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REVISED BIOSTRATIGRAPHY, SYSTEMATICS, AND PALEOBIOGEOGRAPHY
OF THE TRILOBITES FROM THE MIDDLE CAMBRIAN NELSON LIMESTONE,
ANTARCTICA

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Abstract.—A biostratigraphic analysis of the Nelson Limestone, Neptune Range, Antarctica based on the distribution of trilobites in measured sections suggests that the age of the formation is probably late Floran to Undillan; the possibility of a Boomerangian age is considered less likely. The *Nelsonia schesis* and *Amphoton oatesi* zones are also defined. Paleobiogeographic analysis of trilobites in the Nelson Limestone using parsimony analysis of endemism (PAE) suggests that the Neptune Range and other parts of East Antarctica share the closest biogeographic area relationships with Australia rather than with northern Victoria Land or West Antarctica. This may have implications for the tectonic assembly of Antarctica. New specimens of previously described trilobite species from the Nelson Limestone include two new species, *Peishania? neptunensis* and *Poriagraulos kaesleri*. One species, *Dorypyge* sp. cf. *D. australis*, previously known only from the Bowers Terrane of northern Victoria Land, Antarctica, is recognized for the first time in the Neptune Range.

Key Words.—Trilobites, Cambrian, Antarctica, Nelson Limestone, biostratigraphy, paleobiogeography.

INTRODUCTION

The Cambrian biostratigraphy of Antarctica relies principally on trilobites and has been treated in a series of comprehensive studies by Palmer and Gatehouse (1972); Cooper, Begg, and Bradshaw (1990); Cooper, Jago, and Begg (1996); Cooper and Shergold (1991); Jago and Webers (1992); Wolfart (1994); Palmer and Rowell (1995); and Encarnación, Rowell, and Grunow (1999). Cambrian paleontological and biostratigraphic studies have focused primarily on the Ellsworth Mountains of West Antarctica, the Bowers Terrane of northern Victoria Land, the Central Transantarctic Mountains including the Queen Maud Mountains, and the Pensacola Mountains including the Neptune and Argentina Ranges (Fig. 1). Both the Ellsworths and the Bowers terrane were added to Antarctica proper after the end of the Cambrian (Borg and DePaolo, 1991, 1994; Stump, 1995; Webers, Craddock, and Spletstoeser, 1992; Grunow, Hanson, and Wilson, 1996; Duebendorfer and Rees, 1998).

Aspects of Middle Cambrian Antarctic biostratigraphy are based on faunas that come from boulders in moraines. For example, Palmer and Gatehouse's (1972) detailed study of Early and Middle Cambrian trilobites, which used col-

lections made during the initial geological mapping of the region by Schmidt *et al.* (1965), was based mainly on specimens from morainal boulders recovered in the Neptune and Argentina Ranges of the Pensacola Mountains. Some material was also collected in situ from the Neptune Range and also from localities in the Harold Byrd Mountains, but the localities in the Harold Byrds are now known to be Early Cambrian in age (Rowell *et al.*, 1997) and thus will not be considered further.

The work of Palmer and Gatehouse (1972), because of its level of detail and the number of new species figured therein, plays an important role in Middle Cambrian Antarctic biostratigraphy; therefore, additional information about the ranges of taxa listed by Palmer and Gatehouse (1972) that occur in the Nelson Limestone will help to constrain better the biostratigraphy. To this end, collections were made from the Nelson Limestone in the Neptune Range during expeditions led by M. N. Rees and A. J. Rowell in 1989–1990 and A. J. Rowell in 1993–1994 that were funded by NSF through the Office of Polar Programs; these collections can be placed in a precise geological and stratigraphic context described in detail by Evans, Rowell, and Rees (1995). This paper describes and illustrates new trilobite material, including two new species of trilobites,

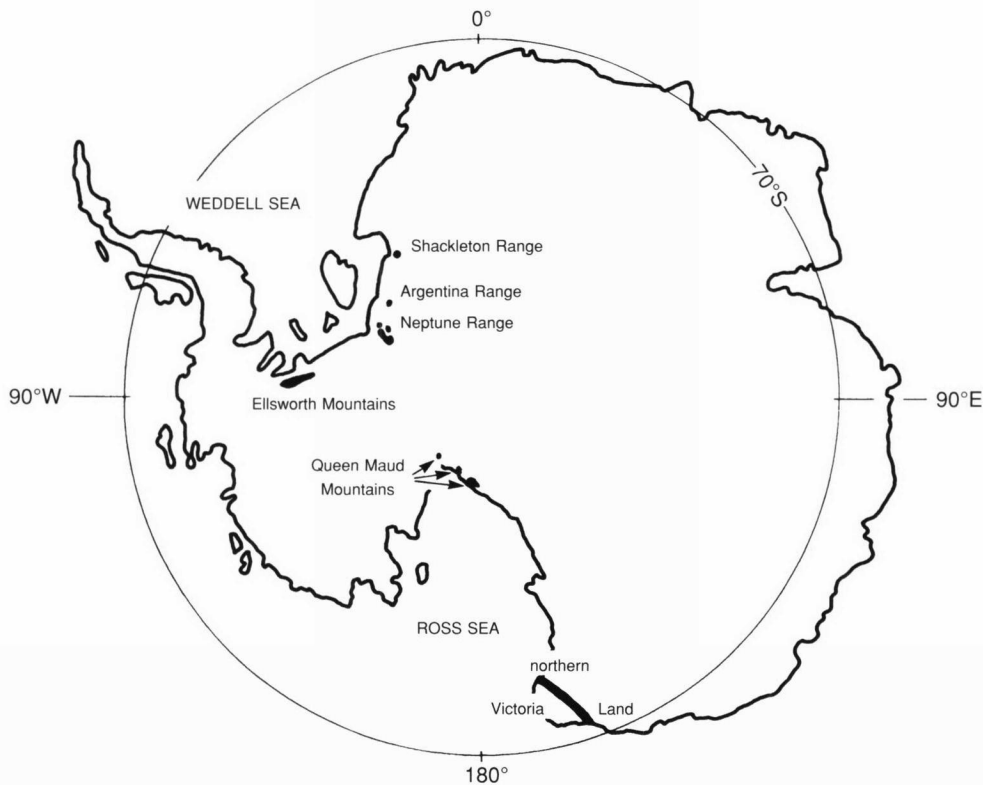


Figure 1. Major outcrops of Cambrian sedimentary rocks and principal localities mentioned in the text. The Argentina and Neptune Ranges are grouped within the Pensacola Mountains, which are in turn part of the northeastern arm of the Transantarctic Mountains (adapted from Rowell and Rees, 1989; used with permission of Cambridge University Press).

revises the biostratigraphy of the Nelson Limestone, and correlates the fauna of the Nelson with other Middle Cambrian faunas in different parts of Antarctica, including northern Victoria Land, the Ellsworth Mountains, and the Queen Maud Mountains (Fig. 1).

STRATIGRAPHIC SETTING OF THE NELSON LIMESTONE

The Nelson Limestone is made up of four primary packages of strata deposited on a carbonate platform (Evans, Rowell, and Rees, 1995). It overlies unconformably the Neoproterozoic and possibly Lower Cambrian Patuxent Formation. (The presence of Lower Cambrian strata has been debated by Rowell, Gonzales, and Evans, 1992; Stump, 1995; and Storey *et al.*, 1996.) The Nelson Limestone is in turn overlain by the volcanoclastic-rich Gambacorta Formation (Schmidt *et al.*, 1965; Stump, 1995; Storey *et al.*, 1996). The Nelson Limestone was deposited in relatively shallow water during what was locally a period of tectonic quiescence (Evans, Rowell, and Rees, 1995). Evans, Rowell, and Rees (1995) recognized three transgressive-regressive sequences in the Nelson. The age of the formation, at least in most of the Neptune Range, is now treated as Middle Cambrian (Palmer and Gatehouse, 1972; Wood, Evans, and Zhuravlev, 1992; Evans, Rowell, and Rees, 1995; Stump, 1995; Storey *et al.*, 1996) and until now as Boomerangian in particular (Evans, Rowell, and Rees, 1995). Although Soloviev and Grikurov (1979) and Soloviev, Popov, and

Samsonov (1984) argued that there were Upper Cambrian fossils in the Nelson Limestone from the southern part of the Neptune Range, this could not be verified based on the collected material examined herein.

Evans, Rowell, and Rees (1995) collected trilobites from various localities in the Neptune Range (Fig. 2) and provided three measured sections for the Nelson Limestone (Fig. 3), all of which contain trilobites. These sections are, from shallowest- to deepest-water settings with localities listed by section in ascending order: Dover Ridge (localities DRF-1, DRF-2, and DRF-3); Nelson Peak (localities NPF-2, NPF-1, and NPF-3); and South Miller Valley Ridge (localities SMVR-89.1, SMVR-89.2, and E93-4). Additional trilobite material comes from an isolated section at Hannah Ridge (locality E93-2, E93-2 [45']) (Fig. 4), whose basal part was covered and thus could not be integrated directly into the litho- and sequence stratigraphy of Evans, Rowell, and Rees (1995); it is inferred to represent possibly a setting outboard of SMVR; and also from a section in the nearby Webb Nunataks not measured because the rocks were poorly exposed (localities E93-9, E93-10, and E93-11).

PREVIOUS IDEAS ON THE BIOSTRATIGRAPHY OF THE NELSON LIMESTONE

Palmer and Gatehouse (1972) divided the Lower and Middle Cambrian of Antarctica into a series of faunules based on the distribution of trilobites. Four of their Middle

Cambrian faunules are most relevant here because they are partly or completely represented in the material collected in situ from the Nelson Limestone. Palmer and Gatehouse (1972) defined these faunules as, from oldest to youngest, the *Amphoton oatesi*, *Schopfaspis granulatus*, *Solenopleura pruina*, and *Nelsonia schesis* faunules; and Palmer and Gatehouse (1972) treated all of these as late Middle Cambrian in age. The *Schopfaspis granulatus* and *Solenopleura pruina* faunules are known exclusively from isolated boulders of the Nelson Limestone recovered from a moraine on Mount Spann in the Argentina Range, approximately 165 miles northeast of the Neptune Range. The *Amphoton oatesi* faunule was collected from the “lower part of the Nelson Limestone” (Palmer and Gatehouse, 1972, p. D5) in the Neptune Range. The *Nelsonia schesis* faunule was collected from the Neptune Range and also from boulders recovered from Mount Spann.

Palmer and Gatehouse (1972) characterized the *Amphoton oatesi* faunule by the presence of *Amphoton oatesi* Palmer and Gatehouse, 1972; *Chondranomocare australis* Palmer and Gatehouse, 1972; *Penarosa trinodus* (Palmer and Gatehouse, 1972); *Kootenia styrax* Palmer and Gatehouse, 1972; *Peronopsis* sp. cf. *P. fallax* (Linnarsson); and their genus and species undetermined 4. Peng and Robison (2000) questionably reassigned the *Peronopsis* sp. cf. *P. fallax* to *Ammagnostus laiwuensis* (Lorenz, 1906). This taxon is valuable for biostratigraphic correlation, as described more fully below. Palmer and Gatehouse’s (1972) genus and species undetermined 4 is nearly identical to *Penarosa trinodus*, though considerably smaller than the type material. Differences in morphology, especially pertaining to the size of the nodes on the anterior part of the cephalon, appear to be ontogenetic.

Palmer and Gatehouse (1972) characterized the *Schopfaspis granulatus* faunule by the presence of *Schopfaspis granulatus* Palmer and Gatehouse, 1972; *Pagetides? antarcticus* Palmer and Gatehouse, 1972; *Liopeshania spannensis* Palmer and Gatehouse, 1972; *Olenoides* sp.; and genus and species undetermined 2. They added that rare mollusks were also present. Notably, *S. granulatus* resembles Palmer and Gatehouse’s (1972) genus and species undetermined 1, which they inferred to be from the older (early Middle Cambrian) *Xystridura multilinia* faunule. Because Palmer and Gatehouse’s (1972) genus and species undetermined 1 is based on only a few poorly preserved specimens, it is not synonymized with *S. granulatus*.

Palmer and Gatehouse (1972) characterized the *Solenopleura pruina* faunule by the presence of *Solenopleura pruina* Palmer and Gatehouse, 1972, and *Suludella? dawnii* Palmer and Gatehouse, 1972. They added that rare orthoid brachiopods are also present.

Finally, Palmer and Gatehouse (1972) characterized the *Nelsonia schesis* faunule by the presence of *Nelsonia schesis* Palmer and Gatehouse, 1972, and *Suludella? spinosa* Palmer and Gatehouse, 1972.

Palmer and Gatehouse (1972) treated the *Schopfaspis granulatus* and *Amphoton oatesi* faunules as being approxi-

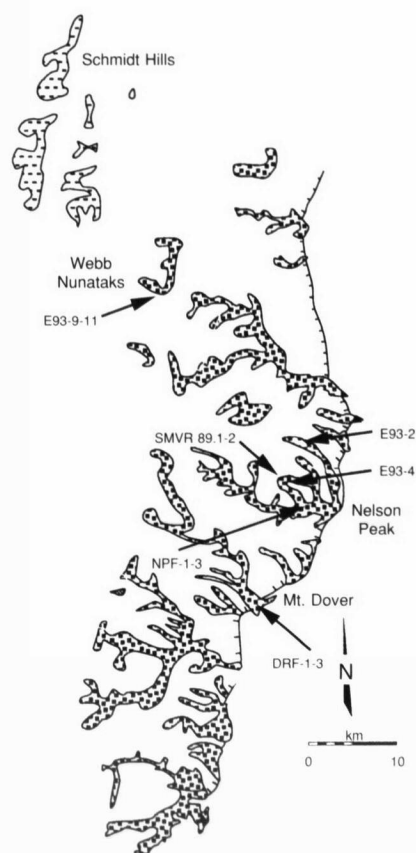


Figure 2. Localities in the Neptune Range mentioned in the text (adapted from Rowell *et al.*, 2001; used with permission of the Geological Society, London, and A. Rowell).

mately late Amgan and early Mayan using the Siberian stage names; they treated the *Solenopleura pruina* and *Nelsonia schesis* faunules as being approximately middle to late Mayan.

