Life Sciences Contributions
Royal Ontario Museum 120

The Ordovician Trilobite *Pseudogygites* Kobayashi in Eastern and Arctic North America

Rolf Ludvigsen

ROM

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LIFE SCIENCES CONTRIBUTIONS
ROYAL ONTARIO MUSEUM
NUMBER 120

ROLF LUDVIGSEN

The Ordovician Trilobite *Pseudogygites* Kobayashi in Eastern and Arctic North America

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The Ordovician Trilobite *Pseudogygites* Kobayashi in Eastern and Arctic North America

Abstract

Pseudogygites Kobayashi is an endemic North American isoteline trilobite which occurs widely in bituminous shale and limestone units of Late Ordovician age (Maysvillian and Richmondian) in southern Ontario and neighbouring areas and the Canadian arctic. The originally designated type species, *Asaphus canadensis* Chapman from Whitby, Ontario, is a junior subjective synonym of *Asaphus*? *latimarginata* Hall from the Watertown area of New York. *Pseudogygites latimarginatus* is rare in the Cobourg Formation of southern Ontario, but is very abundant in the overlying lower Whitby Formation. Three new species are described: *Pseudogygites hudsoni* from Southampton Island, Hudson Bay; *P. akpatokensis* from Akpatok Island, Ungava Bay; and *P. arcticus* from Devon, Bathurst, and Cornwallis islands.

Preservation of both carcasses and undisturbed exuviae of *P. latimarginatus* permits reconstruction of the moulting behaviour of this species.

In ecologic terms, the Cobourg-Whitby contact identifies the level at which the environment changed from shallow, well oxygenated, and warm to shallow, oxygen-poor, and cold. *P. latimarginatus* was probably derived from *Isotelus gigas* by paedomorphosis (neoteny) and its great abundance in the lower Whitby is attributed to fortuitous preadaptation to a new ecologic setting. The four known species of *Pseudogygites* could be iterative paedomorphs of different species of *Isotelus*.

Introduction

The endemic North American trilobite *Pseudogygites* occurs in vast numbers at a few localities in southern Ontario and widely in arctic Canada. Despite the wealth of material, the genus has remained poorly known since it was established by Kobayashi in 1934. Its definition was perfunctory and, furthermore, hidden in a descriptive work on Korean trilobites. Kobayashi chose *Asaphus canadensis* Chapman, 1856 from

Whitby, Ontario, as the type species, but presented no illustrations and, apparently, made no attempt to trace the type specimens. His diagnosis of *Pseudogygites* was brief, but concise: "*Basilicus*-like asaphids; hypostoma forked; isoteliform suture; glabella urceolate, well defined by the dorsal furrow; glabellar furrows rather indistinct." (Kobayashi, 1934:460, 461). As Fritz (1959:1120) suggested, Kobayashi probably based his concept of *Pseudogygites* on the specimen from Ottawa that was illustrated by Raymond (1913:pl. 6, fig. 1) and not on that illustrated by Chapman (1858) from the type area because the Ottawa specimen was the only specimen published at that time showing the attributed diagnostic features. This specimen has also served as a model for the reconstruction of *P. canadensis* in the *Treatise* (Jaanusson, 1959:fig. 253-5a).

The purpose of this paper is to assess critically the material of *Pseudogygites* that occurs in southern Ontario, New York, Southampton Island in Hudson Bay, Akpatok Island in Ungava Bay, and at various localities in the Canadian arctic (Cornwallis, Bathurst, and Devon islands), and to clarify the age and origin of this genus.

Pseudogygites has been recorded from eastern and arctic North America numerous times, but a full description of any species has not been presented since Chapman described *Asaphus canadensis* more than a century ago. Material from Craigleith on Georgian Bay has been illustrated repeatedly, but generally by poorly or indifferently preserved specimens that do not show critical features.

In the absence of concise morphological information, the classification and origin of *Pseudogygites* remain speculative. Raymond (1912:115) suggested that *Pseudogygites* was derived from *Asaphus* and *Basilicus*; Jaanusson (1959) assigned it, with query, to the Isotelinae; and Whittington (1966:712) thought it was possibly related to *Ogygiocaris* or "*Pseudobasilicus*".

The ventral morphology of *Pseudogygites*, in particular, needs clarification. The hypostome has been described as being forked (Raymond, 1912; Kobayashi, 1934), a statement that must be based on Chapman's (1859a) original illustration. Documentation of the morphology of the hypostome is critical because it provides the best evidence for distinguishing *Pseudogygites* from its near-homeomorph, *Ogyginus*.

The assignment of *Pseudogygites* to the Asaphidae naturally implies the presence of a median connective suture crossing the doublure. The available holaspid specimens from southern Ontario, without exception, lack median sutures whereas those from arctic Canada apparently possess such sutures. *Pseudogygites* is unquestionably an asaphid and not a nileid and, therefore, the presence of yoked free cheeks in at least one species is highly pertinent in evaluating the family assignment of other asaphidlike genera that lack median sutures.

Systematic Palaeontology

Repositories

The illustrated specimens are in the Royal Ontario Museum, Toronto (ROM); the Geological Survey of Canada, Ottawa (GSC); the American Museum of Natural

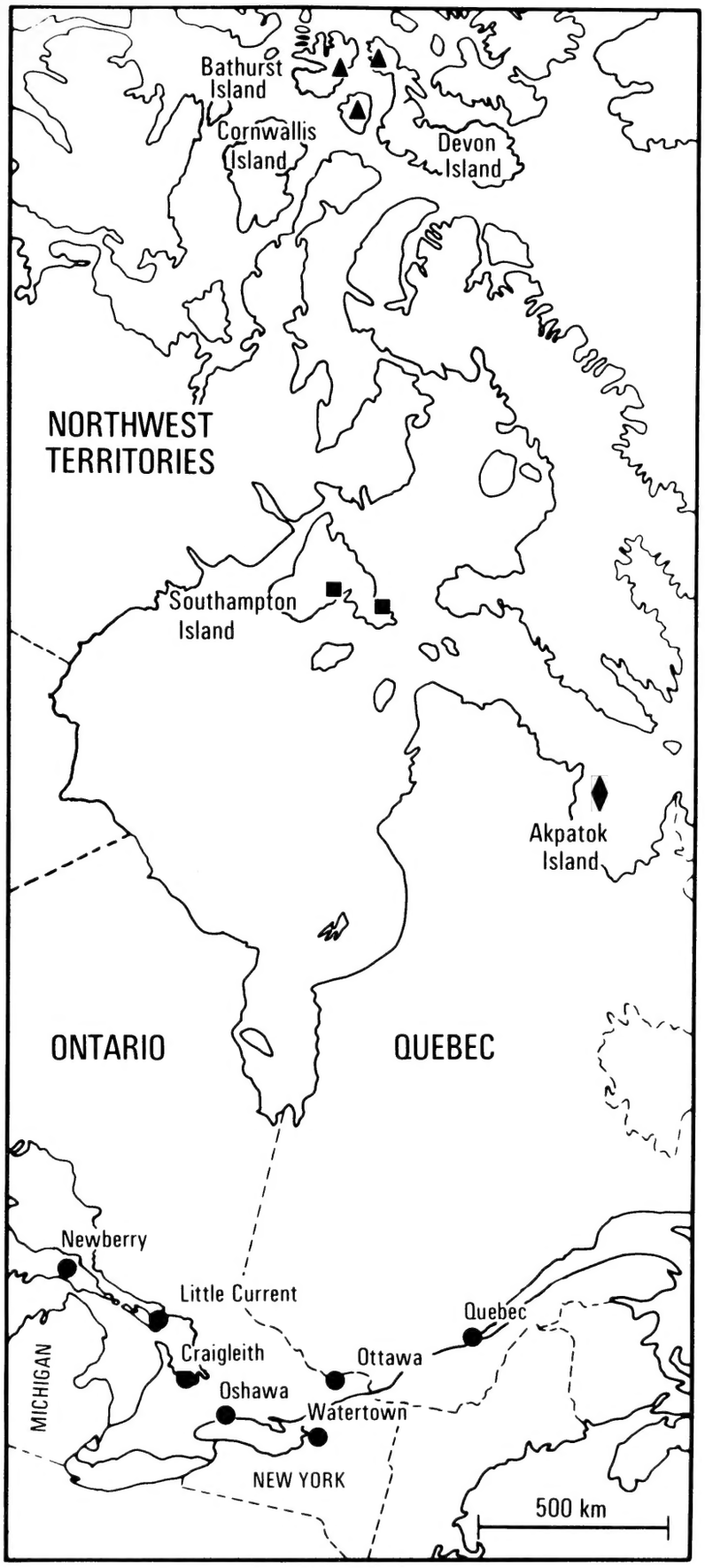


Fig. 1 Locality map of eastern and arctic North America showing occurrences of four species of *Pseudogygites:* circles—*P. latimarginatus* (Hall), squares—*P. hudsoni* n. sp., diamond—*P. akpatokensis* n. sp., triangles—*P. arcticus* n. sp.

History, New York (AMNH); and the Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts (MCZ).

Suborder Asaphinae Salter
Superfamily Asaphacea Burmeister
Family Asaphidae Burmeister

Discussion

Prominent in the diagnosis of the family Asaphidae is the presence of a median connective suture separating the free cheeks. The absence of such a suture has been deemed sufficient evidence to reject otherwise asaphidlike genera from this family (for example, *Brachyaspis* Salter; Jaanusson, 1959:355) and the presence of a median suture has been used to assign otherwise nileidlike genera to this family (for example, *Varvia* Tjernvik; Jaanusson, 1959:354). Therefore, it is of considerable interest to encounter an undoubted asaphid, *Pseudogygites*, which includes species both with and without median connective sutures. All examined specimens of *P. latimarginatus* from southern Ontario possess yoked free cheeks and *P. hudsoni* n. sp. and *P. arcticus* n. sp. from the Canadian arctic possess functional median connective sutures. A parallel situation is found among species of *Isotelus*. Most species of *Isotelus* possess median connective sutures, but a number of recent reports of individuals of *Isotelus gigas* DeKay with yoked free cheeks demonstrate that this is not an uncommon condition (Henningsmoen, 1975; Jaanusson, 1975; this paper, Fig. 6H).

