Late Tremadocian Radiolarian Faunas and Biostratigraphy of the Cow Head Group, Western Newfoundland, Canada

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뉴파운드랜드 Cow Head Group에서 발견한 후기 Tremadocian 방산충 군집과 생충서대 재정립에 관한 연구

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Abstract: Late Tremadocian radiolarian faunas were first recovered from the Cow Head Group, Newfoundland, Canada. Three faunal assemblages were recognized, one from Martin Point and two from Western Brook Pond in Gros Morne National Park. These radiolarian faunas include six families, 11 genera, and 26 species. In these faunas, six genera (*Archeoproventocitum*, *Cowheadia*, *Neopalaeospiculum*, *Protospongontactinia*, *Protoproventocitum* and *Westernbrookia*) and 17 species (*Archeoproventocitum nudiformum*, *A. retiformum*, *Aspiculum densum*, *A. jamesi*, *A. multistratum*, *A. gigantum*, *Cowheadia duplextesta*, *Neopalaeospiculum densum*, *N. laxum*, *N. transformum*, *Pararchoeontactinia stilla*, *Protospongontactinia spongiosa*, *Protoproventocitum nazarovii*, *P. aitchisoni*, *Westernbrookia cancella*, *W. diversa*, and *W. ovata*) are new. Late Tremadocian faunas are characterized by the appearance of proventocitiids and diversification of aspiculmids and reduction of protoentactiniids and echidniniids that had flourished in the early Tremadocian faunas. An examination of the biostratigraphic range of co-occurring conodonts indicates that the radiolarian faunas described here belong to the late Tremadocian, from the Lower Diversity Interval through the *M. diana* Zone to the lower *P. proteus* Zone. With the recovery of conodonts of the *R. manitouensis* Zone from other localities in the study area, the correlation among Martin Point, Western Brook Pond, Broom Point, and St. Paul's Inlet strata has become more precise. Also, the middle and late Tremadocian Cow Head Group can be subdivided into the *R. manitouensis* Zone, the Low Diversity Interval, and the *M. diana* Zone of North America. The lower *P. proteus* Zone of the latest Tremadocian for northern Europe is recognized in the Western Brook Pond South section.

Keywords: Radiolaria, Conodont, biostratigraphy, Late Tremadocian, Cow Head Group

요약: 지금까지 보고된 하부 오르도비스기의 Tremadocian과 Arenigian에 속하는 방산충 군집들 간에는 유사성이나 연관성이 거의 보이지 않았다. Tremadocian에서 Arenigian의 방산충 군집의 진화경향을 알 수 없었던 이유는 후기 Tremadocian 방산충 군집에 대해 알려진 바가 없었기 때문이다. 캐나다 뉴파운드랜드의 Cow Head Group에서 후기 Tremadocian에 속하는 방산충 화석 군집들이 처음으로 발견되었다. 이 새로운 방산충 군집들은 모두 6과, 11속, 26종에 속한다. 이들 가운데 6속 17종이 새로이 발견된 것들이다. Arenigian에서만 보고되었던 Proventocitidae에 속하는 종들

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이 다양하게 산출되었다. 초기 Tremadocian에 변성했던 Protoeactiniidae와 Echidniniidae에 속하는 것들은 감소하고 Aspiculumidae에 속하는 것들은 더욱 분화되어 다양하고 풍부하게 산출되었다. 방산충과 함께 출현하는 코노돈트 연구로 Low Diversity Interval에서 *M. diana* Zone 그리고 하부 *P. proteus* Zone에 속하는 후기 Tremadocian 방산충 군집들로 밝혀졌다. 또한 *R. manitouensis* Zone에 속하는 코노돈트 화석군집이 발견되어 중기와 후기 Tremadocian에 속하는 Cow Head Group이 분포하는 여러 지역 간의 (Martin Point, Western Brook Pond, Broom Point, 그리고 St. Paul's Inlet) 층서대비를 보다 정확하게 할 수 있었고, 코노돈트 생층서에서는 *R. manitouensis* Zone, Low Diversity Interval, *M. diana* Zone, 그리고 하부 *P. proteus* Zone이 식별되었다.

주요어: 방산충, 코노돈트, 생층서, 후기 트레마도시안, Cow Head 층군

Introduction

To date, undisputed Tremadocian radiolarians have been reported only from Nevada (Kozur et al., 1996) and Newfoundland, Canada (Won et al., 2005). However, all of them belong to the early or middle Tremadocian. The radiolarian fauna from Nevada is limited to the early Tremadocian (*Cordylodus angulatus* Zone of conodont), and the Canadian Cow Head radiolarian faunal assemblages are from the early and middle Tremadocian (from the *Cordylodus lindstromi* Zone through the *C. angulatus* Zone to the *Rossodus manitouensis* Zone). The Little Port Complex radiolarian fauna from western Newfoundland (Aitchison et al., 1998) was reported to have been found in basal Tremadocian strata, but a fauna of similar composition was recovered from the Arenigian beds in the Cow Head Group (senior author's observations). Including the Little Port Complex radiolarian fauna, Arenigian radiolarian faunas have been described by Fortey and Holdsworth (1972), Holdsworth (1977), Aitchison (1998), Danelian and Popov (2003), and Maletz and Bruton (2005). The Arenigian fauna reported by Nazarov and Popov (1980) and Nazarov and Ormiston (1993) was reconsidered as lower Darriwilian (lowermost Llanvirn) by Apollonov et al. (1990), but it is known to share the characteristics of Arenigian faunas. The known Tremadocian and Arenigian radiolarian faunas have almost no similarities, and the evolutionary trends from the Tremadocian to the Arenigian faunas have not been discernible to date because of lack of information about the late Tremadocian faunas. The diverse late Tremadocian radiolarian faunas (conodont

zones from the Low Diversity Interval through the *Macerodus diana* Zone to lower *Paraoistodus proteus* Zone) will contribute a great deal to the elucidation of these trends.

The correlations among middle and late Tremadocian strata in the Cow Head Group were previously based, at least partly, on lithologic characteristics because of insufficient fossil data. Using co-occurring conodonts and radiolarians, correlation can now be more precise and is revised herein.

Localities

The radiolarians described in this paper occur in a sequence of late Tremadocian parted limestone or parted mudstone beds of the Cow Head Group on the Great Northern Peninsula of the island of Newfoundland. Locality names and unit number(s) indicating where rock samples were collected, lithologic description, and stratigraphic location (following the designation of James and Stevens, 1986) are as follows (Fig. 1):

1) Martin Point (MP): 49° 46.2' N, 57° 54.6' W, parted limestone from many beds from the base of the MP unit 42d to 6 m above the base.

2) South section of Western Brook Pond (WBPS): 49° 47.0' N, 57° 50.5' W, parted mudstone in most beds of unit 19a, from one nodular limestone fragment in lowermost unit 21, and in a few layers from unit 21 that are between 3.5 and 4.5 m below the base of unit 22.

The conodonts discussed in this paper were isolated from MP units 38b, 40f, 42a, 42b, 42d, WPBS units 5, 8, 10, 12, 15, 19a, 19c, 20, 21, Broom Point unit 105, and St. Paul's Inlet unit 30.

Fig. 1. Locality map showing outcrop area of the four sections that have yielded late Tremadocian radiolarians and/or conodonts.

Biostratigraphy

The first late Tremadocian radiolarian faunas recovered from the Cow Head Group are described in this study. Their biostratigraphic range can be defined by the co-occurring conodonts in the rocks. In addition to the MP and WBPS localities, we collected samples to recover radiolarian faunas of this age at other localities however, those samples contained far more conodonts than radiolarians. Conodonts recovered in this study will contribute to a more precise biostratigraphic age of the previously undescribed radiolarian faunas of the Cow Head Group.

Biostratigraphic range of radiolarian faunas

Late Tremadocian radiolarian faunas were recovered from the lower part of unit 42d at Martin Point (MP) and, from the south section of Western Brook Pond (WBPS), in unit 19a and in two strata from unit 21. The faunal compositions of WBPS unit 19a, MP unit 42d, and WBPS unit 21 are different (Table 1). However, the fauna in the strata between the lowest and upper WBPS unit 21 seems to be fairly constant, even though the number of specimens is quite different. The stratigraphic relation can be securely

documented by co-occurring conodonts as studied below and as shown in Fig. 2 and Table 2.

(A) The conodont fauna recovered from WBPS unit 19a can be assigned to the Low Diversity Interval, which is the interval between the *R. manitouensis* and *M. diana* Zones for North America. The North American zonal index fossils *R. manitouensis* (Figs. 15.13a, b) and *M. diana* (Fig. 15.17) are recognized from WBPS unit 5 and unit 20, respectively. The conodont fauna from WBPS unit 19a lacks diversity and is sparse, as is characteristic of the Low Diversity Interval for North America. The species composition from WBPS unit 19a is similar to that of MP unit 40f (see Table 2). Both fauna from WBPS unit 19a and MP unit 40f is characterized by the co-occurrence of *Glyptocodus floweri*, *D. nowlani* (Fig. 15.15), *Striatodontus prolificus*, *Striatodontus* n. sp. A (reported by Ji and Barnes, 1994), and *V. variabilis* (Fig. 15.18). At least one of these species is characteristic either of the North American Low Diversity Interval (Ross et al., 1997) or of the *D. nowlani* Zone in deeper water zones or the *Striatodontus prolificus*-*S. lanceolatus* Zone in shallow water zones for the St. George Group (Ji and Barnes, 1994) or the upper *P. deltifer* Zone for northern Europe (Löfgren, 2000), respectively. The *D. nowlani* Zone is correlated to the Low Diversity Interval by Pyle and Barnes (2002), which, in turn, is correlated to the upper *P. deltifer* Zone by Löfgren et al. (1999).

(B) A rather abundant and diverse conodont assemblage is found in samples from the base of MP unit 42d to about 6 m above the base. A conodont faunal assemblage similar to that from lower MP unit 42d occurs in WBPS unit 20 (see Table 2.). *S. floweri* and/or *V. variabilis* (Fig. 15.18) with *M. diana* are known to occur together in the *M. diana* Zone in North America (Ross et al., 1977; Löfgren, 2000). As mentioned above, the North American zonal index fossil *M. diana* (Fig. 15.17) has been found in four sections of the Cow Head Group. The conodonts in assemblages containing *M. diana* are relatively abundant and diverse, as well as having their own faunal composition (see Table 2). The *M. diana* Zone

Table 1. Abundance of late Tremadocian radiolarian taxa in strata at the Western Brook Pond South (WBPS) and Martin Point (MP) sections in the Cow Head Group, Newfoundland, Canada

Early Ordovician (late Tremadocian)				
Conodont zone	Low Diversity Interval	<i>Macerodus diana</i> zone	Lower <i>Paraoistodus proteus</i> zone	
Radiolarian faunas	LTRA 1	LTRA 2	LTRA 3	
Locality	WBPS19a	MP42d	WBPS21(L)	WBPS21(U)
<i>Pararchoeontactinia reedae</i> M1	4	2		
<i>Pararchoeontactinia reedae</i> M4	95	74	1	20
<i>Pararchoeontactinia stilla</i> n. sp.	16	10		
<i>Pararchoeontactinia?</i> <i>cowheadensis</i>	3	2		
<i>Palaeospiculum neofurcatum</i>	2	9		
<i>Neopalaeospiculum transformum</i> n. sp.	2	2		
<i>Neopalaeospiculum</i> sp. A	3			
<i>Protoentactinia primigena</i> M1	2	2		
<i>Protoentactinia primigena</i> M2		2		
<i>Protoentactinia gracilispinosa</i>	2	12	4	10
<i>Protoentactinia transformis</i>	5	3		1
<i>Protoentactinia kozuriana</i>	3	4		
<i>Protospongontactinia spongiosa</i> n. sp.	2	6		
<i>Protospongontactinia</i> sp. A		1		
<i>Echidnina bengtsoni</i>	3	6		
<i>Echidnina</i> spp.	2	4		
<i>Archeoproventocitum nudiformum</i> n. sp.	24	25		
<i>Archeoproventocitum retiformum</i> n. sp.	2	5		
<i>Protoproventocitum aitchisoni</i> n. sp.	46	120	6	>1000
<i>Westernbrookia ovata</i> n. sp.	44	40		
<i>Aspiculum multistratum</i> n. sp.	11	10		
<i>Aspiculum densum</i> n. sp.	40	15		
<i>Aspiculum jamesi</i> n. sp. (p type)	50(20)	(65)		
<i>Aspiculum gigantium</i> n. sp.	55	---		
<i>Westernbrookia diversa</i> n. sp.	150	---		
<i>Neopalaeospiculum laxum</i> n. sp.	---	2		
<i>Neopalaeospiculum densum</i> n. sp.	---	2		
<i>Cowheadia duplex</i> n. sp.	---	18		
<i>Aspiculum eccentricum</i> M1	---	70		
<i>Aspiculum eccentricum</i> M2	---	19		
? <i>Aspiculum</i> sp. A	---	3		
<i>Westernbrookia cancella</i> n. sp.	---	2		
<i>Protoproventocitum nazarovi</i> n. sp.	---	---	2	>300

The numbers reported from WBPS19a, WBPS21 (upper strata), and MP42d simply show the relative ratio between taxa within a small fragment of one rock sample among more than 25 (WBPS19a) and 30 (lower part of MP42d) rock samples. All samples contain well-preserved radiolarians. Thus, much more material was examined than is reported in this table. Radiolarians obtained from WBPS21(L) are from only one nodular limestone sample, and those from WBPS21(U) are from one of several samples (see also the section describing the localities and Fig. 2). M1, M2, M4, Morphotype 1, Morphotype 2, Morphotype 4; LTRA, late Tremadocian radiolarian assemblage; p type, pylomate type. Dashed line (---) means absence of the taxon, not only in the representative sample here but also in every examined sample from either WBPS19a or MP42d.

in the Cow Head Group was referred to by Williams et al. (1994) as equivalent to the *P. proteus* Zone. However, the occurrence of the two species in four sections of the Cow Head Group is as follows:

Cow Head South section: *M. diana* was reported first from the middle to upper part of Bed 8, and *P. proteus* first from Bed 9 in Cow Head Group sections (Fähræus and Nowlan, 1978).

Fig. 2. Four Cow Head Group sections (after James and Stevens, 1986) showing revised lithostratigraphic and biostratigraphic correlation of conodont zones among the sections. Conodont names marked with and asterisk are reported by Williams et al. (1994) and/or Johnston and Barnes (1999). LTRA 1-3, late Tremadoican radiolarian assemblages. The occurrence of *P. gracilis* indicated here is only in strata older than the *M. diana* Zone.

St Paul's Inlet section: *M. diana* occurs in unit 39 (Williams et al., 1994), and *P. proteus* was found in STPI unit 13 (Johnston, 1986; Johnston and Barnes, 1999), which may be equivalent to SP unit 43 of James and Stevens' section.