Tröger and Weber (1985) also described material from the Nelson Limestone of the Neptune Range consisting of poorly preserved specimens including fragments of trilobites they assigned to *Amphoton* Lorenz, 1906, and an undefined species. They noted that their stratigraphy did not appear to agree with the inferred order of the two faunules that had been described by Palmer and Gatehouse (1972) (the *Amphoton oatesi* and *Nelsonia schesis* faunules). Because of the fragmentary nature of this material and because they used only line drawings, it is difficult to determine the precise taxonomic affinities of the two trilobites they discussed. It is likely, however, that their *Amphoton* represents *A. oatesi*. This material is housed in the Mining Academy, Freiberg, Germany, and is currently being studied by Cooper and Shergold (personal communication, 2003).

MIDDLE CAMBRIAN BIOSTRATIGRAPHY INCLUDING OTHER REGIONS IN ANTARCTICA

Cooper and Shergold (1991) endorsed the use of aspects of Palmer and Gatehouse’s (1972) faunules, but they added more data from several other regions of Antarctica, including northern Victoria Land and West Antarctica,

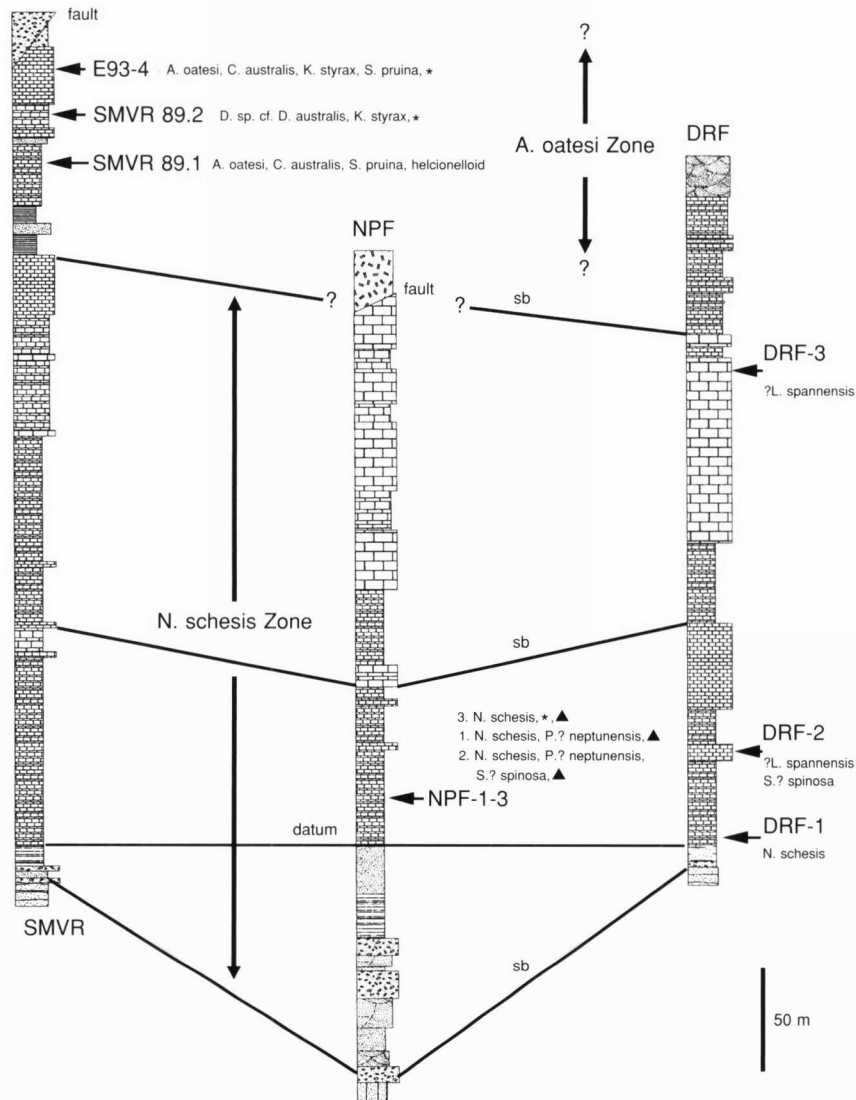


Figure 3. Measured sections of the Nelson Limestone at three localities in the Neptune Range. The lines joining sections demarcate depositional packages separated by a sequence boundary (*sb*). Sections are, from shallowest to deepest water: Dover Ridge (*DRF*); Nelson Peak (*NPF*); and South Miller Valley Ridge (*SMVR*). Trilobites were collected at the following points in the sections: DRF-1 is 1.0 m above the datum, DRF-2 is 49.0 m above the datum, and DRF-3 is 205.0 m above the datum; NPF-1 is 24.5 m above the datum, NPF-3 is 26.0 m above the datum; SMVR-89.1 is 311.0 m above the datum, SMVR-89.2 is 347.0 m above the datum, and E93-4 is about 348.0 m above the datum (A. J. Rowell, personal communication, 2001). Trilobite and other taxa collected are shown for each locality; *, indeterminate inarticulated brachiopods; ▲, tubes or hyolithids (adapted from Evans, Rowell, & Rees, 1995; used with permission of the Society of Economic Paleontology and Mineralogy).

and also expanded greatly the precision and scope of Antarctic biostratigraphy. They divided the Cambrian and Ordovician into a series of biostratigraphic faunas, and here I will focus principally on the biostratigraphic divisions within the Nelson Limestone. They placed elements of Palmer and Gatehouse's (1972) *Schopfaspis granulosa* and *Amphoton oatesi* faunules (along with other taxa) into a new Fauna 3, and they placed elements of Palmer and Gatehouse's (1972) *Solenopleura pruina* and *Nelsonia schesis* faunules (along with other taxa) into a new Fauna 4. Cooper and Shergold (1991) treated their Fauna 3 as being equivalent to the late Amgan and Mayan stages of Russia and the Floran and Undillan stages of Australia, while their Fauna

4 was treated as being equivalent to the late Mayan stage of Russia and the Boomerangian stage of Australia. Cooper and Shergold (1991) also treated trilobites from moraines in the Shackleton Range described by Soloviev and Grikurov (1978, 1979). They assigned these to their Fauna 2, which they treated as generally older though partially overlapping Fauna 3 in age. Cooper and Shergold (1991) treated Fauna 2 as being equivalent to the Toyonian and Amgan stages of Russia and the late Ordian, Templetonian, and Floran stages of Australia.

Cooper and Shergold (1991) also discussed the material Cooper *et al.* (1982) described from Edlin Névé, in the Bowers Terrane, northern Victoria Land, and they assigned

it to their Fauna 4. Taxa recovered from here included poorly preserved species of *Dorypyge* and “*Amphoton*.”

The material Cooper, Begg, and Bradshaw (1990) described from the Spurs Formation, Bowers Terrane, northern Victoria Land at Reilly Ridge, may be slightly younger than the material from the Nelson Limestone discussed here; Cooper and Shergold (1991) assigned it to their Fauna 5, and it is possibly Boomerangian (Cooper, Jago, and Begg, 1996). Cooper, Jago, and Begg (1996) described material from several localities in the Bowers Terrane of northern Victoria Land. They treated their material as ranging in age from Boomerangian (late Middle Cambrian) to Late Cambrian.

Jago and Webers (1992) collected material from a series of localities in the Ellsworths of West Antarctica. Material from the Drake Icefall Formation they treated as being Templetonian and possibly Floran. Material from the Liberty Hills and Springer Peak Formations they treated as being Boomerangian. Material from the Minaret Formation they treated as simply late Middle Cambrian. Later, Duebendorfer and Rees (1998) suggested that the Springer Peak and Minaret Formations might be somewhat younger, with, respectively, Mindyallan and Idamean ages.

Wolfart (1994) described trilobites and a few other taxa from exotic limestone blocks in clastic rocks of the Molar and Spurs Formations from Reilly Ridge in the Bowers Terrane, northern Victoria Land. He identified two distinct faunules of ascending, though slightly overlapping, ages: the *Dorypyge australis-Centonella glomerata* and the *Eurodeois tessensohni* faunules. Wolfart (1994) regarded the former as being age equivalent to the Floran and early Undillan stages and thus also roughly equivalent to Cooper and Shergold’s (1991) Fauna 2. Wolfart (1994) treated his *Eurodeois tessensohni* faunule as being age equivalent to the Undillan and possibly latest Floran stages. Further, he suggested that in its upper part this faunule overlapped (in age) Palmer and Gatehouse’s (1972) *Amphoton oatesi*, *Schopfaspis granulatus*, *Solenopleura pruina*, and *Nelsonia schesis* faunules.

Evans, Rowell, and Rees (1995) treated the Nelson Limestone as Boomerangian. This correlation may be correct, as it matches Cooper and Shergold’s correlation of the *Nelsonia schesis* faunule with their Fauna 4. The correlation is based partly, however, on a typographical error by Cooper and Shergold (1991) (A. J. Rowell, personal communication, 2001), which inadvertently listed the species *Nelsonia schesis* Palmer and Gatehouse, 1972, originally collected in situ from the Neptune Range, as also being present in strata from northern Victoria Land containing a Boomerangian agnostoid.

Encarnación, Rowell, and Grunow (1999) recognized that in the Taylor Formation, Queen Maud Mountains, central Transantarctic Mountains, elements of Palmer and Gatehouse’s (1972) *Amphoton oatesi* and *Nelsonia schesis* faunules (the eponymous taxa) potentially co-occur stratigraphically. Although they referred their species to *Nelsonia* sp. cf. *N. schesis* and *Amphoton* sp. cf. *A. oatesi*, they

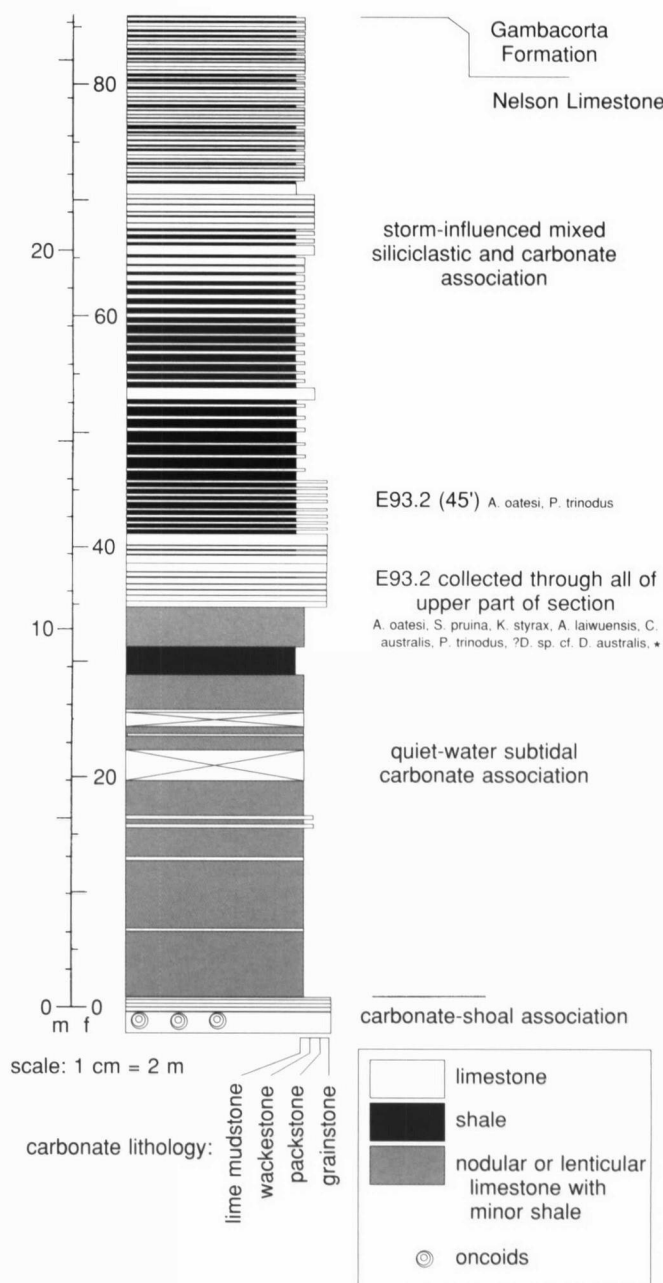


Figure 4. Measured isolated section of the Nelson Limestone at the Hannah Ridge locality. The lower part of the section is scree covered here and was not measured because it was impossible to obtain a meaningful dip (A. J. Rowell, personal communication, 2001); collections were built up by working along strike over 300 m (N-S distance). Trilobite taxa collected are shown for each locality; *, indeterminate inarticulated brachiopods (new).

are identical in all diagnostic characters to the type material from the Nelson Limestone and are treated here as synonyms. The overlap in the ranges of these taxa suggests that the age of these faunules may overlap and that Cooper and Shergold’s (1991) Faunas 3 and 4 may be partly coeval. Encarnación, Rowell, and Grunow (1999) concluded that the Taylor Formation was probably Undillan, though it could be upper Floran or less likely lower Boomerangian.

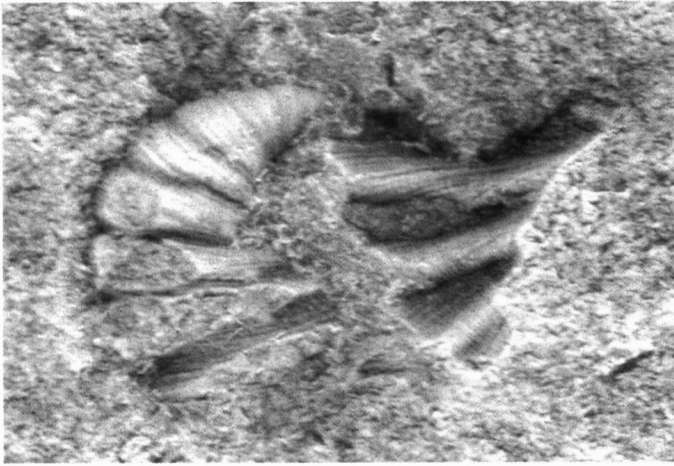


Figure 5. Helcionelloid gen. et sp. indet., Middle Cambrian, Floran–Undillan, Nelson Limestone, Neptune Range, locality SMVR 89.1, Antarctica; lateral view of internal and external mold, KUMIP 311750, $\times 10$ (new).