Whereas the presence of a median connective suture remains an important diagnostic criterion for recognizing Asaphidae, the available evidence from *Pseudogygites* and *Isotelus* suggests that the mere absence of such a suture is not sufficient, in itself, to justify exclusion of a taxon from this family.

In this regard, reference should be made to the family assignment of *Brachyaspis* Salter. The type species, *Brachyaspis rectifrons* (Portlock) from Ireland, lacks a median connective suture. This conclusion led Whittington (1954) to suggest that *B. rectifrons* may not be congeneric with similar trilobites with median sutures from North America which have been assigned to *Brachyaspis*. Jaanusson (1975) and Chatterton and Ludvigsen (1976) suggested that *B. rectifrons* is not an asaphid but a nileid, and Chatterton and Ludvigsen assigned the North American species of "*Brachyaspis*" to a new asaphid genus, *Nahannia*. The absence of a median suture cannot now be taken as good evidence that *B. rectifrons* is a nileid. This taxon may well be an asaphid, but confirmation (that is, an associated hypostome) should be sought. *B. rectifrons* remains an incompletely known taxon and it would be unwise, at the present time, to synonymize *Nahannia* with *Brachyaspis*. Setting aside the question of a median connective suture, the large palpebral lobes and the absence of distinct segmentation on the pygidial axis would still characterize *Nahannia*.

By similar reasoning, the genus *Varvia* which bears "a remarkable similarity to species of *Nileus*" (Fortey, 1975:35) should be removed from the Asaphidae and placed in the Nileidae.

Subfamily Isotelinae Angelin

Genus *Pseudogygites* Kobayashi, 1934

Type Species

The type species is *Asaphus*? *latimarginata* Hall, 1847. The original type species designated by Kobayashi (1934), *Asaphus canadensis* Chapman, 1856 is herein considered a junior subjective synonym of Hall's species.

Diagnosis

A genus of Isotelinae with well-defined flattened borders on cephalon and pygidium, a distinctly outlined glabella which expands in front of the eyes, three pairs of faint lateral glabellar furrows, and genal angles produced into slim spines. Pygidium has 7 to 14 faintly furrowed pleurae and a well-defined axis. Cephalic doublure is broad and flat medially, narrower and convex laterally; it lacks a vincular socket. Median connective suture may be present or fused. Hypostome is deeply notched posteriorly.

Discussion

In establishing *Pseudogygites*, Kobayashi (1934) did no more than present a brief diagnosis and select *Asaphus canadensis* as type species. This species was defined in a series of brief papers in the late 1850s by E.J. Chapman, then Professor of Mineralogy and Geology at the University of Toronto. Chapman's first note in 1856 merely announced the discovery of a new species, *Asaphus canadensis*, in the "Utica Schist" at Whitby, Canada West [Ontario]. A brief description of the new species was presented in 1857, a more complete description and an illustration followed in 1858, and the hypostome was illustrated and described in 1859a. Chapman did not select a type, and the complete specimen on which his only illustration was based (Chapman, 1858:232) cannot now be located in the collections of the University of Toronto or in the Royal Ontario Museum. Chapman (1858) noted that *A. canadensis* occurs in the township of Whitby on Lake Ontario and on Georgian Bay, but the former must be considered the type locality—this being the only locality mentioned in the initial paper. Even in the absence of types, there is little problem in determining the critical features of *A. canadensis*. Chapman's (1858) description and illustration are adequate and a pygidium from the type locality which Chapman identified as *A. canadensis* and presented to the Museum of Palaeontology at the University of Toronto is still extant (Fig. 5H). This specimen, now in the Royal Ontario Museum, is clearly conspecific with the more abundant material from the Craigleith locality of Georgian Bay. An uncrushed specimen from the Eastview Formation at Ottawa was assigned to *Ogygites canadensis* by Raymond (1913) and this specimen appears to have formed the basis for Kobayashi's concept of *Pseudogygites canadensis* and the model for Jaanusson's (1959) reconstruction of the cephalon of *P. canadensis*. The available material suggests that only a single species of *Pseudogygites* occurs at the aforementioned localities on Lake Ontario and Georgian Bay, and in the Ottawa area.

The species *Asaphus*? *latimarginata* Hall, 1847 presents fewer taxonomic problems, but unfortunately it was based on float material consisting of two

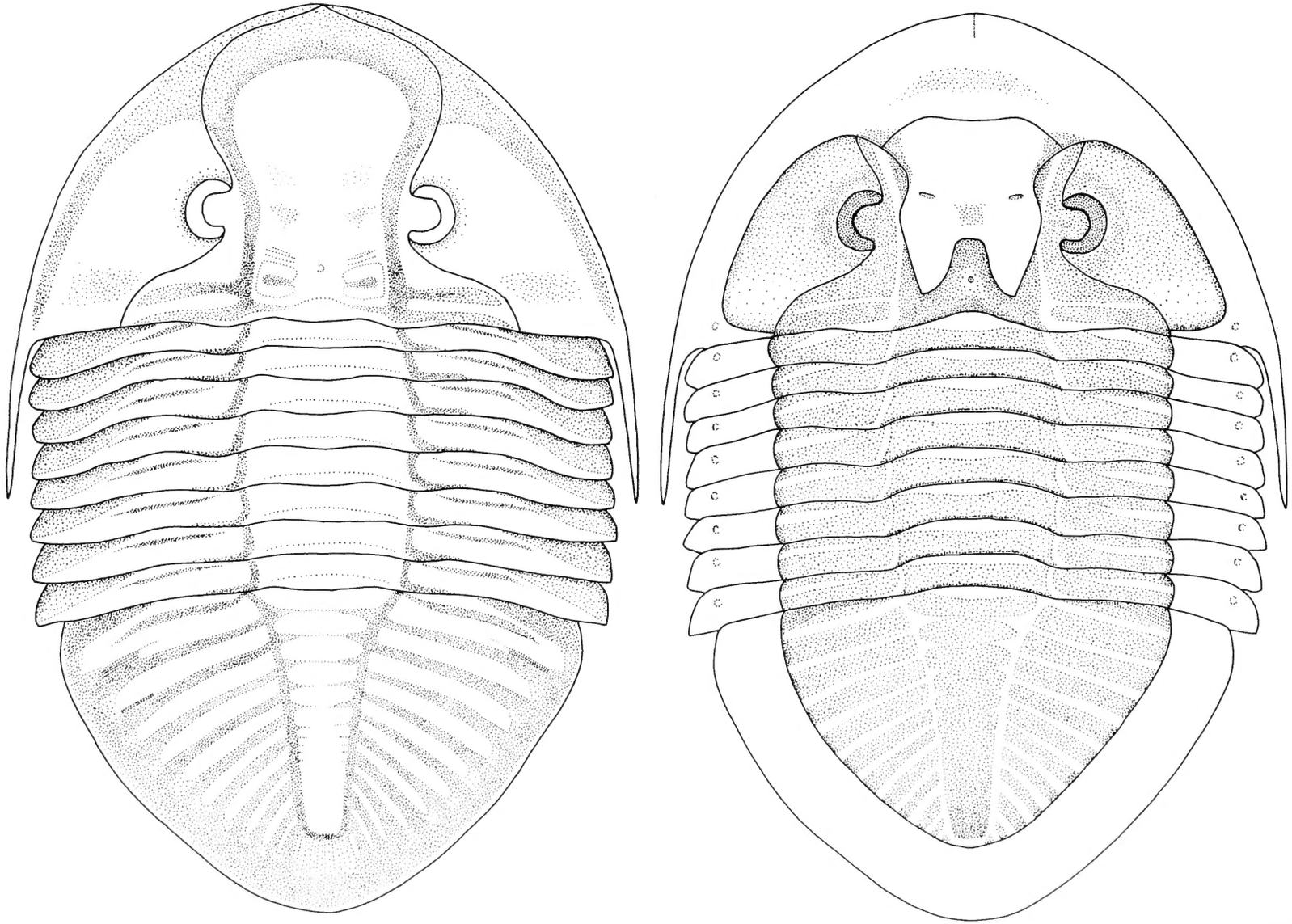


Fig. 2 Reconstruction of *Pseudogygites latimarginatus* (Hall) in dorsal and ventral aspects. Based on ROM 35029 and ROM 35027, approximately × 2, lower Whitby Formation, Craigleith.

incomplete pygidia on loose pieces of shale from Watertown, New York. Both of these specimens are extant and the more complete is selected as lectotype and illustrated photographically for the first time (Fig. 4A).

