

ISSN 1708-5217
ISBN 978-1-897095-70-6

24th Annual Canadian Palaeontology Conference Proceedings No. 12

CPC-2014 Montreal
28 August to 31 August, 2014

Joint conference of the Geological Association of Canada
Palaeontology Division and the Canadian Society of Vertebrate
Palaeontology

Redpath Museum, McGill University



Paleontology Division
Geological Association of Canada

Canadian Society of Vertebrate Palaeontology

biogeography, palaeoecology, and systematics of Permo-Carboniferous taxa. Fossils recovered from formations within this group (Orby Head, Hillsborough River, and Kildare Capes) indicate the presence of typical Permo-Carboniferous assemblages, composed of temnospondyls, parareptiles, diadectids, a caseid or a varanopid, and a sphenacodontid. The parareptile, previously identified as *Mycterosaurus* sp., is known from a partial dentary with multiple teeth similar in morphology to acleistorhinid parareptiles. The recognition of this parareptile represents the first occurrence of a non-synapsid amniote from the PEI redbeds. The diadectid is represented by dental and vertebral elements, and most convincingly by tracks and trackways of *Ichniotherium*. The ambiguous presence of a caseid or varanopid is based on the re-interpretation of a partial pterygoid, previously assigned to Ophiacodontidae, with a unique palatal dentition not known in ophiacodontids. The sphenacodontid, *Bathygnathus borealis*, is known from a partial snout with upper dentition. The teeth are labio-lingually compressed, convex labially, and possess mesial and distal carinae with large denticles. CT data shows that the tooth roots are elongate and do not possess plicidentine. A phylogenetic analysis of sphenacodontids suggests that *Bathygnathus* is more closely related to *Dimetrodon* than to *Sphenacodon* based on the morphology of the teeth and tooth roots, and is deeply nested within the *Dimetrodon* clade as the sister to *D. grandis*.

The re-description of these taxa from PEI provides the basis for an updated faunal list for the vertebrate-bearing formations within the Pictou Group. The presence of a parareptile, diadectid, and possibly three synapsids (caseid and/or varanopid and sphenacodontid), together with the absence of edaphosaurids and definitive ophiacodontids suggests similarities with the upland Bromacker and Richards Spur localities of Germany and Oklahoma, respectively. However, more research and new fossil discoveries are needed to confidently resolve the systematics and palaeoecology of amniotes from the Lower Permian of Atlantic Canada.

RARE CRINOID ASSOCIATIONS FROM THE UPPER ORDOVICIAN NEUVILLE FORMATION, QUÉBEC, CANADA: SMALL CRINOIDS AS PASSENGERS ON BIG CRINOIDS

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Recently discovered crinoid faunas of the Upper Ordovician Neuville Formation in and around Québec City, Canada are being studied. The Formation consists of interbedded grey lime mudstones and calcareous shales which were deposited in relatively deep waters, mostly below storm wave base, on the outer shelf. Brachiopod dominated assemblages and trace fossils are common. However, the beds with abundant fully articulated echinoderms, and trilobites are rare. Most crinoids are found on limestone beds, overlain by muds. These beds are interpreted as mudflows or turbidity currents generated by storms on the shallow parts of the shelf. The Neuville Formation of Québec roughly correlates with various Upper Trenton Group units in Ontario and New York.

Some of the most unique and ecologically informative examples of the Neuville crinoids are

seen in associations between two types of crinoids : large crowns of *Ectenocrinus geniculatus* and small juvenile camerate crinoids of an undescribed species of *Euptychocrinus* that were clearly attached by wrapping their stems around the larger species. This must have occurred while the *E. geniculatus* were alive and elevated well above the seafloor at the time of death and burial. This is evidenced by the fact that the specimens are all complete and the camerate stems are wrapped all the way around “and actually appear knotted or tied to” the stem of the *E. geniculatus*. Although the stems of *E. geniculatus* are not complete, their preserved length would indicate that the base of the crown was located at least 120 mm above the seafloor.