STRATIGRAPHIC DISTRIBUTION OF TAXA WITHIN THE NELSON LIMESTONE

One problem complicating biostratigraphic correlation of the Nelson Limestone and Middle Cambrian sections in general is the absence of a global age standard. Typically, strata from Antarctica have been correlated to Australian stages (e.g., Cooper, Begg, and Bradshaw, 1990; Cooper, Jago, and Begg, 1996; Cooper and Shergold, 1991; Jago and Webers, 1992; Evans, Rowell, and Rees, 1995; Encarnación, Rowell, and Grunow, 1999), and here correlations will be made with the Australian stage names using the general global-correlation scheme of Peng and Robison (2000). This correlation scheme, although not based specifically on Antarctic sections, corresponds closely to schemes that do, e.g., Cooper and Shergold (1991). The stratigraphic distribution of species in the Nelson Limestone (Fig. 3–4) suggests some modification of Palmer and Gatehouse's (1972) biostratigraphy based on faunules. For example, originally Palmer and Gatehouse (1972) held that the *Amphoton oatesi* faunule was older than the *Nelsonia schesis* faunule. Now, however, it can be seen that representatives of their *Nelsonia schesis* faunule lie stratigraphically beneath representatives of their *Amphoton oatesi* faunule. Further, representatives of what Palmer and Gatehouse (1972) called the *Amphoton oatesi* and *Solenopleura pruina* faunules actually co-occur (at localities SMVR 89.1, 89.2, E93-4, and E93-2). On the basis of these results the *A. oatesi* and *S. pruina* faunules should be treated as coeval, and an *A. oatesi* zone is erected. This zone is characterized by *A. oatesi*, *S. pruina*, *Kootenia styrax*, *Chondranomocare australis*, *Penarosa trinodus*, *Dorypyge* sp. cf. *D. australis* Wolfart, 1994, and *Ammagnostus laiwuensis* (Lorenz, 1906). This zone appears to lie in the highstand systems tract of Evans, Rowell, and Rees's (1995) upper sequence. Some of these taxa also allow broader biostratigraphic correlations across Antarctica, as described more fully below.

Although as described above, locality E93-2 from Hannah Ridge is an isolated section where measurements of fossil occurrences relative to a datum are difficult, it possesses all the trilobite taxa found from the measured sections at SMVR, along with *A. laiwuensis*, and therefore E93-2 is treated as coming from the upper part of the Nelson Limestone. Further, it is treated as lying stratigraphically within the *A. oatesi* zone and being from Evans, Rowell, and Rees's (1995) upper sequence.

An *N. schesis* zone in the Neptune Range is erected and is characterized by *N. schesis*, *Suludella?* *spinosa*, *Peishania?* *neptunensis*, and *?Liopeshania spannensis*. These taxa occur in the transgressive systems and highstand systems tracts of Evans, Rowell, and Rees's (1995) lower sequence and the highstand systems tract of their middle sequence. This zone should henceforth be treated as being older than the *A. oatesi* zone. *Amphoton oatesi* and *N. schesis* do co-occur in the Taylor Formation of the Queen Maud Mountains (Encarnación, Rowell, and Grunow, 1999), and the stratigraphic thickness of these zones is presumed to be greatly telescoped there.

The co-occurrence of *?L. spannensis* and *S.?* *spinosa* suggests that the *Schopfaspis granulatus* and *N. schesis* faunules of Palmer and Gatehouse (1972) are coeval. The eponymous representative of the *Schopfaspis granulatus* faunule was recovered from the Webb Nunataks (Table 1) but could not be placed into a precise stratigraphic context. Genus and species undetermined 1 (Palmer and Gatehouse, 1972, pl. 3, 10–12), which occurs in their early Middle Cambrian *Xystridura multilinia* faunule, is very similar to *Schopfaspis granulatus* and could represent an ontogenetic stage of that species. They are treated herein as distinct taxa. If they are conspecific, however, it may imply overlap in the ages of Palmer and Gatehouse's (1972) *X. multilinia* and *S. granulatus* faunules. *Schopfaspis granulatus* co-occurs with *Poriagraulos kaesleri*, new species in the Webb Nunataks (Table 1).

This information on the stratigraphic distribution of fossils in the Neptune Range also implies complexity with Cooper and Shergold's (1991) Faunas 3 and 4. Their faunas were defined on the basis of several taxa, not just those in the Nelson Limestone in the Neptune Range, so aspects of Cooper and Shergold's (1991) biostratigraphic definitions may be correct. Areas of complexity emerge, however, because Fauna 3 was supposed to contain *Amphoton oatesi*, along with other taxa, while Fauna 4 was supposed to contain *Solenopleura pruina* and *Nelsonia schesis*, along with other taxa (Cooper and Shergold, 1991). Instead, based on the results presented here, *A. oatesi* and *S. pruina* appear to occur together and stratigraphically above *N. schesis*.

Other material collected from the Nelson Limestone includes inarticulated brachiopods, segmented tubes and hyolithids from various localities, a helcionelloid from locality SMVR 89.1 (KUMIP 311750; Fig. 5), and an archeocyath, probably *Dictyocyathus neptunensis* (see Wood, Evans, and Zhuravlev, 1992, from locality E93-9).

BIOSTRATIGRAPHIC CORRELATIONS BETWEEN THE NELSON LIMESTONE IN THE NEPTUNE RANGE AND OTHER REGIONS

At least two taxa in the *A. oatesi* fauna in the Nelson Limestone are potentially useful for biostratigraphic correlation: *Dorypyge* sp. cf. *D. australis* and *Ammagnostus laiwuensis*. *Dorypyge australis* was assigned by Wolfart (1994) to his *Dorypyge australis-Centonella glomerata* faunule of Floran to early Undillan age, making it approximately equivalent to Cooper and Shergold's (1991) Fauna 3. *Dorypyge* sp. cf. *D. australis* from the Neptune Range is very similar to, if not conspecific with, *D. australis* from northern Victoria Land.

Jago and Webers (1992) figured a *Dorypygidae* genus and species indet. from the Minaret Formation, Marble Hills, Ellsworth Mountains, West Antarctica, but this material is too poorly preserved to determine if it is closely related to *D. australis*. Cooper *et al.* (1982) also reported poorly preserved specimens of *Dorypyge* (and also *Amphoton*) from Edlin Névé, Bowers Terrane, northern Victoria Land, but again it could not be determined if these specimens were indeed *D. australis* or *A. oatesi*.

Peng and Robison (2000) reported a broad range for *A. laiwuensis* from the upper *Ptychagnostus atavus* Zone to the *Proagnostus bulbosus* Zone, which is late Floran to early Mindyallan. Soloviev and Grikurov (1979) figured agnostoids derived from moraine boulders at Mt. Provender in the Shackleton Range, which Cooper and Shergold (1991) assigned to their Fauna 2. Although this material is poorly preserved and figured, the species they identified as *Peronopsis* sp. cf. *P. fallax* (Linnarsson), *P.* sp. cf. *P. quadrata* (Tullberg), and *P. scutalis* (Salter) are likely referable to *A. laiwuensis*, though they might be referable to *A. wangcunensis* Peng and Robison, 2000, which is slightly younger than *A. laiwuensis*.

The presence of *A. oatesi* and *N. schesis* in the Taylor Formation from the Queen Maud Mountains (Encarnación, Rowell, and Grunow, 1999) suggests that the Taylor Formation and the Nelson Limestone are age equivalent.

Palmer and Gatehouse (1972) reported that *Chondranomocare* Poletaeva in Chernysheva *et al.*, 1956 is restricted to the Amga Stage of Siberia. Wolfart (1994), Peng and Robison (2000), and in part Cooper and Shergold (1991), correlated this stage with the Templetonian and Floran stages. *Peishania* Resser and Endo in Kobayashi, 1935 is known from the Changhian Stage of North China, which is Floran to early Mindyallan (Zhang and Jell, 1987). Jago and Webers (1992) figured a pygidium from a Boomerangian-aged boulder in the Liberty Hills Formation from the Ellsworths that may be referable to *Peishania* and is discussed more fully below.

On the basis of *D.* sp. cf. *D. australis* and correlation with material from northern Victoria Land described by Wolfart (1994), an age range of Floran to early Undillan is indicated for the Nelson Limestone. The presence of *Ammagnostus laiwuensis* suggests an age within the late Floran to early Mindyallan (Peng and Robison, 2000).

Table 1. Taxon distribution among localities in the Webb Nunataks (see Fig. 2).

| E93-9 | E93-10 | E93-11 |
|----------------------------------|----------------------------------|----------------------|
| <i>Poriagraulos kaesleri</i> | <i>P. kaesleri</i> | <i>P. kaesleri</i> |
| <i>Schopfaspis granulatus</i> | indet. inarticulated brachiopods | tubes or |
| indet. inarticulated brachiopods | tubes or hyolithids | hyolithids |
| <i>Dictyocyathus neptunensis</i> | | <i>S. granulatus</i> |

Chondranomocare suggests a Templetonian to Floran age (Palmer and Gatehouse, 1972), and material possibly referable to *Peishania* and correlation with similar material described by Jago and Webers (1992) suggests a Boomerangian age.

The Nelson Limestone in the Neptune Range is considered to be upper Floran to Undillan. A Boomerangian age is considered less likely. This age is similar to, though slightly older than, the Boomerangian age suggested by Cooper and Shergold (1991) and the middle Undillan-early Boomerangian age proposed by Wolfart (1994). Palmer and Gatehouse (1972) suggested the Nelson Limestone was late Amgan to middle Mayan, and this is broadly coeval with the age constraints predicted herein. The age of the Nelson Limestone matches closely that of the Taylor Formation in the Queen Mauds, which Encarnación, Rowell, and Grunow (1999) considered to be Undillan, although they suggested it could be slightly older and upper Floran or less likely early Boomerangian.

Notably, the material and sections Cooper, Begg, and Bradshaw (1990) treated and described from northern Victoria Land have been treated as younger than the Nelson Limestone by Cooper and Shergold (1991), and this age determination is supported by additional information. Cooper, Begg, and Bradshaw (1990) figured material they referred to as *Formosagnostus?* sp. indet., though they did remark that the pygidium was similar to that of *Ammagnostus* Öpik, 1967. This material could be conspecific with *A. histus* Peng and Robison, 2000, a mid-late Mindyallan species (Peng and Robison, 2000). The stratigraphic range of *A. histus* turns out to be everywhere younger than *A. laiwuensis*.

PALEOBIOGEOGRAPHY OF THE NELSON LIMESTONE

Introduction and materials and methods.—Paleobiogeographic information can contribute in an important way to reconstructing the sequence of tectonic events in Antarctica (Duebendorfer and Rees, 1998), and trilobites have played an important role in studies of Cambrian paleogeography (e.g., Jell, 1974; Burrett and Richardson, 1980; Fortey and Cocks, 1992; Babcock, 1994; Lieberman, 1997, 2003). Cocks (1989), Cooper and Shergold (1991), Cooper, Begg, and Bradshaw (1990), Cooper, Jago, and Begg (1996), Jago and Webers (1992), Wolfart (1994), and Palmer and Rowell (1995) have all presented detailed syntheses of early Paleozoic Antarctic paleobiogeography. Five regions were treated in the biogeographic analysis: East

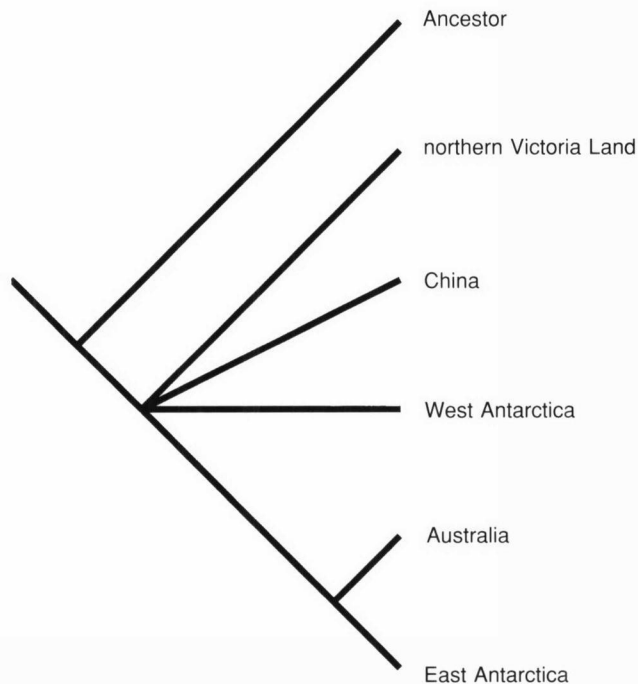


Figure 6. Strict consensus of four most parsimonious paleobiogeographic trees of length four steps produced from PAE of Table 2 using the exhaustive search option of PAUP 4.08b (Swofford, 2001). The consistency index is 0.75, and the retention index is 0.80. The tree was rooted using a hypothetical ancestor as the outgroup and displays the biogeographic relationships between the different regions considered in the text. The bootstrap support for the Australia-East Antarctica relationship is 0.86, and the jackknife support is 0.88 (new).

Antarctica comprising the Neptune and Argentina Ranges (Pensacolas) and the Queen Maud Terrane of the Central Transantarctics, the Bowers Terrane of northern Victoria Land, the Ellsworth-Whitmore Mountains terrane of West Antarctica, Australia, and China. The Queen Maud terrane of Rowell, Gonzales, and Evans (1992) is treated as biogeographically part of East Antarctica because all the trilobite taxa known from there for this time interval are conspecific with species from the Neptune and Argentina Ranges.

Phylogenetic information is very valuable for reconstructing biogeographic patterns (e.g., Brooks and McLennan, 1991, 2002; Lieberman, 2000), but unfortunately phylogenies are not available for the taxa considered herein. In the absence of phylogenetic information, a biogeographic technique that has proven particularly useful in the analysis of biogeographic patterns is parsimony analysis of endemism (PAE), developed by Rosen (1988); this technique has been applied successfully to the analysis of Cambrian and Neoproterozoic biogeographic patterns (e.g., Fortey and Cocks, 1992; Waggoner, 1999). PAE aims to reconstruct a common history for geological regions using patterns of shared taxa (Rosen, 1988; Waggoner, 1999). Because PAE does not incorporate phylogenetic information, it unfortunately cannot distinguish between biogeographic patterns governed by vicariance and biogeographic patterns governed by geodispersal (see discussion by

Lieberman, 1997, 2000). The results can still, however, be used to determine something about overall degree of biogeographic relatedness.

The data matrix used in this analysis is given in Table 2; a hypothetical ancestor is used to polarize the data matrix, with all taxa treated as primitively absent from all regions. The focus here was explicitly on paleobiogeography during the interval corresponding to the deposition of the Nelson Limestone: roughly Floran to Undillan. If different and especially later time periods were considered, conceivably different biogeographic patterns would result.

