contadero Formation) in the San Andres Mountains (Figs 1, 2) where they occur in association with a rare variatrypine representing *Pseudoatrypa*? Available conodont data (Day 1988, 1990) indicate that both *Spinatrypa* and *Pseudoatrypa*? were extinct in New Mexico within or at the end of M.N. Zone 13.

Iowatrypa appears to survive into the very late Frasnian in Nevada based on the reported occurrence of *Iowatrypa* cf. *I. americana* in the *Iowatrypa* Fauna (Uppermost *gigas* Zone) from the Devil's Gate Limestone (Johnson *et al.* 1980). In the NWT (Figs 2, 12), Jones (in McLean *et al.* 1987) reported species of *Atryparia* (= *Costatrypa*), *Pseudoatrypa, Desquamatia (Seratrypa)*, and *Spinatrypa* from the lower part of the Kakisa Formation (presumably from Member 1). This assemblage occurs in the lower part of the interval of T-R cycle IId-2, aligned with that position based on conodont faunas from the Kakisa yielding *Polygnathus brevicarina* described by Klapper & Lane (1985, 1989), Klapper *et al.* (1989). That species is known to be restricted to the M.N. Zone 13 through graphic correlation with the Frasnian composite standard by Klapper (1997: text-fig. 5).

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