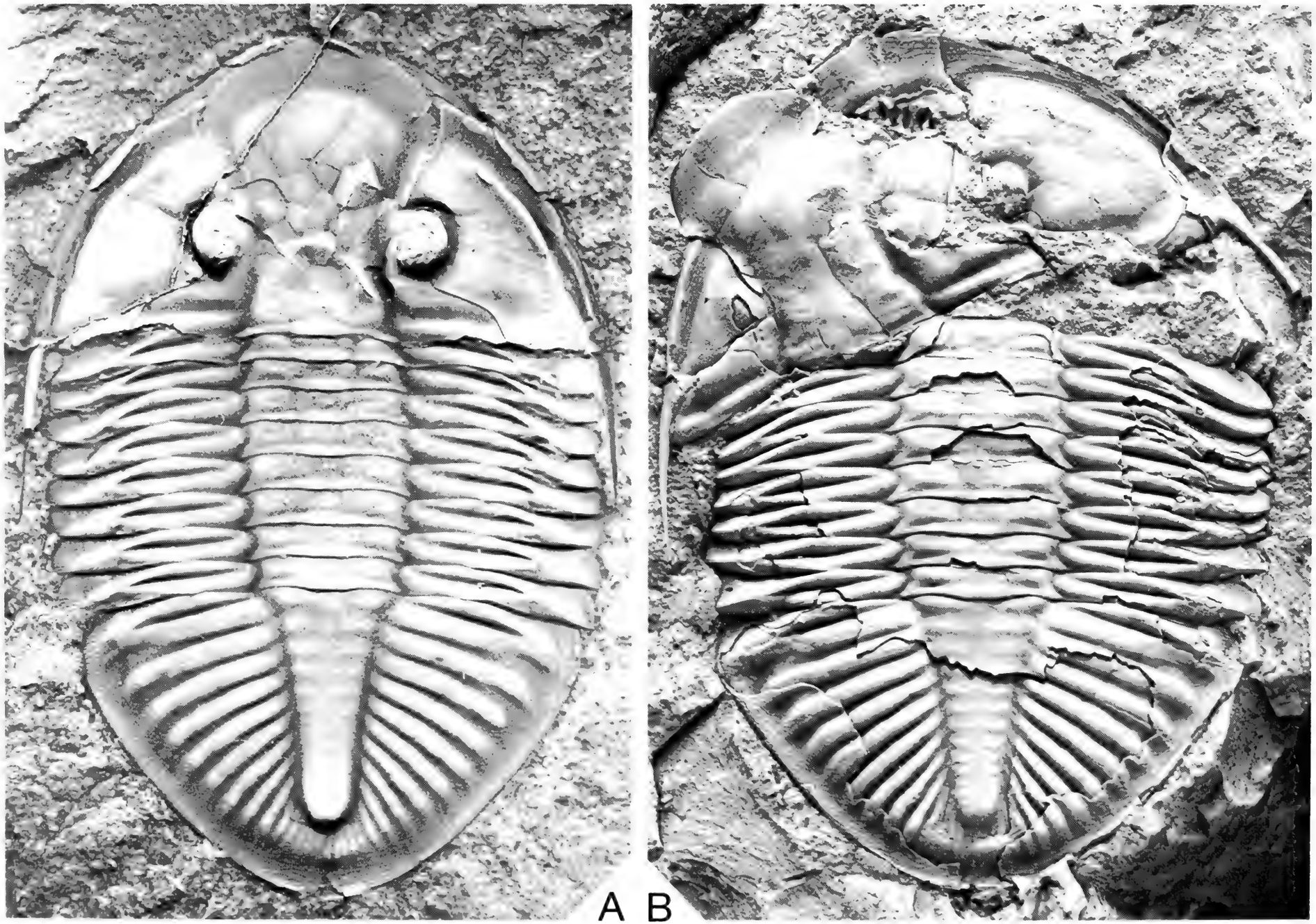
Most authors since the late 1950s have assumed that *Pseudogygites canadensis* and *P. latimarginatus* are synonymous. Chapman did not mention Hall's species in his 1856 paper, an omission that James Hall was quick to point out. In a letter to Chapman in 1856 or 1857 (Chapman, 1857), Hall suggested that *Asaphus canadensis* was identical with *Asaphus*? *latimarginata*. Chapman (1858), however, was reluctant to apply Hall's name to the material from Canada, and, without citing differences, merely stated that the Canadian material was more complete than that from New York. Chapman further marshalled the weight of the opinion of Joachim Barrande who had previously stated (1852:647) that Hall's specimens of *Asaphus* were too incomplete to be determined with any certainty. Hall's figures of *A.*? *latimarginata* are less than satisfactory and somewhat diagrammatic, but the lectotype pygidium is sufficiently well preserved to show that it is conspecific with pygidia from the type locality of *A. canadensis*. Therefore, *Asaphus canadensis* becomes a junior subjective synonym of *A.*? *latimarginata* which now becomes the type species of *Pseudogygites*.

Pseudogygites shares a number of features with *Isotelus*, especially with immature specimens of *Isotelus*. From mature specimens of *Isotelus*, *Pseudogygites* may be distinguished by its flat cephalic borders, long genal spines, well-defined axial furrows on the cephalon and pygidium, longer hypostome, and by the absence of a vincular socket in front of the genal angle (compare Fig. 12D and Fig. 12H).

In dorsal view, *Pseudogygites* is surprisingly similar to the ogygiocaridiniid *Ogyginus* Raymond from the Llanvirnian and Llandeilian of Britain. Whittard (1964) has shown that Jaanusson (1959) was in error in depicting *Ogyginus* with a dorsal intramarginal facial suture. This suture is marginal in front of the glabella and provides one of the few unequivocal differences with *Pseudogygites*. The other obvious difference lies in the hypostome which is forked in *Pseudogygites* and entire in *Ogyginus*. *Pseudogygites* is younger than *Ogyginus* and there is no evidence to show that they are closely related. Raymond (1912) pointed out that the similarity of the two taxa appears to be the result of parallel evolution.

Pseudogygites latimarginatus (Hall, 1847)
Figs. 2, 3, 4, 5, 6A–E, 7A–C, 12A–D

Asaphus? *latimarginata* Hall, 1847:253, pl. 66, figs. 4a, 4b.
Asaphus canadensis Chapman, 1856:482.
Asaphus canadensis—Chapman, 1857:47.
Asaphus canadensis—Chapman, 1858:231, unnumbered figure.
Asaphus canadensis—Chapman, 1859a:1, unnumbered figure.
Asaphus canadensis—Logan, 1863:fig. 201.
Basilicus canadensis—Raymond, 1910:62.
Ogygites canadensis—Raymond, 1912:pl. 1, fig. 2.
Ogygites canadensis—Raymond, 1913:43, pl. 6, fig. 1.
Ogygites canadensis—Parks, 1928:48, 53, 55.
Pseudogygites canadensis—Kobayashi, 1934:461.


A
B

Ogygites latimarginatus—Kay, 1937:pl. 10, unnumbered figure.
Ogygites latimarginatus—Hussey, 1952:pl. 9, fig. 22.
Ogygites latimarginatus—Wilson, 1957:pl. 5, fig. 2.
(*non*) *Pseudogygites latimarginatus*—A.E. Wilson, *in* Thorsteinsson, 1958:87.
Pseudogygites canadensis—Jaanusson, 1959:343, fig. 253-5a.
Pseudogygites latimarginatus—Fritz, 1959:1118, pls. 1, 2.
Pseudogygites latimarginatus—Liberty, 1964:pl. 5, fig. 8.
(*non*) cf. *Pseudogygites latimarginata*—D.E. Jackson, *in* Nelson and Johnson, 1966:567.
Pseudogygites canadensis—Liberty, 1969:71.
Pseudogygites latimarginatus—Norford et al., 1970:pl. 4, fig. 21.
(*non*) *Pseudogygites latimarginatus*—Kerr, 1974:132.
Ogygites canadensis—Levi-Setti, 1975:pls. 3, 58, 59.
Pseudogygites latimarginatus—Ludvigsen:1978, pl. 6, fig. 53.
Pseudogygites latimarginatus—Ludvigsen:1979a, figs. 14, 36, 37.

Diagnosis

A species of *Pseudogygites* with a long preglabellar field (= 18–23% of sagittal cephalic length); a subtriangular pygidium with 12 to 14 distinct pleurae, short and faint pleural furrows evident only on anterior portion of pygidium, well-defined border furrow, and relatively narrow border. Median connective suture is fused.

Lectotype

I select as lectotype of *Pseudogygites latimarginatus* the incomplete internal mould of a pygidium (AMNH 30115, Fig. 4A) originally illustrated by Hall (1847:pl. 66, fig. 4a). The specimen occurs on a piece of brown bituminous shale which was collected loose near Watertown, New York. Curiously, the label on the lectotype cites the collecting locality as "Watertown, N.Y. (Collingwood, Canada)" suggesting that this shale chip was glacial drift from Canada. A bedrock source for the shale does not crop out at Watertown, but some 13 km to the south, on Gulf Stream near Rodman, a thin (5–7 cm) layer of brown bituminous shale occurs as a veneer on the Hillier limestone. A fossil collection from this layer shown to me by J. Riva contains *P. latimarginatus* pygidia (Fig. 6A) and this horizon is, in all likelihood, the source of the lectotype. In Fig. 11, this layer is tentatively referred to the Whitby Formation to differentiate it from the overlying grey, micaceous, and noncalcareous shales of the lower Frankfort Formation (Fisher, 1977).