All taxa from the Nelson Limestone that occurred in more than one region (nonautapomorphous) were coded as either present or absent in the various regions. The criterion used was shared species rather than genera (except in two cases) because some of the generic names used may currently connote para- or even polyphyletic taxa and thus do not convey useful information about biogeographic relationships. The exceptions where shared genera were used rather than shared species involve *D. australis* from northern Victoria Land, *D. sp. cf. D. australis* from the Pensacolas, *D. tenella* Whitehouse, 1945 from Australia, *A. oatesi* from the Pensacolas and the Queen Mauds, and *A. eminens* (Öpik, 1982) from Australia (see discussions under appropriate generic headings). These are cases where the species of the genera are very similar and appear to comprise well-constrained monophyletic groups and likely sister taxa. The data matrix in Table 2 was subjected to a parsimony analysis using the exhaustive search option of PAUP 4.08b (Swofford, 2001). The results from the analysis are expressed as a tree. The closer two regions are on the tree the more recently they and their component biotas shared a common history. Measures of support for various aspects of the tree were assessed using bootstrap and jackknife analyses and tree length frequency skewness distributions.

Results.—Four most parsimonious trees were recovered of length four steps. In the strict consensus of these trees

Table 2. Biogeographic characters and character states for the PAE data matrix. Ancestor refers to the ancestral biogeographic condition for the clades considered. The other regions were the areas considered in the analysis. 0 denotes the primitive condition, absent in a region. Character state 1 denotes the derived condition, present in a region. Character 1 represents the distribution of *Dorypge* sp. cf. *D. australis*, *D. australis*, and *D. tenella*; character 2 represents *Ammagnostus laiwuensis*; and character 3 represents *A. oatesi* and *A. eminens*.

| | character 1 | character 2 | character 3 |
|------------------------|-------------|-------------|-------------|
| Ancestor | 0 | 0 | 0 |
| Australia | 1 | 1 | 1 |
| China | 0 | 1 | 0 |
| East Antarctica | 1 | 1 | 1 |
| northern Victoria Land | 1 | 0 | 0 |
| West Antarctica | 0 | 0 | 0 |

Australia and the Pensacolas plus the Queen Maud terrane (East Antarctica) group together to the exclusion of West Antarctica, northern Victoria Land, and China (Fig. 6). The consistency index of this tree is 0.75, and the retention index is 0.80. Bootstrap analyses performed with PAUP 4.08b (Swofford, 2001) using 1,000 bootstrap replications (each replication used a branch and bound search with furthest addition sequence) and with groups retained compatible with the 50-percent majority rule consensus tree, indicated strong support for the Australia-East Antarctica relationship (0.86). Jackknife analyses using the same basic protocol and with 35-percent character deletion showed strong support (0.88) for the Australia-East Antarctica relationship. The g_1 statistic recovered with PAUP 4.08b (Swofford, 2001) is -0.67 . This value is significant at $p < 0.01$ for six taxa according to Hillis (1991).

Discussion.—The biogeographic pattern that emerges from this analysis is the Pensacolas plus Queen Maud terrane-Australia grouping to the exclusion of all other regions. These regions group together due to the presence of *A. oatesi* and the closely related *A. eminens*, which occur exclusively in East Antarctica and Australia, respectively. No taxa are shared exclusively between the Ellsworth-Whitmore Mountain terrane and East Antarctica. (There is the enigmatic material from both the Ellsworths and the Neptune Range possibly referable to *Peishania*, but this genus occurs also in China, and the precise generic identities of the material from the Ellsworths and the Pensacolas could not be well constrained.) On the basis of the resultant biogeographic patterns, admittedly based on limited data, it seems likely that in the Middle Cambrian Australia and the Pensacolas plus the Queen Maud terrane were closer to each other than either was to the Ellsworth-Whitmore Mountains terrane, northern Victoria Land, or China.

Rowell, Gonzales, and Evans (1992), Rowell *et al.* (1995), Borg and DePaolo (1994), Encarnación and Grunow (1996), Duebendorfer and Rees (1998), Grunow and Encarnación (2000), and Boger and Miller (2004) presented a variety of geological evidence that the Bowers Terrane, the Ellsworth-Whitmore Mountains area, the Queen Maud Terrane, and Australia were in close association during the time interval in question. Duebendorfer and Rees (1998) argued specifically that during the Cambrian the terranes may have been part of a single large terrane that lay outboard of Coats Land and extended toward the Neptune and Argentina ranges. They suggested further that the Queen Maud terrane was closer to the Neptune and Argentina ranges, and this aspect of their interpretation is supported by the biogeographic patterns discussed and presented herein, because the Queen Mauds solely possess trilobite taxa known from the Pensacolas.

The closer biogeographic grouping between Australia and the Pensacolas-Queen Mauds may be problematic if only geographic distance of the various regions is considered, but the relevant parts of Australia and East Antarctica may actually have been joined (see the paleogeog-

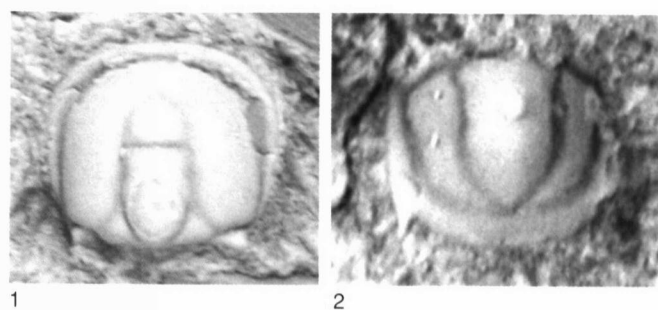


Figure 7. *Ammagnostus laiwuensis* (Lorenz, 1906), Middle Cambrian, Floran-Undillan, Nelson Limestone, Neptune Range, locality E93-2, Antarctica; 1, dorsal view of cephalon, KUMIP 311796, $\times 8$; 2, dorsal view of pygidium, KUMIP 311797, $\times 15$ (new).

ographies of Duebendorfer and Rees, 1998, and Boger and Miller, 2004) and thus been connected by shallow water, while deeper water inhospitable to trilobites and their larvae may have physically separated these regions from the more outboard terranes. Based on the results presented herein it is impossible to determine if the Ellsworth-Whitmore Mountains terrane was closer to East Antarctica, as suggested by Duebendorfer and Rees (1998), or closer to other parts of Gondwana including Australia, as suggested by Dalziel and Grunow (1992) (see discussion by Grunow, 1999, and Grunow and Encarnación, 1999). The relatively poor degree of resolution in the area cladogram in general may be attributable at least partly to the low diversity of the component faunas and their endemic nature.

SYSTEMATIC PALEONTOLOGY

Morphological terminology used follows Whittington *et al.* in Kaesler (1997) and Harrington *et al.* in Moore (1959). Classification follows Whittington *et al.* in Kaesler (1997), Harrington *et al.* in Moore (1959), Sundberg (1994), and Jell and Adrain (2003). All material is housed in the Division of Invertebrate Paleontology (KUMIP) of the Natural History Museum and Biodiversity Research Center, The University of Kansas.

Order AGNOSTIDA Salter, 1864

Family AMMAGNOSTIDAE Öpik, 1967

Genus AMMAGNOSTUS Öpik, 1967

AMMAGNOSTUS LAIWUENSIS (Lorenz, 1906)

Figure 7

Ammagnostus laiwuensis (Lorenz); Peng and Robison, 2000, p. 27, fig. 20 (see for more complete synonymy).

?*Peronopsis* sp. cf. *P. fallax* (Linnarsson); Soloviev and Grikurov, 1979, p. 62, pl. 1, 6–7.

?*Peronopsis* sp. cf. *P. quadrata* (Tullberg); Soloviev and Grikurov, 1979, p. 63, pl. 2, 8–9.

?*Peronopsis scutalis* (Salter); Soloviev and Grikurov, 1979, p. 62, pl. 2, 10–12.

Material examined.—KUMIP 311591, 311592, 311664, 311795–311814, and numerous unnumbered specimens in the collections of the KUMIP.

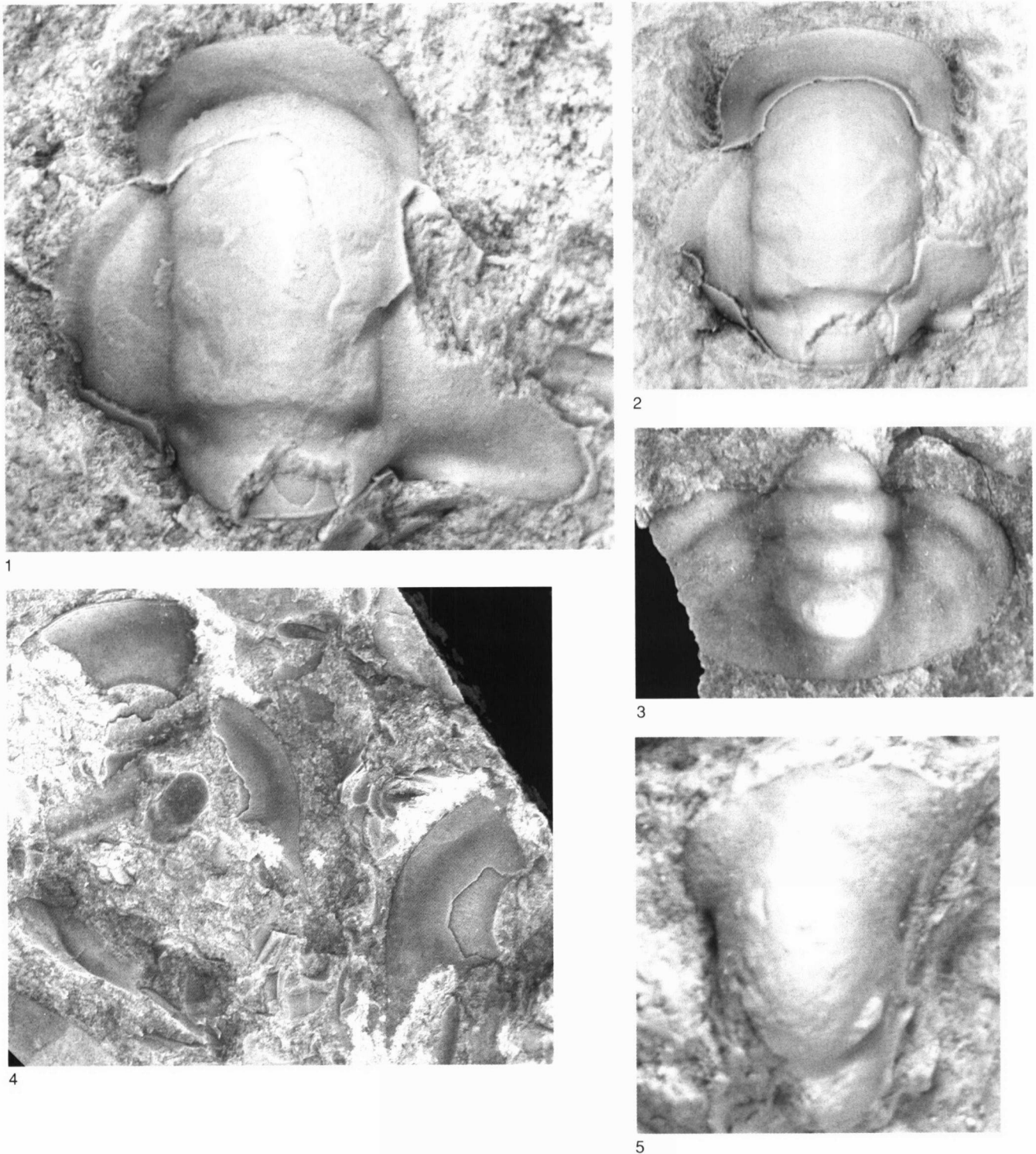


Figure 8. *Amphoton oatesi* Palmer and Gatehouse, 1972, Middle Cambrian, Floran–Undillan, Nelson Limestone, Neptune Range, locality E93-2, Antarctica; 1, dorsal view of cranidium, KUMIP 311672, $\times 9$; 2, dorsal view of cranidium, KUMIP 311671, $\times 6$; 3, dorsal view of pygidium, KUMIP 311669, $\times 11$; 4, dorsal view of librigenae, KUMIP 311666–311668 (from left to right), $\times 4.5$; 5, ventral view of hypostome, KUMIP 311670, $\times 12$ (new).

Occurrence.—Locality E93-2 from the Nelson Limestone, Neptune Range, and questionably from moraines on Mt. Provender in the Shackleton Range (see Soloviev and Grikurov, 1979, and Cooper and Shergold, 1991).