Western Brook Pond: *M. diana* occurs only in unit 20, and the lowest occurrence of *P. proteus* is in unit 21 (this study).

Martin Point: *M. diana* was reported to occur in unit 42a, b, c (Williams, Barnes, O'Brien, and Boyce, 1994) and in the lowest part of MP unit 42d (from the base to less than 5 m above the base of the unit in this study), and *P. proteus* occurs first about 11 m (designated as DMP16) above the base of unit 42d

(Johnston and Barnes, 1999).

According to Williams et al. (1994), *P. proteus* co-occurs with *M. diana*. Their report about conodonts was based on unpublished data from F. H. C. O'Brien and C. R. Barnes and modified from Fåhrus and Nowlan (1978), Johnston (1986 in Johnston and Barnes, 1999), and Stouge and Bagnoli (1988). However, no published papers report the co-occurrence of *P. proteus* and *M. diana*. Also, in the present study, *P. proteus* was not found with *M. diana*. According to Löfgren (1997), the first appearance of *P. proteus* is from the base of the *P. proteus* Zone. However, according to Löfgren (1993, Fig. 6) *P. proteus* occurs in the uppermost *P. deltifer*

Table 2. Tremadocian conodonts from Western Brook Pond and Martin Point, Newfoundland

	Western Brook Pond	Martin Point
Rossodus manitouensis Zone	WBPS unit 5: <i>R. manitouensis</i> Repetski, 1982; <i>Acanthodus lineatus</i> Furnish, 1938; <i>A. uncinatus</i> Furnish, 1938; <i>Cordylodus</i> sp.; <i>Scolopodus sexplicatus</i> Jones, 1971; <i>Variabilicomus bassleri</i> Furnish, 1938	MP unit 38b: <i>R. manitouensis</i> ; <i>Chosonodina herfurthi</i> Müller, 1964; <i>V. bassleri</i>
Low Diversity Interval	WBPS units 8, 10, 12, 15: <i>Acodus</i> sp., <i>A. uncinatus</i> ; <i>Paraoistodus gracilis</i> Lindström, 1955; <i>Polycostatus minutus</i> Ji and Barnes, 1994; <i>Striatodontus prolificus</i> Ji and Barnes, 1994; <i>V. bassleri</i> WBP unit 19a: <i>Decoriconus peselephantis</i> (Lindström, 1955); <i>Drepanodus arcuatus</i> Pander, 1856; <i>Glyptocomus floweri</i> (Repetski, 1982); <i>P. numarcuatus</i> Lindström, 1955; <i>Scolopodus acontiodiformis angularis</i> Repetski, 1982; <i>S. filiosus</i> Ethington and Clark, 1964; <i>Striatodontus</i> sp. A Ji and Barnes, 1994; <i>S. prolificus</i> ; <i>V. bassleri</i> ; <i>V. variabilis</i> Lindström, 1955. WBP unit 19c: <i>P. gracilis</i>	MP unit 40f: <i>Decoriconus peselephantis</i> ; <i>Drepanodus arcuatus</i> ; <i>Drepanoistodus nowlani</i> Ji and Barnes, 1994; <i>P. gracilis</i> ; <i>P. numarcuatus</i> ; <i>Scolopodus filiosus</i> ; <i>Striatodontus</i> sp. A; <i>S. prolificus</i> ; <i>V. bassleri</i> ; <i>V. variabilis</i>
Marcerodus diana Zone	WBPS unit 20: <i>D. peselephantis</i> ; <i>Drepanoistodus</i> cf. <i>D. forceps</i> Lindström, 1955; <i>D. arcuatus</i> ; <i>D. concavus</i> ; <i>G. floweri</i> ; <i>Macerodus</i> sp.; <i>M. diana</i> Fähræus and Nowlan, 1978; <i>Paltodus</i> sp. A; <i>Paltodus</i> sp. B; <i>P. numarcuatus</i> ; <i>P. minatus</i> ; <i>S. filiosus</i> ; <i>S. acontiodiformis angularis</i> ; <i>S. prolificus</i> ; <i>Variabilicomus</i> ? sp. (reported by Löfgren, 1997); Genus et sp. indet. A	MP unit 42d: <i>D. peselephantis</i> ; <i>D.</i> cf. <i>D. forceps</i> ; <i>D. arcuatus</i> ; <i>D. concavus</i> ; <i>Macerodus</i> sp.; <i>M. diana</i> ; <i>Paltodus</i> sp. A; <i>Paltodus</i> sp. B; <i>P. numarcuatus</i> ; <i>S. filiosus</i> ; <i>S. acontiodiformis angularis</i> ; <i>Striatodontus</i> sp. A; <i>S. prolificus</i> ; <i>V. variabilis</i> ; Genus et sp. indet. A
Lower Paraoistodus proteus Zone	WBPS lowest unit 21: <i>Acodus d. deltatus</i> Lindström, 1955; <i>Cornuodus longibasis</i> (Lindström, 1955); <i>D. peselephantis</i> ; <i>D. arcuatus</i> ; <i>D.</i> aff. <i>D. forceps</i> ; <i>Paltodus d. deltifer</i> Lindström, 1955; <i>P. proteus</i> Lindström, 1955; <i>P. numarcuatus</i> ; <i>Scandodus</i> sp.; Genus et sp. indet. B. WBPS upper unit 21: <i>Acodus d. deltatus</i> ; <i>Tripodus</i> sp.	

Zone in the Storeklev section at Hunneberg, Sweden. Thus, *P. proteus* seems to be present in strata older than those that belong to the *P. proteus* Zone. However, even if *P. proteus* and *M. diana* should occur together, the faunal compositions of the *M. diana* Zone (equivalent to the upper *P. deltifer* Zone for northern Europe) and the *P. proteus* Zone are quite different, as seen in Table 2.

(C) Samples from the lowermost part of WBP unit 21 contain well-preserved conodonts. The faunal composition is clearly distinguished from that of the *M. diana* Zone from WBPS unit 20 and the lower part of MP unit 42d because it includes the co-occurrence of numerous and typical *Paltodus deltifer deltifer* (Figs. 15.19, 15.20), *Paraoistodus proteus* (Figs. 15.21, 15.22), *A. deltatus deltatus* (Figs. 15.23, 15.24), and *P. numarcuatus*. *P. deltifer deltifer* occurs in northern Europe from the *P. deltifer* Zone to the lower *P. proteus* Zone. The co-occurrence of *P. deltifer deltifer* and *P. numarcuatus*, and plentiful *P. proteus*

means the fauna belongs to the latest Tremadocian (Löfgren, 1997). Such a combination means that the conodont fauna from WBPS unit 21 can be correlated to the lower part of the *P. proteus* Zone of northern Europe. The three species mentioned above have not been reported from North America (Midcontinent Realm). To date, the presence of *P. deltifer* has not been reported in the Cow Head Strata equivalent to the *P. deltifer* Zone. The first occurrence of *P. deltifer deltifer* in the Cow Head Formation is not in the *P. deltifer* Zone but in the *P. proteus* Zone at WBPS may mean that, at least at the Western Brook Pond area during the latest Tremadocian, the northern European faunal influence was much stronger than was that of North America. In North America, *R. manitouensis* and *M. diana* are used as zonal index fossils for the middle and late Tremadocian, respectively. *V. variabilis* occurs in both provinces, but *P. deltifer deltifer* and *P. numarcuatus* are not present in North America (Midcontinent Realm), and *R.*

manitouensis and *M. diana*e are generally not found in Europe.

The upper part of WBPS unit 21 yields *A. deltatus* and *Tripodus* sp. From the occurrence of fairly plentiful graptolites in WBPS unit 21, James and Stevens (1986) determined that it belongs to Lancefieldian Zone 2. WBPS unit 21 has been correlated to WBP (north section) unit 1 and was assigned to the latest Tremadocian by them. Williams et al. (1994) reported the graptolite zonal index species of the *Aorograptus victoriae* Zone in WBP unit 5; it is limited to the Tremadocian.

Correlation among sections of the Cow Head Group

Conodont faunas that belong to the *R. manitouensis* Zone were recovered from Broom Point (BP) unit 105, MP unit 38b, St. Paul's Inlet (SP) unit 26 (Won et al., 2005), and WBPS unit 5. Consequently, the conglomerate beds above the *R. manitouensis* Zone in BP units 107-110, MP unit 39, SP unit 31, and WBPS unit 8 may be coeval (see Fig. 2). Further, *M. diana*e occurs above the conglomerate bed in MP unit 41, SP unit 38, and WBPS unit 19c. Such a simple correlation at WBPS units is difficult because of numerous conglomerate strata in WBPS, as seen in Fig. 2. The palaeoceanographic position is deeper from BP to SP to MP to WBPS (James and Stevens, 1986); in general, the beds thin toward the deeper water conditions. However, the sediments deposited between the *R. manitouensis* Zone and *M. diana*e Zone are thickest (among these sections) in the WBPS section and include many intervals with conglomerate or grainstone grading up to thin conglomerate. Unlike beds at BP, MP and SP, these thick sedimentary rocks at WBPS seem to be turbidites.

The first appearance datum (FAD) of *P. gracilis* (Fig. 15.14) in several sections of the Cow Head Group is in late Tremadocian strata (see Fig. 2) and it seems to be useful for approximate correlation among different sections (Fig. 2): the species occurs in WBPS units 15 and 19 and MP unit 40f in this study. The species was also reported from MP unit 42b and from

St. Paul's Inlet (SP) from 43 m above the section measured by Johnston (1986) and by Johnston and Barnes (1999). The position of 43 m may be above the base of unit 37 of James and Stevens (1986). The presence of *P. gracilis* was also indicated as from SP unit 33 by Williams et al. (1994) on the basis of unpublished data. The *P. gracilis* zone was established by Johnston and Barnes (1999) and is equivalent to the *A. victoriae* graptolite Zone, limited to the latest Tremadocian. Unlike the findings of the comparison between the *P. proteus* Zone and the *P. gracilis* Zone by Williams et al. (1994), the *P. gracilis* Zone is younger than the *P. proteus* Zone (Pyle and Barnes, 2002; Pyle and Barnes 2003; Pyle et al., 2003). Löfgren (2002) stated the *P. gracilis* subzone as the third among four subzones of the *P. proteus* Zone. As it is, the FAD of *P. gracilis* and the application of the *P. gracilis* Zone vary from locality to locality and from researcher to researcher. As seen in Figure 2, *P. gracilis* occurs much earlier than *P. proteus* in the Cow Head Group. Even for local Newfoundland use of the conodont zone, the FAD of *P. gracilis* is not appropriate for zonation because of its extreme rarity. In the late Tremadocian portion of the Cow Head Group, most of the samples contain no *P. gracilis*; where it was recovered, only one or two specimens were found in this study. The first appearance of *P. gracilis* in Öland, Sweden, as reported by Van Wamel (1974), is from the *D. arcuatus* Zone, which is time-equivalent to the *P. deltifer* Zone (see Löfgren, 1994), and, in turn, may be equivalent to the Low Diversity Interval.

Stratigraphic correlation is here revised (see Fig. 2) so that the lower part of the St. Paul's Member at WBPS is equivalent to the uppermost Broom Point Member in BP and SP sections. According to the conodont faunal data, the uppermost part of the Broom Point Member at MP is correlated to lower St. Paul's Member at SP.

James and Stevens (1986) reported that Bed 9 at BP is not exposed in the area of their figure 45. On the other hand, the strata from units 111 to 119 belong to Bed 9, and the boundary between units 110 and 111

is interpreted as location of the boundary between the Tremadocian and Arenigian in their figure 10. However, the boundary is between middle and late Tremadocian.

Characteristics of the Radiolarian Faunas

Three late Tremadocian radiolarian assemblages (LTRA 1-3, Table 1) were recognized. Faunas from MP unit 42d and WBPS unit 19a are diverse, but the fauna from the WBP lowermost unit 21 is very sparse and low in diversity. The fauna from the upper part of WBP unit 21 consists of only a few species, with two making up more than 99 percent of this fauna that seems to have survived in marginal ecological conditions. The faunal composition of MP unit 42d and WBPS unit 19a is similar, but both assemblages can be distinguished by the presence or absence of the following species: *Aspiculum eccentricum* Morphotypes 1 and 2, *A. gigantum*, *Cowheadia duplex* testis, *Westernbrookia diversa*, *W. cancella*, *Neopaleospiculum laxum*, and *N. densum* (Table 1). These differences appear to have biostratigraphic significance when we consider the co-occurring conodont faunas. As mentioned in the section concerning biostratigraphy, WBPS unit 19a has conodonts of the "Low Diversity Interval", while lowest MP unit 42d yields conodonts of the *M. diana* Zone.

The characteristics of latest Tremadocian faunas can be summarized as follows:

1) The late Tremadocian faunas are characterized by the very abundant and diverse taxa that belong to the family Aspiculumidae. The similarly diverse and abundant *Parechidnina* from early Tremadocian strata have disappeared and been replaced in the late Tremadocian by diverse and plentiful *Aspiculum* and *Westernbrookia* species.

2) The appearance of the fairly abundant and diverse forms that belong to the new family Proventocitiidae also distinguishes the late Tremadocian radiolarian faunas from the older ones. However, as noted, the middle Tremadocian radiolarian faunas are

very sparse and low in diversity. Thus, neither the real faunal assemblage characteristics, nor the diversity or abundance of Proventocitiidae of the middle Tremadocian faunas could be formally established. Unlike the spicule system of Protoentactinidae, Palaeospiculumidae, and Archeoentactinidae, the shape of the spicule of Proventocitiidae is inconstant between specimens, as well as intraspecifically and interspecifically.

3) Taxa that belong to Archeoentactinidae and Palaeospiculumidae are rare, as they are in the early Tremadocian faunas, and Echidnidae and Protoentactinidae are much less abundant and much less diverse than in the early Tremadocian faunas.

4) In the early and middle Tremadocian radiolarian faunas (Won et al., 2005), unfused rays or branches of spicules of the Echidnidae, Protoentactinidae, and Palaeospiculumidae are common, and fused rays do not appear before the middle Tremadocian. Mostly or totally fused spherical shell walls in representatives of the three families are found in the late Tremadocian.

5) Proventocitiid make up 99 percent of the lowermost and upper parts of the latest Tremadocian WBPS unit 21 fauna.

Systematic Paleontology

All type specimens are deposited at the National Type Collection of Invertebrate and Plant Fossils, Geological Survey of Canada (GSC). Occurrence of the new species can be seen in Table 1; that of previously reported species is described under the corresponding taxon.

Order POLYCYSTINA Ehrenberg, 1838

Suborder SPUMELLARIA Ehrenberg, 1875

Family ARCHEOENTACTINIDAE Won in Won and Below, 1999

Genus *Pararchoentactinia* Won and Iams, 2002

Type species. - *Pararchoentactinia reedae* Won and Iams, 2002, p. 13.