Occurrences

CRAIGLEITH AND COLLINGWOOD AREA

Old collections of *P. latimarginatus* at the University of Toronto and the Royal

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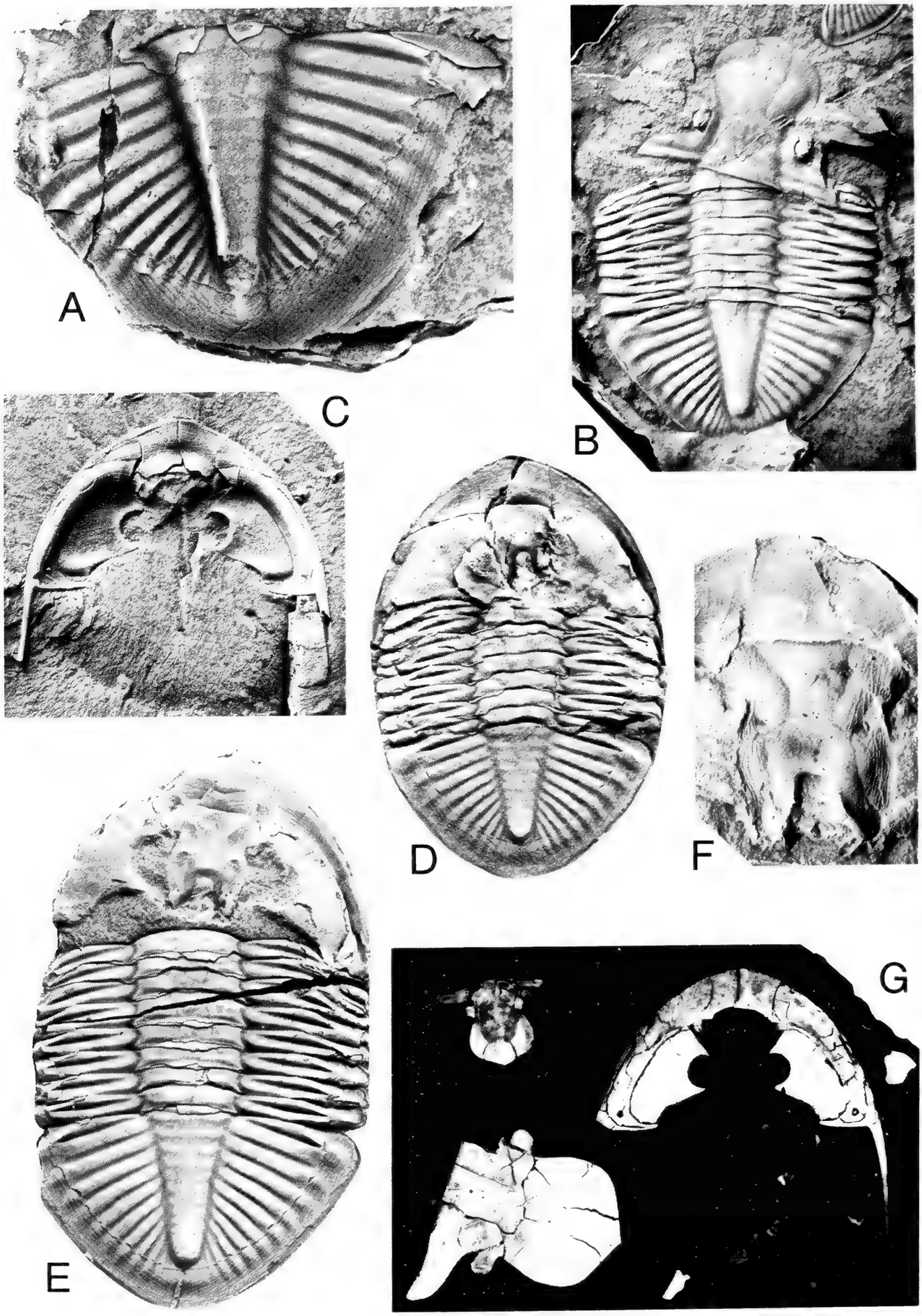
Fig. 3 *Pseudogygites latimarginatus* (Hall)

A Dorsal view of latex impression of external mould of entire exoskeleton, ROM 35029, × 3.5, lower Whitby Formation, Craigleith (carcass).

B Dorsal view of dismembered exoskeleton, ROM 30015, × 2.5, lower Whitby Formation, Craigleith (exuvia; note displaced and overturned hypostome).


A
B
C
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E
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G

Ontario Museum are labelled "Utica Shale, Collingwood, Ontario". Collingwood undoubtedly refers to the township of Collingwood and not to the town which is located in the adjacent township of Nottawasaga. Presumably, these specimens were collected from the lower Whitby Formation exposed along the shore of Georgian Bay between Craigleith and Camperdown (Parks, 1928:fig. 2). Recent collections have been made by members of the Department of Invertebrate Palaeontology, Royal Ontario Museum, from the lower Whitby Formation, 2 km west of Craigleith Station. Both of these occurrences are herein identified as "lower Whitby Formation, Craigleith". *P. latimarginatus* also occurs sparingly in the upper Cobourg Formation, about 3 km east of the town of Collingwood, on the south side of Highway 26.

MANITOULIN ISLAND

P. latimarginatus has been recorded from the lower Whitby Formation in and near the town of Little Current (Caley, 1936; Liberty, 1968). Hussey (1952) has illustrated a specimen from "Collingwood, Manitoulin Island". According to Liberty (1968), *Pseudogygites* sp. occurs in the highest Lindsey Formation (= Cobourg Formation) in Little Current. These localities are no longer accessible (T.E. Bolton, pers. comm. to J. Riva, 1975). *P. latimarginatus* does not occur in the Whitby and Sheguiandah Formations exposed farther south near the village of Sheguiandah.

NORTHERN MICHIGAN

P. latimarginatus has been recorded from drift near Newberry, northern Michigan (Ruedemann and Ehlers, 1924). The genus was recorded from the Groos Quarry Member at the Bichler Quarry, north of Escanaba (Hussey, 1952).

OSHAWA-WHITBY AREA

Old collections of *P. latimarginatus* in the Royal Ontario Museum are labelled "Collingwood Shale, Whitby, Ontario". Whitby possibly refers to the township of Whitby. These collections probably came from the lower Whitby Formation exposed in creek beds in Whitby or nearby Oshawa (Parks, 1928:55; Liberty, 1969:67). In the Canada Cement Quarry at Bowmanville *P. latimarginatus* is very abundant in the lower Whitby Formation and rare in the upper part of the Cobourg Formation.

Fig. 4 *Pseudogygites latimarginatus* (Hall)

- A Dorsal view of exfoliated pygidium, lectotype, AMNH 30115, × 2.3, Whitby Formation (?), Watertown, New York (original of Hall, 1847:pl. 66, fig. 4a).
- B Dorsal view of latex impression of external mould of dismembered individual lacking free cheeks, ROM 158, × 1.1, lower Whitby Formation, Oshawa (exuvia; lower cephalic unit was apparently carried away by the moulting trilobite).
- C Ventral view of yoked cheeks, ROM 35031, × 1.8, lower Whitby Formation, Craigleith.
- D Dorsal view of weathered internal mould of entire exoskeleton; glabella has been removed to expose hypostome, ROM 35033, × 1.2, lower Whitby Formation, Craigleith (carcass).
- E,F Dorsal view of internal mould of thorax and pygidium and external mould of yoked cheeks and hypostome, × 2.0, and ventral view of latex impression of external mould of hypostome and doublure, × 4.0, ROM 35027, lower Whitby Formation, Craigleith (exuvia).
- G Bedding surface (immersed in water) showing two cranidia and one yoked cheek, ROM 35023, × 2.0, lower Whitby Formation, Craigleith.

NEW YORK STATE

See discussion under Lectotype.

OTTAWA AREA

P. latimarginatus has been reported from both the Eastview and Billings Formations (Wilson, 1957; Baird, 1972). Old collections in the Royal Ontario Museum labelled "The Butts, Rideau River, Ottawa" probably came from the Billings Formation.

QUEBEC AREA

P. latimarginatus was also reported from the lower Utica Shale at Beauport and Montmorency Falls near Quebec by Ells (1888) and Low (1892). J. Riva (pers. comm., 1977) has questioned these occurrences and notes that he has never seen *P. latimarginatus* in either Utica or Trenton collections from this area.

Age

Pseudogygites latimarginatus first appears in the grey and tan argillaceous limestones of the Cobourg Formation of southern Ontario (Sproule, 1936; Liberty, 1969), but it is never a common fossil in this unit. Its numerical acme is reached at and near the base of the overlying black and dark brown bituminous shales and black limestones regionally assigned to the lower Whitby, Eastview, or Billings Formations (Fig. 11). The species has a short vertical range in these units, but a considerable geographic range, apparently occurring along a 1700 km long belt between northern Michigan and Quebec (Fig. 1). Liberty (1969) noted that the species is confined to the entire 10 m thick lower member of the Whitby Formation at Craigleith and similar vertical ranges are implied for other areas.

Sweet and Bergström (1976) assigned the Cobourg and Hillier Formations to Midcontinent conodont Fauna 11 and noted that the *Amorphognathus superbus – A. ordovicicus* transition of the North Atlantic zonation occurs within the uppermost

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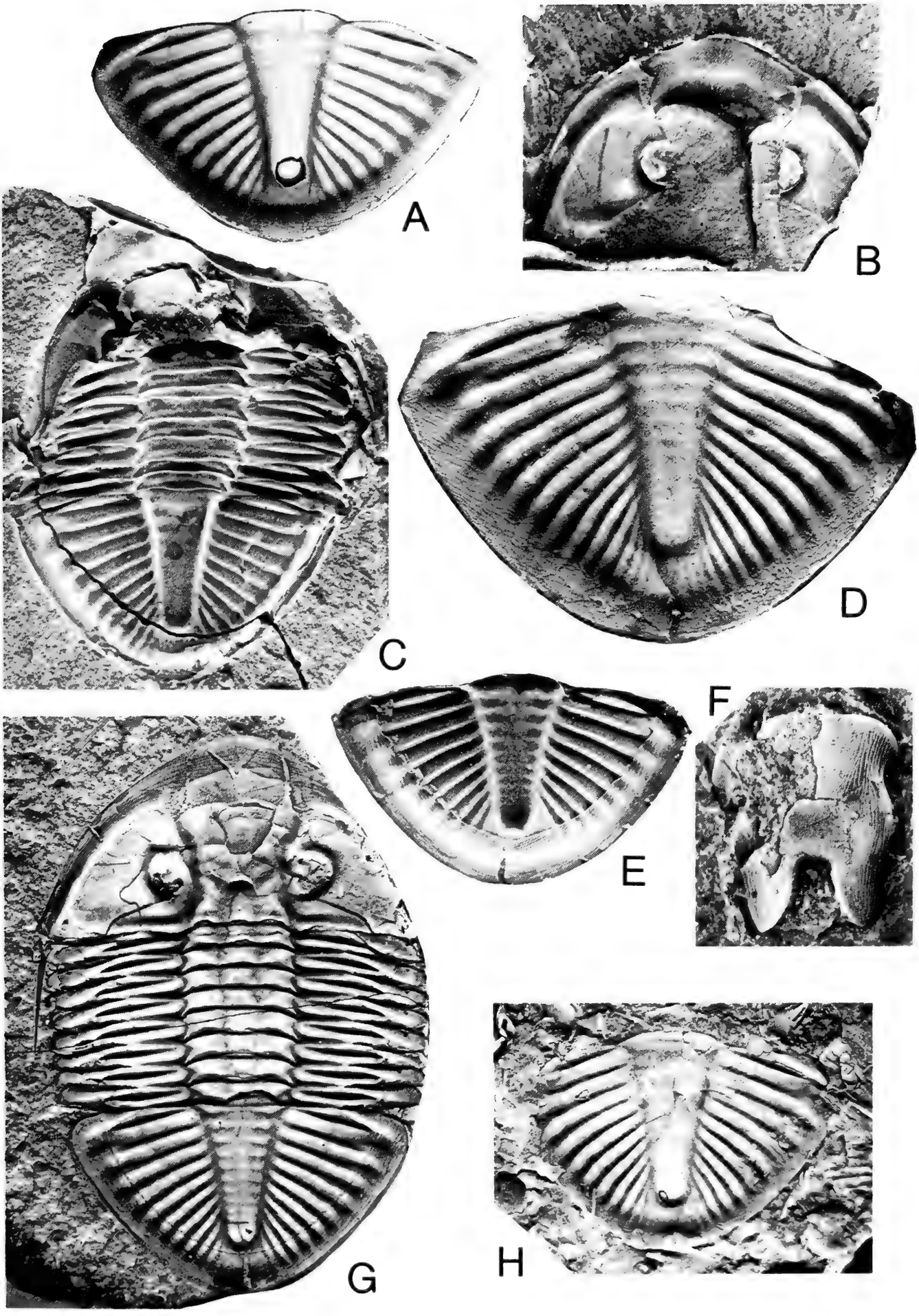
Fig. 5 *Pseudogygites latimarginatus* (Hall)