Discussion.—Peng and Robison (2000) listed this species as questionably present in Antarctica, but the material from the Nelson Limestone appears to be within the range of variation they documented for this species from other

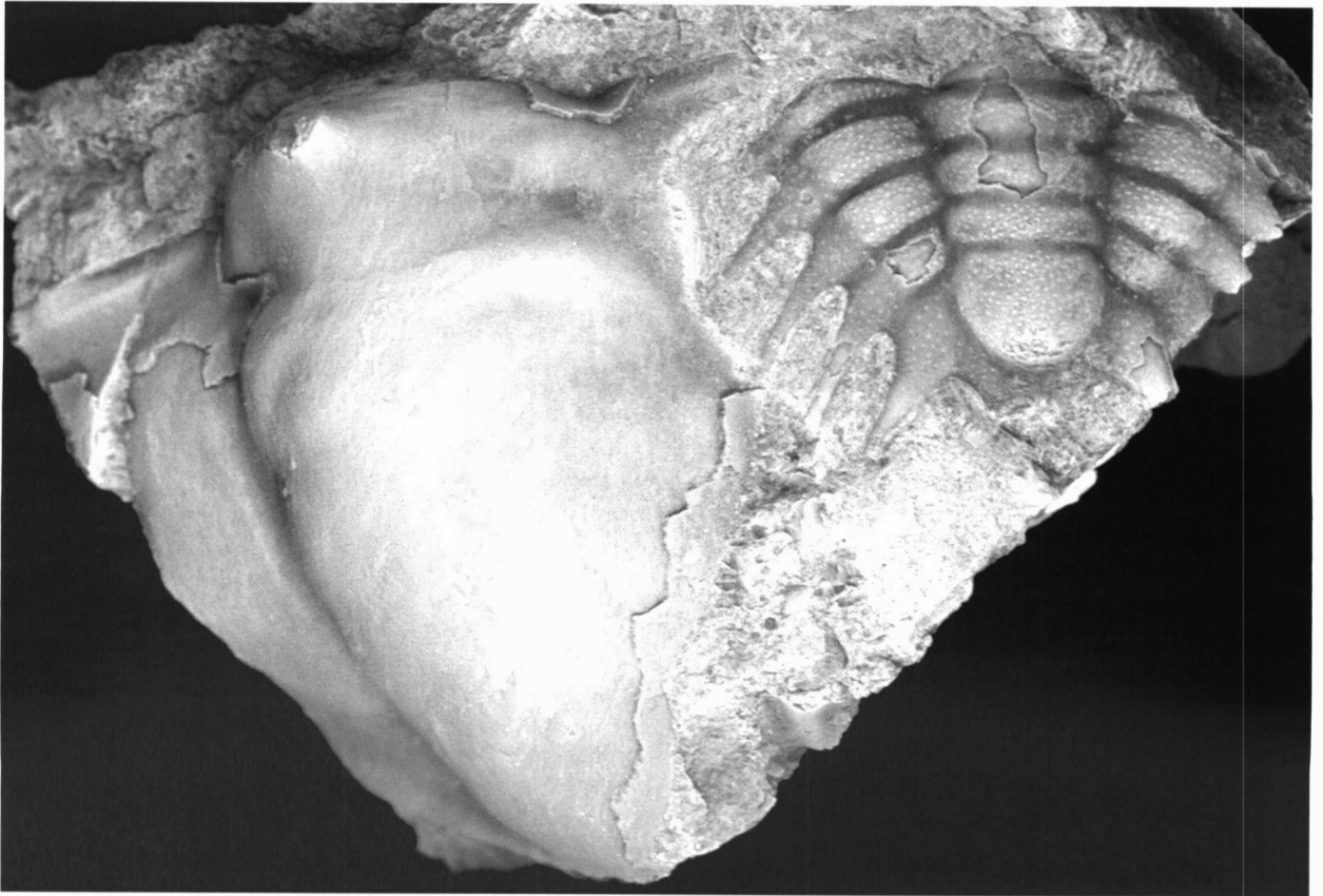


Figure 9. Middle Cambrian, Floran–Undillan, Nelson Limestone, Neptune Range, locality SMVR 89.2, Antarctica, $\times 5$; *Dorypyge* sp. cf. *D. australis* Wolfart, 1994, dorsal view of pygidium (on right), KUMIP 311632; and *Kootenia styra* Palmer and Gatehouse, 1972, dorsolateral view of cranidium (on left), KUMIP 311631 (new).

localities including Australia, China, and Laurentia. Palmer and Gatehouse (1972) treated this species as *Peronopsis* sp. cf. *P. fallax* (Linnarsson). Some of Soloviev and Grikurov's (1979) figured material from moraines in the Shackleton Range that they referred to as *P.* sp. cf. *P. fallax*, and indeed to other species of *Peronopsis* Hawle and Corda, may also belong to *A. laiwuensis*; however, because it is poorly preserved and also because the photographs are poor, it is conceivable that this species might represent *A. wangcunensis* Peng and Robison, 2000. Soloviev and Grikurov's (1979) material is therefore referred only questionably to *A. laiwuensis*. *Peronopsis deons* Jago and Webers, 1992 also shows similarities to *A. laiwuensis*, though it represents a different species.

Order CORYNEXOCHIDA Kobayashi, 1935

Suborder CORYNEXOCHINA Kobayashi, 1935

Family DOLICHOMETOPIDAE Walcott, 1916

Genus AMPHOTON Lorenz, 1906

AMPHOTON OATESI Palmer and Gatehouse, 1972

Figure 8, 13.2

Amphoton oatesi Palmer and Gatehouse, 1972, p. 17, pl. 4, 8, 11–13; Soloviev and Grikurov, 1978, p. 193; Soloviev

and Grikurov, 1979, p. 55; Cooper and Shergold, 1991, p. 463; Wolfart, 1994, p. 10.

Amphoton sp. cf. *Amphoton oatesi* Palmer and Gatehouse; Encarnación, Rowell, and Grunow, 1999, p. 498, fig. 3b–c.

Amphoton sp. Evans, Rowell, and Rees, 1995, p. 33.

?*Amphoton?* sp. Tröger and Weber, 1985, p. 364, pl. 1, 1–10.

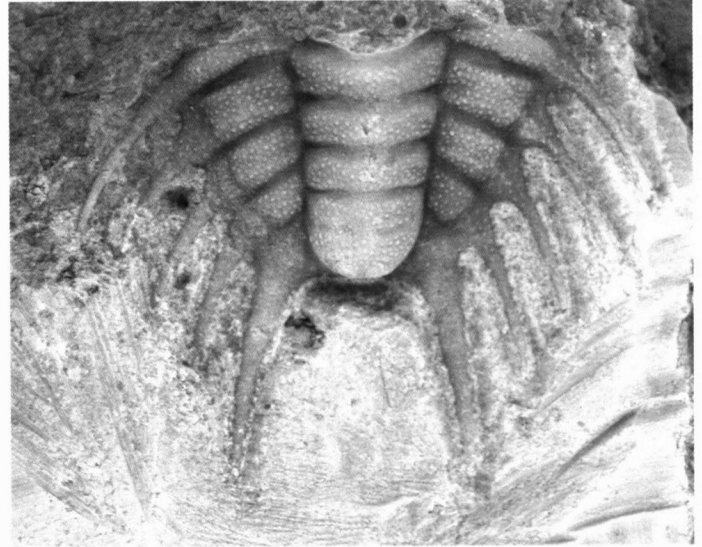
Material examined.—KUMIP 198572, 198574, 311665–311743, and numerous unnumbered specimens in the collections of the KUMIP.

Occurrence.—Localities E93-2, E93-2 (45'), E93-4, and SMVR 89.1, from the Nelson Limestone in the Neptune Range; and the Taylor Fm., from a 3-m-thick carbonate layer in the upper part of the succession at Taylor Nunatak, Shackleton Glacier area, Queen Maud Mountains, Transantarctic Mountains (see Encarnación, Rowell, and Grunow, 1999).

Discussion.—The material from the Nelson Limestone in the Neptune Range, Antarctica figured by Tröger and Weber (1985) and referred to as *Amphoton?* sp. could not be examined, and the only illustrations are line drawings. This makes it impossible to determine precise taxonomic identities. The material Evans, Rowell, and Rees (1995)



1



2

Figure 10. *Dorypyge* sp. cf. *D. australis* Wolfart, 1994, Middle Cambrian, Floran–Undillan, Nelson Limestone, Neptune Range, locality SMVR 89.2, Antarctica; 1, dorsal view of cranidium, KUMIP 311635, $\times 6$; 2, dorsal view of pygidium, KUMIP 311633, $\times 4.5$ (new).

mentioned was brought back from Antarctica, including the material they referred to as *Amphoton*, and in fact the material they collected forms the core of this study. Based on analysis, the material is identical in all respects with the type material of *A. oatesi*. Similarly, Encarnación, Rowell, and Grunow's (1999) figured material from the Queen Maud Mountains, which they referred to as *A. sp. cf. A. oatesi*. Although it is based on a limited number of specimens, it appears to be within the range of variation for specimens of *A. oatesi* collected from the Nelson Limestone in the Neptune Range and is therefore referred to that species.

The material of *A. oatesi* from the various localities seems to be overall fairly homogeneous though variation, often apparently preservational, occurs in the length of the occipital spine and the genal spine. One occasional and slight difference recognized between specimens from different localities involves the specimens from SMVR 89.1. In these the lateral margins of the glabella are more strongly divergent, when proceeding from S0 to the frontal lobe, relative to specimens from other localities. Specimens of *A. oatesi* from this locality are less abundant in collections than those from other localities and it could not be determined whether this inconsistent minor difference represents some sort of taphonomic artifact; it is treated as a subtle example of intraspecific variation.

Several hypostomes are associated with abundant remains of *A. oatesi*, though none has been found in place. These hypostomes seem to be approximately the right size and correct estimated geometry. They also conform in several respects with hypostomes of specimens of *Amphoton* figured by Zhang and Jell (1987) and a hypostome assigned to *Fuchouia* figured by Jago and Webers (1992). They are tentatively assigned to *A. oatesi*. They may, however,

belong to a co-occurring taxon such as *Chondranomocare australis*.

Amphoton oatesi is closely similar to *Horonastes eminens* Öpik, 1982 from the Currant Bush Limestone, Northern Territory, Australia; and in fact *Horonastes* is likely a junior synonym of *Amphoton* (P. A. Jell, personal communication, 2004). These species do differ in a few characters, however, which leads me to conclude that they are distinct but very closely related. In particular the glabellar furrows are more prominently incised in *A. eminens*; the cranidial anterior border is relatively longer (sag.) in *A. oatesi*; the entire cranidial anterior border is developed as a flattened shelf in *A. oatesi*, whereas in *A. eminens*, anterior of what Öpik (1982) referred to as the frontal glabellar recess, the anterior border, in lateral view, is broken up into distinct topographies, a short (sag.) anterior one that is flattened and akin to the shelf in *A. oatesi*, and a posterior, dorsally arched raised lip (the development of this distinct feature on *A. eminens* is attributable to the presence of what Öpik [1982] termed the interocular knob on the border); and the pygidial axial margins converge more strongly posteriorly in *A. eminens*.

Family DORYPYGIDAE Kobayashi, 1935

Genus DORYPYGE Dames, 1883

DORYPYGE sp. cf. DORYPYGE AUSTRALIS

Wolfart, 1994

Figure 9–11

Dorypyge australis Wolfart, 1994, p. 41, pl. 1,2–4, fig. 8.

Material examined.—KUMIP 311632–311638 and questionably 311639.

Occurrence.—Locality SMVR 89.2, and questionably from locality E93-2, from the Nelson Limestone in the Neptune Range.

Discussion.—Material referred to this species from northern Victoria Land and the Nelson Limestone is represented by relatively scanty remains, but for the characters that can be examined they appear identical. At this time, therefore, the material from the Nelson Limestone is treated as *D. sp. cf. D. australis*. Characters specimens share include the condition of the pygidial marginal spines, with five large spine pairs and the last of these spine pairs being the longest (exsag.). Further, at the posterior margin of the pygidium there are two small pairs of lateral spines, effectively reduced to nubbins, that are developed. The cephalon from the Nelson Limestone also have the characteristic swollen glabella that expands anteriorly, effaced of furrows, and with a small node on L0. Finally, the prosopon from specimens of both localities is covered with distinct, coarse granules.

There is one poorly preserved pygidium from the top of the Nelson at locality E93-2, which appears to conform in the aspects of its morphology that are preserved to pygidia of *D. sp. cf. D. australis*, and it is tentatively assigned to that species. Based on the condition of the spines it appears to differ from other taxa like *K. styrax* also known from locality E93-2 and appears instead likely referable to *D. sp. cf. D. australis*. There is a fragmentary hypostome (Fig. 11) preserved with other material assigned to *D. sp. cf. D. australis* from SMVR 89.2 that is tentatively referred to this species; it is the first time a hypostome has been illustrated for the species.

Cooper and Shergold (1991) identified material referable to *Dorypyge* sp. in their Fauna 4 in northern Victoria Land, from allochthonous blocks in the Spurs Formation at Reilly Ridge, and from the Edlin Formation at Edlin N ev ; but this material was not examined here, and it could not be determined whether this material was conspecific with *D. australis*.

Jago and Webers (1992) figured a partial cephalon and a partial pygidium from the Minaret Formation of the Ellsworth-Whitmore Mountains block that they assigned to the Dorypygidae. This material appears to be a dorypygid, but it is too poorly preserved to determine its affinities.

Sundberg (1994) described a series of characters whereby material referable to *Dorypyge* can be distinguished from *Kootenia* (and *Olenoides*). Based on his discussion this species belongs in *Dorypyge* and also *K. styrax* is referable to *Kootenia*.

Dorypyge australis closely resembles *D. tenella* Whitehouse, 1945 from the Middle Cambrian of Australia (P. A. Jell, personal communication, 2004). In particular, their prosopon is nearly identical in relative size of the granules and their distribution on the cranidium, and also the shape and relative size of the pygidial pleural spines is very similar. There are a few subtle differences between these taxa, however. In particular: the cephalic axial furrows in *D. australis* appear to diverge slightly more in their path from S0 to the anterior end of the ocular lobe; the nodes on the



Figure 11. *Dorypyge* sp. cf. *D. australis* Wolfart, 1994, Middle Cambrian, Floran–Undillan, Nelson Limestone, Neptune Range, locality SMVR 89.2, Antarctica; ventral view of hypostome, KUMIP 311634, $\times 9$ (new).

first two pygidial axial rings are more prominent in *D. tenella*; and the anterior margins of the first three pygidial axial rings are more uniformly convex in *D. tenella*, whereas in *D. australis*, when following the anterior margin of the axial ring from the axial furrow to the midline, the anterior margin of the ring is broadly convex but arches first slightly anteriorly, then slightly posteriorly, and then slightly anteriorly such that the anterior margins of the pygidial axial rings are weakly sinusoidal. Based on these minor differences *D. australis* and *D. tenella* are treated as distinct species, but they are very closely related and likely to be sister taxa.

Genus KOOTENIA Walcott, 1889

KOOTENIA STYRAX Palmer and Gatehouse, 1972

Figure 9, 12

Kootenia styrax Palmer and Gatehouse, 1972, p. 18, pl. 4, 4–5; Cooper and Shergold, 1991, p. 464; Wolfart, 1994, p. 10.

Material examined.—KUMIP 311641–311663.

Occurrence.—Localities E93-2, E93-4, and SMVR 89.2 from the Nelson Limestone in the Neptune Range.

Discussion.—Wolfart (1994, p. 44, pl. 12, 10a–c and fig. 9) illustrated a poorly preserved cranidium from his *Eurodeois tessensohni* faunule in northern Victoria Land, which he referred to as *Kootenia?* sp. indet. The material does indeed appear to represent a species of *Kootenia* based on Sundberg’s (1994) criteria, but it is too poorly preserved to determine its affinities with *K. styrax*.