Pararchoentactinia reedae sensu stricto Won and Iams, 2002

Fig. 3. Various states of the spicule in the Proventocitiidae Aitchison, 1988: 1. Spicule of *Archeoproventocitum* n. gen. 2. Spicule transformed to an internal meshwork in *Protoproventocitum* n. gen. 3. Spicule as an internal spicule in *Cowheadia* n. gen.

Morphotype 1

Figs. 4.3, 4.4

Pararchoeontactinia reedae Won and Iams, 2002, p. 13.

Diagnosis. - See Won and Iams, 2002, p. 13.

Description. - The skeleton consists of a spherical shell wall and a point-centered six-rayed spicule. The shell wall has a small diameter, and its surface is rough. The meshwork of the shell wall is made up of straight or slightly curved bars that are interwoven in a disorderly fashion, but this meshwork is variable: fine to coarse, and loose to somewhat compact. No basal layer has been observed. Spinules or traces of spinules are developed on the proximal parts of the rays (Fig. 4.4). Many of the spinules are not joined to the shell wall.

Discussion. - Morphotype 1 from Late Cambrian strata in the Cow Head Group shows many morphological variations - shell size, presence or absence of a basal layer, layered or non-layered shell wall, fine to coarse and compact to loose meshwork of the shell wall - but it is characterized by the disorderly fashioned shell wall structure. All specimens of M1 from late Tremadocian rocks in the Cow Head Group have a very small shell, and the shell is non-layered and has no basal layer, but it is still disordered and variable in texture.

Representative specimens. - GSC 125611, 125612.

Occurrence. - Late Cambrian to late (not latest) Tremadocian units in the Cow Head Group, Newfoundland, Canada (see also Table 1).

Pararchoeontactinia reedae sensu lato Won and Iams, 2002

Morphotype 4

Figs. 4.1, 4.2

Description. - The spherical skeleton has a point-centered six-rayed spicule and a thick spongy shell wall that is characterized by its non-layered, and compact nature. Many branched spinules arise from the proximal parts of the rays and are connected to the shell wall. Rarely, unconnected spinules may be present on the rays. Some specimens have six long spines (Fig. 4.1), and others appear to have very short (Fig. 4.2) or no spines

Discussion. - Under the microscope, specimens of Morphotype 4, from the late Tremadocian, can be separated into two types - those with spines and those without spines. Specimens without spines appear to be a spherical mass of spongy shell. However, under SEM examination, these specimens (that appeared to have no spines under light microscope examination) can be seen to actually have very short spines. It is unclear why two such groups are developed only in MP 42d, not in WBPS19s fauna.

Representative specimens. - GSC 125609, 125610.

Occurrence. - From Late Cambrian to late Tremadocian units in the Cow Head Group, Newfoundland, Canada (see also Table 1).

Pararchoeontactinia stilla n. sp.

Figs. 4.6-4.12

Diagnosis. - A drop-like shell with a point-centered

six-rayed spicule having densely distributed spinules on proximal part of each ray; shell wall consisting of branching and fusing of spinules and minor spicules

Description. - The point-centered spicule consists of six rays and spinules that are densely developed mainly along the proximal parts of the rays. The shell wall is characterized by numerous orthogonally arranged minor spicules. None of the minor spicules are attached to the six rays of the main spicule. The spinules on the rays are branched or furcated and fused to one another and to minor spicules. Some specimens with a small shell wall possess no minor spicules.

Discussion. - *Pararchoentactinia stilla* n. sp. shares some characteristics with species of the genus *Archoentactinia* Won, 1999 that have minor spicules. However, the minor spicules of *Archoentactinia* are attached to the main spicules. *P. stilla* may have evolved from *P. reedae*; in a specimen of *P. reedae*, one minor spicule (arrow on Fig. 4.5b) is recovered amidst the spongy shell wall. The shell wall having minor spicules is the diagnostic characteristics of *P. stilla*. *P. stilla* also has densely distributed, well-developed spinules (Figs. 4.7b, c, 4.12), one of the most diagnostic characteristics of *P. reedae*. Some specimens (Figs. 4.9-4.11) appear to have no minor spicules. A specimen (Fig. 4.12) with one minor spicule may indicate that the very small and/or poorly preserved shell wall without a minor spicule (Figs. 4.9-4.11) may be a juvenile or poorly preserved form of *P. stilla*.

Etymology. - *Stilla* (Lat.), a drop.

Types. - Holotype, GSC-125616; paratypes, GSC-125614, 125615, 125618-125620.

Pararchoentactinia cowheadensis? Won, Iams, and Reed, 2005

Figs. 6.12, 6.13.

Diagnosis and description. - Won, Iams, and Reed, 2005, p. 438.

Representative specimens. - GSC 125642, 125643.

Occurrence. - From early to late Tremadocian units in the Cow Head Group, Newfoundland, Canada (see also Table 1).

Family ASPICULUMIDAE Won, Iams, and Reed, 2005

Diagnosis. - Won, Iams, and Reed, 2005, p. 438-441.

Genus *Aspiculum* Won, Iams, and Reed, 2005

Type species. - *Aspiculum eccentricum* Won, Iams, and Reed, 2005, p. 441.

Diagnosis. - See Won, Iams, and Reed, 2005.

Aan the early Paleozoic taxa may of the shell wall.sion PS 19a.eccentricum is multimodal variation in ratio of the thick shell wDiscussion. - Species of the genus *Aspiculum* share the common characteristics of eccentricity of the internal structure and variability in the presence or absence of a pylome (or opening). The development of the eccentricity was mentioned in the discussion section of *Aspiculum* in Won et al. (2005). The presence of specimens with or without a pylome within the same taxon is not a unique phenomenon. This condition has also been found in other taxa of the families *Aspiculumidae* and *Proventocitiidae*.

Some species of *Aspiculum* shows diversity not only in the shell wall meshwork structure, but also in their internal structure. Whereas the internal structure of post-early Paleozoic radiolarians is constant within a species, we infer that the variable internal structure in the early Paleozoic taxa may reflect the diversification of the earliest radiolarians. Variation in the internal structure of some species of *Aspiculum* includes presence or absence of a basal layer and the diameter of the basal layer, which determines the thickness of the shell wall. Where a basal layer is developed, its meshwork may be two- or three-dimensional. Development of the large basal layer is related to the appearance of the two-dimensional meshwork structure of the shell (Figs. 13.8, 3.15). The appearance of the two-dimensional meshwork structure in *Aspiculum* seems to lead to a new genus, *Westernbrookia*, whose shell wall is characterized by a two-dimensional meshwork with a trace of three-dimensional meshwork. The presence or absence of the basal layer is not critical to distinguishing these early taxa, as mentioned in the discussion section of *Parechidhina jamesi* (Won

and Iams, 2002) and has been seen to vary at the species level also in *Pararcheontactinia reedae* Won and Iams, 2002, *Spongontactinia inusitata* Won, 1997, and *S. invenusta* (Aitchison, 1993), as reported by Won (1997).

Aspiculum densum n. sp.

Figs. 12.13-12.16

Diagnosis. - A spherical skeleton with a compact eccentric internal structure, no internal cavity, and numerous thin outer spines. Where present, pylome ornamented by numerous spinules.

Description. - The outer appearance of the spherical skeleton is loosely spongy (Figs. 12.13, 12.16); however, internally, there is a dense, quasi-layered mass that fills the shell (Figs. 12.14, 12.15). The innermost part of the shell may be slightly more loosely meshed than the area directly beneath the outer surface and is eccentrically positioned. A pylome may or may not be developed; its presence may be indicated by a bundle of many spinules. Numerous short, thin, radially arranged spines are present.

Discussion. - In some specimens where a pylome is not present or not distinguishable under the stereomicroscope, the outer appearance is similar to that of *Pararcheontactinia reedae* Morphotype 4 having very short or no spines or of *Protospongontactinia spongiosa* n. sp. because of the compact spongy meshwork of the shell surface. However, *A. densum* differs from them by the numerous outer spines and eccentric internal arrangement.

Etymology. - Densus (Lat.), dense.

Types. - Holotype, GSC 130873; paratypes, GSC 130874-130876.

Aspiculum eccentricum Won, Iams, and Reed, 2005

Figs. 13.1-13.15

Aspiculum eccentricum Won, Iams, and Reed, 2005, p. 441.

Diagnosis. - See Won, Iams, and Reed, 2005.

Emended diagnosis. - Spherical shell with the internal structure eccentrically positioned. Meshes on

the shell surface grading across a specimen from dense to coarse, size of mesh openings on the shell surface ranging widely. Internal structure variable; inner cavity delineated by a basal layer of the shell or lacks this layer; where the basal layer absent, shell consisting of a continuous meshwork; where the basal layer present, cavity diameter variable, and the meshwork structure of the basal layer two- or three-dimensional. Pylome, where present, occurring where the meshes are densest.

Description. - The irregular gradation of the mesh from dense to coarse on the shell surface is one of the most characteristic features of this species. The range in the mesh opening size is commonly great within a specimen, but it varies from very great (Figs. 13.1-13.5, 13.15) to relatively uniform (Figs. 13.7-13.8). Where a pylome is developed, it is on the densest surface meshwork. The pylome may be absent (Fig. 13.1), or it is indistinct (Fig. 13.2a), or it is very small (Won et al., 2005, figs. 5.10a, b), or it is well developed (Figs. 13.3-13.8, 13.14, 13.15). Eccentric placement of the internal structure can be easily observed in many specimens (Figs. 13.6b, 13.9-13.15), but the internal structure is diverse, that is, an inner cavity may be surrounded by a meshed basal layer (Figs. 13.6b, 13.11-13.15) or not (Fig. 13.9). The basal layer can be obscure (Figs. 13.10a, b), definite, or not developed (Fig. 13.9). The basal layer may be simply the inner surface of the shell wall where all mesh bars have the same robustness (Figs. 13.11, 13.12) or a pronounced layer (Figs. 13.6a,b, 13.13-13.15) whose mesh bars are stouter than those of overlying shell wall. Where the surrounding delicate meshwork of the basal layer is partly (Figs. 13.6a, b), almost (Fig. 13.15) or not preserved (Figs. 13.7-13.8), it appears as a one-layered shell wall having a three- (Fig. 13.7) or two-dimensionally latticed structure (Figs. 13.8, 13.15). The cavity surrounded by the basal layer seems to be not completely empty (Figs. 13.10a, b, 13.11, 13.13a, b); skeletal elements in the basal layer connected to the layer can be observed. The diameter of the cavity defined by the basal layer is variable (Figs. 13.11-13.15) and determines the thickness of the shell wall. That is, the greater the diameter, the thinner the wall. Because of

Fig. 4. The scale bar on the first figure applies to all the other figures, and is equivalent to a length noted in parentheses (μm). 1, 2, *Pararcheontactinia reedae* sensu lato, Won and Iams, 2002, Morphotype 4. 1, GSC 125609 (WBPS21-4c-a4), (33.3). 2, GSC 125610 (MP42d-j24), (22.2): very short spines. 3, 4, *Pararcheontactinia reedae* sensu lato, Won and Iams, 2002, Morphotype 1. 3, GSC 125611 (WBPS19-k1), (20). 4, GSC 125612 (MP42d-g43), (11.1): spinules along the rays. 5, *Pararcheontactinia reedae* sensu lato, Won and Iams, 2002, GSC 125613 (MP42d-j19); 5a, b, (30.3, 12.5): minor spicule (arrow). 6-12, *Pararcheontactinia stilla* n. sp. 6, GSC 125614 (WBPS19-q8); 6a, (25, 12.5): minor spicule (arrow). 7, GSC 125615 (WBPS19-E6); 7a, b, (36.3, 14.2); 7c, (14.2): spinules along the ray. 8, Holotype, GSC 125616 (WBPS19-E4); 8a, b, (28.5, 12.3): minor spicules. 9, GSC 125617 (WBPS19-u6), (28.5). 10, GSC 125618 (WBPS19-e5), (24.3). 11, GSC 125619 (MP42d-k1), (12.5): spinules are branched and fused. 12, GSC 125620 (WBPS19a-x17), (15.3): one minor spicule (arrow). 13-14, *Palaeospiculum neofurcatum* Won, Iams, and Reed, 2005. 13, GSC 125621 (MP42d-d5), (45.5). 14, GSC 125622 (MP42d-d1); 14a, b, (45.4, 20): fused spinules on 14b.

the eccentric placement of the basal layer, the thickness of the shell wall within a specimen is not constant. The pylome is developed on the densest meshwork, which is also the thinnest part of the shell wall (Figs. 13.6b, 13.14). The number of spines varies, but in many specimens there are as many as eight major outer spines (Figs. 13.1-13.4, 13.10, 13.11, 13.13-13.16), and in some specimens more than eight, and the spines vary in length and diameter (Figs. 13.5, 13.7, 13.8).

Discussion. - *A. eccentricum* varies in the size of the mesh openings on the shell surface, the presence or absence of a pylome and basal layer, shell wall thickness (the size of inner cavity), meshwork structure of the basal layer, number of outer spines, and quality of preservation. If we consider only the internal characteristics, such as the presence or absence of the basal layer and its diameter, we can see diverse forms of *A. eccentricum* as mentioned above, but these can be roughly grouped into two types: those having a thick shell wall (Figs. 13.1-13.5, 13.9-13.13) and those with a thin shell wall (Figs. 13.6-13.8, 13.14, 13.15). Generally, the thinner the shell wall, the larger the basal layer/inner cavity diameter. In addition, the pylome is larger and more distinct, the meshwork of the basal layer is denser, and the difference in mesh opening sizes is smaller on the shell surface where the shell wall is thin. Such diverse and variable internal structures and the presence of two forms also is known in *A. jamesi* n. sp. (Figs. 14.14-14.20) and *A. gigantium* n. sp. (Figs. 11.5-11.11). In all three of these species, if the basal layer/inner cavity is large and the outermost skeletal detail is commonly not preserved, the shells may

appear to be two-dimensionally latticed, giving them a quite different outer appearance (Figs. 11.11a, 13.8, 14.11). While the thin-walled forms are very rare in *A. jamesi* and *A. gigantium*, they are relatively common in *A. eccentricum*, and the two forms are defined as discrete morphotypes only in *A. eccentricum*.

Representative specimens. - GSC 130877-130891.

Aspiculum eccentricum s. s. Won, Iams, and Reed,
2005

Morphotype 1

Figs. 13.1-13.5, 13.9-13.13

Aspiculum eccentricum Won, Iams, and Reed, 2005,
p. 441.

Description. - The spherical shell is characterized by a moderately to very thick shell wall and an inner cavity/basal layer that may or may not (Fig. 13.9) be present. If present, its size is variable and determines the shell wall thickness (Figs. 13.10-13.13). There is a tendency in specimens where the basal layer/cavity is large for a pylome to be well developed. A pylome may (Figs. 13.3-13.5) or may not (Fig. 13.1) be developed, or its presence is obscure in some specimens (Figs. 13.2a, b). As many as eight or, rarely, numerous major spines may be present; length and diameter of spines vary.