Paleozoic crinoids were passive suspension feeders, using their tube feet to capture small swimming and floating micro-organisms from the surrounding water currents. A likely scenario follows. The juvenile *Euptychocrinus* n. sp. probably cemented their embryonic holdfasts to the stem of their hosts. During growth, the stem of typical Paleozoic crinoids becomes longer due to the addition of new plates and calcite accretion onto older ones. Hence the relationship between the host *E. geniculatus* and its residents, namely the small crowns of *Euptychocrinus* n. sp., must have continued for an appreciable amount of time. The small camerates obviously benefited greatly from this partnership because attachment to the elevated stems of *E. geniculatus* would have raised them above the muddy seafloor along with the organisms living there. Although they were feeding at the same level, they probably did not compete for the exact same food supplies. *Euptychocrinus* n. sp. with its narrow food grooves and small closely spaced tube feet would have eaten a narrow range of very small food particles. *E. geniculatus* must have had wider food grooves along with larger gaps between adjacent tube feet which would have enabled it to capture a wider set of larger food items. Thus it seems unlikely that the specimen of *E. geniculatus* were harmed by their relationship with the small individuals of *Euptychocrinus* n. sp.

A mature individual of *Euptychocrinus* n. sp., with a partial stem, was also discovered, thus, the adult mode of life of this species remains unknown.

PHYLOGENY & TAPHONOMIC DECAY OF THE HEMICHORDATE *RHABDOPLEURA* - A LIVING GRAPTOLITE

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Graptolites are an important component of early-middle Paleozoic biotas. Here we present a phylogenetic analysis incorporating data from extant the species of pterobranchs *Cephalodiscus* and *Rhabdopleura* and representatives of each of the major graptolite orders. Our results reveal two well supported clades within the Pterobranchia: the cephalodiscids, and *Rhabdopleura* plus all graptolites. *Rhabdopleura* nests among the benthic, encrusting graptolite taxa and shares all of the important synapomorphies that unite the graptolites. Therefore, rhabdopleurids can be regarded as extant members of the Subclass Graptolithina, a sister taxon to the Subclass Cephalodiscida. The nesting of

Rare crinoid associations from the Upper Ordovician Neuville Formation, Québec, Canada: small crinoids as passengers on big crinoids

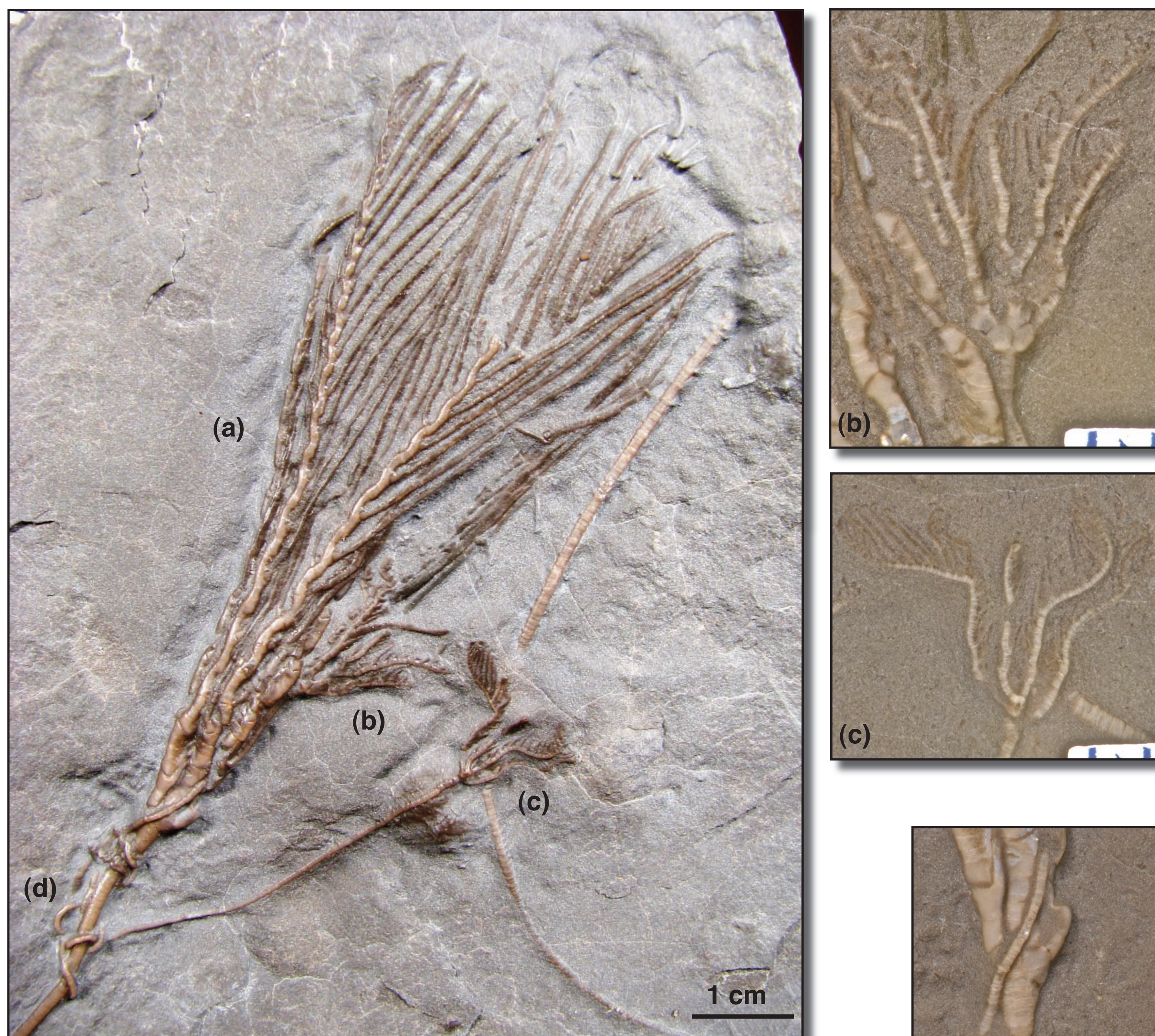
BROWER, James C.¹, Iellamo, John² and Cournoyer, Mario E.²