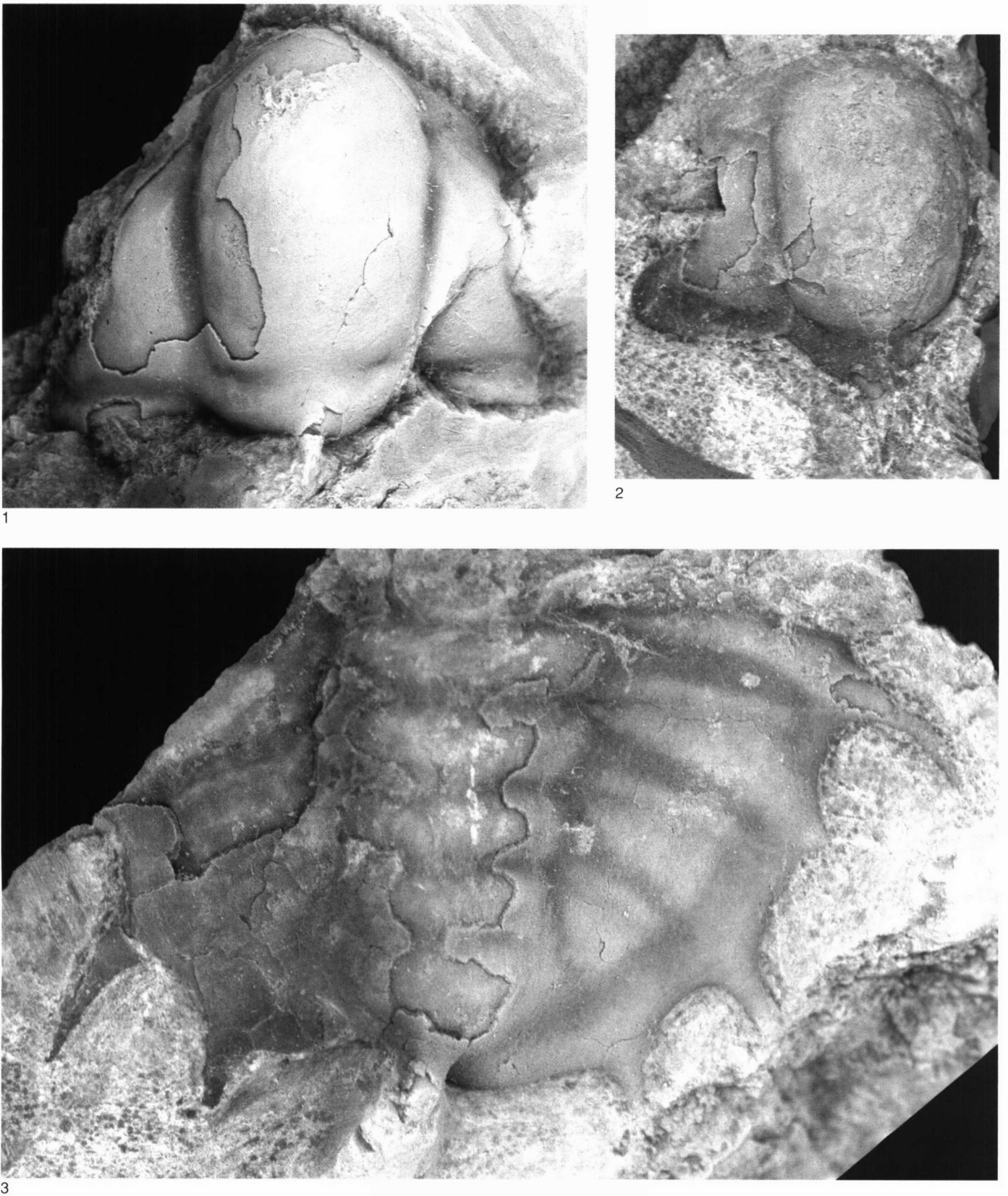


Figure 12. Middle Cambrian, Floran–Undillan, Nelson Limestone, Neptune Range, locality SMVR 89.2, Antarctica, *Kootenia styrax* Palmer and Gatehouse, 1972; 1, dorsal view of cranidium, KUMIP 311644, $\times 4.5$; 2, dorsal view of cranidium, KUMIP 311645, $\times 5$; 3, dorsal view of pygidium, KUMIP 311643, $\times 6.75$ (new).

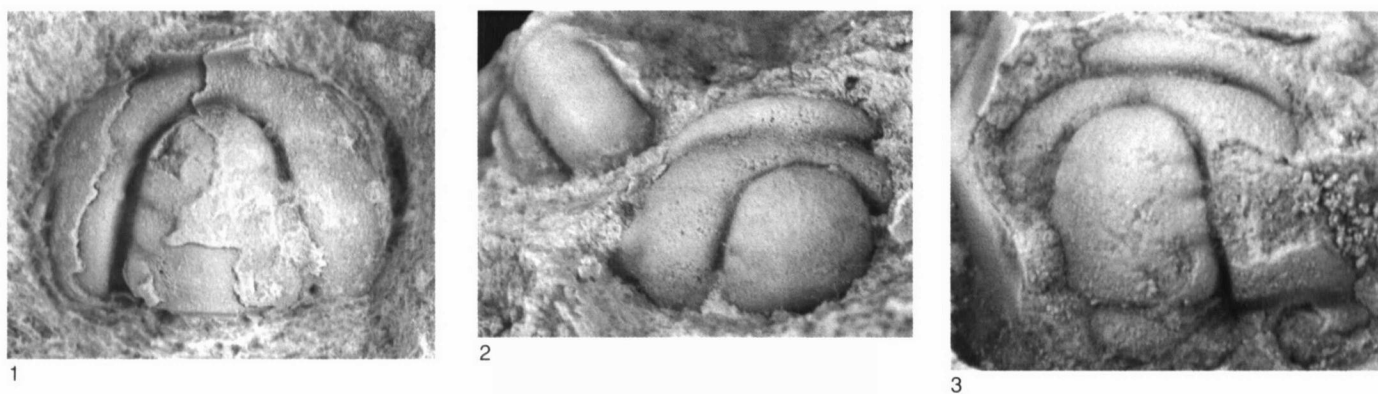


Figure 13. Middle Cambrian, Floran–Undillan, Nelson Limestone, Neptune Range, Antarctica; 1, *Solenopleura pruina* Palmer and Gatehouse, 1972, dorsal view of cranidium, locality E93-2, KUMIP 311752, $\times 5$; 2, locality E93-4, *Solenopleura pruina* Palmer and Gatehouse, 1972, dorsal view of cranidium, KUMIP 311754, and *Amphoton oatesi* Palmer and Gatehouse, 1972, anterodorsal view of cranidium, KUMIP 311701, $\times 8$; 3, *Solenopleura pruina* Palmer and Gatehouse, 1972, locality E93-2, dorsal view of cranidium, KUMIP 311754, $\times 10$ (new).

Order PTYCHOPARIIDA Swinnerton, 1915

Suborder PTYCHOPARIINA Richter, 1933

Family SOLENOPLEURIDAE Angelin, 1854

SOLENOPLEURA Angelin, 1854

SOLENOPLEURA PRUINA

Palmer and Gatehouse, 1972

Figure 13

Solenopleura pruina Palmer and Gatehouse, 1972, p. 26, pl. 5, 19–22; Soloviev and Grikurov, 1979, p. 69, pl. 4, 32–38; Cooper and Shergold, 1991, p. 464; Wolfart, 1994, p. 83.

Material examined.—KUMIP 311752–311788.

Occurrence.—Localities E93-2, E93-4, and SMVR 89.1 from the Nelson Limestone in the Neptune Range; and also from moraines on Mt. Spann in the Argentina Range

(Palmer and Gatehouse, 1972; Soloviev and Grikurov, 1979).

Discussion.—*Solenopleura reillyense* Wolfart, 1994 from the *Eurodeois tessensohni* faunule in northern Victoria Land appears to be closely related to *S. pruina*. Both share the arched preglabellar field, the conical glabella, the deeply impressed cephalic axial furrows, and the granulose prosopon. The pygidium of *S. reillyense* is of dubious affinity and as Wolfart (1994) discussed may not be referable to that species or even that genus. Differences between the two species include the anterior cephalic border, which is relatively longer (sag.) in *S. pruina*; the posterior cephalic border, which laterally arches more strongly posteriorly in *S. pruina*; and the fixigenae, which are relatively slightly narrower in *S. pruina*. *Solenopleura* as defined currently likely represents a para- or even polyphyletic genus, as

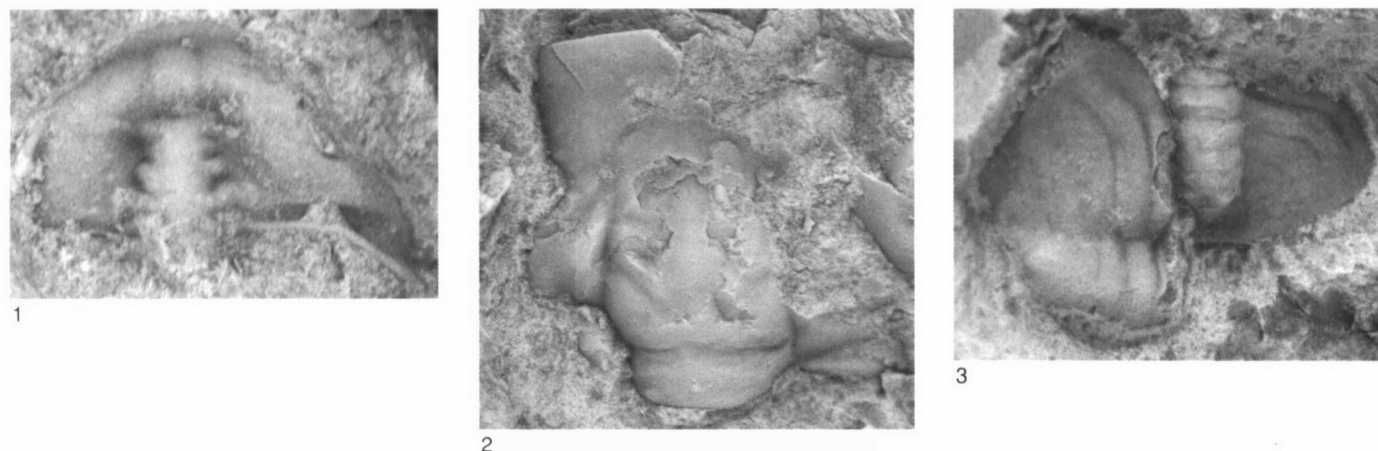


Figure 14. Middle Cambrian, Floran–Undillan, Nelson Limestone, Neptune Range, Antarctica; 1, locality E93-2(45'), *Penarosa trinodus* (Palmer and Gatehouse, 1972), dorsal view of cranidium, KUMIP 311559, $\times 7.5$; 2–3, locality E93,2, *Chondranomocare australis* Palmer and Gatehouse, 1972, 2, dorsal view of cranidium, KUMIP 311569, $\times 5$, 3, dorsal view of pygidia, KUMIP 311566, 311567, $\times 3.6$ (new).

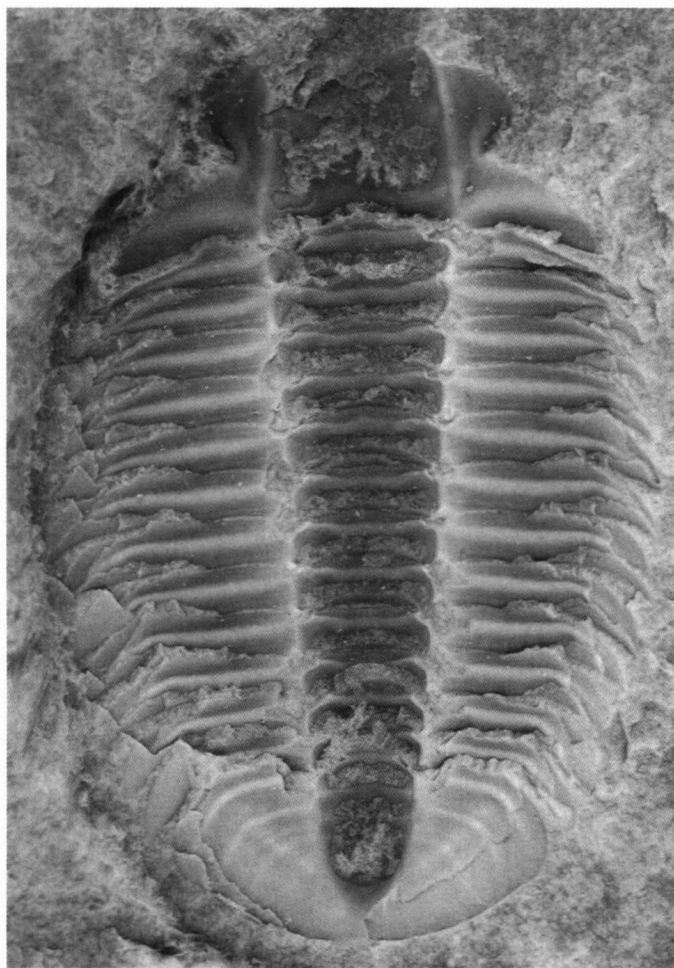


Figure 15. *Chondranomocare australis* Palmer and Gatehouse, 1972, Middle Cambrian, Floran–Undillan, Nelson Limestone, Neptune Range, locality E93-2, Antarctica; ventral view of external mold of nearly complete individual, KUMIP 311573, $\times 4.2$ (new).

Cooper, Jago, and Begg (1996, p. 378) intimated. Thus, the relationships of *S. pruina* to such taxa as *Sohopleura drakensis* Jago and Webers, 1992, and *Reillopleura braddocki* Cooper, Jago, and Begg, 1996, cannot be determined. It is not inconceivable that *S. pruina* and *S. reillyense* might instead be referable to *Sohopleura* Jago and Webers, 1992, to *Reillopleura* Cooper, Jago, and Begg, 1996, or even to some other genus but until a detailed phylogenetic analysis of this family can be performed this cannot be determined with any degree of precision. At this time, therefore, the species is retained within *Solenopleura*.

Solenopleura pruina and thus *S. reillyense* are also similar to Cooper, Jago, and Begg's (1996) *Solenopleuridae* gen. et sp. indet. (1996, p. 378, fig. 6L–M) from the Spurs Formation, northern Victoria Land, and these taxa may all be closely related and perhaps form a clade of sister species. Cooper, Jago, and Begg's (1996) species differs in having a slightly more prominent eye ridge, a slightly more

granulose prosopon, a more prominent node on L0, and a slightly less conical glabella.