- A Dorsal view of pygidium, ROM 35026, × 2.0, lower Whitby Formation, Craigleith.
- B Dorsal view of latex impression of external mould of yoked cheeks, ROM 35032, × 2.0, lower Whitby Formation, Craigleith (note presence of short fused median suture on front part of doublure).
- C Ventral view of external mould of thorax and pygidium and internal mould of portion of yoked cheeks and hypostome, ROM 35024, × 2.0, lower Whitby Formation, Craigleith (exuvia; note telescoped thoracic segments).
- D Dorsal view of latex impression of external mould of pygidium, ROM 807 U, × 1.2, Billings Formation (?), Rideau River, Ottawa.
- E Ventral view of latex impression of internal mould of pygidium, ROM 35025, × 2.0, lower Whitby Formation, Craigleith.
- F Ventral view of hypostome, ROM 35028, × 2.6, Cobourg Formation, Collingwood.
- G Dorsal view of internal mould of entire exoskeleton; front portion of cephalon has been removed to expose broad doublure, ROM 35030, × 2.0, lower Whitby Formation, Craigleith (carcass).
- H Dorsal view of latex impression of external mould of pygidium, ROM 154, × 1.0, lower Whitby Formation, Oshawa (specimen identified as *Asaphus canadensis* Chapman by E.J. Chapman).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Hillier Formation. They concluded that the Cobourg and Hillier are mid-Edenian to mid-Maysvillian in age or, in terms of the British sequence, latest Caradocian to early Ashgillian.

In the Craigleith area, the lower Whitby Formation is assignable to the upper part of the *Climacograptus pygmaeus* Zone (Ruedemann and Ehlers, 1924; Riva, 1974; J. Riva, pers. comm., 1977). In western New York, the *C. pygmaeus* Zone occurs in the "Atwater Creek" and "Deer River" Members (= lower Frankfort; Fisher, 1977; Riva, 1974) which overlie the *P. latimarginatus* horizon on top of the Hillier Formation. In northern Michigan near Newberry *P. latimarginatus* occurs associated with *C. pygmaeus* Zone graptolites on loose pieces of shale (Ruedemann and Ehlers, 1924). These may have been derived from the nearby outcrops of the "Haymeadow Creek" Member (= lower Bill's Creek Formation, Liberty, 1968) which also contains graptolites referable to the *C. pygmaeus* Zone (Berry, 1970). In Ottawa, the Billings Formation contains graptolites of the *C. pygmaeus* Zone (J. Riva, pers. comm., 1977).

In eastcentral North America *Pseudogygites latimarginatus* occurs within the *Climacograptus pygmaeus* Zone and possibly in slightly older strata, but it does not occur in the succeeding *Climacograptus manitoulinensis* Zone. Riva (1974) considered the *C. pygmaeus* Zone correlative with the lower half of the *Pleurograptus linearis* Zone of Britain which Williams et al. (1972) have interpreted as straddling the Caradocian-Ashgillian boundary.

Description

Entire exoskeleton is oval in outline; length (sag.) is 1.5 times maximum width at midthorax. Cephalon and pygidium are of equal length and each is slightly longer than one-third total length. Convexity is difficult to determine because of the compressed state of nearly all specimens, but it appears to be moderate to slight.

Cephalon is parabolic to semicircular in outline; twice as wide across base of genal spines as long (sag.) and, apparently, moderately vaulted. Glabella is well defined by furrows; it occupies less than one-third cephalic width at level of eyes and it is outlined laterally by moderately deep and wide (tr.) axial furrows. These converge slightly from posterior margin towards a line joining palpebral lobes then diverge and curve around the broadest part of glabella to become preglabellar furrows. Preglabellar field is flat and broad, about one-fifth the length (sag.) of cephalon. An occipital furrow does not occur on holaspid specimens, but on meraspid specimens (Fig. 12B) it is a straight, medially impressed furrow located immediately behind the

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Fig. 6 A–E *Pseudogygites latimarginatus* (Hall)

A Dorsal view of pygidium, AMNH 42302, × 1.2, Whitby Formation, Gulf Stream near Rodman, New York.

B–E Dorsal and oblique lateral views of incomplete and uncompressed cephalon, × 2.0, detail of anteromedial portion of cranidium, × 9.0, and detail of front portion of glabella, × 27.0, ROM 37775, lower Whitby Formation, Craigleith.

F–H *Isotelus gigas* DeKay

Detail of anteromedial portion of cephalon, × 9.0, dorsal view of cephalon, × 3.0, and ventral view of doublure showing fused median connective suture, × 4.8, ROM 35367, Verulam Formation, Lakefield Quarry, Lakefield, Ontario.

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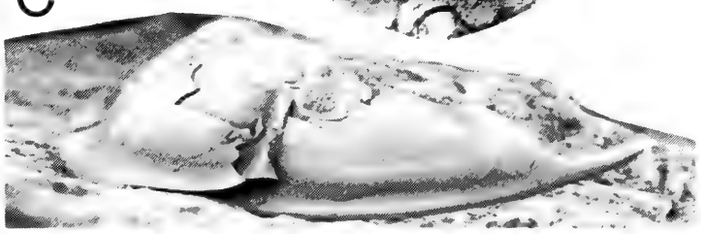

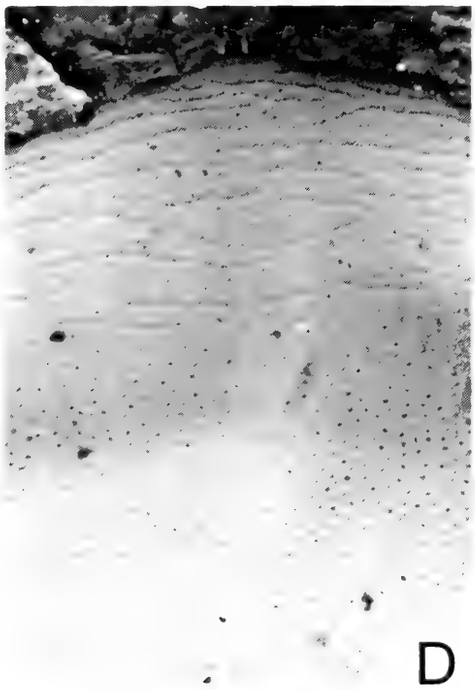

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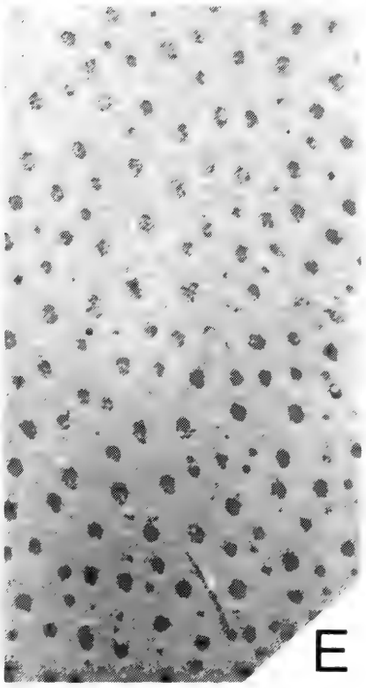

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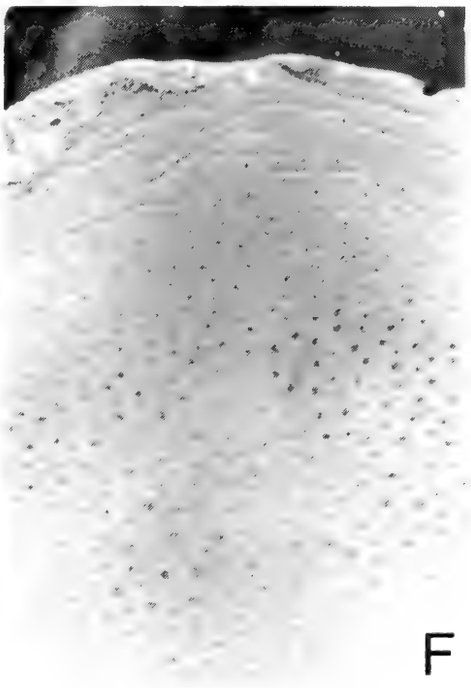