Discussion. - See discussion section for Morphotype 2 of *A. eccentricum*.

Aspiculum eccentricum s. l. Won, Iams, and Reed,
2005

Morphotype 2

Figs. 13.6-13.8, 13.14, 13.15

Fig. 5. The scale bar on the first figure applies to all the other figures, and is equivalent to a length noted in parentheses (μm). 1, 2, 3?, *Neopalaeospiculum transformum* n. sp. A. 1, Holotype, GSC 125623 (WBPS19-q23); 1a, (18.1); 1b, (8.33): fused spinules; 1c, (11.1): shell surface showing short branches. 2, GSC 125624 (WBPS19-i11); 2a, (20), 2b, (12.5): meshed structure and mostly unfused branches. 3, GSC 125625 (MP42d-j48); 3a, (40); 3b (40): underside of 3a; 3c, (12.5): partly fused mesh structure (in a circle). 4, 6, *Neopalaeospiculum laxum* n. sp. 4, GSC 126256 (MP42d-j48); 4a, (25): neopalaeospiculimid spicule structure; 4b, (12.5): underside of 3a; 4c, (12.5): fused meshwork structure. 6, Holotype, GSC 125628 (MP42d-h13); 6a, (30.3): internal structure; 6b, (30.3): underside of 6a; 6c, (8.69): spinules and their branches are fused. 5, *Neopalaeospiculum* sp. A, GSC 125627 (WBPS19a-n19): note internal spicule portions thinner than outer ones; 5a, (18.1); 5b, (14.2): internal structure of 5a, but broken after photo was made. 7, 8, *Neopalaeospiculum densum* n. sp. 7, GSC 125629 (MP42d-f20); 7a, (22.2): dense meshwork structure; 7b, (7.14): orthogonally arranged spicule structure. 8, Holotype, GSC 125630 (MP42d-j30); 8a, (25); 8b, (8.33), internal neopalaeospiculimid structure.

Description. - The spherical shell is characterized by a large pronounced basal layer whose delicate outer meshwork is commonly not preserved. In the rare specimens in which the delicate outer meshwork is preserved (Figs. 13.6a, b, 13.14), the eccentric placement of the basal layer can be detected. In specimens where the outer meshwork is not preserved, the basal layer appears as a simple one-layered shell wall (Figs. 13.7, 13.8,) consisting of two- or three-dimensional meshwork. The pylome is consistently well developed on the densest part of the meshwork, and its margin is denticulate (surrounded by thorns, see Figs. 13.7, 13.8b). The size difference among mesh openings is not great on the delicate shell surface (Figs. 13.6a, 13.14). Some specimens display as many as eight major spines, while others have numerous spines that vary in length and diameter.

Discussion. - Morphotype 2 has a larger inner cavity than Morphotype 1. Also, a pylome is always large and well developed in Morphotype 2, whereas in Morphotype 1, the pylome may be well, poorly, or not developed. Generally, specimens with a thick shell wall have a poorly developed pylome or none at all. Morphotype 1 is characterized by a thick shell wall and considerable variation in mesh opening size on the surface.

Aspiculum gigantium n. sp.

Figs. 11.1-11.10, 11.11?

Diagnosis. - A large subspherical skeleton, the shell wall characterized by irregularly interwoven, open, three-dimensional meshwork. Shell wall with or without a large basal layer/internal cavity. Internally

diverse structure that may be eccentric. Numerous, rather uniform outer spines.

Description. - The subspherical skeleton is unusually large and consists of very delicate, loose, and open meshwork with more than 10 and fewer than 30 outer spines. Some specimens consist of uniformly delicate meshwork from the innermost to outermost parts of the shell (Figs. 11.1-11.6). Other specimens (Figs. 11.7-11.11) consist of three parts even though differentiation into multi-shell layers is not clear. The outermost part, which is commonly not well preserved (Figs. 11.9-11.11), consists of delicate, fine to loose spongy skeletal elements (Figs. 11.7, 11.8), rarely outermost layered structure remains (Fig. 11.7b). The middle part forms a spherical to subspherical shell layer that is angularly interwoven (Figs. 11.7-11.11). Rarely, the second part of the shell wall is densely and angularly two- or three-dimensionally latticed (Fig. 11.11a). The inner part of the middle shell layer consists of a loose, open, and delicate meshwork of diverse structure (Figs. 11.7b, 11.9b, 11.10, 11.11b). The shell center, where the outer spines originate, is eccentrically positioned (Figs. 11.5, 11.6, 11.11b), or the quasi layers (Fig. 11.5) or the (basal) layer are eccentric (Fig. 11.8). Because of the loose and open meshwork structure, it is difficult to identify a pylome.

Discussion. - *A. gigantium* n. sp., *A. eccentricum*, and *A. jamesi* share the diversity of the presence or absence of the basal layer and pylome and the eccentric inner structure. Also, as in Morphotype 2 of *A. eccentricum* and several specimens of *A. jamesi*, some specimens of *A. gigantium* may have a well-developed, large-diameter basal layer. Unlike the

Fig. 6. The scale bar on the first figure applies to all the other figures, and is equivalent to a length noted in parentheses (μm). 1, *Protoentactinia primigena* s. s. Won, Iams, and Reed, 2005, Morphotype 1, GSC 125631 (WBPS 19a-i39) (36.3). 2, *Protoentactinia primigena* s. l. Won, Iams, and Reed, 2005, Morphotype 2, GSC 125632 (MP42d-k23) (50). 3, 4, *Protoentactinia gracilis* Kozur, Mostler, and Repetski, 1996. 3, GSC 125633 (MP42d-d7) (45.5). 4, GSC 125634 (WBPS19a-k19) (22.2). 5, 6, *Protoentactinia kozuriana* s.s. Won, Iams, and Reed, 2005. 5, GSC 125635 (MP42d-j35) (16.6). 6, GSC 125636 (MP42d-j33) (14.2). 7, 8, *Protoentactinia transformis* Won, Iams, and Reed, 2005: shell wall fused, but note trifurcated branch structure on the shell wall. 7, GSC 125637 (MP 42d-k31); 7a, b, (28.5, 12.8). 8, GSC 125638 (WBPS19a-q38); 8a- c, (30.3, 30.3, 12.5). 9, *Protospongentactinia* sp. A, GSC 125639 (MP42d-f26); 9a, (40); 9b, (16.6): internally positioned stout trifurcated branches and disorderly fused shell wall meshwork. 10, 11, *Protospongentactinia spongiosa* n. sp. 10, Holotype, GSC 125640 (WBPS19-q39); 10a, (25): echidninid spicule system; 10b, c (28.5, 12.5): underside of 10a shows spongy shell wall without trifurcated branch structure. 11, GSC 125641 (WBPS19-i38), (41): echidninid spicule structure inside of the spongy shell wall. 12, 13, *Pararacheoentactinia?* *cowheadensis* Won, Iams, and Reed, 2005. 12, GSC 125642 (MP42d-g59), (33.3). 13, GSC 125643 (WBPS19a-q6); 13a, b, (28.5, 10): six-rayed internal spicule.

diameter of the basal layer of *A. eccentricum* and *A. jamesi* that ranges from very small to very large, the basal layer is moderately large in *A. gigantium*. In the three species, the basal layer generally has a three-dimensional meshwork structure, but, rarely, two-dimensional meshwork structure is developed (see Figs. 11.11a, 13.9, 14.11). The appearance of the angularly meshed layer may signal relation to the two-dimensional meshwork of the shell wall of a new genus, *Westernbrookia* (Figs. 11.13-11.16, 12.1-12.10, 15.1-15.12). This species is characterized by a polygonally latticed, and relatively dense meshwork that can be regarded as a two-dimensional shell wall rather than a basal layer (or middle layer), even though spongy or three-dimensional meshwork structure is still developed on or in it. Most importantly, transitional forms (Figs. 11.11a, b, 11.12) indicate that, through the development of a two-dimensional basal layer, *A. gigantium* is closely related to *Westernbrookia ovata* n. sp.

Etymology. - Giganteus (Lat.), giant, gigantic.

Types. - Holotype, CGS 125707; paratypes, GSC 125708-125716, 125717?

Aspiculum jamesi n. sp.

Figs. 14.1-14.11, 14.13-14.20

Diagnosis. - Spherical shell with innermost structures slightly eccentric. Shell wall with three-dimensional web-like or spongy mesh and generally uniform meshwork. Pylome (if present) quasi-tubular and protruding. Inner cavity/basal layer of the shell present

or absent; if present, its size variable, and thus the thickness of the shell wall also variable. As many as eight major outer spines developed.

Description. - The spherical to subspherical shell is characterized by fairly uniform three-dimensional web-like or spongy meshwork. The variations in internal structure can be observed in Figures 14.13-14.20. The shell wall is indistinctly multi-layered (Fig. 14.13); a full spongy meshwork is present without a basal layer/inner cavity (Fig. 14.14); innermost mesh bars are curved to form a very small sphere (Figs. 14.15a, b, 14.16); or a definite inner cavity (basal layer) with variable diameter is developed (Figs. 14.17-14.20). Where the basal layer is large and its meshwork is stout, the covering of loose meshwork may be partly (Fig. 14.10), mostly (Fig. 14.20), or even completely missing (Fig. 14.11). Rarely, the basal layer has two-dimensional structure, like the outer shell of multi-shelled entactiniid taxa (Fig. 14.11). Because of the slight eccentricity of the internal structure, the thickness of the shell wall differs within a specimen. The thickest part of the shell wall seems to be where a pylome is developed. (Compare the thickest part of the eccentric shell wall of Figure 14.18 and the pylome of Figures 14.5, 14.9, and 14.10.). However, the pylome may present or absent. If present, its margin varies from inconspicuous (Fig. 14.4) to having a low margin (Fig. 14.3) to a well-developed tube-like projection. The protruding pylome margin is marked by clustered long thorns or spinules (Figs. 14.5-14.7, 14.9) or by protruding roughly cylindrical

Fig. 7. The scale bar on the first figure applies to all the other figures, and is equivalent to a length noted in parentheses (μm). 1, *Echidnina bentgsoni* Kozur, Mostler, and Repetski, 1996, GSC 125644 (MP42d-g4); 1a, (25); 1b, (25): underside of 1a. 2-9, *Echidnina* spp.: explanation of each specimen is noted in the discussion section of *Echidnina* spp. 2a, b, GSC 125645 (MP42d-j18), (30.3, 30.3): 2b is underside of 2a. 3a-c, GSC 125646 (MP42d-j17) (28.5, 11.1, 30.3): 3c is underside of 3a, b. 4a, b, GSC 125647 (MP42d-d8), (45.4, 25). 5a-c, GSC 125648 (MP42d-h5), (40, 50, 28.5): 5b is underside of 5a, and 5c is a broken part of 5a. 6a-d, GSC 125649 (GP25-C24), (50, 13.8, 50, 12.5); 6c and 6d are undersides of 6a, b. 7a, b, GSC 125650 (GP 7-1) (22.2, 22.2); 7b is a different view of 7a. 8, GSC 125651 (GP 6-10), (36.3). 9, GSC 125652 (GP25-B2-57).

meshed structure (Figs. 14.8, 14. 11). Not more than eight rod-like spines are developed.

Discussion. - *A. jamesi* differs from *A. eccentricum* by the markedly smaller and relatively uniform meshwork of the shell wall (excluding the basal layer, when present) and, if a pylome is present, a margin that protrudes as a neck-like structure. *A. eccentricum* is characterized by the mesh size grading from fine to coarse within a specimen, and its pylome is simply denticulated and developed on the densest meshwork. Thus, the outer appearance is quite different, and these species are easily differentiated. However, *A. jamesi* exhibits variations in its internal structure (as seen in Figs. 14.13-14.20), including the nature and presence or absence of a basal layer (inner cavity); variation in shell wall thickness (and associated diameter of inner cavity, where a basal is layer present); and presence or absence of the pylome, as in *A. eccentricum*. These two species also have common characteristics, such as the eccentric position of the innermost part of the shell wall. Furthermore, in specimens where the basal layer/cavity is large, the pylome is more prominent and well developed. Thus, *A. jamesi* can exhibit a spectrum of characteristics ranging between two "end members". One has a thin shell wall with a large-diameter basal layer and well-developed pylome (Fig. 14.11), as in Morphotype 2 of *A. eccentricum*. The other "end-member" (Fig. 14.1) has a thick shell wall without a basal layer or a pylome, similar to many of the specimens of Morphotype 1 of *A. eccentricum*. Some forms with mixtures of the characteristics of the end members (Figs. 14.5, 14.9, 14.10) suggest the close relation between the two types: a three-dimensional web-like or spongy meshwork with a simple pylome (Fig. 14.4) or a pylome (Fig. 14.3) with a low margin or a high, protruding pylome (Fig.

14.8), or a spongy shell wall with a basal layer whose thickest part may be occupied by the pylome (Fig. 14.9). However, unlike Morphotype 2 of *A. eccentricum*, specimens of *A. jamesi* with a thin shell wall and large-diameter basal layer are very rare.

Due to the robust nature of the mesh bars in specimens of *A. jamesi* from unit 42d at Martin Point, the pylome is commonly well preserved and fairly easily recognized. In contrast, specimens from unit 19a at Western Brook Pond are found with or without a pylome. Identification of a pylome in WBPS unit 19a specimens is made more difficult because the shell wall and pylome meshwork are delicate, even when originally present.

Etymology. - In honor of Noel. P. James, who has contributed much to our knowledge of the stratigraphy of the Cow Head Group.

Types. - Holotype, GSC 130897; paratypes, GSC 130892-130896, 130898-130910.

Aspiculum multistratum n. sp.

Figs. 12.11-12.12

Diagnosis. - A spherical skeleton with a multi-layered shell wall consisting of a dense meshwork that is irregularly and incompletely layered and inconsistently two- or three-dimensionally meshed.