Family NEPEIDAE Whitehouse, 1939

Genus PENAROSA Öpik, 1970

PENAROSA TRINODUS (Palmer and Gatehouse, 1972)

Figure 14.1

Trinepea trinodus Palmer and Gatehouse, 1972, p. 25, pl. 4, 1–2; Wolfart, 1994, p. 10.

Trinepea trinoda Palmer and Gatehouse; Cooper and Shergold, 1991, p. 464.

Penarosa trinodus (Palmer and Gatehouse); Jell, 1977, p. 119.

Genus and species undetermined 4 Palmer and Gatehouse, 1972, p. 32, pl. 4, 3.

Material examined.—KUMIP 311559–311561.

Occurrence.—Localities E93-2 and E93-2 (45') from the Nelson Limestone in the Neptune Range.

Discussion.—Jell (1977) discussed why *Trinepea trinodus* is instead referable to *Penarosa*, with *Trinepea* a junior subjective synonym of *Penarosa* (see also Jell and Adrain, 2003), and Jell's (1977) taxonomy is followed herein. Palmer and Gatehouse (1972) treated their genus and species undetermined 4 as being potentially distinct from *P. trinodus* because it has only a single median node on the cranidial brim and because the cephalic border is more downsloping, although they did suggest that it might represent an earlier ontogenetic stage of that species. Jell (1977) described that these characters, especially the geometry and number of nodes, can vary within and among nepeid taxa due to preservational circumstances, and it appears likely that this is the case here. Therefore, genus and species undetermined 4 likely represents a juvenile of *P. trinodus*.

Family ANOMOCARIDAE Poulsen, 1927

Genus CHONDRANOMOCARE

Poletaeva in Chernysheva et al., 1956

CHONDRANOMOCARE AUSTRALIS

Palmer and Gatehouse, 1972

Figure 14.2–14.3, 15

Chondranomocare australis Palmer and Gatehouse, 1972, p. 21, pl. 3, 18–24; Cooper and Shergold, 1991, p. 464; Wolfart, 1994, p. 10.

Material examined.—KUMIP 311566–311590.

Occurrence.—Localities E93-2, E93-4, and SMVR 89.1 from the Nelson Limestone in the Neptune Range.

Discussion.—Wolfart (1994) figured a species from northern Victoria Land in his *Eurodeois tessensohni* faunule that he treated as a related genus within the Anomocaridae, *Sudanomocarina* Jell in Jell and Robison, 1978. Jell and Adrain (2003), however, subsequently referred this genus to the Proasaphiscidae, and these two genera now appear to be not particularly closely related.

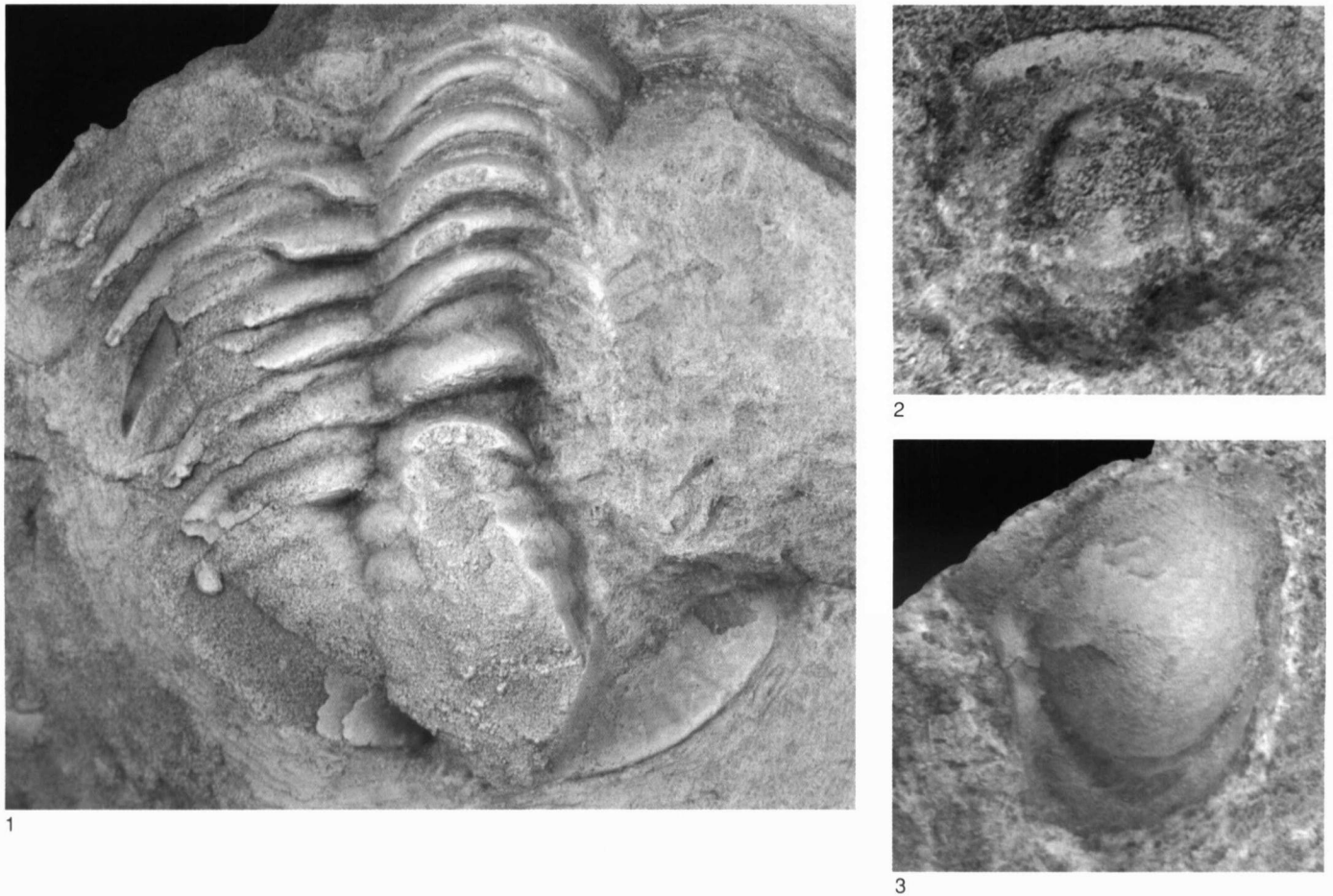


Figure 16. ?*Liopeishania spannensis* Palmer and Gatehouse, 1972, Middle Cambrian, Floran–Undillan, Nelson Limestone, Neptune Range, Antarctica; 1, locality DRF-3, dorsal view of partial thorax and pygidium, KUMIP 311562, $\times 6$; 2, locality DRF-3, dorsal view of cranium, KUMIP 311565, $\times 8$; 3, locality DRF-2, ventral view of hypostome, KUMIP 311564, $\times 11$ (new).

Family ANOMOCARELLIDAE Hupé, 1953

LIOPEISHANIA Zhang, 1963

?LIOPEISHANIA SPANNENSIS

Palmer and Gatehouse, 1972

Figure 16

Liopeishania spannensis Palmer and Gatehouse, 1972, p. 22, pl. 4, 9–10, 14–22; Cooper and Shergold, 1991, p. 464; Wolfart, 1994, p. 99.

Material examined.—KUMIP 311562–311565.

Occurrence.—Localities DRF-2 and DRF-3 from the Nelson Limestone in the Neptune Range; and boulders from a moraine on Mt. Spann, Argentina Range (Palmer and Gatehouse, 1972).

Discussion.—This material is very poorly preserved, but for those characters that can be determined it does seem to match *L. spannensis*, in particular, the flat, distinct, shelflike anterior cephalic border, the short (sag.) preglabellar field, the relatively broad (tr.) glabella, the roughly transverse glabellar furrows, the shape of the pygidium and pygidial axis, the nature of the pygidial bor-

der, and the possession of approximately seven pygidial axial rings. Due to the nature of the material and its preservation, it is assigned only questionably to *L. spannensis*. Originally Palmer and Gatehouse (1972) referred this genus to the Asaphiscidae, but subsequently Zhang and Jell (1987) treated the closely related *Peishania* as part of the Anomocarellidae, and Jell and Adrain (2003) assigned *Liopeishania* to that same family. Wolfart (1994, p. 99, pl. 19, 1a–c) figured *Liopeishania?* *angusta* Wolfart, 1994 from his *Eurodeois tessensohni* faunule in northern Victoria Land. *Liopeishania?* *angusta* differs from *L. spannensis* in several characters. In particular, in the former, the anterior cephalic border and the preglabellar fields are shorter (sag.), the glabellar furrows are much more weakly incised, the glabellar margins are less convergent, and S0 is more convex anteriorly. Further evaluation of this genus and the Anomocarellidae is required before it can be determined if *L.?* *angusta* is indeed referable to *Liopeishania*. Wolfart (1994) suggested that this species may in fact belong to *Peishania* Resser and Endo in Kobayashi, 1935 or some other genus.

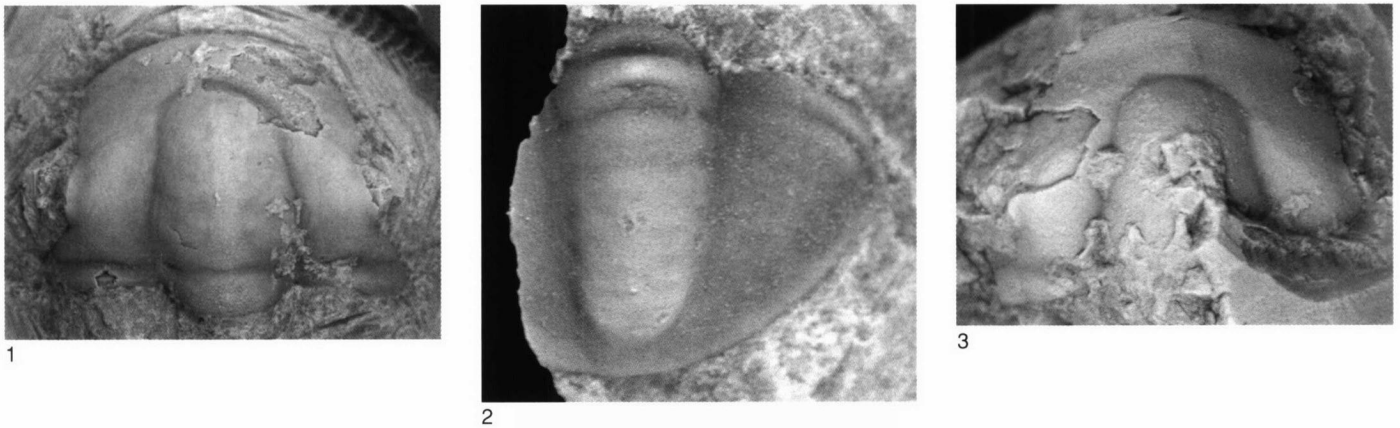


Figure 17. *Peishania? neptunensis* new species, Middle Cambrian, Floran–Undillan, Nelson Limestone, Neptune Range, Antarctica, locality NPF-2; 1, dorsal view of holotype cranidium, KUMIP 218051, $\times 4$; 2, dorsal view of paratype partial pygidium, KUMIP 218053, $\times 10$; 3, dorsal view of partial cranidium, KUMIP 218052, $\times 5.75$ (new).

PEISHANIA? Resser and Endo in Kobayashi, 1935
PEISHANIA? NEPTUNENSIS new species

Figure 17

Diagnosis.—Anterior cephalic border moderately short (sag., exsag.), developed as sloping, flat to faintly convex field; preglabellar field long (sag.); cephalic axial furrows moderately incised; glabellar furrows faintly incised; glabella moderately arched (tr., sag.); fixigenae very broad (tr.); pygidial axis with eight or nine rings; anterior margins of pygidial rings sinuous; pygidial pleural and interpleural furrows faintly incised; pygidial border weakly developed, scooped out and flattened.

Description.—Cranidial length (sag.) approximately 75 percent of width (tr.). Anterior cephalic border moderately short (sag., exsag.), developed as sloping, flat to faintly convex field, length (sag.) approximately 33 percent length (sag.) of L0; anterior margin of anterior border weakly convex in dorsal aspect. Preglabellar field long, length (sag.) approximately equal to 80 percent length (sag.) of

L0. Cephalic axial furrows moderately incised; glabellar furrows faintly incised. Glabella moderately arched (tr., sag.). Anterior margin of frontal lobe gently rounded in dorsal view. Lateral margins of glabella posterior of LA moderately expand posteriorly. Fixigenae very broad (tr.), width (tr.) opposite eye lobes roughly equal to 60 percent width of glabella. Posterior margins of L0 strongly convex in dorsal view; L0 with faint node variably developed. Eye lobes prominently developed. Anterior of eye lobes facial sutures form 0 to 20 degree angle with sagittal line; immediately posterior of eye lobes facial suture forms roughly 50–60 degree angle relative to sagittal line. Cephalic posterior border furrow transverse to sinusoidal; cephalic posterior border deflected posteriorly distally. Prosopon of very fine, small, evenly distributed granules.

Pygidium with semicircular profile. Pygidial axis gently inflated, posteriorly arches weakly ventrally in dorsal aspect; margins of pygidial axis converge gently posteriorly; pygidial axis with eight or nine rings; anteriormost axial ring bears node; pygidial axial ring furrows faintly incised;

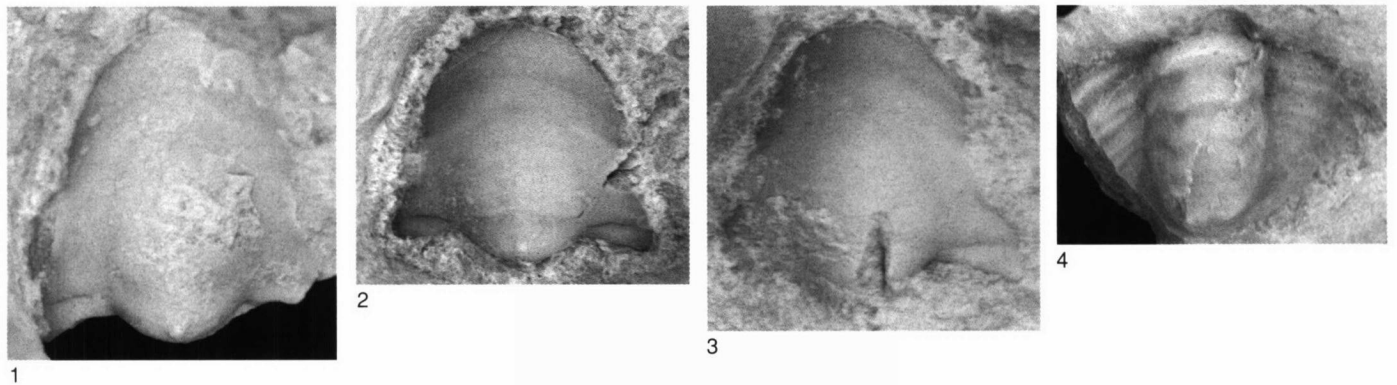


Figure 18. Middle Cambrian, Floran–Undillan, Nelson Limestone, Neptune Range, Antarctica; 1–3, *Poriagraulos kaesleri* new species, locality E93-9, Webb Nunataks; 1, dorsal view of cranidium, KUMIP 311605, $\times 7$; 2, dorsal view of holotype cranidium, KUMIP 311603, $\times 6$; 3, dorsal view of cranidium, KUMIP 311604, $\times 7$; 4, *Suludella? spinosa* Palmer and Gatehouse, 1972, locality NPF-2, dorsal view of pygidium, KUMIP 218049, $\times 4.5$ (new).

anterior margins of pygidial rings sinuous; pygidial axial terminus gently rounded posteriorly. Pygidial pleural and interpleural furrows faintly incised. Pygidial border weakly developed, scooped out and flattened.

