The Earliest Annelids: Lower Cambrian Polychaetes from the Sirius Passet Lagerstätte, Peary Land, North Greenland

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Source: Acta Palaeontologica Polonica, 53(1) : 137-148

Published By: Institute of Paleobiology, Polish Academy of Sciences

URL: https://doi.org/10.4202/app.2008.0110

The earliest annelids: Lower Cambrian polychaetes from the Sirius Passet Lagerstätte, Peary Land, North Greenland

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Conway Morris, S. and Peel, J.S. 2008. The earliest annelids: Lower Cambrian polychaetes from the Sirius Passet Lagerstätte, Peary Land, North Greenland. *Acta Palaeontologica Polonica* 53 (1): 137–148.

Apart from the Phyllopod Bed of the Burgess Shale (Middle Cambrian) polychaete annelids are practically unknown from any of the Cambrian Lagerstätten. This is surprising both because their diversity in the Burgess Shale is considerable, while to date the Chengjiang Lagerstätte which is equally impressive in terms of faunal diversity has no reliable records of any annelids. Here we describe, on the basis of about 40 specimens, *Phragmochaeta canicularis* gen. et sp. nov. from the Lower Cambrian Sirius Passet Lagerstätte of Peary Land, North Greenland. This makes it by far the oldest known polychaete, with a likely age of lower to middle Atdabanian, The body consists of approximately 20 segments, each bearing notochaetae and neurochaetae. The former appeared to have formed a felt-like covering on the dorsum, whilst the neurochaetae projected obliquely to the longitudinal axis. Apart from minor differences in chaetal size at either end there is no other tagmosis. Details of the head are obscure, and presence of palps, tentacles and eyes are conjectural. Jaws appear to have been absent. The gut was straight, and flanked by massive longitudinal musculature. *P. canicularis* was evidently benthic, propelling itself on the neurochaetae, with the dorsal neurochaetae conferring protection. Its stratigraphic position and generalized appearance are consistent with *P. canicularis* being primitive, but the phylogenetic relationships within the polychaetes remain problematic, principally because of paucity of relevant morphological information.

Key words: Annelida, Polychaeta, *Phagmochaeta*, metazoan evolution, Cambrian, Sirius Passet Lagerstätte, Greenland.

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Introduction

More than 30 Burgess Shale-type faunas are now known from the Lower and Middle Cambrian of Laurentia, South China, Australia, and Siberia (as well as a few other scattered localities). These faunas are typified by arthropods, brachiopods, priapulans and sponges, and despite unique occurrences of particular taxa (such as halkieriids in Sirius Passet and fish in Chengjiang) they otherwise show quite a high degree of faunal homogeneity and temporal conservation. In the cynosure of such Lagerstätte, the celebrated Burgess Shale of British Columbia, a notable component of the fauna are polychaete annelids. First described by Walcott (1911, 1931) they were rescrutinized by Conway Morris (1979), and his observations were very largely confirmed by Eibye-Jacobsen (2004). Despite this considerable diversity and disparity of forms in the Burgess Shale it is noteworthy that the fossil record of Cambrian polychaetes is otherwise exceptionally meager. Apart from the report herein from Sirius Passet, in our opinion the only other bona-fide example is a single specimen from the Spence Shale of Utah (Robison 1969; see also Conway Morris 1979: 268, pl. 9: 130, 131). In this context it seems surprising, especially given its extraordinary richness, that no convincing polychaetes have been recognized in the Chengjiang Lagerstätte. A putative annelid has been illustrated by Chen et al. (1996: 142, figs. 175, 176; see also Chen and Zhou 1997: 37, fig. 34). These authors identify appendages as parapodia, but there seems to be no evidence for associated chaetae. An associated sclerite is also identified at the base of each supposed parapodium, and it is possible that this animal is better identified as a lobopodian arthropod. In any event its polychaete affinities seem very much open to question.

There is, it is true, a considerable roster of early fossil worms that have been assigned to the polychaetes but their status is almost universally problematic. Within the Ediacaran assemblage taxa such as *Dickinsonia* have been compared to spintherid polychaetes (Wade 1972). This is, however, widely regarded as a case of convergence and whilst the status and phylogenetic affinities of the Ediacaran biotas are still controversial, there is no convincing identification of any sort of annelid. A significant component of the Cambrian fauna are the palaeoscolecidans (which as a group range to the Silurian), and these too have been assigned to the annelids (see Conway Morris 1977: 85–87; Conway Morris

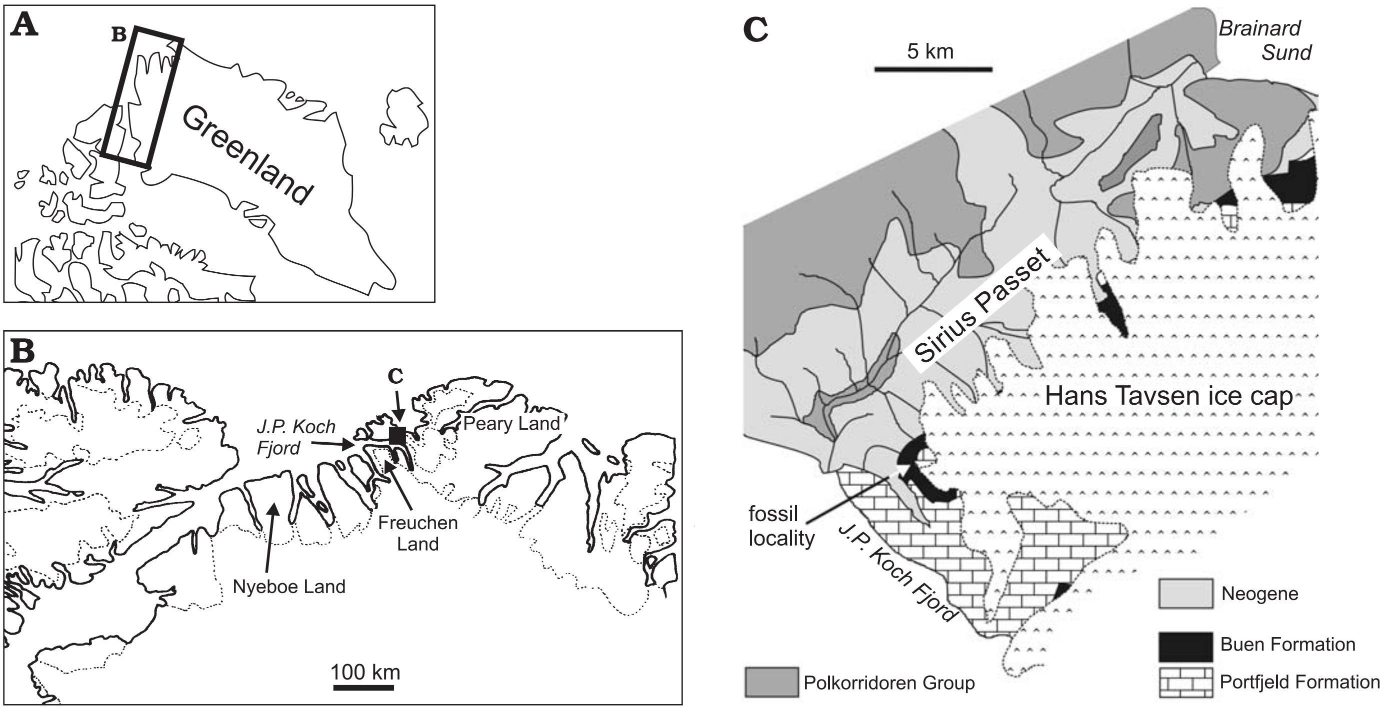


Fig. 1. Locality map of North Greenland (**A**, **B**), with position of the Sirius Passet Lagerstätte (**C**) and its simplified geological context.