Description. - The spherical to subspherical or oval skeleton consists of multiple layers and has as many as six fairly robust rod-like spines. It has the appearance of a multi-shelled entactiniid. However, the shell layers are not continuous. The partly two-dimensional meshwork structure of the layers, while not uniform, is rather well developed. The innermost part of the shell is eccentrically placed. The surface meshwork of the shell is densely interwoven. It is unclear at this time whether a pylome is present since

Fig. 8. The scale bar on the first figure applies to all the other figures and is equivalent to a length noted in parentheses (μm). 1-4, 7, 8, *Archeoproventocitum nudiformum* n. sp. 1a, b, Holotype, GSC 125653 (WBPS19a-e19), (28.5, 15.3): one median bar. 2a, b, GSC125654 (WBPS19a-e20), (40.4, 16.6): two-median bars. 3, GSC 125655 (WBPS19a-e18), (50.5). 4, GSC 125656 (MP42d-g47), (25.0). 7, GSC 125659 (WBPS19a-a14), (22.2). 8, GSC 125660 (WBPS19a-e21), (28.5): rays joined by an inter-ray loop. 5, 6, Forms transitional between *A. nudiformum* and *Protoproventocitum aitchisoni* n. sp., GSC 125657 (MP42d-g20), (35.7): fusing and branching of the branches and rays of the spicule. 6, GSC 125658 (WBPS19a-d6), (20): still showing transitional characteristics between *A. nudiformum* and *P. aitchisoni*, but three-dimensional meshwork of the shell wall and dense meshwork at apical area are diagnostic characteristics of protoproventocitiids. 9-12, Transitional forms between *A. nudiformum* n. sp. and *A. retiformum* n.sp.: from 9 to 12, note the gradually increasing area of the apical meshwork. 9, GSC 125661 (WBPS19a-d23), (25). 10, GSC 125662 (WBPS19a-b17), (28.5). 11, GSC 125663 (WBPS19a-a20), (28.5). 12, GSC 125664 (WBPS19a-j2), (25). 13-18, *Archeoproventocitum retiformum* n. sp. 13, GSC 125665 (MP42d-o2), (28.5). 14, GSC 125666 (WBPS19a-a1), (33.3). 15, GSC 125667 (WBPS19a-j2), (25). 16, Holotype, GSC 125668 (WBPS19a-a9), (26.3): incompletely meshed. 17, GSC 125669 (MP42d-h16), (25). 18, GSC 125670 (MP42d-il2), (22.2).

most of specimens are imperfectly preserved.

Discussion. - Because of the presence of the multiple shell layers, *A. multistratum* n. sp. is easily distinguished from the other species of *Aspiculum*. The incompletely developed layers of the shell wall of this species appear to be similar to that of some haploteniatumids (Won et al., 2002). However, the pronounced eccentricity of the internal structure of the shell easily distinguishes *A. multistratum* from them.

Etymology. - multi (Lat.), numerous; stratum (Lat.), layer.

Types. - Holotype, GSC 130871; paratype, GSC 180372.

?Aspiculum sp. A

Fig. 14.12

Description. - A spherical spongy shell with a tubelike pylome that forms a discrete part of the spherical shell wall. No major spines are developed.

Discussion. - Only four specimens of *?Aspiculum* sp. A were found, and only in unit 42d at Martin Point. The long pylome in this specimen is somewhat similar to that in *A. jamesi*, but it differs by the absence of the major spines. Also, the pylome of *A. jamesi* appears to be an extension of the shell meshwork and that of *?Aspiculum* sp. A is a discrete shape not related to the spherical shell wall. Specimens of *?Aspiculum* sp. A are present in Arenigian Cow Head strata (senior author's observation). Thus, even though only four specimens have been found in late Tremadocian faunas to date, the form may not be a

variant of *A. jamesi*. Further studies are needed.

Representative specimen. - GSC 130911.

Westernbrookia n. gen.

Type species. - *Westernbrookia diversa* n. sp.

Diagnosis. - Oval, subspherical, or spherical skeleton consisting of a layered shell wall with dense polygonal meshwork on which delicate fine skeletal may developed; internal structure extremely diverse, some eccentricity in internal structures; pylome present.

Discussion. - *Westernbrookia* n. gen. is characterized by a layered shell wall consisting of polygonal meshwork structure. The nature of the shell wall suggests a phylogenetic relation to the basal layer of *Aspiculum* as mentioned in the discussion section for *A. gigantium*. A few specimens (e.g., Fig. 11.11) resemble both *A. gigantium* and *Westernbrookia ovata* n. sp. The diverse internal structures of *A. gigantium* appear also in *Westernbrookia*, even though most specimens of the latter appear to be empty because of loss of the delicate internal elements. Also, some specimens of *Westernbrookia* have a cage-like inner structure (Figs. 11.16a, b, 15.4, 15.7, 15.8, 15.12). Perhaps the inner shell and/or cage-like inner hollow sphere (or its modifications) of multi-shelled taxa may have developed from such an internal structure.

The two-dimensionally meshed shell layer of *Westernbrookia* differs from a typical two-dimensionally latticed shell wall by having a delicate skeletal cover and internal meshwork elements that are connected to

Fig. 9. The scale bar on the first figure applies to all the other figures and is equivalent to a length noted in parenthesis (μm). 1-12, *Protoproventocitum aitchisoni* n. sp.: note poorly preserved, or poorly developed, or lack of the additional shell wall (1-7) and well-developed additional shell wall (8-12). 1, GSC 125671 (WBPS19a-a17), (25). 2, GSC 125672 (WBPS19a-x18), (25): original ray structure of the proventocitiid spicule (arrows). 3, GSC 125673 (WBPS19a-d20), (20). 4, GSC 125674 (MP42d-g10), (20). 5, GSC 125675 (WBPS21c-d22), (36.3). 6, GSC 125676 (MP 42d-g48), (25). 7, GSC 125677 (MP42d-g55), (28.5). 8, Holotype, GSC 125678 (MP42d-j22), (30.3). 9, GSC 125679 (MP42d-g54), (33.3). 10, GSC 125680 (MP42d-21), (22.5). 11, GSC 125681 (MP42d-i4), (40). 12, GSC 125682 (WBPS21c-c2), (37). 13-19, 20?, *Protoproventocitum nazarovi* n. sp. 13, GSC 125683 (WBPS21c-c11), (40). 14, GSC 125684 (WBPS21c-h1), (40). 15, Holotype, GSC 125685 (WBPS21c-c5), (44.4). 16, GSC 125686 (WBPS21c-b1), (50.5). 17, GSC 125687 (WBPS21c-e15), (44.4). 18, GSC 125688 (WBPS21c-e13), (40). 19, GSC 125689 (WBPS21c-d9), (40): trace of additional shell wall (arrow). 20, GSC 125690 (WBPS21c-e4), (28.5): trace of three-dimensional meshwork (arrow) and polygonal meshwork.

it. Depending on how densely the delicate skeletal elements originally covered the polygonally meshed shell layer, that layer may appear to be smooth (Fig. 15.1) or rough (Figs. 12.3, 12.7-10, 15.2, 15.11, 15.12). The density and thickness of the outer delicate shell wall differs among specimens, as well as intraspecifically and interspecifically.

Etymology. - Western Brook, for the Western Brook Pond section from which the fossils were collected.

Westernbrookia diversa n. sp.

Figs. 15.1-15.12

Diagnosis. - An oval, spherical, or subspherical skeleton characterized by densely and polygonally meshed shell that may or may not be covered by spongy material, and by diverse inner structures; as many as eight outer spines; pylome present.

Description. - The oval, spherical, or subspherical skeleton has a shell wall perforated by a pylome and has as many as eight major spines. The shell wall consists of dense polygonal meshwork and is commonly two-, less commonly three-dimensionally meshed. The shell wall surface is smooth or covered by fine or spongy material. The meshwork of the inner part of the shell wall is commonly open and loose, forming an internal structure that differs from specimen to specimen (Figs. 15.3-15.12). Rarely, more densely interwoven internal meshwork structure can be observed (Fig. 15.5). The meshwork of some inner parts forms a spherical outline like a basal layer or inner shell (Figs. 15.8, 15.12). The eccentric structure of the shell wall can be observed in some broken specimens (Figs. 15.3, 15.5-15.9). The shell wall is

opened by a slightly protruded pylome (Figs. 15.1, 15.2).

Discussion. - *W. diversa* n. sp. differs from *W. ovata* n. sp. by the presence of as many as eight major outer spines, small shell size, and stouter elements of the internal meshwork. *W. ovata* is characterized by more than 15 outer spines, large shell, and more delicate internal elements that are generally not observable, that is, the shell appears to be empty, presumably because the internal elements have been destroyed. *W. diversa* occurs only in WBPS unit 19a, whereas *W. ovata* has been found in WBPS unit 19a and MP unit 42d.

Etymology. - Diversus (Lat.), diverse.

Types. - Holotype, GSC130913; paratypes, GSC 130912, 130914-130923.

Westernbrookia ovata n. sp.

Figs. 11.12-11.16, 12.1-12.6

Diagnosis. - A spherical to oval layered shell wall consisting of dense polygonally latticed meshwork covered by delicate spongy skeletal material; internal irregular structure of fine, curved bars; more than 12 short spines; pylome developed near pole of the long axis of the prolate skeleton.

Description. - A spherical to oval shell is characterized by a polygonally latticed layer. The layer may be/have been covered by spongy skeletal material (Figs. 11.12, 12.3, 12.6). The layer is generally two-dimensionally latticed (Figs. 11.13, 11.16, 12.2, 12.5) or rarely three-dimensionally meshed (Figs. 11.14, 11.15, 12.1), even when overlying spongy material is not preserved. The internal structure is rarely

Fig. 10. The scale bar on the first figure applies to all the other figures and is equivalent to a length noted in parenthesis (μm). 1-4, *Protoproventocitium aitchisoni* n. sp.: note diverse internal meshwork structure. 1a, b, GSC 125691 (WBPS19a-11), (40, 12.5): proventocitiid spicule structure showing rays and their branches and an inter-ray bar (arrow on 1b). 2, GSC 125692 (MP42d-g12), (36.3). 3, GSC 125693 (MP42d-p13), (36.3). 4, GSC 125694 (WBPS21c-f24), (23.2). 5-9, *Protoproventocitium nazarovi* n. sp. 5a, b, GSC 125695 (WBPS21c-d10), (45.4, 12.6): joined inter-ray bars form an apical polygonal mesh. 6, GSC 125696 (WBPS21c-d12), (33.3): internal meshwork formed by joined rays and their branches separated from the additional shell wall. 7, GSC 125697 (WBPS21c-d6), (33.3): internal meshwork attached to the shell wall. 8, GSC 125698 (WBPS21c-c3), (28.5): rays of the proventocitiid spicule form a part of the shell wall. 9a, b, GSC 125699 (WBPS21c-d11), (42.5, 20): apical ring structure (upper arrow) may be a trace of an inter-ray loop and skeletal elements along dotted line connected to spines may have been originally one ray of the proventocitiid spicule. 10-16, *Cowheadia duplex-testa* n. sp. 10, GSC 125700 (MP42d-f8), (25). 11a, b, Holotype, GSC 125701 (MP42d-g18), (36.3, 36.3). 12, GSC 125702 (MP42d-i16), (13.3). 13, GSC 125703 (MP42d-g25), (25). 14, GSC 125704 (MP42d-g22), (20). 15, GSC 125705 (MP42d-c23), (20): inter-ray bars form a C shape. 16, GSC 125706 (MP42d-i17), (22.2): inter-ray bars form a ring, that is, an inter-ray loop.

preserved because it is extremely delicate. Where preserved, it is eccentrically located (Fig. 11.15) and variable (Figs. 11.14-11.16, 12.5-12.6). The pylome, whose diameter is somewhat variable, is developed near the pole of the long axis of the shell (Figs. 12.3, 12.4). Numerous spines are developed, typically more than 12. The length and the diameter of the spines may vary or be the same within a specimen, but they are generally short.

Discussion. - Transitional characteristics shared by some specimens (Fig. 11.11a) of *W. ovata* and *A. gigantum* suggest a close relation between the two species and two genera.

Types. - Holotype, 125726; paratypes, GSC 125718-125725, 130865-130866.

Etymology. - Ovatus (Lat.), oval.

Westernbrookia cancella n. sp.

Figs. 12.7-12.10

Diagnosis. - A spherical, two-dimensionally latticed shell wall covered by a thick and delicate spongy layer; delicate internal framework. More than 10 stout major spines; pylome present.

Description. - The spherical shell wall consists of thick spongy material on a stout meshwork layer. The delicate spongy layer is partly preserved; commonly, traces remain along the outer spines or on the shell surface meshwork. The two-dimensional shell layer is polygonally meshed. The thickness of the mesh bars may be similar or wider than the mesh openings (Fig. 12.8). Traces of internal meshwork structure can be

observed (Figs. 12.9b, 12.10b). More than 10 stout outer spines and a pylome (Fig. 12.8) are present.

Discussion. - *W. cancella* n. sp. differs from other species of *Westernbrookia* by possessing the numerous stout outer spines, much smaller polygonally latticed shell diameter and much thicker spongy layer whose remnants appear as spinules along the outer spines.

Etymology. - Cancellata (Lat.), latticed.

Types. - Holotype, GSC 130868; paratypes, GSC 130867, 130869, 130870.

Family ECHIDNINIDAE Kozur, Mostler, and Repetski, 1996

Diagnosis. - See Kozur, Mostler, and Repetski, 1996, p. 248; see also Won and Iams (2002) and Won, Iams, and Reed (2005).

Genus *Echidnina* Bengtson, 1986

Type species. - *Echidnina runnegari* Bengtson, 1986, p. 202.

Emended diagnosis. - Won and Iams, 2002, p. 24. See also expanded diagnosis by Won and Iams, 2005, p. 446.

Echidnina bengtsoni Kozur, Mostler, and Repetski, 1996
Fig. 7.1

Echidnina bengtsoni Kozur, Mostler, and Repetski, 1996, p. 249.

Echidnina bengtsoni Won and Iams, 2005, p. 447.

Diagnosis and description. - Kozur, Mostler, and Repetski, 1996, p. 249.

Fig. 11. The scale bar on the first figure applies to all the other figures and is equivalent to a length noted in parenthesis (μm). 1-10, 11?, *Aspiculum gigantium* n. sp. 1, Holotype, GSC 125707 (WBPS19a-h5), (58.8). 2, GSC 125708 (WBPS19a-h16), (71.4). 3, GSC 125709 (WBPS19a-o9), (57.1). 4, GSC 125710 (WBPS19a-L31), (55.5). 5, GSC 125711 (WBPS19a-h17), (66.6). 6, GSC 125712 (WBPS19a-o8), (40). 7a, b, GSC 125713 (WBPS19a-m7), (66.6, 66.6); 7b is underside of 7a. 8, GSC 125714 (WBPS19a-h1), (671.4). 9a, b, GSC 125715 (WBPS19a-p14), (57.1, 57.1); 9b is underside of 9a. 10, GSC 125716 (WBPS19a-j18), (55.5). 11a, b, GSC 125717 (WBPS19a-m3), (55.5, 55.5); 11b is under side of 11a. 12-16, *Westernbrookia ovata* n. sp. 12, GSC 125718 (WBPS19a-L21), (64.5). 13, GSC 125719 (WBPS19a-j4), (50). 14, GSC 125720 (WBPS19a-o2), (33.3). 15, GSC 125721 (WBPS19a-o4), (50). 16a, b, GSC 125722 (WBPS19a-L36), (40, 18.1); 16b shows an inner structure that resembles an inner shell, but whose meshwork appears to be incompletely developed.

Representative specimen. - GSC 125644.