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INTRODUCTION

Recently discovered crinoid faunas of the Upper Ordovician Neuville Formation in and around Québec City, Canada, are being studied. The Formation consists of interbedded grey lime mudstones and calcareous shales which were deposited in relatively deep waters, mostly below storm wave base, on the outer shelf. Brachiopod dominated assemblages and trace fossils are common. However, the beds with abundant fully articulated echinoderms and trilobites are rare. Most crinoids are found on limestone beds, overlain by muds. These beds are interpreted as mudflows or turbidity currents generated by storms on the shallow parts of the shelf. The Neuville Formation of Québec roughly correlates with various Upper Trenton Group units in Ontario and New York.

Some of the most unique and ecologically informative examples of the Neuville crinoids are seen in associations between two types of crinoids : large crowns of *Ectenocrinus geniculatus* and small juvenile camerate crinoids of an undescribed species of *Euptychocrinus* that were clearly attached by wrapping their stems around the larger species. This must have occurred while the *E. geniculatus* were alive and elevated well above the seafloor at the time of death and burial. This is evidenced by the fact that the specimens are all complete and the camerate stems are wrapped all the way around "and actually appear knotted or tied to" the stem of the *E. geniculatus*. Although the stems of *E. geniculatus* are not complete, their preserved length would indicate that the base of the crown was located at least 120 mm above the seafloor.