and Robison 1986). It is now clear, however, that palaeoscolecidans are closely related to the priapulans, with the papillate bands representing rows of distinct sclerites that have no association with chaetae, let alone parapodia. Finally, brief mention should be made of *Myoscolex ateles* from the Lower Cambrian of South Australia. In a detailed reappraisal by Dzik (2004) this worm was assigned to the annelids, with at least some similarity claimed to exist with the opheliids. This echoes the earlier remarks by Glaessner (1979), but is in conflict with a proposed affinity to the anomalocaridid arthropods (Briggs and Nedin 1997). Having examined some material with Romilly Everett (personal communication June 2005) we conclude that an assignment to the annelids is unlikely. In particular, the identification of phosphatic rod-like structures as chaetae (Dzik 2004) seems to be forced, but it must also be admitted that the comparison to the stem-group arthropods is not free of difficulties.

Institutional abbreviation.—MGUH, The Geological Museum of the University of Copenhagen (Museum Geologicum Universitatis Hauniensis), now part of the Natural History Museum of Denmark.

The Sirius Passet Lagerstätte

Whilst the Sirius Passet Lagerstätte (Conway Morris et al. 1987; Peel et al. 1992; Conway Morris 1998) does not match the richness of either the Burgess Shale or Chengjiang Lagerstätten it has yielded an impressive variety of organisms showing exceptional preservation, notably trilobites (Blaker 1988; Blaker and Peel 1997; Babcock and Peel in press) and other arthropods (Budd 1993, 1994, 1995, 1997, 1998, 1999; Williams et al. 1996; Budd and Peel 1998), halkieriids (Conway Morris and Peel 1990, 1995), and sponges (Rigby 1986).

All the fossils, including the annelids described herein, were collected at the south-western end of the broad valley connecting J.P. Koch Fjord and Brainard Sund in north-west Peary Land, central North Greenland (latitude 82°47.6’ N, longitude 42°13.7’ W) at an altitude of 450 m above sea level (Fig. 1). Almost 6000 fossiliferous slabs were selected during visits between 1985 and 2006 (Peel 1990; Peel et al. 1992; Conway Morris 1998) from extensive talus slopes derived from the lower part of the Buen Formation (Conway Morris 1998: figs. 52, 55).

The Buen Formation forms part of the southern shelf succession of the Franklinian Basin of North Greenland and the Canadian Arctic Islands (Surlyk 1991). The formation (325 m thick) consists of a lower, sand-dominated, member overlain by an upper member dominated by dark grey-green mudstones and siltstones in its type area in southern Peary Land (Peel and Sønderholm 1991; Ineson and Peel 1997; Blaker and Peel 1997). It thickens to around 700 m in northern Peary Land where it comprises a mud-rich transitional succession into deep water trough deposits of the Polkorridoren Group (Peel and Sønderholm 1991). Dark grey to black mudstones at the fossiliferous locality form part of this transitional succession from the shelf to the slope. To the south they lie in faulted contact with pale dolomites of the underlying Portfjeld Formation, and to the north with bioturbated mudstones and sandstones of the Buen Formation.