Occurrence. - From the early Tremadocian strata of the Windfall Formation, Nevada, USA, and the early to late Tremadocian units of the Cow Head Group, Newfoundland, Canada (see also Table 1).

Echidnina spp.

Figs. 7.2-7.9

Description. - The spherical shell has a large empty inner space, and the shell wall consists of the deformed/transformed spicule whose echidninid characters may or may not be detectable, depending on specimen orientation and breakage. Rarely, a major spicule may be developed.

Discussion. - The late Tremadocian faunas include sparse echininids unlike those of the early Tremadocian. That is, except for *Echidnina bengtsoni*, all specimens consist of transformed spicules. Each form is extremely rare in these faunas, and the echininids display a variety of spicule structures and diverse states of transformation, such as, *inter alia*, partly fused spicules whose original structure is unclear (Figs. 7.3a, b, c); spicules fused and forming an irregular meshwork (Figs. 7.2a, b); spicules that have a median bar (Figs. 7.4a, b); and transformed spicules forming angular meshwork with a major spicule with a short median bar (Figs. 7.5a-c). Some echidninids have a major spicule that is much larger than the spicules forming the shell wall. The presence of the major spicule is rarely observed in Late Cambrian (Figs. 7.7a, b, 7.8), early Tremadocian (Figs. 7.6a-d, 7.9), and late Tremadocian (Figs. 7.5a-c) faunas in the Cow Head Group. At this time it is unclear whether the development of the major spicule is speciation or

simply variants. The major spicule is point-centered (Fig. 7.8), or meeting point-centered (an articulation point; Fig. 7.7b, or has a median micro-bar (Figs. 7.5a, b, 7.6c, d), or a long median bar (Fig. 7.9).

Representative specimens. - GSC 125645-125652.

Occurrence. - From the Late Cambrian and early to late Tremadocian units of the Cow Head Group, Newfoundland, Canada (see also Table 1).

Family PALAEOSPICULUMIDAE Won in Won and Below, 1999

Diagnosis. - Won in Won and Below, 1999, p. 339.

Expanded diagnosis - Point-centered spicular skeleton, the spicule consisting of rays with subsidiary elements on all or some rays that may or may not form a shell wall; where a shell wall is developed, the shell wall elements fused or unfused.

Discussion. - Palaeospiculumidae that occur from the Middle Cambrian to the middle Tremadocian may or may not have a shell wall made up of unfused elements. Shell walls formed by partly fused subsidiary elements occur in middle Tremadocian strata. In the late Tremadocian units, completely fused shell wall meshwork structures can be found. This variation over time requires an expanded diagnosis of the family Palaeospiculumidae. The evolutionary trend from unfused subsidiary elements on the rays to fused meshwork appears also in the Protoentactinidae Kozur, Mostler, and Repetski, 1996 and Echidninidae Kozur, Mostler, and Repetski, 1996.

Genus *Palaeospiculum* Won in Won and Below, 1999

Type species. - *Palaeospiculum burkensis* Won in Won and Below, 1999

Fig. 12. The scale bar on the first figure applies to all the other figures and is equivalent to a length noted in parenthesis (μm). 1-6, *Westernbrookia ovata* n. sp. 1, GSC 125723 (MP42d-i8), (52.2). 2, GSC 125724 (MP42d-h22), (42.6). 3, GSC 125725 (MP42d-f27), (44.4). 4, Holotype, GSC 125726 (WBPS19a-x1), (50). 5, GSC 130865 (MP42d-n5), (40). 6, GSC 130866 (MP42d-e1), (40). 7-10, *Westernbrookia cancella* n. sp. 7, GSC 130867 (MP42d-j44), (50). 8, Holotype, GSC 130868 (MP42d-h23), (44.4). 9a, b, GSC 130869 (MP42d-o1), (50, 13.6): remnants of internal meshwork. 10a, b, GSC 130870 (MP42d-06), (50, 14.2): internal meshwork (arrow). 11-12, *Aspiculum multistratum* n. sp. 11a, b, Holotype, GSC 130871 (WBPS19a-m9), (42.5, 40): 11b is under side of 11a). 12a, b, GSC 130872 (WBPS19a-i22), (33.3, 16.6). 13-16, *Aspiculum densum* n. sp. 13, Holotype, GSC 130873 (WBPS19a-i16), (33.3). 14, GSC 130874 (WBPS19a-a7), (28.5). 15, GSC 130875 (WBPS19a-q27), (33.3). 16, GSC 130876 (WBPS19a-h1), (28.5).

Palaeospiculum neofurcatum Won, Iams, and Reed,
2005

Figs. 4.13, 4.14

Palaeospiculum neofurcatum Won, Iams, and Reed,
2005, p. 451.

Diagnosis and description. - See Won, Iams, and Reed, 2005, p. 451.

Representative specimens. - GSC 125621, 125622.

Discussion. - In general, the spiny spherical shell wall of *P. neofurcatum* consists mainly of peripherally positioned unfused spinules. Spinules of one specimen (Figs. 4.14a, b) have the fused structure, but spinules of the outer shell wall are unfused.

Occurrence. - From middle and late Tremadocian units of the Cow Head Group, Newfoundland, Canada (see also Table 1).

Neopalaeospiculum n. gen.

Type species. - *Neopalaeospiculum laxum* n. sp.

Diagnosis. - A six-rayed spicular skeleton with a spherical shell wall made up of partly or completely fused meshwork. Four or five radially arranged first-order spinules developed at one or two nodes on the rays, these spinules with or without second- or, at most, third-order spinules, also radially arranged. Spinules near the shell wall possessing branches, and both elements forming a thin one-layered, three-dimensionally interwoven shell wall.

Discussion. - *Neopalaeospiculum* differs from *Palaeospiculum* by the nature of the shell wall. *Palaeospiculum* may or may not form a spherical shell wall, depending on how well subsidiary elements on the rays are developed. Those subsidiary elements (spinules without branches) that form a spherical shell

wall are not fused. In contrast, the shell wall of *Neopalaeospiculum* consists of fused spinules and their branches forming a meshwork. In *Palaeospiculum*, the six rays of the spicule are stout among skeletal elements, but the main spicule rays are slender in *Neopalaeospiculum*. In addition, in *Neopalaeospiculum* sp. A, the internal part of the spicule is clearly more slender than the outer part (Figs. 5.5a, b). Such a slender internal spicule structure is one of the common features in late Palaeozoic taxa.

Neopalaeospiculum has the spicule system that was derived from *Palaeospiculum hexaradiatum* Won and Iams 2002, *P. multifurcatum* Won, Iams and Reed, 2005, and *P. neofurcatum* Won, Iams, and Reed, 2005. However, *Neopalaeospiculum* differs from *Palaeospiculum* by its spherical shell wall of fused meshwork. The first appearance datum of *P. hexaradiatum* with first-order spinules is in the Late Cambrian; this datum for *P. multifurcatum* with second-order spinules is early Tremadocian, that of *P. neofurcatum* with third-order spinules is middle Tremadocian, and the new genus *Neopalaeospiculum* with third-order spinules and fused shell-wall meshwork is from the late Tremadocian. The changing of the shell wall structure from unfused elements to fused meshwork may reflect an evolutionary trend like that seen in the Protoentactinidae and Echininidae.

Neopalaeospiculum laxum n. sp.

Figs. 5.4, 5.6

Diagnosis. - A point-centered six-rayed spicule and a spherical shell wall with fused, very thin, loose, and coarse meshwork. Four, five, or, rarely, six spinules arising at one or two nodes on the rays, and third-

Fig. 13. The scale bar on the first figure applies to all the other figures and is equivalent to a length noted in parenthesis (μm). 1-5, 9-13, *Aspiculum eccentricum* s. s. Morphotype 1 Won, Iams, and Reed, 2005. 1, GSC 130877 (MP42d-h27), (66.6): no pylome on the densest part of shell wall. 2a, b, GSC 130878 (MP42d-g20), (40): meshwork of the shell wall is dense and has several openings, and if one of them were the pylome, it is unclear which; 2b, the underside of 2a, shows coarse meshwork. 3, GSC 130879 (MP42d-h7), (50). 4, GSC 130880 (MP42d-g30), (50). 5, GSC 130881 (MP42d-h14), (50). 9, GSC 130882 (MP42d-h27), (66.6): no internal cavity and no basal layer. 10a, b, GSC 130883 (MP42d-b6), (50, 20): a poorly developed basal layer with three-dimensional meshwork. 11, GSC 130884 (MP42d-b7), (50): meshwork developed in the basal layer. 12, GSC 130885 (MP42d-f11), (40): stout basal layer eccentrically positioned. 13a, b, GSC 130886 (MP42d-f2), (40, 15.3): three-dimensional thick basal layer, in which internal meshwork developed. 6-8, 14, 15, *Aspiculum eccentricum* s. l. Morphotype 2 Won, Iams and Reed, 2005. 6a, b, GSC 130887 (MP42d-f4), (66.6, 66.6): 6b, the underside of 6a, shows a partly broken pylome on the densest meshwork and on the area where shell wall is thinnest. 7, GSC 130888 (MP42d-g34), (50). 8a, b, GSC 130889 (MP42d-g7), (31.2): two-dimensional meshwork structure and denticulated pylome margin. 14, GSC 130890 (MP42d-g31), (40): pylome positioned on the densest meshwork and thinnest shell wall. 15, GSC 130891 (MP42d-g15), (41.6).

order spinules (maximum) developed. Spinules or their branches joined, forming fused meshwork. Some unfused free spinules or branches on the meshwork.

Description. - The skeleton is composed of a six-rayed spicule and a spherical meshed shell wall. Each ray of the spicule possesses four to five, rarely six, radially developed spinules at one or two nodes. These first-order spinules bear second-order spinules. Third-order spinules are less common. Distally developed spinules and their branches form the fused meshwork of the shell wall. Some spinules project outward free on the meshwork. The meshwork is loose, very coarse, and three-dimensionally interwoven.

Discussion. - The internal structure of *N. laxum* n. sp. is the same as that of *Palaeospiculum neofurcatum* Won, Iams, and Reed, 2005. *N. laxum* differs from *N. transformum* n. sp. by the shell wall structure. In the former, branches are long and most of them are fused to other branches or spinules, forming fused meshwork. In *N. transformum*, branches are short and many of them are not connected to the other branches or spinules.

Etymology. - *Laxus* (Lat.), loose.

Types. - Holotype, GSC 125628; paratype, GSC 125626.

Neopalaeospiculum densum n. sp.

Figs. 5.7, 5.8

Diagnosis. - A neopalaeospiculimid spicule surrounded by a spherical, thin shell wall composed of fine meshwork.

Description. - The thin shell wall consists of very dense meshwork that is three-dimensionally interwoven. Neither branch nor spinule structure can be observed on the shell wall. Internally, the neopalaeospiculimid structure can be observed (Fig. 5.8b). Outer spines are not developed.

Discussion. - *N. densum* n. sp. differs from *N. laxum* n. sp. by the smooth shell wall structure and much denser meshwork of the shell wall.

Etymology. - *Densus* (Lat.), dense.

Types. - Holotype, GSC 125630; paratype, GSC 125629.

Neopalaeospiculum transformum n. sp.

Figs. 5.1, 5.2, 5.3?

Diagnosis. - A spherical shell wall surrounding a point-centered neopalaeospiculimid spicule formed by branches and spinules of the spicules, both of which make an incomplete meshwork structure. Short branches covering the shell surface.

Description. - Spinules on the rays are fused and form the spherical shell wall. Short branches on the shell surface are partly fused, thus the shell wall surface shows an incompletely fused meshwork structure. The point-centered neopalaeospiculimid spicule is the stoutest among the skeletal elements.

Discussion. - This species shows characteristics transitional or intermediate between typical *Neopalaeospiculum* and *Palaeospiculum*. The dense spherical shell wall is that of *Neopalaeospiculum*, but the stout spicule structure is reminiscent of *Palaeospiculum*. In one specimen, rare incompletely

Fig. 14. The scale bar on the first figure applies to all the other figures and is equivalent to a length noted in parenthesis (μm). 1-11, 13-20, *Aspiculum jamesi* n. sp.; note pylome (indicated by arrow). 1, GSC 130892 (WBPS19a-i5), (40); no pylome. 2, GSC 130893 (WBPS19a-r7), (33.3). 3, GSC 130894 (WBPS19a-q9), (40). 4, GSC 130895 (WBPS19a-q15), (43.4). 5, GSC 130896 (WBPS19a-g36), (40). 6, Holotype, GSC 130897 (MP42d-i5), (50). 7, GSC 130898 (MP42d-k3), (28.5). 8, GSC 130899 (WBPS19a-q12), (44.4). 9, GSC 130900 (WBPS19a-i1), (40). 10, GSC 130901 (WBPS19a-g32), (40). 11, GSC 130902 (WBPS19a-h17), (40). 13-20, note diverse internal structure. 13, GSC 130903 (WBPS19a-q10), (40). 14, GSC 130904 (WBPS19a-k12), (25). 15a, b, GSC 130905 (WBPS19a-i10), (33.3, 12.5). 16, GSC 130906 (WBPS19a-h26), (33.3). 17, GSC 130907 (WBPS19a-q17), (33.3). 18, GSC 130908 (WBPS19a-i3), (50). 19, GSC 130909 (WBPS19a-g7), (45.4). 20, GSC 130910 (WBPS19a-i14), (40). 12, ?*Aspiculum* sp. A. GSC 130911 (MP42d-i25), (25).

fused mesh (Fig. 5.3c in the circle) more strongly supports the transitional character between *Palaeospiculum* with its unfused shell wall and *Neopalaeospiculum* with a fused shell wall.

Types. - Holotype, GSC 125623; paratype, GSC 125624.

Neopalaeospiculum sp. A

Fig. 5.5

Protoentactinia? sp. A Won, Iams, and Reed, 2005, p. 458.

Description. - The point-centered six-rayed neopalaeospiculumid spicule is enclosed by a spherical, thin shell wall composed of fused meshwork. The distal parts of the rays protrude beyond the shell wall as outer spines. This species is characterized by the internal spicule thinner than the outer spines.

Discussion. - The internal segment of the spicule suddenly thins from where the shell wall is developed, and its outer segment, which protrudes from the shell wall as an outer spine, is much thicker. In early Paleozoic radiolarians, the inner and outer parts of the spicule have the same diameter. Variation between delicate inner and stout outer parts of the spicule is quite common in late Paleozoic taxa. The earliest specimen in which this character has been found comes from a middle Tremadocian unit of the Cow Head Group (Won et al., 2005); another specimen is from a late Tremadocian fauna discussed in this paper. The older of these two was misassigned as *Protoentactinia?* sp. A by Won et al. (2005). The taxonomic assignment of this form was provisional because of the few specimens, but its internal structure was misunderstood.

Representative specimen. - GSC 125627.

Occurrence. - From a middle Tremadocian Broom Point South unit and late Tremadocian units in the Cow Head Group, Newfoundland, Canada (see also Table 1).