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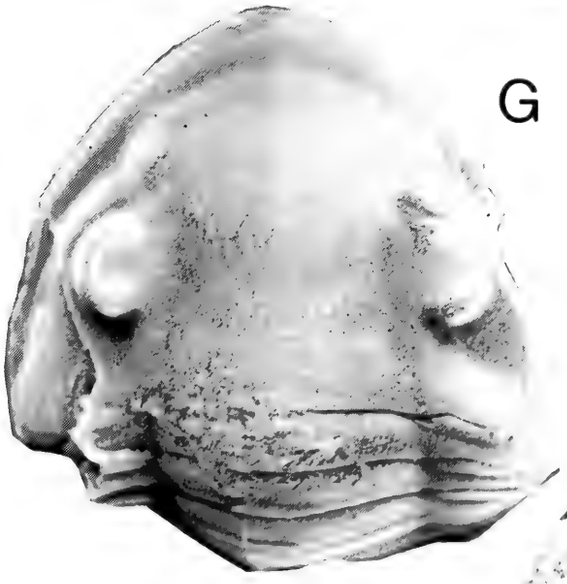

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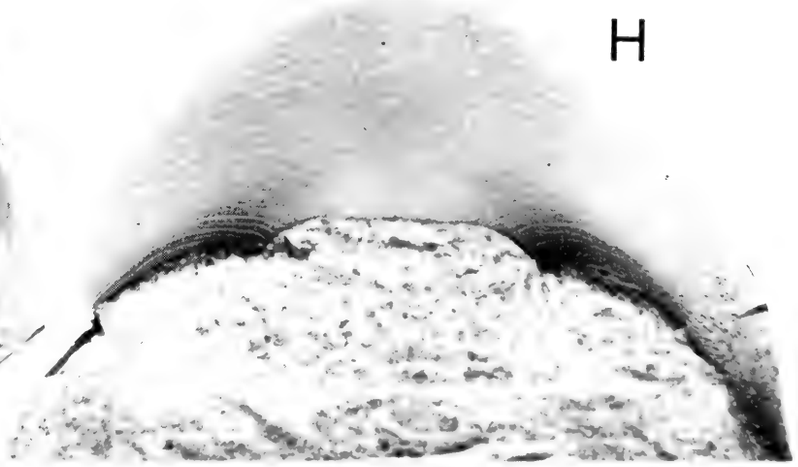


median glabellar tubercle. A "pseudo-occipital furrow" does cross the posterior portion of the glabella (Fig. 3A), but this furrow is merely the impression of the front edge of the articulating half ring of the first segment. Three pairs of lightly impressed lateral glabellar furrows are evident on well-preserved specimens. First furrow is a composite furrow; it comprises a posterior furrow which is lenticular in outline and transversely directed and surrounded by a yoke-shaped ridge which opens adaxially; its anterior portion consists of a pair of obliquely disposed shallow slitlike furrows. Second furrow is an oval to triangular depression located in line with palpebral lobes. Third furrow is a very faint concavity located just in front of a line joining anterior edges of palpebral lobes. None of these furrows extends to the axial furrow. A tiny median glabellar tubercle is situated in line with the anterior part of the first glabellar furrow. Palpebral lobe consists of elevated, laterally-convex flap which is located near the axial furrow just behind midlength of cranidium. Palpebral furrow is crescent-shaped and very faint. Holochroal eye surface is strongly curved in a horizontal plane, moderately so in a vertical plane. Free cheek is almost as wide (tr.) as glabella and slopes gently from shallow furrow at base of eye to lateral border furrow which defines a 90 degree arc from near genal corner to juncture with axial furrow. Lateral border is narrow near genal angle; becomes wider and flatter towards the front to merge with preglabellar field. Posterior border furrow is firmly impressed on fixed cheek. It is slightly offset anteriorly at facial suture and continues on free cheek as a shallow depression that does not reach the lateral border furrow. Posterior branch of facial suture swings outward and backward in an arcuate curve from eye. Anterior branch of facial suture curves outward and forward along a path parallel to axial furrow, then curves adaxially to cross anterior margin on sagittal line. Genal spine is long, slim, and backwardly directed. It attenuates to a fine point opposite fifth thoracic segment. Cephalon is covered by minute, shallow, circular pits which are approximately 100 μm in diameter (Fig. 6D). Fine wrinkles parallel the cephalic margin on the anterior and lateral borders.

Cephalic doublure is one-third the length (sag.) of cephalon and flat to gently concave in front of hypostome. A vestige of a median connective suture is evident as a short (sag.) fused suture on anterior part of doublure. Laterally, doublure becomes much narrower and sharply incurved. A small panderian opening is located inside the genal corner. A vincular socket is not present. Doublure carries fine terrace lines that run subparallel with cephalic margin.

Hypostome is rectangular in outline, five-sixths as wide (tr.) as long (exsag.). Its posterior margin is located below the first glabellar furrows. A deep rounded posteromedial notch extends forward for one-third the length of the hypostome and separates a pair of subtrapezoidal posterior projections. The ventral surface of each projection is flat and faces obliquely outward. Anterior margin is convex forwardly with a faint posterior curvature medially. Hypostome is widest across triangular anterior wings, behind these it narrows into a pair of U-shaped antennal notches and then expands into rounded shoulders which carry low carinae along their lateral margins. Central body is quadrate, slightly inflated, and not defined by furrows; its posterior margin is defined by a shallow square depression located in front of posterior notch. Maculae are relatively deep, anterolaterally directed slots located near the posterolateral margins of the central body and slightly anterior of midlength of hypostome. Median portion of hypostome is smooth; its flanks carry terrace lines that run subparallel with lateral margins.

Thorax consists of eight segments. Moderately vaulted axis is slightly narrower (tr.) than one-third cephalic width; widens a little from first to fourth segment, then narrows slightly towards pygidium. Axis is transversely divided by a furrow that shallows towards sagittal line and which separates an anterior portion from a shorter posterior portion. The latter portion mirrors the articulating half ring of the next segment. Axial furrow on each segment is scalloped, convex side facing inward. Inner portion of pleura is subhorizontal; outer portion declines gently. Firmly impressed pleural furrow proceeds diagonally from anterior side of pleura, near axial furrow, to midlength of pleura on upper part of declined portion, and terminates just inside broad anterolateral facet. Anastomosing terrace lines on facets; remaining thorax is finely pitted. Declined portion of pleura is encased by flat doublure which contains a small panderian opening.

Pygidium is subtriangular in outline with bowed lateral margins and is only slightly inflated; width equals 1.3 to 1.5 sagittal length. Prominent facets occur at anterolateral corners. Axis is moderately convex and well defined by firmly impressed axial furrows which are convergent at about 15 degrees and are straight or slightly convex adaxially. Anterior portion of axis is crossed by five to seven shallow axial ring furrows which become faint to imperceptible close to sagittal line. Posterior portion of axis is unfurrowed and its termination is bluntly rounded to square-tipped. Posterior end of axis is well in front of border furrow. Pleural field is somewhat inflated and bounded by distinct border furrows. Concave border is narrow and it maintains the same width around the lateral and posterior edges of pygidium. Interpleural furrows are continuous from axial furrow to border furrow and nearly straight. There are 10 or 11 firmly impressed interpleural furrows lateral to axis and an additional three or four faint interpleural furrows behind axial termination. The direction of the interpleural furrows changes gradually from slightly posterior of transverse near front of pygidium to sagittal behind axis. Length (exsag.) of pleurae decreases from front to back. Pleural furrows are narrow (tr.) slitlike depressions on the posterolateral flanks of each of the first five or six pleurae. Only on the two most anterior pleurae do the pleural furrows continue to the axial furrow as extremely faint furrows. Fine terrace lines on border run at a low angle to margin; remainder of pygidium is finely pitted. On interior, axial ring furrows are more prominent than on exterior, and continue posteriorly to axial termination. Doublure is broad (about twice as wide as border) and reaches as far forward as tip of axis. Doublure carries terrace lines that run subparallel to margin.

Discussion

The description of each of the following species of *Pseudogygites* will take the form of a comparison with *P. latimarginatus*.

Raymond (1913:43) synonymized *Asaphus halli* Chapman, 1858 and *Asaphus hincksii* Chapman, 1859b with *Ogygites canadensis* (Chapman). The illustration of *A. halli* presented by Chapman (1858:236) shows an asaphid trilobite with a ribbed pygidium and a cephalon with rounded genal corners and an indistinct glabella. The cranidium is transversely divided by a W-shaped furrow which joins the facial suture slightly in front of the eyes. Another furrow is forwardly convex and terminates at the axial furrows of the first thoracic segment. The peculiar transverse cephalic furrows are probably fractures. In any case, the remaining cephalic features of *A. halli* clearly

exclude it from *Pseudogygites latimarginatus* and, because no type specimen exists, this species remains unrecognizable. Likewise, *Asaphus hincksii* cannot be considered synonymous with *P. latimarginatus* because this species was described as having a smooth pygidium. However, *A. hincksii* does deserve notice because in the description of that species Chapman (1859b) noted and illustrated the morphological feature to which the name of *panderian opening* was later applied—apparently independently of its discovery two years earlier by Pander in *Asaphus expansus*.

Pseudogygites hudsoni n. sp.
Figs. 7D, 8B–G, 10A

cf. *Pseudogygites latimarginata* (Hall), D.E. Jackson, *in* Nelson and Johnson, 1966:567.
?*Pseudogygites* sp., Jackson, 1971.

Diagnosis

A species of *Pseudogygites* with a short preglabellar field (= 12% of sagittal cephalic length); a semicircular pygidium with 9 to 10 distinct pleurae with faint but complete pleural furrows, poorly defined border furrow, and relatively broad border. Median connective suture is functional.