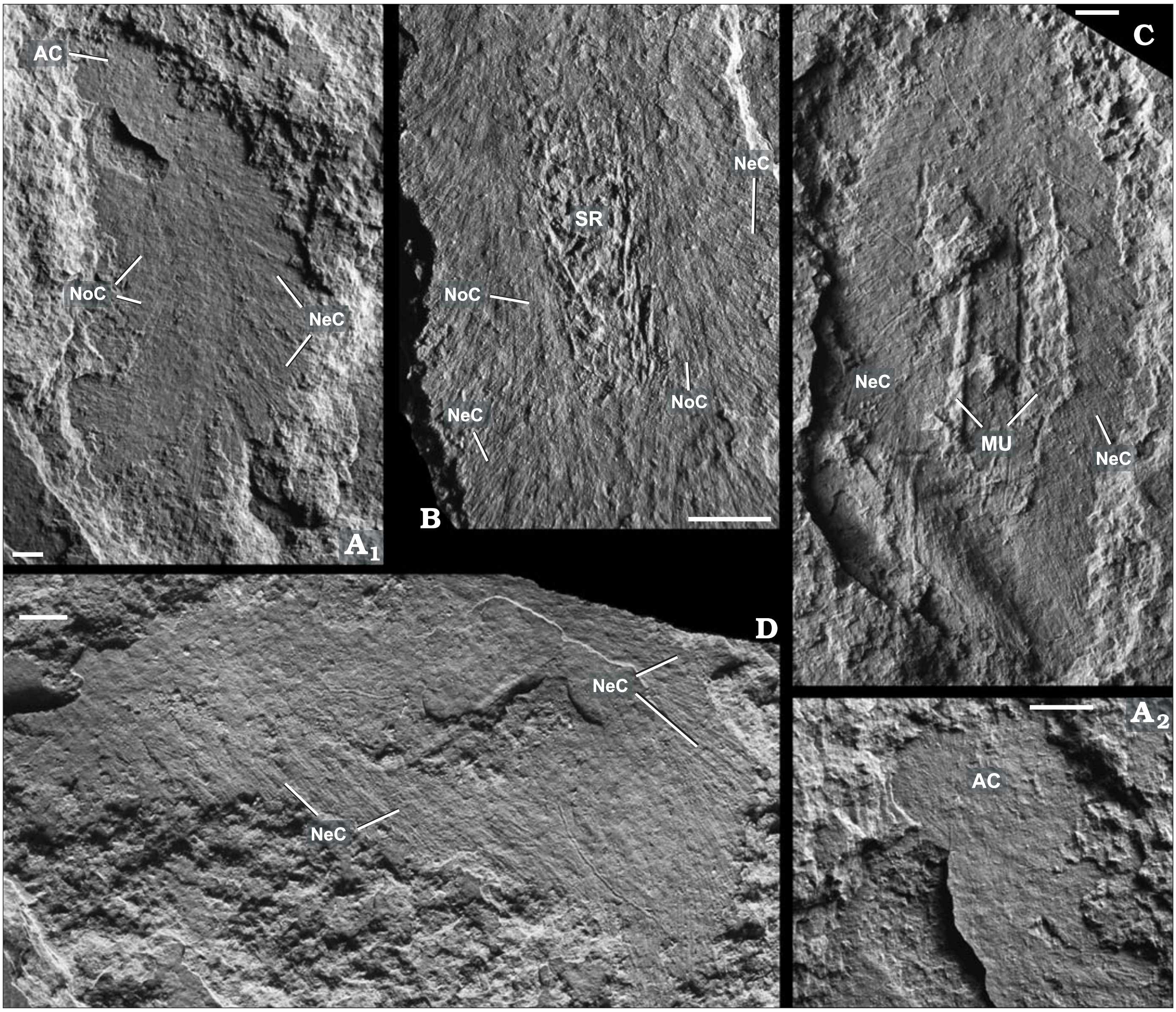
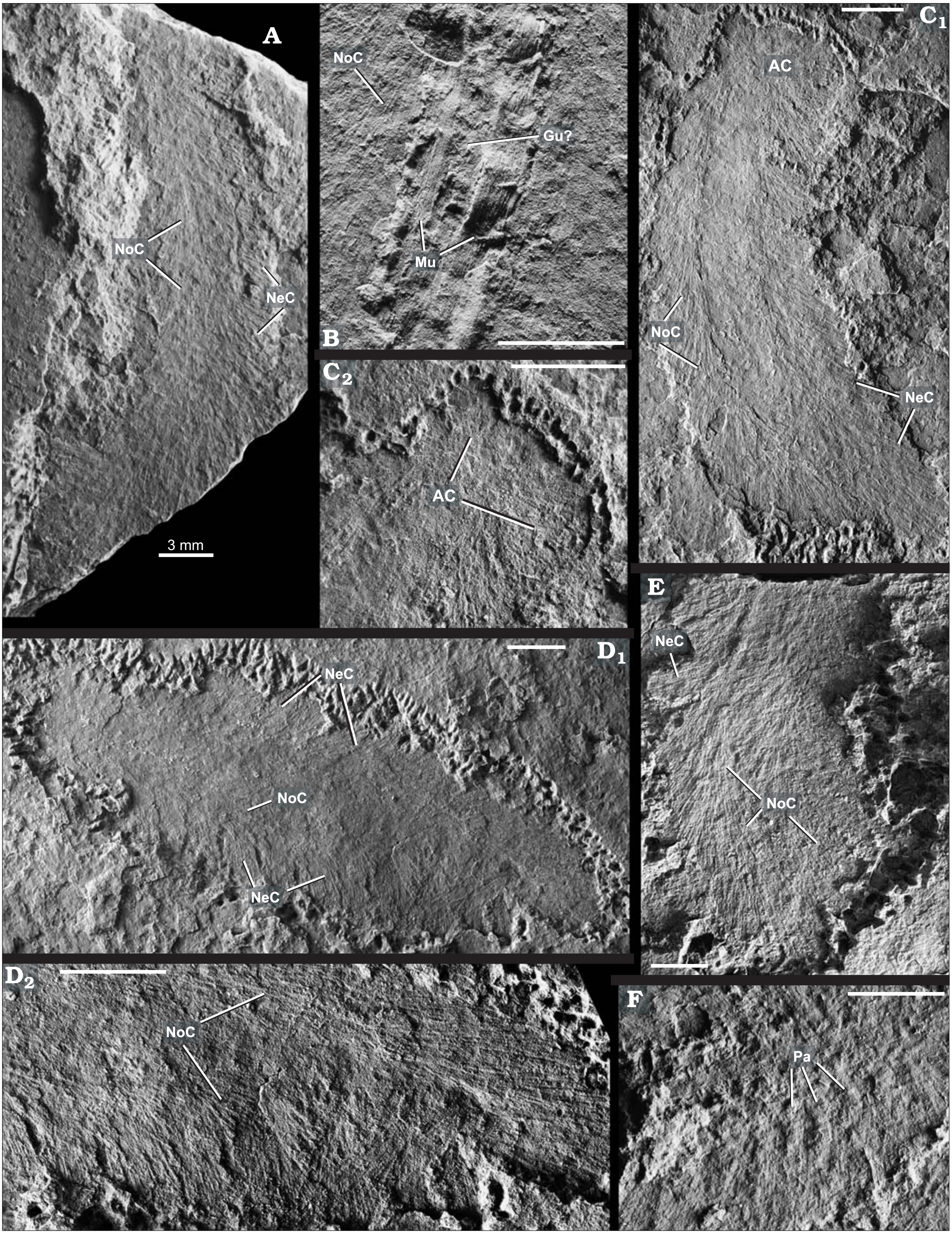


Fig. 2. Polychaete annelid *Phragmochaeta canicularis* gen. et sp. nov., Lower Cambrian (Atdabanian), Buen Formation, Sirius Passet Lagerstätte, Peary Land, North Greenland. **A**. MGUH 28.880, dorsal view (A_1) with anterior enlarged (A_2). **B**. MGUH 28.881. **C**. MGUH 28.882. **D**. MGUH 28.883. All specimens coated with ammonium chloride sublimate. Scale bars 2 mm. Abbreviations: AC, anterior chaetae (probably the notochaetae); NeC, neurochaetae; NoC, notochaetae; MU, muscles flanking the gut; SR, segmental rods.

The Sirius Passet Lagerstätte contains the oldest Lower Cambrian trilobites known from North Greenland. The occurrence of *Buenellus higginsi* Blaker, 1988 indicates the *Nevadella* Zone as used in Laurentia (Palmer and Repina 1993; Blaker and Peel 1997; Babcock and Peel in press). This is now correlated with Stage 3 of the provisional Cambrian Series 2 in the emerging global stratigraphic scheme for the Cambrian (Babcock et al. 2005). In the upper member of the formation, the occurrence of the olenelloid trilobites *Olenellus* (*Mesolenellus*) *hyperboreus* (Poulsen, 1974) and *O. svalbardensis* Kielan, 1960 indicates the *Olenellus* Zone of Laurentian usage (Blaker and Peel 1997), equivalent to the provisional Series 2 Stage 4 of the Cambrian (Babcock et al. 2005).

Description

The majority of specimens are incomplete, either because of rock breakage or because the extremities remain concealed within the sediment and are difficult to prepare. Even in the relatively few specimens with either end preserved these regions are usually indistinct. Where size measurements are possible, values for length are found to range from ca. 25–35 mm (Figs. 2A, 3D), whilst widths (which are more readily measurable) range from 1.8–12 mm. The greatest width is also seen in the longest complete specimen, so by extrapolation of a length to width ratio of c.1:3 this suggests that the species did not exceed ca. 40 mm in length. The attitude of


A
NoC
NeC
3 mm
NoC
Gu?
Mu
B
C1
AC
NoC
NeC
C2
AC
D1
NeC
NoC
NeC
E
NeC
NoC
D2
NoC
F
Pa

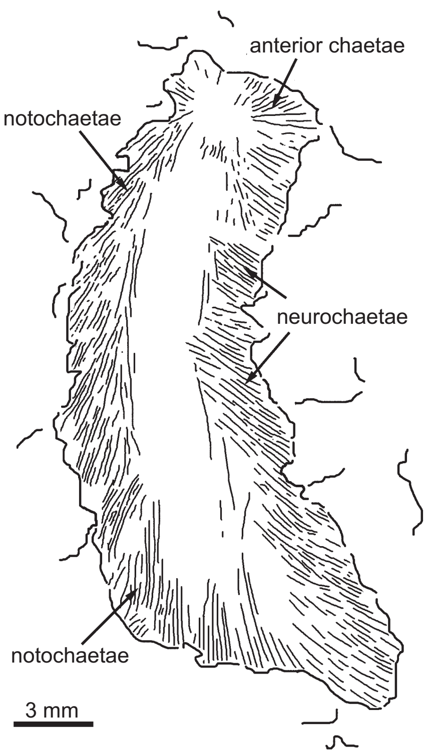


Fig. 4. Explanatory camera-lucida sketch of the holotype, MGUH 28.886; compare to Fig. 3C.

the specimens is always parallel to the bedding plane, but otherwise varies from being straight (Fig. 3D) to gently or strongly recurved (Figs. 2D, 5F).