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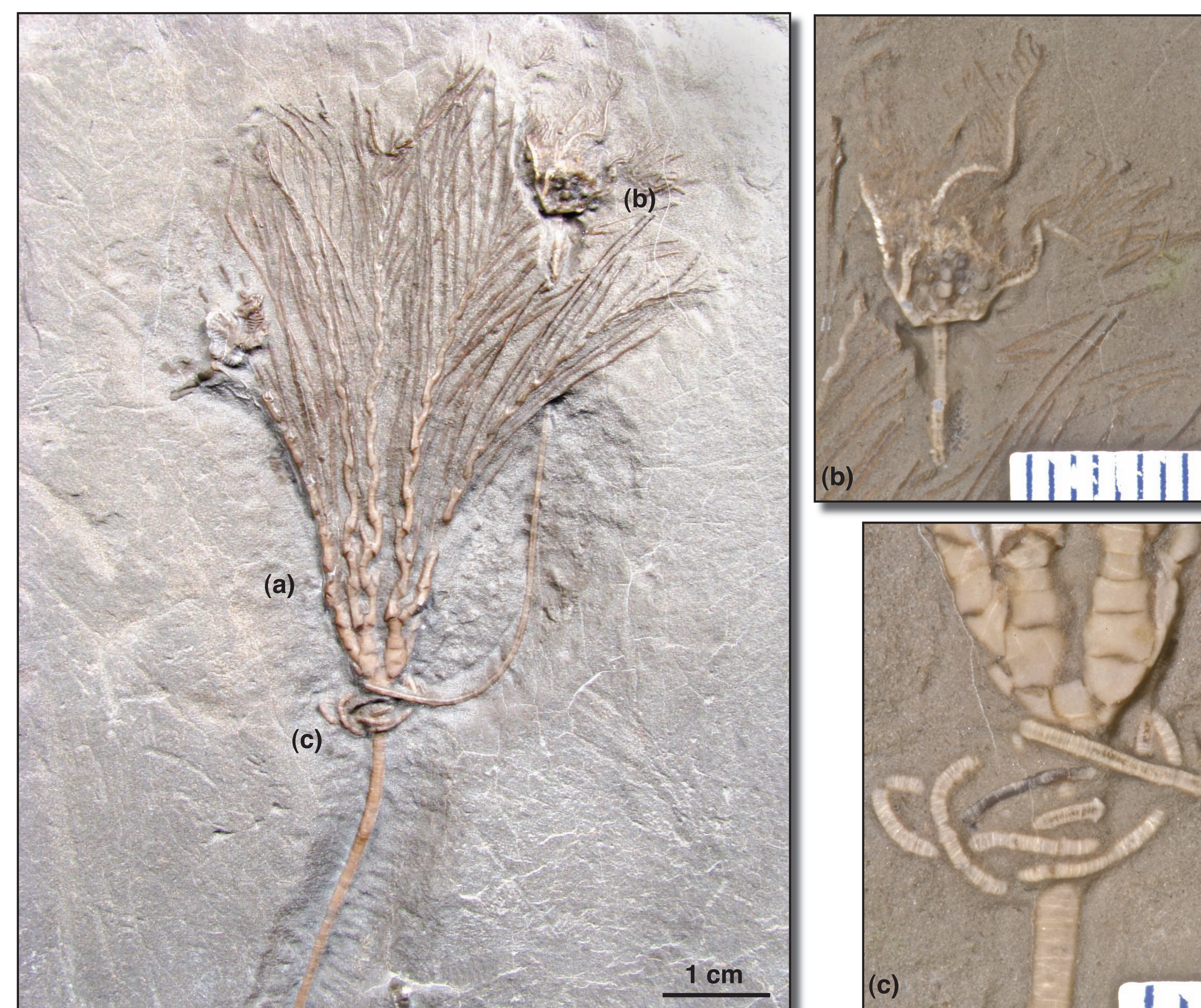
The large crown (a) with the long stem segment belongs to the disparid crinoid *Ectenocrinus geniculatus*. Two small juvenile camerate crinoids of an undescribed species of *Euptychocrinus* are also present, one immediately to the right (b) and the other further to the right of the crown of *E. geniculatus* (c). The juvenile camerates were clearly attached by wrapping their stems around the column of *E. geniculatus* (d).

PARTNERSHIP

Paleozoic crinoids were passive suspension feeders, using their tube feet to capture small swimming and floating micro-organisms from the surrounding water currents. A likely scenario follows. The juvenile *Euptychocrinus* n. sp. probably cemented their embryonic holdfasts to the stem of their hosts. During growth, the stem of typical Paleozoic crinoids becomes longer due to the addition of new plates and calcite accretion onto older ones. Hence the relationship between the host *E. geniculatus* and its residents, namely the small crowns of *Euptychocrinus* n. sp., must have continued for an appreciable amount of time.

The relationship must have been long enough for the juvenile camerates to develop reasonably long stems. Unfortunately little is known about the ages of Recent or fossil crinoids. Assuming that the Ordovician camerates were similar to Recent comatulid crinoids, their approximate age can be estimated. In general, the juvenile camerates resemble the late pentacrinid growth stages of living comatulids. Data listed by Clark (1921, p. 513-590) for three modern comatulids from cold water areas, *Antedon bifida*, *Hathrometra sarsii*, and *Promachocrinus kerguelensis*, suggest that the pentacrinid growth stages of these species end at about nine months to 2.5 years when the larval stems are shed. These data certainly imply that the young camerates were attached to their host for a minimum of some months.