Holotype

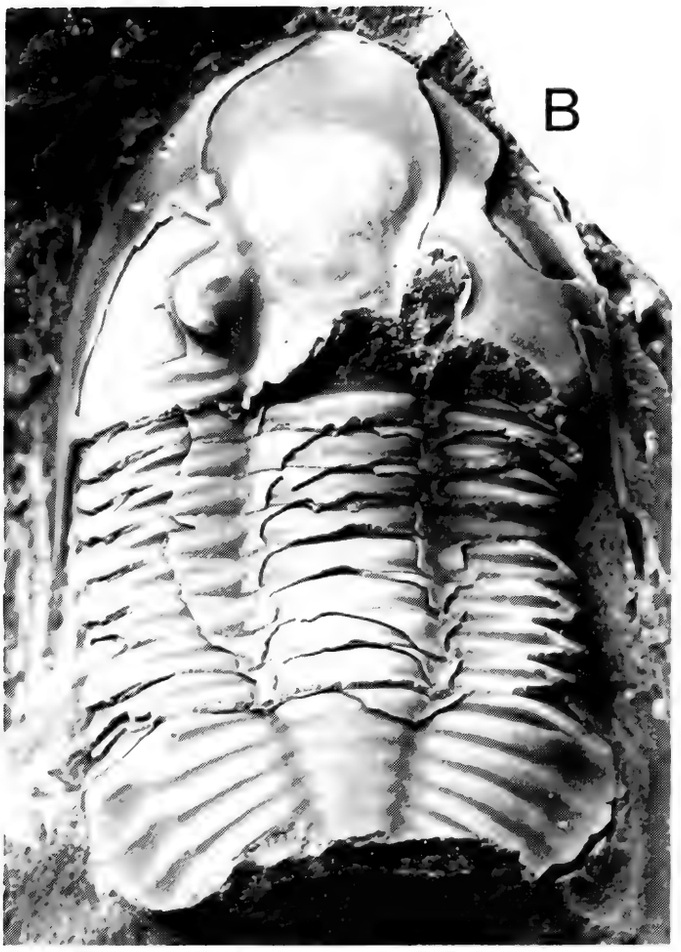
A complete, but compressed and exfoliated cranidium (GSC 47517) collected from rubble of the "Oil Shale interval" (= Boas River Shale) near East Bay, Southampton Island by S.J. Nelson (GSC loc. C-26369). According to Nelson and Johnson (1976:fig 3), the "Oil Shale interval" at East Bay is about 17 m thick.

Occurrences

SOUTHAMPTON ISLAND

GSC loc. 84651, Boas River Shale, 0 to 0.7 m above base of exposure, central Southampton Island, 64°22′50″N, 84°31′10″W, collected by B.V. Sanford. GSC loc. 84653, same locality and collector as above, 0.7 to 2.3 m above base of exposure. GSC loc. C-26369, "Oil Shale interval" (= Boas River Shale), near East Bay, 64°01′N, 81°28′W, collected by S.J. Nelson.

Fig. 7 A–C *Pseudogygites latimarginatus* (Hall)
- A Dorsal view of latex impression of external mould of entire exoskeleton, ROM 35034, × 1.5, lower Whitby Formation, Bowmanville (carcass; note deformed thoracic segments on the left side, probably indicating an unsuccessful attempt at moulting).
- B,C Dorsal and oblique lateral views of nearly complete uncompressed specimen, GSC 7817, × 1.5, Eastview Formation, Ottawa.
- D *Pseudogygites hudsoni* n. sp.
  Bedding plane with three cranidia and a pygidium, GSC 47510, × 2.8, Boas River Shale, Southampton Island (GSC loc. 84651).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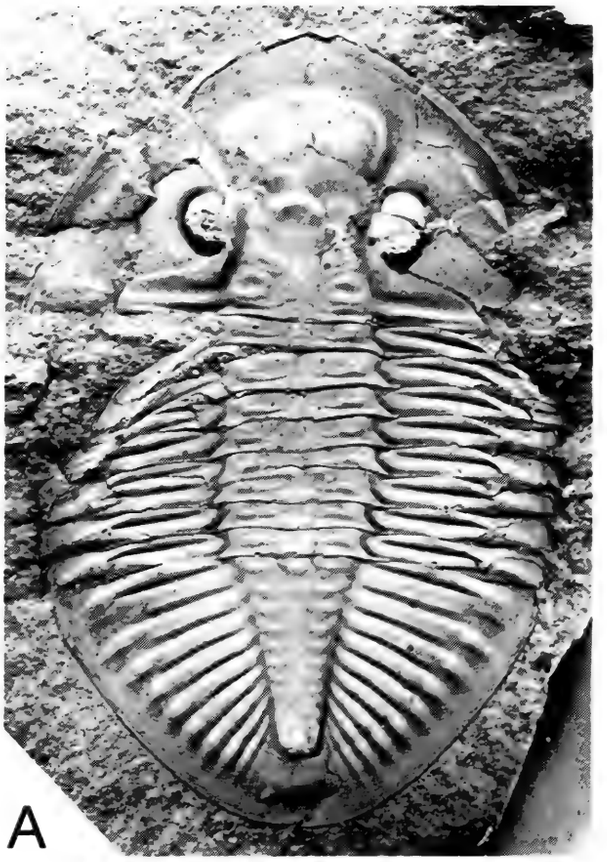
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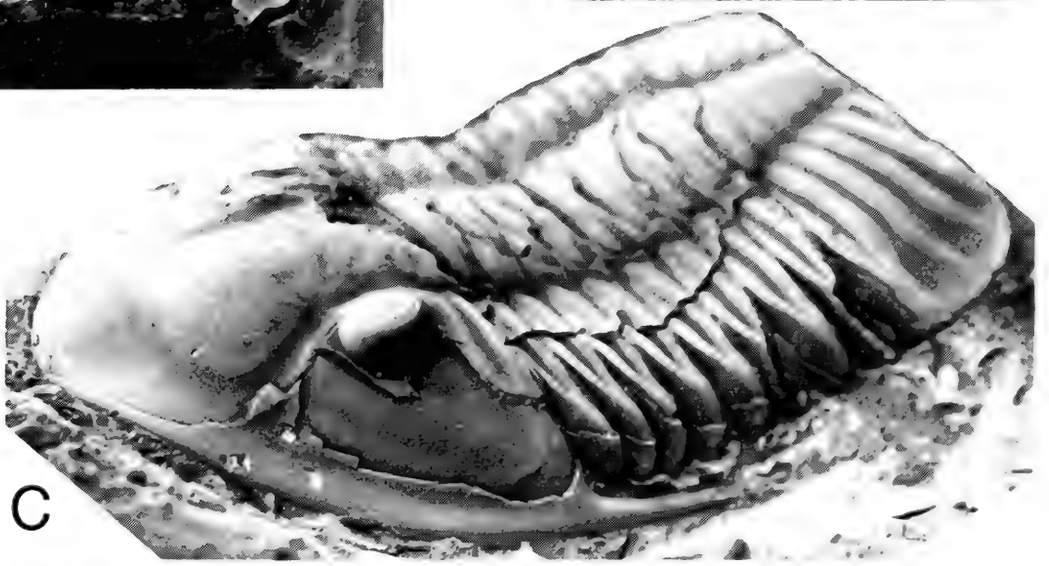
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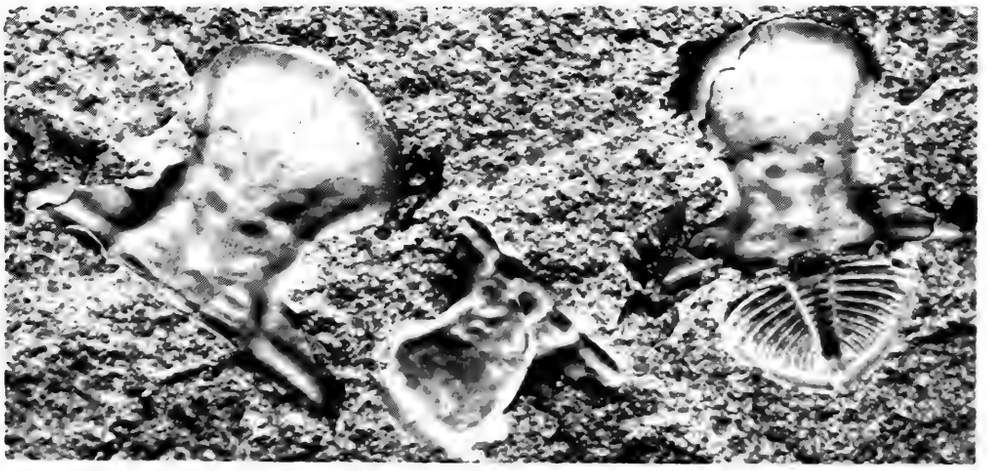
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Age

The type material of *Pseudogygites hudsoni* n. sp. was selected from three lots of fossils. One was collected by S.J. Nelson from rubble of the "Oil Shale interval" near East Bay, Southampton Island (Nelson and Johnson, 1966, 1976) and the other two were collected by B.V. Sanford from the Boas River Shale in central Southampton Island (Sanford, 1970; Heywood and Sanford, 1977). According to Nelson and Johnson (1976), the "Oil Shale interval" is Richmondian in age and occurs at the top of the Ordovician section on Southampton Island, between the Churchill River Group and the Silurian, and is a separate and younger unit than the Boas River Shale which, according to Heywood and Sanford (1977), is Edenian in age and occurs between the Bad Cache Rapids Group and the Churchill River Group.