The most obvious feature on all specimens is the chaetae (e.g., Figs. 2B, 5C), which form prominent fans. In many specimens further differentiation is difficult, but in appropriate material it is clear that on either side of each segment they form two bundles. As with the majority of polychaetes it seems reasonable to interpret the respective bundles as the standard notochaetae and neurochaetae. Differentiation is based on the assumption that the broad naked area that is flanked by obliquely inclined bundes (Fig. 5D) is the ventral view, whilst the other set of bundles that run sub-parallel to the longitudinal axis are dorsal. As noted below this is consistent with the neurochaetae and notochaetae adopting respectively a locomotory and protective role. The chaetae of each bundle are relatively robust and may also have been somewhat flattened. Under high magnification the chaetae sometimes show a longitudinal structure. The number of chaetae per bundle is difficult to estimate precisely, but appears to have been typically ca. 15.

Notochaetae and neurochaetae are distinguished on the basis of both position and orientation (Figs. 2A, 3D, E, 6C). The former are generally less completely preserved, but are arranged sub-parallel to the body axis and appear to have been relatively short. The notochaetae are directed posteriorly, except around the anterior where they appear to have extended forwards (Figs. 2A, 3C). By definition the notochaetae are on the dorsal surface, and in appropriately preserved specimens they are seen to overlie the neurochaetae. In the majority of specimens the extent of coverage by the notochaetae appears to be restricted to the dorsal margins. This may, however, be effectively a preservational artefact because in MGUH 28.884 and MGUH 28.888 (Fig. 3A, E) notochaetae are seen to cover almost the entire dorsum. There is some evidence that the anterior-most notochaetae were not only significantly smaller but were also composed of smaller bundles (Figs. 2A, 3C).

The neurochaetae are almost invariably more prominent, and project at an oblique and posterior angle to the body axis (e.g., Fig. 5B). The parapodia are also sometimes visible (Figs. 5E, 6A, B), and were closely spaced and arose along the ventro-lateral margins, being separated by a broad and more-or-less featureless ventral zone (Fig. 5E). As with the notochaetae the anterior-most bundles appear to be smaller (Fig. 6D), while towards the posterior the neurochaetae were more elongate (Figs. 2D, 3D, 6A).

Little else is known of the external aspect. In no specimen is the anterior clearly preserved. So far as can be told there were no palps, antennae, or other appendages. So too evidence is lacking for eyes, and also gills. Estimates of segment numbers must rely on counts of chaetal bundles, and given the degree of overlap and incompleteness of specimen numbers are somewhat tentative. An average size specimen, however, appears to have possessed ca. 20 segments.

Several features of the internal anatomy are preserved, although some interpretations are not straightforward. A few specimens show a dark trace (but less evident in the material when coated with sublimate; Fig. 6A) which is interpreted as the alimentary canal. In two cases gut contents have been identified. One (unillustrated) consists of a bolus of fine-grained, indeterminate material, while in the posterior region of MGUH 28.899 (Fig. 6F) there is a semi-continuous gut fill of more particulate matter. No jaw has been identified in this species. In one specimen (Fig. 6D) an elongate strand extends from close to the anterior. This could be identified as an everted proboscis, but this structure lies at a different level and we consider it more likely to be a fortuitous association.

A more prominent feature of the internal anatomy are two parallel strands in the mid-region of the body (Fig. 6B, F; see also Fig. 5A, C) which presumably originally flanked the gut. These strands, assuming they represent the same structure, show a somewhat variable appearance. In MGUH 28.885

← Fig. 3. Polychaete annelid *Phragmochaeta canicularis* gen. et sp. nov., Lower Cambrian (Atdabanian), Buen Formation, Sirius Passet Lagerstätte, Peary Land, North Greenland. **A**. MGUH 28.884. **B**. MGUH 28.885. **C**. MGUH 28.886, dorsal view (C_1) with anterior enlarged (C_2). **D**. MGUH 28.887, dorsal view (D_1) with flank enlarged (D_2). **E**. MGUH 28.888. **F**. MGUH 28.895. All specimens coated with ammonium chloride sublimate. Scale bars 3 mm. Abbreviations: AC, anterior chaetae (probably the notochaetae); GU?, presumed gut; NeC, neurochaetae; NoC, notochaetae; MU, muscles flanking the presumed gut; Pa, parapodia.