The small camerates obviously benefited greatly from this partnership because attachment to the elevated stems of *E. geniculatus* would have raised them above the muddy seafloor along with the organisms living there. Although they were feeding at the same level, they probably did not compete for the exact same food supplies. *Euptychocrinus* n. sp. with its narrow food grooves (or ambulacrae) and small closely spaced tube feet would have eaten a narrow range of very small food particles. *E. geniculatus* must have had wider food grooves along with larger gaps between adjacent tube feet which would have enabled it to capture a wider set of larger food items. Thus it seems unlikely that the specimens of *E. geniculatus* were harmed by their relationship with the small individuals of *Euptychocrinus* n. sp.



SPECIMEN MPEP700.26

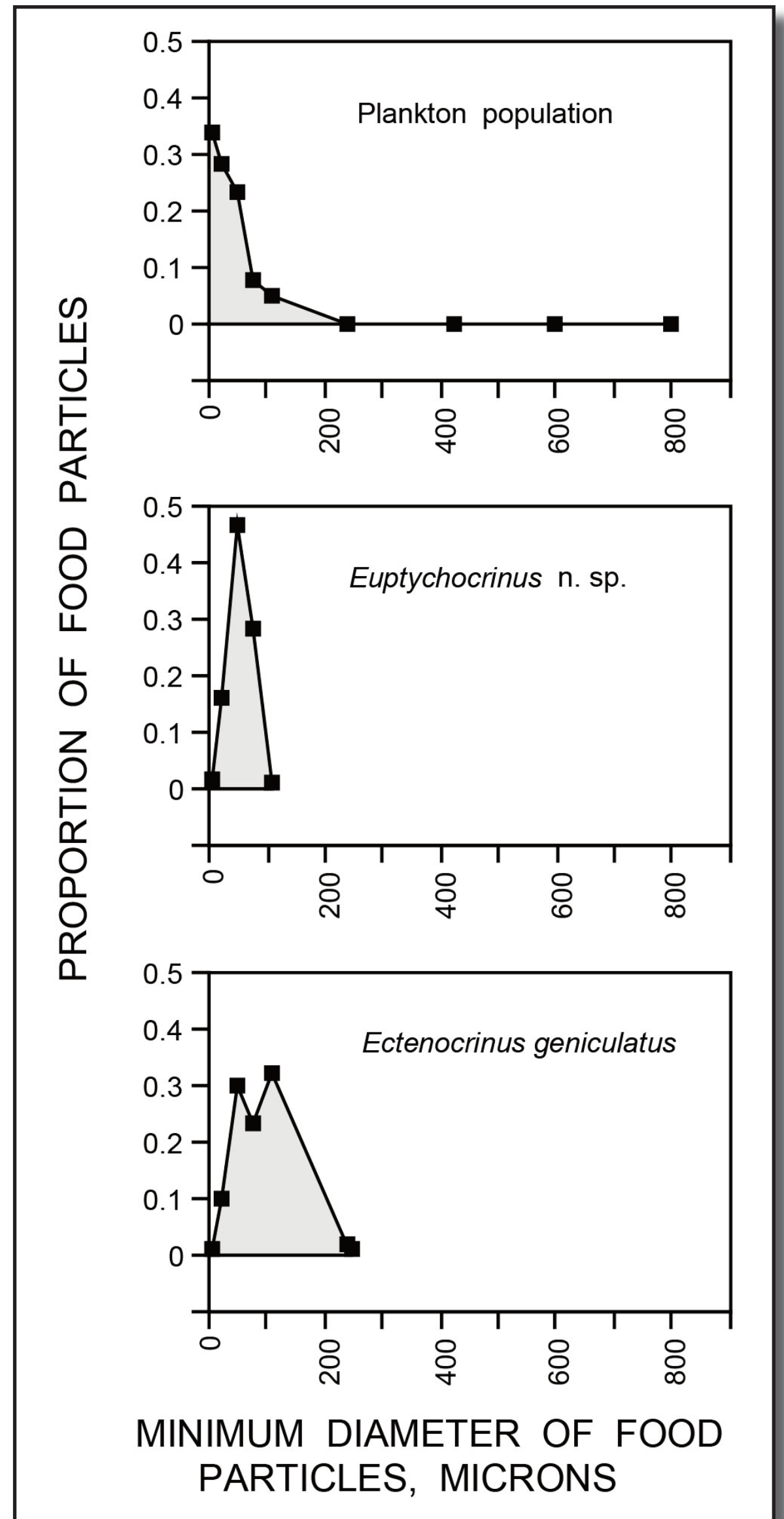
The large crown (a) with the long stem segment belongs to the disparid crinoid *Ectenocrinus geniculatus*. One small juvenile camerate crinoid of an undescribed species of *Euptychocrinus* is also present, on the upper right portion of the crown of *E. geniculatus* (b). The juvenile camerate was clearly attached by wrapping its stem around the column of *E. geniculatus* (c).