Family PROTOENTACTINIIDAE Kozur, Mostler, and Repetski, 1996

Genus *Protoentactinia* Kozur, Mostler, and Repetski, 1996

Noblella Kozur, Mostler, and Repetski, 1996

Paulanoblella Kozur and Repetski, 2002

Type species. - *Protoentactinia gracilispinosa* Kozur, Mostler, and Repetski, 1996, p. 253.

Diagnosis. - See Kozur, Mostler, and Repetski, 1996, p. 253.

Expanded diagnosis. - See Won, Iams, and Reed, 2005, p. 453.

Protoentactinia gracilispinosa Kozur, Mostler, and Repetski, 1996
Figs. 6.3, 6.4

Protoentactinia gracilispinosa Kozur, Mostler, and Repetski, 1996, p. 253.

Protoentactinia gracilispinosa Won, Iams, and Reed, 2005, p. 453.

Diagnosis, Description, Discussion. - See Won, Iams, and Reed, 2005

Representative specimens. - GSC 125633, 125634.

Occurrence. - Early Tremadocian part of the Windfall Formation, Nevada, U.S.A., and early to late Tremadocian units in the Cow Head Group, Newfoundland, Canada (see also Table 1).

Fig. 15. The scale bar on the first figure applies to all the other figures and is equivalent to a length noted in parenthesis (μm). 1-12, *Westernbrookia diversa* n. sp.; note diverse internal structure. 1, GSC 130912 (WBPS19a-o14), (33.3). 2, Holotype, GSC 130913 (WBPS19a-h27), (40). 3, GSC 130914 (WBPS19a-n2), (28.5). 4, GSC 130915 (WBPS19a-m10), (40). 5, GSC 130916 (WBPS19a-n5), (45.4). 6, GSC 130917 (WBPS19a-i32), (40). 7, GSC 130918 (WBPS19a-n3), (33.3). 8, GSC 130919 (WBPS19a-o18), (33.3). 9, GSC 130920 (WBPS19a-m13), (28.5). 10, GSC 130921 (WBPS19a-n10), (30.3). 11, GSC 130922 (WBPS19a-o6), (33.3). 12, GSC 130923 (WBPS19a-m5), (40). 13a, b, *Rossodus manitouensis* Repetski, 1982, GSC 130924 (SP30-Co1), (40); 13a is outer side and 13b is inner side of coniform (or c element). 14, *Paracodylodus gracilis* Lindström 1955, GSC 130925 (MP40f-b5), (83.3), S element of Type B. 15, *Drepanoistodus nowlani* Ji and Barnes, 1994, GSC 130926 (MP40f-b6), (83.3), c element. 16, *Paraoistodus numarcuatus* (Lindström, 1955), GSC 130927 (WBPS20-1), (63.6), M element. 17, *Marceroodontus diana*e Fähræus and Nowlan, 1978, GSC 130928 (MP42d-Co1), (40), a element. 18, *Variabiliconus variabilis* Lindström, 1955, GSC 130929 (MP42d-Co2), (55.5), Pb element. 19, 20, *Paltodus deltifer deltifer* Lindström, 1955. 19, GSC 130930 (WBPS21L-1), (55.5), Sa element. 20, GSC 130931 (WBPS21L-2), (57.1), Sc element. 21, 22, *Paraoistodus proteus* Lindström, 1955. 21, GSC 130932 (WBPS21L-3), (44.6), Sd element. 22, GSC 130933 (WBPS21L-4), (47.2), Pb element. 23, 24, *Acodus deltatus deltatus*, Lindström, 1955. 23, GSC 130934 (WBPS21L-5) (76.9), Sa element. 24, GSC 130935 (WBPS21L-6) (66.6), sb element.

Protoentactinia kozuriana sensu stricto Won, Iams,
and Reed, 2005

Morphotype 1

Figs. 6.5, 6.6

Protoentactinia kozuriana Won, Iams, and Reed,
2005, p. 455.

Diagnosis and Description. - See Won, Iams, and
Reed, 2005

Discussion. - Specimens of *P. kozuriana* in the late
Tremadocian faunas are all Morphotype 1 and much
smaller than those from the early Tremadocian.

Representative specimens. - GSC 125635, 125636.

Occurrence. - From early to late Tremadocian units
in the Cow Head Group, Newfoundland, Canada (see
also Table 1).

Protoentactinia primigena sensu stricto Won, Iams,
and Reed, 2005

MORPHOTYPE 1

Fig. 6.1

Protoentactinia gracilispinosa s. l. Kozur, Mostler,
and Repetski, 1996: Won and Iams, 2002, p. 30.

Protoentactinia primigena s. s. Won, Iams, and
Reed, 2005, p. 456.

Diagnosis, Description, and Discussion. - See Won,
Iams, and Reed, 2005

Representative specimen. - GSC 125631.

Occurrence. - From Late Cambrian to late
Tremadocian units in the Cow Head Group,
Newfoundland, Canada (see also Table 1).

Protoentactinia primigena sensu lato Won, Iams and
Reed, 2005

MORPHOTYPE 2

Fig. 6.2

Protoentactinia gracilispinosa s. l. Kozur, Mostler,
and Repetski, 1996: Won and Iams, 2002, p. 30.

Protoentactinia primigena s. l. Won, Iams, and
Reed, 2005, p. 456.

Diagnosis, Description, and Discussion. - See Won,
Iams, and Reed, 2005

Representative specimen. - GSC 125632.

Occurrence. - From Late Cambrian to late
Tremadocian units in the Cow Head Group,
Newfoundland, Canada (see also Table 1).

Protoentactinia transformis Won, Iams, and Reed,
2005

Figs. 6.7, 6.8

Protoentactinia transformis Won, Iams, and Reed,
2005, p. 457.

Diagnosis, description, and discussion. - See Won,
Iams, and Reed, 2005

Representative specimens. - GSC 125637, 125638.

Occurrence. - From early to late Tremadocian units
in the Cow Head Group, Newfoundland, Canada (see
also Table 1).

Genus *Protospongentactinia* n. gen.

Type species. - *Protospongentactinia spongiosa* n. sp.

Diagnosis. - Protoentactiniid internal structure and a

meshed or spongy spherical shell wall.

Discussion. - The genus *Protospongentactinia* differs from *Protoentactinia* by the lack of the trifurcated branch structure of the shell wall. The development of the fused meshwork of the shell wall in *Protospongentactinia* is an evolutionary trend, one that is also seen in echidniniids and palaeospiculimids. The trifurcated structure of the spicule with a fused shell wall may be equivalent to the apophyses of the internal spicule of Retentactiniinae Won, 1997, which is a junior synonym of Spongentactiniinae Nazarov, 1975. *Protospongentactinia* differs from spongentactiniids by the unmodified repeated trifurcated internal structure.

Etymology. - Proto (Gr.), before; spongentactinia, a genus name.

Protoentactinia spongiosa n. sp.

Figs. 6.10, 6.11

Diagnosis. - Protoentactiniid internal structure with a spherical spongy shell wall.

Description. - The internal spicule system has the protoentactiniid structure within a large spherical empty inner space that is surrounded by a thick spongy shell wall. The shell wall contains no trifurcated branch structures, but it consists of fully developed spongy meshwork. The shell bears some thin, short outer spines.

Discussion. - The outer appearance of *Protospongentactinia spongiosa* n. sp. is very similar to that of *Protoentactinia transformata* Won, Iams, and Reed, 2005, but differs by its spongy meshwork structure. *P. transformata*, whose outermost part is partly fused, is a transitional form between *Protoentactinia* with a shell wall consisting of trifurcated branches and *Protospongentactinia* with a shell wall of spongy meshwork.

Etymology. - Spongiosus (Lat.), spongy.

Types. - Holotype, GSC 125640; paratype, GSC 125641.

Protospongentactinia sp. A

Fig. 6.9

Description. - The spherical shell wall consists of irregularly and well-fused coarse meshwork; the form has the protoentactiniid internal spicule system. Furcated branch structures can rarely be observed on the shell wall.

Discussion. - The meshed shell wall in *Protospongentactinia* sp. A appears to be developed by the fusion and modification of the trifurcated branches. A shell wall with fusion and modification of the branches can be seen also in *Protoentactinia deformis* Won, Iams, and Reed, 2005. However, the protoentactiniid characteristic of in *Protospongentactinia* sp. A can be identified only by its internal structure.

Representative specimen. - GSC 125639.

Family PROVENTOCITIIDAE Aitchison, 1998

1972 Radiolaria familia nova Fortey and Holdsworth conical and spicular forms. 1972, p. 39-40.

1977 Radiolaria familia nova Fortey and Holdsworth 1972 - Holdsworth 1977, p. 169.

Assigned genera. - *Proventocitum* Nazarov, 1988; *Archeoproventocitum* n. gen.; *Cowheadia* n. gen.; *Protoproventocitum* n. gen.

Emended diagnosis. - Spicular or shelled form with or without a spicule as the internal structure. Spicular skeleton consisting of several sinuous rays that are commonly irregularly branched and connected by an inter-ray bar(s) or an inter-ray loop. Spicule encompassed by a shell wall or transformed by joining rays and branches to construct the shell wall. Distal parts of the rays and branches of the spicule in the shelled forms developed as outer spines; some spines developed as apical or subapical and as lateral and/or branched outer spines. Shelled forms with or without opening.

Discussion. - The first report describing the proventocitiids was by Fortey and Holdsworth (1972), and they mentioned the close relation between the spicular form and conical form of Radiolaria familia nova species. When Holdsworth (1977, p. 169) wrote again about the family, he excluded the spicular form and described the family as "Paleozoic latticed or spongy conical shells, open at base, with spirally

disposed lateral spines and also apical spines". Aitchison (1998) established the family Proventocitiidae on the basis of conical forms of Radiolaria familia nova spp. (Fortey and Holdsworth, 1972) and of *Proventocitum procerulum* from Kyzylzharskay Suite, Kazakhstan (Nazarov and Popov, 1980) and *P. procerulum* from the Ballantrae Complex, Scotland (Aitchison, 1988). Thus, they viewed spicular form of Radiolaria familia nova spp. as unrelated to the conical form. However, the many specimens intermediate between the spicular and conical shelled form and the shelled form with a spicule as the internal structure from Cow Head faunas strongly suggest that the shelled (or conical) form is closely related to the spicular form (all displayed specimens on Figs. 3, 8, 9, 10).

In this report three new genera are established. *Archeoproventocitum* n. gen. includes a naked spicular form as well as one in which rays and branches have a tendency to join, forming a two-dimensional meshwork. The spicule in *Protoproventocitum* is transformed to a conical shell form by branching of the spicule and subsequent fusion of the branches (Fig. 3.2). In *Cowheadia* n. gen., the basic proventocitiid spicule is developed as the internal structure in a spherical shelled form (Fig. 3.3).

One of the evolutionary trends in the Proventocitiidae is well displayed in forms from *Archeoproventocitum* through *Protoproventocitum* to *Proventocitum* and is similar to that in the Echidninae, Palaeospiculidae, and Protoentactinidae. In these four families, the earliest representative is an unfused spicular form; later, a shell wall is developed or the skeletal elements of the spicule are fused to produce a shell wall without a definite inner space; finally, a layered shell whose inner surface lines an inner cavity is developed (see also the discussion section of *Protoproventocitum* n. gen. and *P. nazarovi* n. sp.). Also, the co-occurrence of the three proventocitiid genera in the late Tremadocian suggest the possibility of the earlier appearance of proventocitiids than the late Tremadocian and that the spicular form may be the oldest one. In the late early Tremadocian fauna (*C.*

angulatus Zone) from Nevada (Kozur et al., 1996) and from Newfoundland (Won et al., 2005) and the middle Tremadocian fauna (*R. manitouensis* Zone) from Newfoundland (Won et al., 2005) these forms are rare and low in diversity. Thus, the faunal characteristics of late early and middle Tremadocian fauna are not yet well known, unlike earliest Tremadocian fauna (Won et al., 2005). The sudden blooming of diverse and abundant proventocitiids in the late Tremadocian faunas may support this suggestion. Also, the spicular form as the internal structure in the shelled forms *Cowheadia* n. gen. and *Protoproventocitum* n. gen. may indicate that ontogenesis is an abbreviated recapitulation of the evolution of the phyletic lineage (pylogenesis) to which it belongs. Genus *Proventocitum* Nazarov, 1988, which was the basis for establishing the family Proventocitiidae, is a conical layered shelled form lacking an internal structure. The gradual merging of the internal spicule to the shell wall from older to younger species of *Protoproventocitum* in late Tremadocian fauna in this study may be the origin of the Arenigian lineage *Proventocitum*.

Archeoproventocitum n. gen.

Type species. - *Archeoproventocitum nudiformum*. n. gen., n. sp.

Diagnosis. - Spicular skeleton consisting of several sinuous rays with branches centered at the apical portion. Rays connected by an inter-ray bar(s) or an inter-ray loop. One to several inter-ray spines developed. Transformation of the spicule by development of fused rays and branches forming the meshwork of an apical or partially to completely closed shell wall.

Discussion. - The proventocitiid spicule in *Archeoproventocitum* has a tendency to form a two-dimensional meshwork by fusing rays and their branches. Depending on the degree of fusion, an apical, hemispherical, or almost closed spherical meshwork can be formed (Figs. 8.9-8.18). The late Tremadocian *Archeoproventocitum* can be separated into three forms by the degree of joining of rays and branches. In the first form, the spicule consists of

several irregular sinuous rays joined by an inter-ray bar(s) or an inter-ray loop in the apical portion (Figs. 8.1-8.5, 8.7, 8.8). This kind of spicule is present also in the shelled form - e.g., as the internal structure in *Cowheadia* n. gen. In the second form, the joining of the rays and branches of the spicule is mainly around the apical part; thus, an apical to partial meshwork (Figs. 8.9-8.11, 8.12) is formed. In the third form, the spicule transforms to an almost closed shell wall composed of two-dimensional meshwork sheet, thereby losing the spicule structure (Figs. 8.13-8.17).

The gradual transitional morphologies from the first to the third form may reflect their close relation. The oldest proventocitiids may be the first form of *Archeoproventocitum*, that is, *A. nudiformum* n. sp. In the other families mentioned above, the earliest forms are typically naked and the simplest spicule, and then they evolve to more complex forms.

The second form is very rare. Thus, only the first and third forms are treated here as discrete species. The apparently gradual transition from first to third forms may reflect the fact that the rays and branches of the spicule tend to join easily. This tendency may be better demonstrated later, in the Arenigian, and may lead to a new species that has a two-dimensionally completely latticed spherical shell (senior author's observation). The rays and branches of the spicule tend to join as not only two- but also three-dimensional meshwork (Figs. 8.5, 8.6). The development of a three-dimensional meshwork defines the genus *Protoproventocitum*.

Archeoproventocitum nudiformum n. sp.