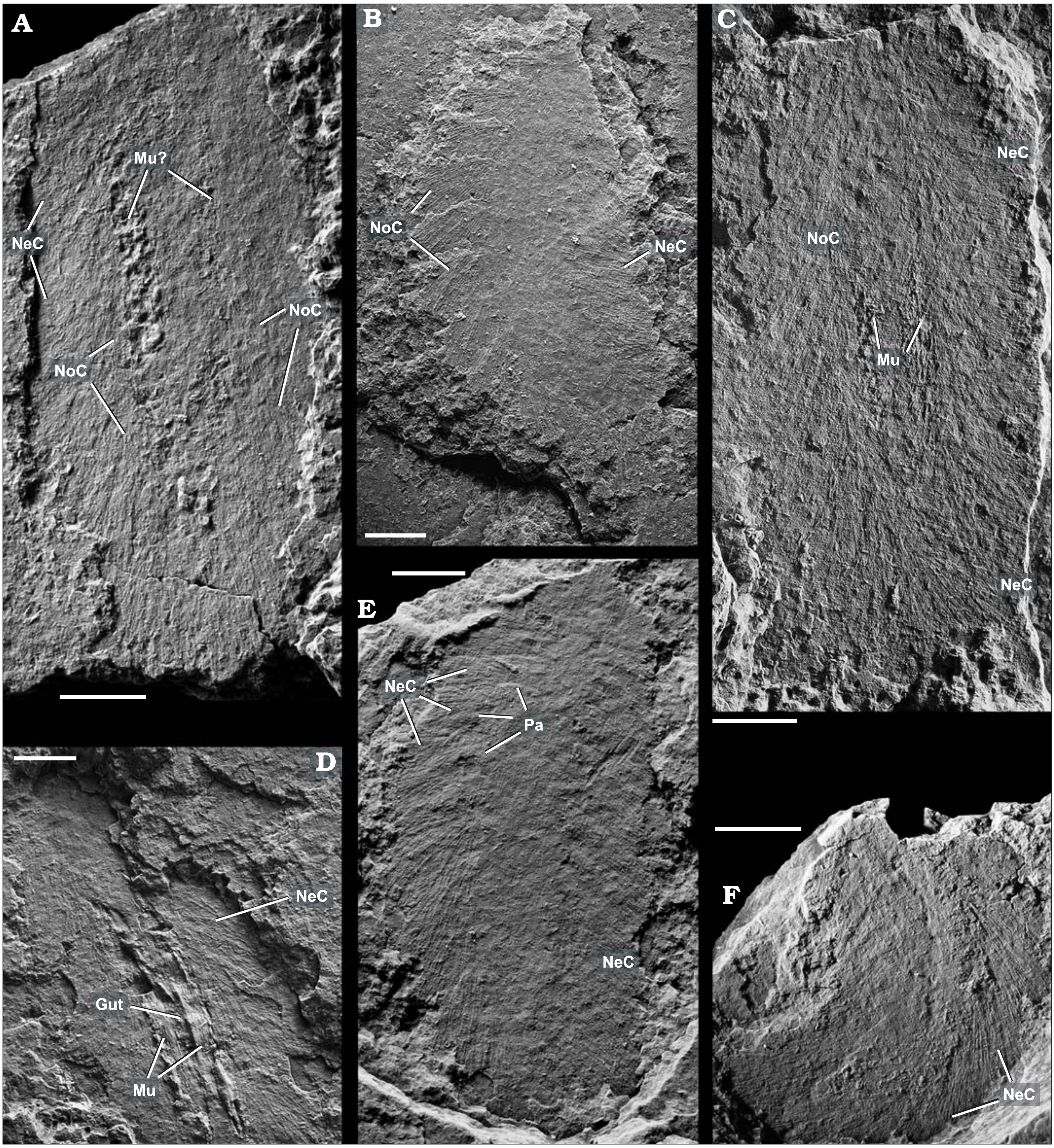


Fig. 5. Polychaete annelid *Phragmochaeta canicularis* gen. et sp. nov., Lower Cambrian (Atdabanian), Buen Formation, Sirius Passet Lagerstätte, Peary Land, North Greenland. **A**. MGUH 28.889. **B**. MGUH 28.890. **C**. MGUH 28.891. **D**. MGUH 28.885. **E**. MGUH 28.892. **F**. MGUH 28.893. All specimens coated with ammonium chloride sublimate. Scale bars 3 mm. Abbreviations: Gut, gut (alimentary canal); MU, muscles flanking the gut; MU?, presumed muscles flanking the gut; NeC, neurochaetae; NoC, notochaetae; Pa, parapodia.

(Figs. 3B, 5D) the strands show a fine longitudinal fibrosity, consistent with it representing muscular tissue (Budd 1998). In other specimens these longitudinal strands may display a more complex arrangement, which in MGUH 28.898 (Fig. 6E) consists of a series of irregular, tube-like structures. In MGUH 28.882 (Fig. 2C) the strands have prominent relief, but the intervening area is also partially mineralized. A more problematic arrangement, only clearly seen in MGUH 28.881 (Fig.

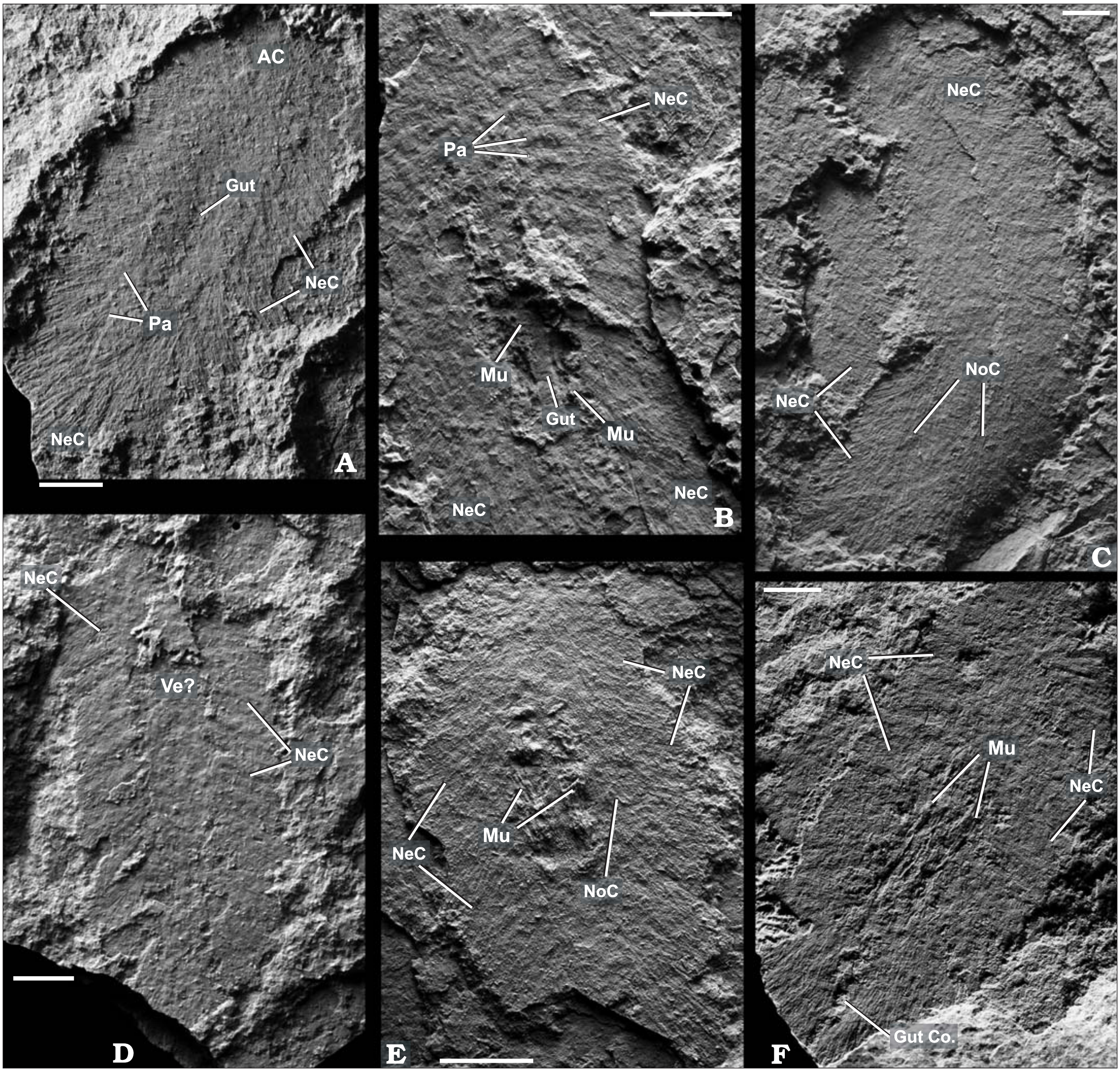


Fig. 6. Polychaete annelid *Phragmochaeta canicularis* gen. et sp. nov., Lower Cambrian (Atdabanian), Buen Formation, Sirius Passet Lagerstätte, Peary Land, North Greenland. **A**. MGUH 28.894. **B**. MGUH 28.895. **C**. MGUH 28.896. **D**. MGUH 28.897. **E**. MGUH 28.898. **F**. MGUH 28.899. All specimens coated with ammonium chloride sublimate. Scale bars 3 mm. Abbreviations: AC, anterior chaetae (probably the notochaetae); Gut, gut (alimentary canal); Gut Co, gut contents; MU, muscles flanking the gut; NeC, neurochaetae; NoC, notochaetae; Pa, parapodia; Ve?, presumed ventral surface.