FOOD PARTICLES

Although the food grooves and covering plates of *Euptychocrinus* n. sp. and *Ectenocrinus geniculatus* are unknown, it is still possible to apply the methods of filtration theory discussed by Baumiller (1993) and Brower (2007, 2011, 2013) to model the approximate size distributions of food particles collected by the crinoids. Most food particles were caught by the tube feet located along the food grooves of the ramules of *Ectenocrinus geniculatus* and those on the pinnules of *Euptychocrinus* n. sp. The main arms principally serve to convey food particles to the mouth. Hence, the estimates of the food groove widths are based on the average width of the pinnules and the ramules. In typical Ordovician crinoids the food grooves are about 60 percent of the width of the arms, ramules or pinnules.

The plankton population illustrates the size distribution of the food items that were available for capture, and the data are obtained from plankton in modern oceans. Note that the food particle distributions of the two Ordovician crinoids are skewed toward larger food items. This is because crinoids are more efficient at catching larger food particles than smaller ones. The food particles utilized by *Euptychocrinus* n. sp. are restricted to a relatively narrow range of small food particles because of its narrow food grooves and small and closely spaced food-catching tube feet.

Conversely, the larger and more widely separated tube feet (or podia) and the wider food grooves of *Ectenocrinus geniculatus* allowed the capture of a wider range of food items. If the two species competed for food, this competition was limited to common items within the smaller food particles.