Figs. 3.1, 8.1-8.4, 8.7, 8.8

Radiolaria familia nova spp., spicular form. Fortey and Holdsworth, 1972, p. 40, pl. 2, figs. 2, 5; text-fig. 1a.

Diagnosis. - Skeleton consisting of several sinuous rays having irregular branches connected by an inter-ray bar(s) or an inter-ray loop. One to several inter-ray spines developed.

Description. - The spicule differs from specimen to specimen because the number, shape, and length of

the inter-ray bar that connect(s) the rays and spines is not constant nor is the number of the rays and branches. There are several sinuous rays connected by one (Figs. 3.1, 8.1a, b) or two median bars (Fig. 8.2b) in the simple form, but the number of rays may exceed five in complicated forms, depending on the criteria used to distinguish the rays and spines where they are connected by several inter-ray bars that form an inter-ray loop (Fig. 8.8). Counting the rays is not easy because it is commonly difficult to distinguish ray from inter-ray spine. Rays are generally long and have branches, and spines are short and not branched. However, some short ones are branched.

Discussion. - *A. nudiformum* n. sp. is characterized by the sinuous rays that have branches; the rays are connected by an inter-ray bar(s) or an inter-ray loop. This species was reported as *Radiolaria familia nova* sp. spicular form by Fortey and Holdsworth (1972). They described it as an irregularly branching, triradiate spicular form. The three rays of their triradiate spicular form do not arise at a point but rather are connected by an inter-ray bar (as seen in Fig. 3.1), which can be observed with SEM, but depending on the angle of view not observable with a light microscope.

Types. - Holotype, GSC-125653; paratypes, GSC125654-125656, GSC 125659, 125660.

Archeoproventocitum retiformum n. sp.

Figs. 8.13-8.18

Diagnosis. - Spherical to subspherical shelled form not completely closed by the remarkably large mesh(es) or incompletely meshed. No proventocitiid spicule structure, but its remnants surviving as curved and/or branched outer spines; rarely sinuous rays present.

Description. - The shell wall is generally spherical to subspherical. Its meshwork is not completely closed (Figs. 8.13, 8.16), or one or two meshes are very large (Figs. 8.17, 8.18). Meshwork of the shell wall is irregular, generally polygonal, and varies in the size of the mesh opening. No spicule structure remains; the sinuous rays are rarely preserved (Fig. 8.13). Some of

the branched (Figs. 8.13-8.18) or curved (Fig. 8.15) outer spines may be remnants of the spicule structure.

Discussion. - In *A. retiforma* n. sp., the rays and branches of the proventocitiid spicule are quite thoroughly joined, forming the latticed shell wall while losing the original spicule structure. Because of the presence of intermediate forms (Figs. 8.9-8.12), the close relation of *A. nudiforma* n. sp. and *A. retiforma* n. sp. can be seen. *A. retiforma* differs from the two-dimensionally latticed Paleozoic entactiniid shell by the presence of larger mesh opening(s) or the incompletely formed meshwork, some curved and/or branched outer spines, and lack of internal spicule. (See also the discussion section for the genus *Archeoproventocitum*.) The well-developed two-dimensional meshwork of *A. retiforma* may be related to the development/origin of unreported Arenigian proventocitiids (author's observation) that have a two-dimensional, completely closed spherical shell wall with an apical loop structure.

Etymology. - Rete (Lat.), a net; forma (Lat.), form.

Types. - Holotype, GSC-125668; paratypes, GSC 125664-125667, GSC 125669, 125670.

Cowheadia n. gen.

Diagnosis. - Proventocitiid spicule as the internal structure of a spherical shelled form; distal parts of rays and branches of the spicule protruding out of the shell wall as outer spines.

Discussion. - *Cowheadia* n. gen. differs from *Archeoproventocitum* n. gen. by the development of the closed spherical shell wall(s) that encompass the proventocitiid spicule as the internal structure (see Fig. 3.3). In *Archeoproventocitum*, the spicule has no shell wall or the spicule itself is transformed into two-dimensional shell wall. In *Protoproventocitum*, branching and fusing of these branches of the spicule forms the thick three-dimensional shell wall where the original part of the transformed spicule is positioned mainly as part of internal framework.

Etymology. - Cow Head, for the Cow Head Group strata from which fossil was collected.

Cowheadia duplextesta n. sp.

Figs. 3.3, 10.10-10.16

Diagnosis. - Proventocitiid spicule developed as a stout internal structure in a spherical two-layered shell wall having irregularly distributed and variably oriented outer spines that are the distal parts of the rays and branches of the spicule. Proventocitiid spicule consisting of several rays connected by an inter-ray bar(s) or an inter-ray loop. Thin double layers of the shell wall consisting of angular and dense meshwork.

Description. - The two-layered spherical shell wall encompasses the stout proventocitiid spicule. The spicule is the basic form of the proventocitiid spicule that consists of several rays connected by an inter-ray bar (Fig. 10.10) or bars forming a c-shape (Fig. 10.15) or, rarely, an inter-ray loop (Fig. 10.16). The meshwork of the shell wall is angular and dense. Parts of rays and branches also form a part of meshwork element (Figs. 10.12, 10.14, 10.15). Elements of the shell wall are much more delicate than those of the internal spicule. The shell wall is clearly separated into two closely positioned layers (Figs. 10.11a, b), but in a few specimens only one layer is evident (Fig. 10.14). It is unclear whether the one-layered shell wall is original or secondary. The outer spines are not evenly distributed on the shell wall because they are the distal parts of the irregular spicule. Thus, outer spines are more or less concentrated on the shell wall above the apical part of the internal spicule.

Discussion. - The internal structure of *Cowheadia duplextesta* n. sp. is similar to that of the spicule of *Archeoproventocitum nudiforma* n. sp. having no shell wall. It may reflect the phylogenetic relationship between *Archeoproventocitum* and *Cowheadia*.

Etymology. - Duplex (Lat.), double; testa (Lat.), shell.

Types. - Holotype, GSC-125701; paratypes, GSC125700, GSC 125702-125707.

Protoproventocitum n. gen.

Diagnosis. - Open or closed, conical to sub-conical

shelled form with a well- or poorly developed apical portion. An internal transformed proventocitiid spicule present or incorporated into the meshwork of the shell wall. Shell wall spongy or one-layered with three-, rarely two- dimensional meshwork. Apical shell wall distinguished by denser meshwork than that of the major part of shell wall. Meshwork commonly coarser toward antapical side. Outer spines highly variable in their position, length, and diameter.

Discussion. - *Protoproventocitum* n. gen. is closely related, on the one hand, to *Archeoproventocitum* n. gen. and, on the other, to *Proventocitum* Aitchison, 1988. By connecting the rays and branches and with additional branching and fusing of the branches, the spicular form (*Archeoproventocitum*) acquires a three-dimensional meshwork whose apical part is covered by the densest mesh (*Protoproventocitum*). Their close relation is well illustrated by the transitional form (Figs. 8.5, 8.6) and the *Protoproventocitum* specimen (Figs. 3.2, 10.1a, b) showing the transformed proventocitiid spicule as its internal structure.

Protoproventocitum species show a tendency, from old to younger faunas, for the meshwork of the shell wall to become denser. Also, a gradual merging of the internal spicule to the shell wall can be observed among younger *Protoproventocitum* (Figs. 10.6-10.9). This tendency culminates in the development of a new lineage, the Arenigian *Proventocitum*. *Proventocitum* differs from *Protoproventocitum* by the layered dense meshwork and definite inner space without an internal spicule structure.

Etymology. - Proto (Lat.), a parent substance of; proventocitum, a genus name.

Protoproventocitum aitchisoni n. sp.

Figs. 3.2, 8.6, 9.1-9.12, 10.1-10.4

Diagnosis. - Cone-shaped spongy shells with or without opening. Definite apical portion covered by dense meshwork. Transformed proventocitiid spicule forming a shell wall characterized by three-dimensional meshwork with diverse and irregular meshes. Commonly mesh openings slightly coarser from apical to antapical tip. Outer spines varied in

length, number, and position, but some developed as apical or sub-apical and/or lateral spines.

Description. - Branching and joining of the branches and rays of the proventocitiid spicule form a three-dimensionally shell wall (Figs. 8.6, 9.1-9.3) on which more branching and fusing make up an additional thick shell wall (Figs. 9.8-9.12, 10.3). Two-layered structure can be observed (Fig. 10.3) in typically developed specimens, where densest meshwork covers the apical portion of the internal meshwork and coarsest meshwork is developed on the antapical portion. A few specimens show the original spicule structure (Figs. 9.2, 10.1a, b), but, in general, a total transformation to three-dimensional meshwork (Figs. 10.2-10.4) characterizes this species. The inner meshwork derived from the rays and branches of the spicule is commonly stouter (Fig. 10.2). In some specimens, the thickness of mesh bars is the same as that of surrounding (outer) shell wall meshwork (Fig. 10.4). The apical part is commonly clearly separated, like a cephalon (Figs. 9.2, 9.6-9.8), or it is connected smoothly (Figs. 9.4, 9.9) to the major part of the shell wall. In both types, the meshwork of the apical shell wall is always most dense. Toward the antapical side, mesh size of the shell wall gradually becomes coarser, and the shell is opened or closed, but if open, there is no constant and definite opening form. The antapical opening appears to be a result of the presence of larger meshes (Figs. 9.7, 9.12) or incompletely connected meshwork (Figs. 9.6, 9.8, 9.11). Position, length, and number of the outer spines vary, but some of them appear as apical, or sub-apical, or lateral major spines (Figs. 9.5, 9.8, 9.10, 9.12).

Discussion. - *P. aitchisoni* n. sp. is similar to the familia nova spp. conical form of Fortey and Holdsworth, 1972 in having a prominent apical portion and gradually larger size of the meshes of the shell wall from apex to antapical tip. However, familia nova spp. conical form seems to have a layered shell wall lining a definite inner space, and it has prominent apical or sub-apical and several lateral major spines as in *Proventocitum*.

The specimens shown in Figures 8.5 and 8.6 are

actually transitional forms between *A. nudiforma* n. sp. and *P. aitchisoni* n. sp. The specimen in Figure 8.5 having more diagnostic characteristics of *P. nudiforma* than *P. aitchisoni* shows the spicular structure, but it is transformed to three-dimensional meshwork by fusing of the rays and their branches. The specimen in Figure 8.6 has dense meshwork on its apical portion, which is one of the most diagnostic characteristics of *Protoproventocitum*, even though the specimen shows no conical form with a thick shell wall. Specimens without the additional thick shell wall (Figs. 9.1-9.4) occur mainly in samples from WBPS unit 19a, and in some faunal assemblages the ratio between specimens with or without additional shell wall is 1:1. In contrast to this, most of the specimens from MP unit 42d have the well-developed additional shell wall.

Etymology. - In honor of Dr. Jonathan C. Aitchison, who established the family. Proventocitiidae.

Types. - Holotype, GSC-125678; paratypes, GSC 125671-125677, 125679-125682, 125691-125694.

Protoproventocitum nazarovi n. sp.

Figs. 9.13-9.19, 9.20?, 10.5-10.9

Diagnosis. - Subspherical or subconical shell with a slightly protruding apical portion covered by fine meshwork. Proventocitiid spicule transformed to three-dimensional meshwork or rarely merged to the shell wall meshwork. Outer spines variable in position, length, and diameter. Shell wall generally closed.

Description. - This subconical (Figs. 9.19, 10.5, 10.9) to subspherical (Figs. 9.13-9.18, 10.7, 10.8) shelled form has a weakly developed apical portion where fine meshwork is developed. The transformed proventocitiid spicule may form the internal meshwork (Fig. 10.6) or may be attached (Fig. 10.7) to the shell wall or merged with the meshwork of the shell (Figs. 10.8, 10.9a, b). Rarely, the spicule structure can be observed in the apical portion as a very small ring (Fig. 10.9b, upper arrow) or polygonal mesh structure (Fig. 10.5b). The ring is equivalent to the apical loop of the proventocitiid spicule, and the polygonal mesh is the connected inter-ray bars. The shell wall appears to be spongy or three-dimensionally meshed in

completely preserved specimens. However, in specimens where layering can be observed, the inner meshwork of the shell wall may be dense (Figs. 9.14, 9.17, 9.19, 10.7-10.9). Where the outer meshwork is not preserved, the shell wall appears to be two-dimensionally latticed (Figs. 9.18, 9.19, 10.8). Both the inner and outer part of the shell wall meshwork is coarser toward the antapical side; thus, the shell wall is thicker toward the antapical tip (Figs. 9.14, 9.17, 10.9). The varied outer spines appear to be centered in the apical portion (Figs. 9.13-9.15). In some specimens, some of the spines develop as apical to sub-apical and lateral major spines (Fig. 10.5a).

Discussion. - The shell wall with denser meshwork and smaller mesh opening size differences and a less prominent apical portion combine to form a much less conical shell form in *P. nazarovi* than in *P. aitchisoni*. The development of denser meshwork not only across the whole of the shell wall but also in the inner surface of the shell wall produces a smooth wall lining the inner cavity in *P. nazarovi* (Fig. 10.9b).

Specimens of *Protoproventocitum* make up 99 percent of the latest Tremadocian faunas in the Cow Head Group in Western Brook Pond unit 21. They are mainly *P. aitchisoni* and *P. nazarovi*, but some specimens have characteristics intermediate between these species. Moreover, specimens of *P. nazarovi* themselves show variations in shell wall structure - from a massive three-dimensional shell wall (Figs. 9.13, 9.15, 10.5) to a layered shell wall (Figs. 9.14, 9.17-9.19, 10.5, 10.8, 10.9) - and in the degree of merging of the internal spicule structure to shell wall (Figs. 10.6-10.9). Development of these changes connects this genus to a new lineage of proventocitiids in the earliest Arenigian (author's observation), *Proventocitum* Nazarov, 1988. This genus was reported from Arenigian by Fortey and Holdsworth (1972), by Aitchison (1998), and from the Llandellian by Nazarov and Popov (1980). One other Arenigian *Proventocitum* reported by Noble and Danelian (2004) is poorly preserved. *Proventocitum* is characterized by a dense, one-layered shell with two- or three-dimensional meshwork, no internal spicule

structure, and apical or sub-apical and lateral major spines. The major spines in *Proventocitum* appear to have been developed from some of the larger spines of *Protoproventocitum*, in which spines vary in length and diameter. Some of the larger spines in some specimens of *Protoproventocitum* (Figs. 9.5- 9.7, 9.9-9.11, 9.15, 10.5) can be easily compared to the apical or sub-apical or lateral major spines of *Proventocitum*; such major spines are well developed in several specimens of *Protoproventocitum* (Fig. 10.5).

Etymology. - In honor of Dr. Boris B. Nazarov, who established the first proventocitiid taxon, *Proventocitum*.

Types. - Holotype, GSC-125685; paratypes, GSC125683, 125684, 125686-125689, 125695-125699.

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