2B), consists of segmentally arranged rod-like structures that in being inclined adaxially serve to define a chevron-like arrangement. Closer to the midline in this specimen there is also a series of block-like structures which may represent muscles. The somewhat variable appearance of these strands make it difficult to decide whether they represent taphonomic variants of the same structure or are distinct organs. At the least, however, the prominent fibrous strands probably represent massive internal musculature.

Mode of life

The great majority of the Sirius Passet fauna appears to have been benthic, being either sessile (e.g., sponges) and vagrant, mostly in the form of diverse arthropods and the halkieriids. Evidence of infaunal activity is restricted to narrow and simple trace fossils, and there is no reason to think that these are a product of this polychaete. Indeed such evidence as we have suggests that *Phragmochaeta* was epifaunal. Thus, it is assumed that the worm locomoted by virtue of its neuropodial chaetae, with the dorsal equivalents forming a protective thatch. The mode of feeding remains uncertain, and the rare gut contents (Fig. 6F) are not particularly informative.

Phylogenetic affinities

These fossils are clearly polychaetes, and are important in as much as they are stratigraphically the oldest yet recorded. Nevertheless, their exact relationships within the annelids (and various fossils attributed to this group) are difficult to resolve. To the first approximation this worm appears to be very generalized, notably with its closely similar noto- and neurochaetae. These only differ in relative orientation, and show no particular differences, other than relatively subdued size differences at either end of the body. The absence (whether originally wanting or were simply small and concealed) of key features, such as palps and antennae, that might help to refine the phylogenetic position, is a considerable draw-back in reliably comparing *Phragmochaeta* with the extraordinarily diverse assemblage of living annelids.

The diversity of polychaete taxa in the Burgess Shale is striking (Conway Morris 1979; Eibye-Jacobsen 2004), both in comparison to the monospecific occurrence in the Sirius Passet Lagerstätte and, as noted above, the almost total absence of this group from all other Burgess Shale-type faunas. Comparisons are further hindered because *Phragmochaeta* shows no particular similarity to any of the Burgess Shale taxa. The overall arrangement of the noto- and neurochaetae somewhat resembles *Canadia spinosa* (Conway Morris 1979), but the differentiation of chaetal shape in this Burgess Shale taxon is much more pronounced than in *Phragmochaeta*. The Sirius Passet taxon also resembles *Burgessochaeta setigera* in as much as in this Burgess Shale taxon the noto- and neurochaetae are effectively identical and similar in form to *Phragmochaeta*. Their overall arrangement is, however, dissimilar, especially in terms of their much wider segmental spacing, and the fact that in *Burgessochaeta* the notochaetae form distinct bundles quite unlike the thatch-like arrangement in *Phragmochaeta*.

Not only are comparisons with other Cambrian taxa difficult, but the wider position of *Phragmochaeta* in the annelids is also problematic. In part, this is because of the problems with establishing the overall pattern of annelid phylogeny. This difficulty is now well-appreciated, and given the advances in many other areas of metazoan phylogeny somewhat surprisingly a resolution of annelid relationships has proved unexpectedly problematic. This problem is further compounded because not only are many of the nodes, especially at deeper levels in the annelidan tree, weakly supported, but there is a general lack of concordance between the traditional morphological approach (see Bartolomaeus et al. 2005) and molecular data (e.g., Rousset et al. 2007; Struck et al. 2007; see also McHugh 2005). As Rousset et al. (2007: 54) remark that despite their analysis being “the most ambitious attempt yet to resolve annelid relationships […] overall resolution remains discouraging: rarely [have] so many taxa […] been sequenced for so many nucleotides with such sparing results”.

Given, therefore, the existing lack of resolution in annelid phylogeny it seemed that any phylogenetic analysis of *Phragmochaeta* would have to rely on a morphological data matrix and accordingly we chose the widely used scheme offered by Rouse and Fauchald (1997). This approach was also employed in the recent analyses of the fossil polychaetes *Kenostrychus* (Sutton et al. 2001) and *Arkonips* (Farrell and Briggs 2007), respectively from the Silurian and Devonian. As with these two other fossil polychaetes, a significant number of the character states identified by Rouse and Fauchald (1997) for use amongst extant taxa remain unknown. In addition we made a few minor changes in the coding of some character states for *Arkonips* (Farrell and Briggs 2007). As with the phylogenetic analyses of *Kenostrychus* and *Arkonips* we only employed about a third of the families included by Rouse and Fauchald (1997), specifically excluding meiofaunal groups and the great majority of families with sedentary life habits. Our list of families was, therefore, similar to that used by Sutton et al. (2001) and Farrell and Briggs (2007), but included a number of additional groups, such as the maldanids and orbiniids. The program we employed was PAUP version 4.0b10, and here on the basis of 1061 trees we present a strict consensus tree (Fig. 7), and as an appendix also the 50% majority-rule consensus tree. Given that the data matrix is very largely derived from the compilation offered by Rouse and Fauchald (1997) it is unsurprising that to the first approximation the trees we obtained are similar. It is even less remarkable, given its paucity of characters, that the position of *Phragmochaeta* is largely unresolved and little can be said about its putative primitiveness. Again unsurprisingly the position of the two fossil polychaetes considered here, *Arkonips* and *Kenostrychus*, is much the same as previously indicated (Sutton et al. 2001; Farrell and Briggs 2006).

Systematic palaeontology

Phylum Annelida Lamarck, 1809

Class Polychaeta Grube, 1850

Family Phragmochaetidae nov.

Remarks.—A monogeneric family, diagnosis as for genus.

Genus *Phragmochaeta* nov.

Derivation of the name: An oblique reference to the thatch-like appearance of the chaetae, hence reeds (Greek *phragmites*).

Type and only species: *Phragmochaeta canicularis*.

Diagnosis.—As for species.

Phragmochaeta canicularis sp. nov.

Figs. 2–6.