SIZE DISTRIBUTION OF FOOD PARTICLES

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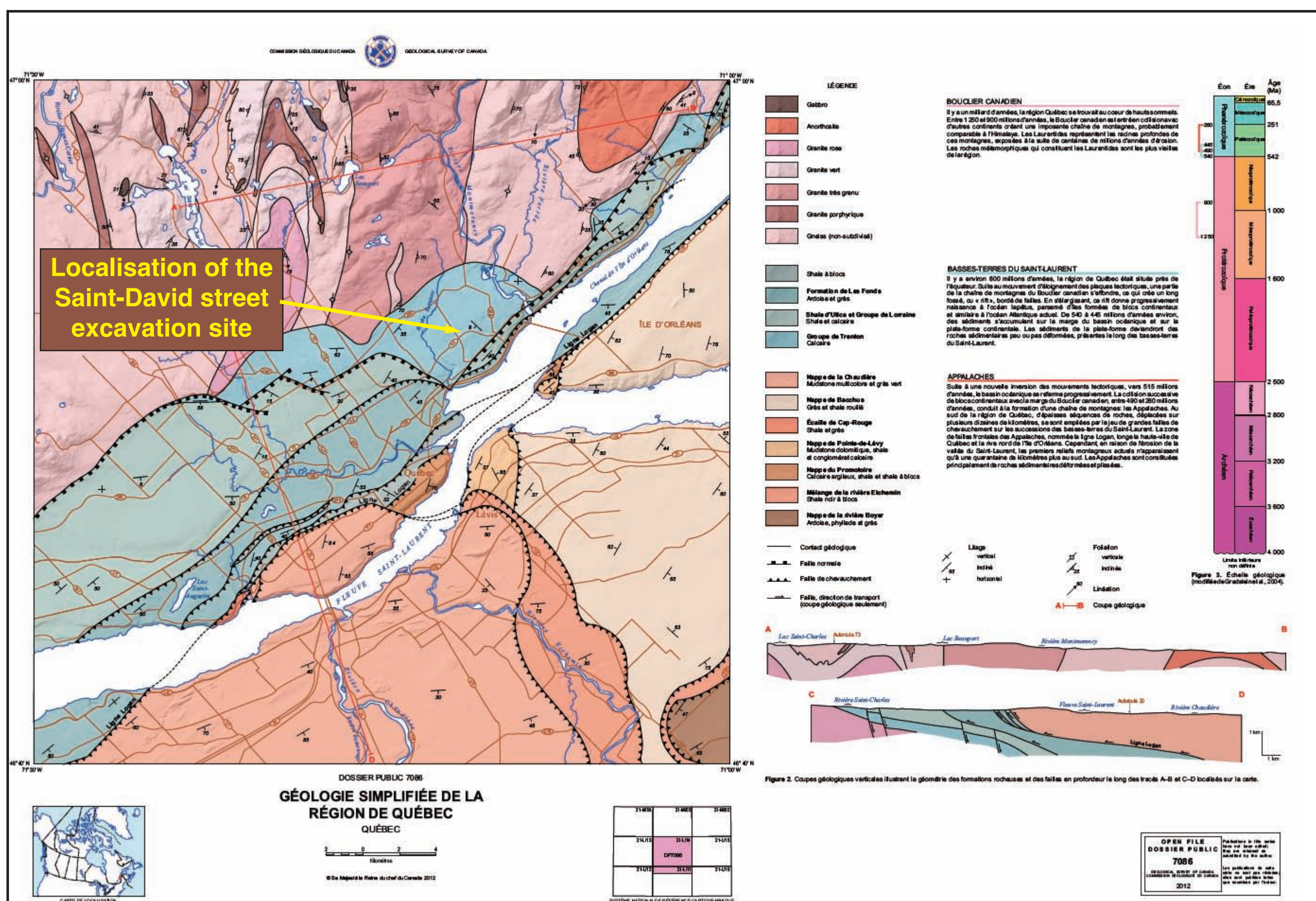
Mature individual of *Euptychocrinus* n. sp., with a partial stem (on the left) and a *Cincinnatiocrinus varibrachialis* individual (on the lower right). Until more complete specimens are found, the adult mode of life of this species will remain unknown.

ACKNOWLEDGMENTS

The authors are grateful to Mr. Michel Bédard, co-owner of Les Entreprises GÉVILCO (Québec) for providing access to the construction site and rock dumps. A special thank you to Kevin Brett for providing information regarding the Neuville Formation and Daniel Lavoie for helping out with the general geological setting of the Québec City area.

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SIMPLIFIED GEOLOGICAL MAP OF THE QUÉBEC CITY AREA AND LOCALISATION OF SITE

Faunal list

- | | | | |
|--------------|---------------------------------|-------------------|---|
| Conularida | <i>Conularia trentonensis</i> | Crinoidea | |
| Bryozoa | branching form | Cladida | <i>Dendrocrinus</i> n. sp. * |
| | dome form | | <i>Plicodendrocrinus proboscidiatus</i> † |
| Brachiopoda | | Disparida | <i>Quinequecaudex</i> ? sp. † |
| Inarticulata | <i>Pseudolingula</i> sp. | | <i>Ectenocrinus simplex</i> |
| Trilobita | <i>Ceraurus pleurexanthemus</i> | | <i>Ectenocrinus geniculatus</i> † |
| | <i>Flexicalymene senaria</i> | Camerata | <i>Cincinnatiocrinus varibrachialis</i> † |
| | <i>Hypodicranotus</i> sp. | | Undescribed disparid * |
| | | Rhombifera | <i>Rhaphanocrinus</i> n. sp. * |
| | | | <i>Euptychocrinus</i> n. sp. * |
| | | Cystoidea | |
| | | Rhombifera | <i>Homocystites anatiformis</i> |
| | | | cf. <i>Homocystites</i> n. sp. * |
| | | Stylophora | |
| | | Mitrata | <i>Ateleocystites</i> sp. † |
| | | Undet. Echinoderm | |

* - new species
† - new occurrence