Types.—Holotype KUMIP 218051 (Fig. 17.1), partial cephalon and paratype KUMIP 218053, partial pygidium (Fig. 17.2), both from locality NPF-2, Nelson Limestone, Neptune Range, Antarctica.

Etymology.—Named for the Neptune Range in Antarctica.

Other material examined.—KUMIP 218052, 311593–311595, and 311598.

Occurrence.—Localities NPF-1 and NPF-2 from the Nelson Limestone in the Neptune Range.

Discussion.—Zhang and Jell (1987) provided a detailed discussion of this genus and commented on characters it shares with *Liopeshania*. Wolfart (1994) also considered characters shared by *Peishania* and *Liopeshania*. This new species has the following characters in common with *Peishania*: the anterior border is relatively short (sag., exsag.); the anterior margins of the frontal lobe are relatively transverse in dorsal view; the glabellar furrows are indistinct; the glabella arches relatively strongly dorsally medially; anterior of the eye the facial sutures tend to arch only weakly laterally; the fixigenae are relatively strongly arched dorsally and are relatively broad (tr.); the margins of the pygidial axis converge gently posteriorly; the anterior margins of the pygidial rings are sinuous and proceeding from left to right arch first anteriorly, then posteriorly, then anteriorly, then posteriorly, and finally anteriorly; the pygidial axial terminus is gently rounded posteriorly; the pygidial pleural and interpleural furrows are faintly incised; the pygidial border is scooped out and flattened; and the prosopon is covered with fine granules. On the basis of these characters it is likely that this new species belongs to *Peishania*. There are some characters present in *P.?* *neptunensis*, however, that do not occur in other species of *Peishania*. For example, in *P.?* *neptunensis*: the preglabellar field is relatively longer (sag.); the anterior border is more sloping and less developed as a flattened shelf; the glabella is narrower (tr.); and the pygidial border is shorter (sag., exsag.).

At this time and in the absence of complete character information, phylogenetic information, and information about primitive versus derived character states in the Anomocarellidae, this material is questionably referred to *Peishania*.

Jago and Webers (1992, p. 112, pl. 3, 16–18 and pl. 4, 1–2) figured and discussed some pygidia from a Boomerangian boulder in the Ellsworths that they referred to as *Asaphiscidae* gen. et sp. indet. It may represent a species of *Peishania* and instead be referable to the Anomocarellidae (based on Jell and Adrain's 2003 classification). *Peishania?* *neptunensis* from the Nelson Limestone and Jago and Weber's (1992) material share the following characters: the margins of the pygidial axis con-

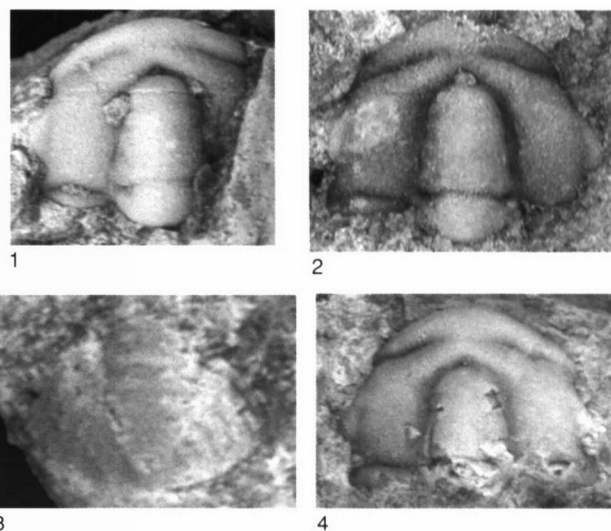


Figure 19. *Nelsonia schesis* Palmer and Gatehouse, 1972, Middle Cambrian, Floran–Undillan, Nelson Limestone, Neptune Range, Antarctica, locality NPF-1; 1, dorsal view of cranidium, KUMIP 311501, $\times 10$; 2, dorsal view of cranidium, KUMIP 218055, $\times 10$; 3, dorsal view of pygidium, KUMIP 218056, $\times 15$; 4, dorsal view of cranidium, KUMIP 311500, $\times 10$ (new).

verge gently posteriorly; there are approximately eight pygidial axial rings (though the exact number is difficult to determine in Jago and Weber's 1992 specimens because of the indistinctness of the axial ring furrows); the pygidial axial terminus is gently rounded posteriorly; the pygidial pleural and interpleural furrows are faintly incised; and the pygidial border is scooped out and flattened. There are, however, some differences between these two Antarctic taxa. In particular, in Jago and Weber's (1992) material the pygidial axial furrows and axial ring furrows are more indistinct, and the pygidial axial border is more strongly flattened, but there are species of *Peishania* that Zhang and Jell (1987) figured that possess these characters. Again, at this time and because of the limited nature of the material, Jago and Weber's (1992) species is only tentatively assigned to *Peishania*.

Family CONOKEPHALINIDAE Hupé, 1953

Genus SULUDELLA? Yegorova and Savitskiy, 1968

SULUDELLA? SPINOSA Palmer and Gatehouse, 1972

Figure 18.4

Suludella? *spinosa* Palmer and Gatehouse, 1972, p. 24, pl. 6, 16–18, 20–23; Cooper and Shergold, 1991, p. 464; Wolfart, 1994, p. 10.

Material examined.—KUMIP 218045, 218047–218049, and 311630.

Occurrence.—Localities NPF-2 and DRF-2 from the Nelson Limestone in the Neptune Range; and a boulder from a moraine on Mt. Spann, Argentina Range (Palmer and Gatehouse, 1972).

Discussion.—Palmer and Gatehouse (1972) figured two species that they referred questionably to *Suludella*. Because

of the limited new material uncovered during the course of this study it is still difficult to determine whether this species belongs to *Suludella* or instead represents a new but related genus, and therefore the questionable generic status of this species is retained. No new material of their other species *S.?* *davnii* Palmer and Gatehouse, 1972 was uncovered during the course of this investigation. Wolfart (1994, p. 78, pl. 18,3) figured an incomplete cranidium from northern Victoria Land in his *Eurodeois tessensohni* faunule that he referred to *Suludella?* sp. indet., but the specimen is so incomplete and poorly preserved that it is impossible to determine its taxonomic affinities.

Family ALOKISTOCARIDAE Resser, 1939

Genus SCHOPFASPIS Palmer and Gatehouse, 1972

SCHOPFASPIS GRANULOSUS

Palmer and Gatehouse, 1972

Schopfaspis granulatus Palmer and Gatehouse, 1972, p. 24, pl. 6, 16–18, 20–23; Wolfart, 1994, p. 8.

Schopfaspis granulosa Palmer and Gatehouse; Cooper and Shergold, 1991, p. 464.

?Genus and species undetermined 1 Palmer and Gatehouse, 1972, p. 31, pl. 3, 10–12; Wolfart, 1994, p. 8.

Material examined.—KUMIP 311599–311602.

Occurrence.—Localities E93-9 and E93-11 from the Nelson Limestone in the Neptune Range; and moraines on Mt. Spann, Argentina Range (Palmer and Gatehouse, 1972).

Discussion.—Palmer and Gatehouse (1972) figured two cranidia and one free cheek that they referred to their genus and species indeterminate 1. This species is poorly preserved but appears indistinguishable from *S. granulatus* and therefore may be referable to that species. Palmer and Gatehouse (1972) had assigned the boulder in which this undetermined genus and species occurred to their *Xystridura multilinia* faunule, which they held to be considerably older than their *S. granulatus* faunule that contained the eponymous *S. granulatus*. It now appears that the boulder containing putative members of the *X. multilinia* faunule may also contain a representative of what Palmer and Gatehouse (1972) treated as a different faunule. Because of the poor state of preservation of Palmer and Gatehouse's (1972) genus and species indeterminate 1, however, at this time it is only synonymized questionably with *S. granulatus*.

Family AGRAULIDAE Raymond, 1913

Genus PORIAGRAULOS Zhang, 1963

Type species.—*Poriagraulos nanum* (Dames, 1883).

Included species.—*Poriagraulos kaesleri* new species.

Discussion.—*Poriagraulos* Zhang, 1963 was discussed by Zhang and Jell (1987) and *P. nanum* (Zhang and Jell, 1987, p. 116, pl. 47, 15, pl. 48, 5) from the Hsichuang Formation of North China is closely similar to *P. kaesleri* (P. A. Jell, personal communication, 2004). In particular, they share: the long anterior cranial border (sag., exsag.); the broad

(tr.) fixigenae; the weakly incised cephalic axial and glabellar furrows; the facial sutures immediately anterior of the eye lobe being roughly parallel and forming a 0 to 20 degree angle relative to a sagittal line; the gently convex preglabellar field with the length (sag.) roughly equal to the length (sag.) of L0; the long (sag.) L0, bearing a median node and arching strongly posteriorly; and the prosopon consisting of fine granules. They do differ in the condition of a few characters, including: the cranial anterior border is relatively longer (sag.) in *P. kaesleri*; the cranial posterior border furrow is more deeply incised in *P. kaesleri*; and the fine granules are more prominently developed on the cranial anterior border of *P. nanum*.

PORIAGRAULOS KAESLERI new species

Figure 18.1–18.3

Diagnosis.—Cephalic axial furrows and glabellar furrows faintly incised; anterior border evenly sloping, deflected ventrally; preglabellar field relatively long (sag., exsag.); eye lobes and eye ridges weakly developed; L0 arches strongly posteriorly medially; prosopon of faint granules.

Description.—Cranial length (sag.) approximately 90 percent of width (tr.). Anterior cephalic border long (sag., exsag.), developed as sloping, flat to faintly convex field, length (sag.) approximately 150 percent length (sag.) of L0; anterior margin of anterior border strongly convex in dorsal aspect. Preglabellar field long, length (sag.) approximately equal to length (sag.) of L0. Cephalic axial furrows and glabellar furrows faintly incised to effaced. Glabella moderately arched (tr., sag.). Anterior margin of frontal lobe gently rounded. Lateral margins of glabella posterior of LA weakly expand posteriorly. Fixigenae broad (tr.), width (tr.) opposite eye lobes roughly equal to 30 percent width of glabella. Posterior margins of L0 convex in dorsal view; L0 with faint node variably developed. Eye lobes weakly developed. Anterior of eye lobes facial sutures form 0–20 degree angle with sagittal line; immediately posterior of eye lobes facial suture forms roughly 60–70 degree angle relative to sagittal line; at posterior ends facial sutures roughly parallel sagittal line. Cephalic posterior border furrow transverse; cephalic posterior border deflected posteriorly distally. Prosopon of fine, small granules distributed evenly over cranial surface excepting anterior border where they are generally lacking.

Types.—Holotype KUMIP 311603 (Fig. 18.2), cranidium from locality E93-9, Middle Cambrian, Nelson Limestone, Webb Nunataks, Neptune Range.

Etymology.—Named for Roger L. Kaesler, who has been an important mentor to me during my career at the University of Kansas.

Other material examined.—KUMIP 311604–311624.

Occurrence.—Localities E93-9, E93-10, and E93-11 from the Nelson Limestone in the Webb Nunataks, Neptune Range.

Discussion.—Unfortunately no librigenal or pygidial remains are known for this species or *P. nanum*.

Family PTYCHOPARIIDAE Matthew, 1887**Genus NELSONIA Palmer and Gatehouse, 1972****NELSONIA SCHEISIS Palmer and Gatehouse, 1972**

Figure 19

Nelsonia schesis Palmer and Gatehouse, 1972, p. 28, pl. 6, 3–4, 6–14; Cooper and Shergold, 1991, p. 464; Wolfart, 1994, p. 10; Evans, Rowell, and Rees, 1995, p. 32; Jell and Adrain, 2003, p. 410.

Nelsonia sp. cf. *Nelsonia schesis* Palmer and Gatehouse; Encarnación, Rowell, and Grunow, 1999, p. 498, fig. 3a.

Material examined.—KUMIP 218050, 218054–218056, 311500–311558, and several unnumbered specimens in the KUMIP.

Occurrence.—Localities NPF-1, NPF-2, NPF-3, and DRF-1 from the Nelson Limestone in the Neptune Range; a boulder from a moraine on Mt. Spann, Argentina Range (Palmer and Gatehouse, 1972); and the Taylor Formation, from a 3 m thick carbonate horizon in the upper part of the succession at Taylor Nunatak, Shackleton Glacier area, Queen Maud Mountains, Transantarctic Mountains (see Encarnación, Rowell, and Grunow, 1999).

Discussion.—Encarnación, Rowell, and Grunow's (1999) figured material from the Queen Maud Mountains, which they referred to as *N. sp. cf. N. schesis*, although based on a limited number of specimens, appears to be within the range of variation for specimens of *N. schesis* collected from the Nelson Limestone in the Neptune Range and is therefore referred to that species.

Due to a typographical error by Cooper and Shergold (1991), *N. schesis* was listed as also being present in the Spurs Formation of northern Victoria Land; subsequently, Evans, Rowell, and Rees (1995), using that information from Cooper and Shergold (1991), also treated the species as present in northern Victoria Land; however, Encarnación, Rowell, and Grunow (1999) corrected the error.

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