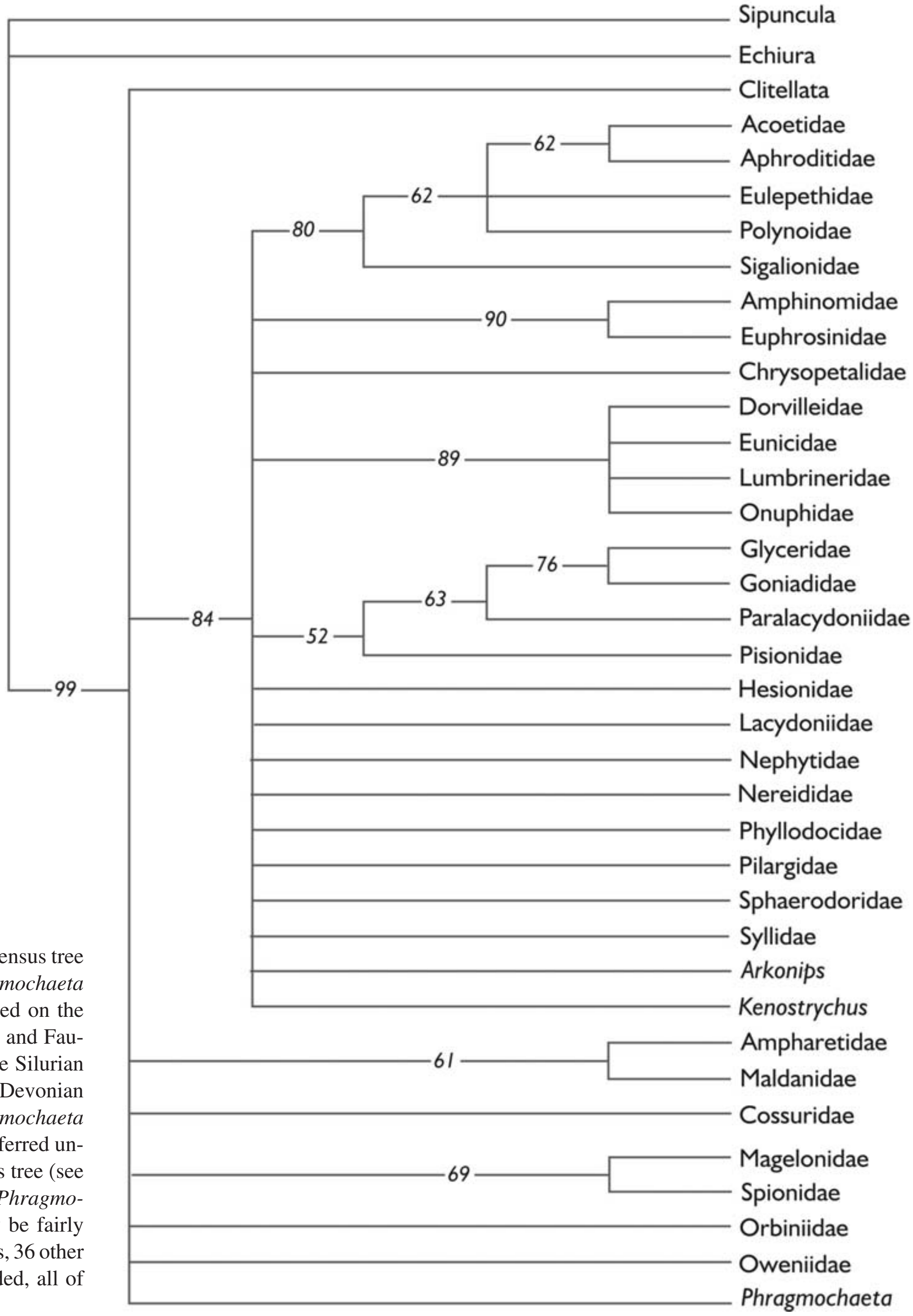


Fig. 7. A cladogram in the form of a strict consensus tree based on 1061 trees of the position of *Phragmochaeta* gen. nov. in the Annelida. Data matrix is based on the same 124 character states employed by Rouse and Fauchald (1997: 176, appendix 1a), apart from the Silurian *Kenostrychus* (Sutton et al. 2001) and the Devonian *Arkonips* (Farrell and Briggs 2007) and *Phragmochaeta* itself. Bootstrap values shown have been transferred unchanged from the 50% majority rule consensus tree (see Appendix 2). Note the phyletic position of *Phragmochaeta* is very poorly constrained, but it may be fairly basal. The outgroup chosen was the sipunculans, 36 other groups were included, and 124 characters coded, all of which were unweighted.

Derivation of the name: From the Latin for dog (canis), an oblique reference to Sirius (hence dog-star) Passet.

Holotype: MGUH 28.886. (Fig. 3C); complete specimen preserved in dorsal view.

Type locality: Peary Land, central North Greenland, at the south-western end of the broad valley connecting J.P. Koch Fjord and Brainard Sund (Fig. 1). Latitude 82°47.6’ N, longitude 42°13.7’ W, altitude of 450 m above sea level.

Type horizon: Lower part of Buen Formation (Lower Cambrian, provisional Series 2, Stage 3).

Material.—The holotype and MGUH 28.880–28.885, 28.887–28.899.

Diagnosis.—Medium-sized polychaete, ca. 20 segments. Notochaetae, simple, transverse across dorsum. Neuropodia lobate, neurochaetae oblique to body axis, otherwise similar to notochaetae. Chaetae possibly flattened, otherwise simple. At anterior both notochaetae and neurochaetae reduced in size, at posterior neurochaetae somewhat more elongate. Details of head not known. No jaws. Gut straight, flanked by massive musculature.

Stratigraphic and geographic range.—Buen Formation (Stage 3 of provisional Cambrian Series 2, equivalent to *Nevadella* Zone), Peary Land (North Greenland).

Acknowledgements

Comments by two anonymous referees greatly improved the paper. Mona Bjørklund (Uppsala, Sweden), Jon Ineson (Copenhagen, Denmark), Paul Smith (Birmingham, U.K.), and Poul Schiøler (Lower Hutt, New Zealand) are thanked for support and companionship in the field within a logistic framework coordinated by the Geological Survey of Greenland (now Geological Survey of Denmark and Greenland) and Danish Polar Center. Financial support from the Carlsberg Foundation, National Geographic, St John's College, Cambridge, Geological Survey of Greenland and the Swedish Research Council (*Vetenskapsrådet*) is gratefully acknowledged. Stefan Ekman (Museum of Evolution, Uppsala, Sweden) is thanked for advice and for running several versions of PAUP. Cambridge Earth Sciences Publication 9040.

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Appendix 1

Data matrix of character states used in cladistic analysis. The 124 characters employed are the same ones as given by Rouse and Fauchald (1997: 176).

	5	10	15	20	25	30	35	40	45	50	55	60	65	70	75	80	85	90	95	100	105	110	115	120	124
Sipuncula	00000	00000	00000	00000	00000	00000	00000	00000	00000	00000	00000	00000	00000	00000	00000	00000	00000	00010	00000	00000	10000	00000	00000	00000	0000
Echiura	00000	00010	00000	00000	00000	00000	00000	00000	00000	00000	00000	00000	00000	00000	00000	00000	00000	00010	0??0?	00000	01001	00000	00000	00000	1000
Clitellata	10001	00000	00000	00000	00000	00011	01000	01000	00000	00000	00000	00000	00000	10000	00000	00000	00000	00110	00001	00001	01001	00000	00000	01010	0000
Acoetidae	10000	00011	11100	00000	01101	10011	00100	01000	00110	10001	11001	00000	00010	00100	00101	00000	00000	10010	0????	?????	????1	00100	00000	01010	0001
Ampharetidae	10000	00010	00110	10000	10001	10011	00010	00100	00010	01000	00000	00011	00001	00010	00000	01100	00011	00010	01000	00100	01011	00000	00000	01100	0010
Amphinomidae	10000	00011	11100	00000	01011	00111	00001	01000	00011	00001	10001	10000	00000	10000	10000	00001	00000	00110	01000	10000	01001	10100	00000	01010	0000
Aphroditidae	10000	00011	10100	00000	01101	10011	00100	01000	00110	10001	11001	00000	00010	00100	00101	00000	00000	10010	01000	1000?	01001	00100	00000	01010	0001
Chrysopetalidae	10000	00011	11100	00000	01101	100?1	00100	01000	00110	00101	10001	00000	00010	00100	00110	00000	00000	00110	00100	????0	01001	00110	10010	01000	0000
Cossuridae	10001	00000	00000	00000	00001	10011	01000	01000	00011	00000	00000	00000	00000	00000	00000	00000	00000	001??	?????	?0010	01001	00000	00000	01000	0000
Dorvilleidae	10000	10001	11100	00000	01011	10011	01000	01000	00010	10001	10001	00000	10010	10000	10000	00000	10000	00110	0??00	10000	01001	00111	00001	01000	0000
Eulepethidae	10000	00011	11100	00000	01101	100?1	00100	01000	00110	10001	11001	00000	00010	00100	00101	00000	00000	10010	?????	?????	??0?1	00100	00000	01010	0000
Eunicidae	10000	10001	11100	00000	01011	10011	01000	01000	00010	10001	10001	10000	10010	10000	10000	00000	11000	00110	01000	10000	01001	00111	00001	01001	0000
Euphrosinidae	10000	00011	11100	00000	010?1	00111	00001	01000	00010	00101	10001	10000	00010	10000	10000	00001	00000	00110	01000	1000?	01001	10100	00000	01010	0000
Glyceridae	10000	00011	01100	00000	01100	00011	01000	01000	00010	10001	10001	00000	00010	00100	00100	10000	00000	00101	10010	1000?	10001	00110	10100	01000	0000
Goniadidae	10000	00011	01100	00000	01100	00011	01000	00000	10010	10001	10001	00000	00010	00100	00100	10000	000?0	?0?01	00010	00010	10001	00110	10100	01000	0000
Hesionidae	10000	00011	11100	00000	01101	10011	10000	00010	00110	10001	10001	00000	00010	00100	00110	00000	00000	00110	10100	10000	01001	00110	10100	01000	0000
Lacydoniidae	10000	00011	01100	00000	01101	10011	10000	00010	00110	10001	00101	00000	00001	00100	00000	00000	00000	001??	?????	?????	??0?1	00110	10100	01000	0000
Lumbrineridae	10000	10001	11000	00000	00001	10011	01000	01000	00010	10001	00011	00000	10010	10000	10000	00000	11000	00110	01000	????0	??0?1	00111	00000	01000	0000
Magelonidae	10000	00010	00110	00001	00000	00011	01000	00100	00010	00000	00000	00001	00010	10010	00000	00010	00000	001??	?????	00010	01001	00000	00000	01001	0100
Maldanidae	01000	00010	00000	00000	00001	10011	01000	00100	00010	01000	00000	00000	00001	100?0	0?000	000?0	00010	00110	01000	00100	01001	00000	00000	01000	1100
Nephytidae	10000	00011	01100	00000	01101	10011	10000	01000	00111	00001	10001	00000	00010	00100	00110	00000	00000	00101	10010	1000?	01001	00100	00010	01000	0000
Nereididae	10000	00011	01100	00000	01101	10011	10000	00010	00110	10001	10001	00000	00010	00100	00110	00000	00000	00110	10001	10000	01001	00110	10000	00000	0000
Onuphidae	10001	00001	11100	00000	01011	10011	01000	01000	00010	10001	10001	10000	10010	10000	10000	00000	11000	00110	01000	?0?00	01001	00111	00001	01000	0000
Orbiniidae	10001	00000	00000	00000	00001	10011	01000	01000	00011	00000	00000	00101	01001	10010	00000	00010	00000	00110	0??00	1000?	010?1	00000	00000	01010	0000
Oweniidae	00101	00000	00111	01000	0000?	?0011	01000	00001	00010	01000	00000	00000	00000	10010	00000	00010	00000	00110	01000	00000	01?01	00000	00000	01000	0100
Paralacydoniidae	10000	00011	01100	00000	0110?	?00?1	10000	00000	10010	10001	10001	00000	00???	00100	00000	00000	000?0	?0???	?????	?????	??0?1	00110	10100	01000	0000
Phyllodocidae	10000	00011	11100	00000	01101	10011	10000	00010	00110	10001	00101	00000	00010	00100	00000	00000	00000	00101	00010	10000	10001	00110	10000	01000	0000
Pilargidae	10000	00011	11100	00000	01101	100?1	10000	00010	00110	10001	10001	00000	00010	00100	00000	00000	000?0	?0???	?????	?????	??0?1	00100	00000	01010	0000
Pisionidae	10000	00011	01100	00000	01100	00011	10000	00010	00110	10001	10001	00000	00010	00100	00101	00000	00000	00101	00010	00100	10001	00110	10010	01000	0000
Polynoidae	10000	00011	11100	00000	01101	10011	00100	00010	00110	10001	11001	00000	00010	00100	00101	00000	00000	10010	01000	10000	01001	00100	00000	01010	0000
Sigalionidae	10000	00011	11100	00000	01101	10011	00100	01000	00110	10001	11001	00000	00010	00100	00101	00000	00000	10010	01000	10000	01001	00110	10001	01000	0000
Sphaerodoridae	10000	00011	11100	00000	01101	10011	10000	00010	00110	10000	00001	00000	00010	00100	00000	01000	00000	00110	0??00	0010?	10001	00110	10010	01000	0000
Spionidae	10000	00011	10110	10001	00001	01011	01000	01000	00010	00010	00000	00101	01001	100?0	0?000	000?0	00000	00110	0??00	00010	01001	00000	00000	01001	0100
Syllidae	10000	00011	11100	00000	01101	10011	01000	00010	00110	10001	10001	00000	00010	00100	00100	01000	00000	00110	00100	10000	01001	00110	10001	01000	0000
Arkonips	00100	00011	11100	01000	0110?	???01	00000	00010	00111	00001	10000	00000	0?001	?????	??0??	?????	?????	0?1??	?????	?????	????1	0000?	?????	??00?	????
Phragmochaeta	?????	?????	?????	?????	?????	???11	?0???	?0001	00011	??1?0	00000	0000?	???00	?????	??0??	?????	?????	0?1??	?????	?????	????1	0000?	?????	??00?	????
Kenostrychus	10000	00011	111??	00000	0110?	????1	01000	01000	00011	00001	10001	1000?	0?0??	?????	?????	?????	?????	?????	?????	?????	????1	??1??	?????	??00?	????

Appendix 2

A cladogram in the form of a 50% majority rule consensus tree of 1061 trees. Details otherwise as given in Fig. 7.