An evaluation of published evidence suggests that the fossiliferous "Oil Shale interval" rubble and the Boas River Shale is the same unit and, further, that this unit is probably of late Maysvillian age and occurs between the Bad Cache Rapids Group and the Churchill River Group (Fig. 11). The "Oil Shale interval" rubble and the Boas River Shale contain the same species of *Pseudogygites*, occur along the same belt, and the available hand samples are indistinguishable lithologically. According to Riva (1974:5), the graptolites of the Boas River Shale and of the "Oil Shale interval" probably belong to the *Climacograptus manitoulinensis* Zone and, as such, are probably somewhat younger than those of the lower Whitby Formation of southern Ontario, which belong to the *C. pygmaeus* Zone. The Churchill River Group and the Red Head Rapids Group which overlie the Boas River Shale on Southampton Island have yielded conodonts of "late Maysvillian to Richmondian age, probably Richmondian" (Barnes, 1974:235).

Discussion

The following features distinguish *Pseudogygites hudsoni* n. sp. from *P. latimarginatus* (Hall).

CEPHALON

The preglabellar field is shorter and the glabella expands more in front of the eyes. A faint sagittal depression is present on the front part of the glabella. The lateral glabellar furrows are deeper. A median connective suture crosses the doublure.

HYPOSTOME

The single available hypostome of *P. hudsoni* is very similar to that of *P. latimarginatus*, but the maculae are deeper and the posterior notch narrower (tr.).

PYGIDIUM

The pygidium is semicircular in outline. The axial ring furrows are greater in number (up to 12), more distinct, and continue to near the axial termination. The pleurae are fewer in number and the pleural furrows are faint, but continuous from the lateral border furrow to the axial furrow.

Pseudogygites arcticus n. sp.
Figs. 8A, 9, 10B–D

Pseudogygites latimarginatus (Hall), A.E. Wilson, *in* Thorsteinsson, 1958:87.
Pseudogygites latimarginatus—Kerr, 1974:132.

Diagnosis

A species of *Pseudogygites* with a short preglabellar field (= 8–10% of sagittal cephalic length); a semicircular pygidium with seven to nine faint pleurae and very faint but complete pleural furrows, well-defined border furrow, and relatively narrow border. Median connective suture is functional.

Holotype

An incomplete external mould of a cranidium (ROM 35388) from the base of a 7 m thick tongue of the Cape Phillips Formation within the lowest part of the Allen Bay Formation on Grinnell Peninsula, Devon Island (74°41′N, 95°35′W); collected by G.S. Nowlan and C.R. Barnes.

Occurrences

DEVON ISLAND

Same locality and collectors as holotype.

CORNWALLIS ISLAND

Cape Phillips tongue within the lower Allen Bay Formation (75°10′N, 95°10′W); collected by J. Arengi. See Thorsteinsson and Kerr (1968:7).

BATHURST ISLAND

GSC loc. 67001, 18 m above base of Cape Phillips Formation, Driftwood Bay (75°57′N, 97°50′W); collected by J.W. Kerr.

Age

In commenting on the age significance of *Pseudogygites arcticus* (as *P. latimarginatus*) in Member A of the Cape Phillips Formation on Cornwallis Island, Thorsteinsson (1958:90) stated: "The graptolites with which *P. latimarginatus* is associated in Cape Phillips strata appear to bear no relation to Collingwood or Utica forms. Moreover, the association of *P. latimarginatus* with *Climacograptus latus* indicates that either the former ranges higher than previously recorded or the latter ranges lower." Thorsteinsson's assessment of *P. arcticus* as being younger than *P. latimarginatus* in the Collingwood Shale (= lower Whitby) is supported herein. John Riva has examined graptolites associated with *P. arcticus* and identified two species: one is a probable new species of *Glyptograptus* with extremely long virgella, antisicular spines, and mesial spine on th 1^1 and the other is a species of *Glyptograptus* or "*Pseudoclimacograptus*". He stated (pers. comm., 1977) that these graptolites are puzzling, but they all are younger than the *Climacograptus*

pygmaeus Zone. Barnes (1974:233, 234) noted that conodont collections from the lower part of the Allen Bay and Cape Phillips Formations on Ellesmere, Somerset, and Bathurst islands (including samples from *P. arcticus*-bearing beds) belong to conodont Fauna 12 of late Maysvillian to Richmondian age.

Discussion

The following features distinguish *Pseudogygites arcticus* n. sp. from *P. latimarginatus* (Hall).

CEPHALON

The preglabellar field is shorter and the glabella expands farther laterally in front of the eyes. A firmly impressed sagittal furrow is present on the front part of the glabella. The lateral glabellar furrows are fainter and the median glabellar tubercle appears transversely stretched. The palpebral lobes are located farther forward. A median connective suture crosses the doublure.

HYPOSTOME

The posterior projections are longer and more pointed, the lateral shoulders are not as rounded, and the central body is more inflated.

PYGIDIUM

The pygidium is semicircular in outline. The pleural lobes are inflated, so that they stand as high as the axis. The axial ring furrows are faintly impressed. The axis is relatively shorter (sag.). The pleurae are not very distinct and the pleural furrows are continuous from the lateral border furrow to the axial furrow. The lateral border is narrower.

The cranidium of *Pseudogygites arcticus* is rather similar to that of *P. hudsoni* in having a short preglabellar field and a glabella that expands markedly in front of the eyes and which contains a short sagittal furrow on its front part. The pygidium and hypostome of *P. arcticus* and *P. hudsoni* differ markedly.

Fig. 8 A *Pseudogygites arcticus* n. sp.
Dorsal view of small pygidium, GSC 47511, × 4, lower Cape Phillips Formation, Driftwood Bay, Bathurst Island (GSC loc. 67001).

B–G *Pseudogygites hudsoni* n. sp. All from Boas River Shale, Southampton Island.

B Ventral view of hypostome, GSC 47512, × 2 (GSC loc. 84653).

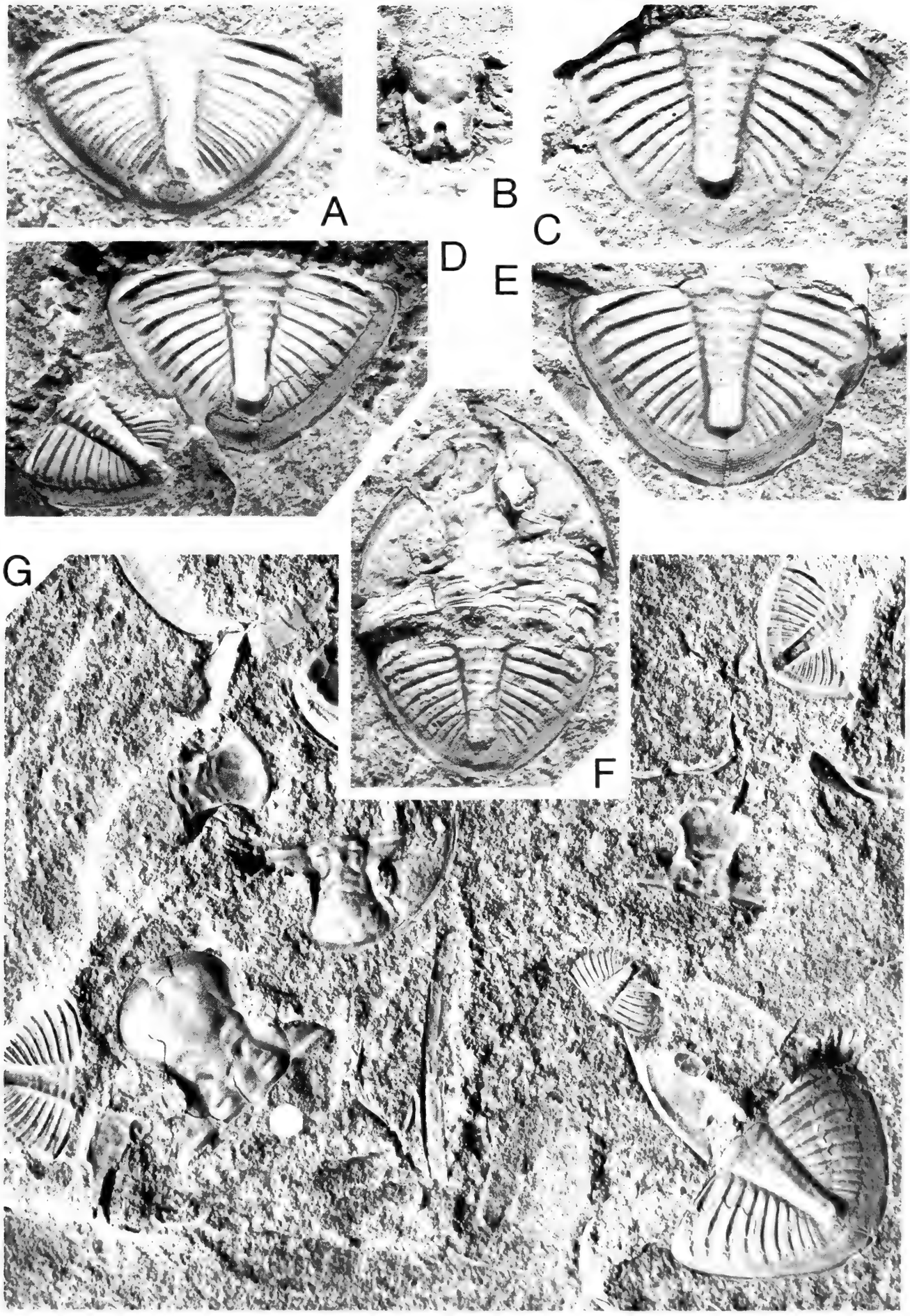
C Dorsal view of latex impression of external mould of pygidium, GSC 47513, × 2.4 (GSC loc. 84651).

D Dorsal view of two pygidia, GSC 47514, × 2.4 (GSC loc. C–26369).

E Dorsal view of exfoliated pygidium, GSC 47515, × 2.8 (GSC loc. 84653).

F Dorsal view of dismembered specimen, probably a moult association, GSC 47516, × 2 (GSC loc. 84651).

G View of bedding plane with a number of cranidia and pygidia. Holotype is cranidium in lower left corner marked by white dot, GSC 47517, × 2.6 (GSC loc. C–26369).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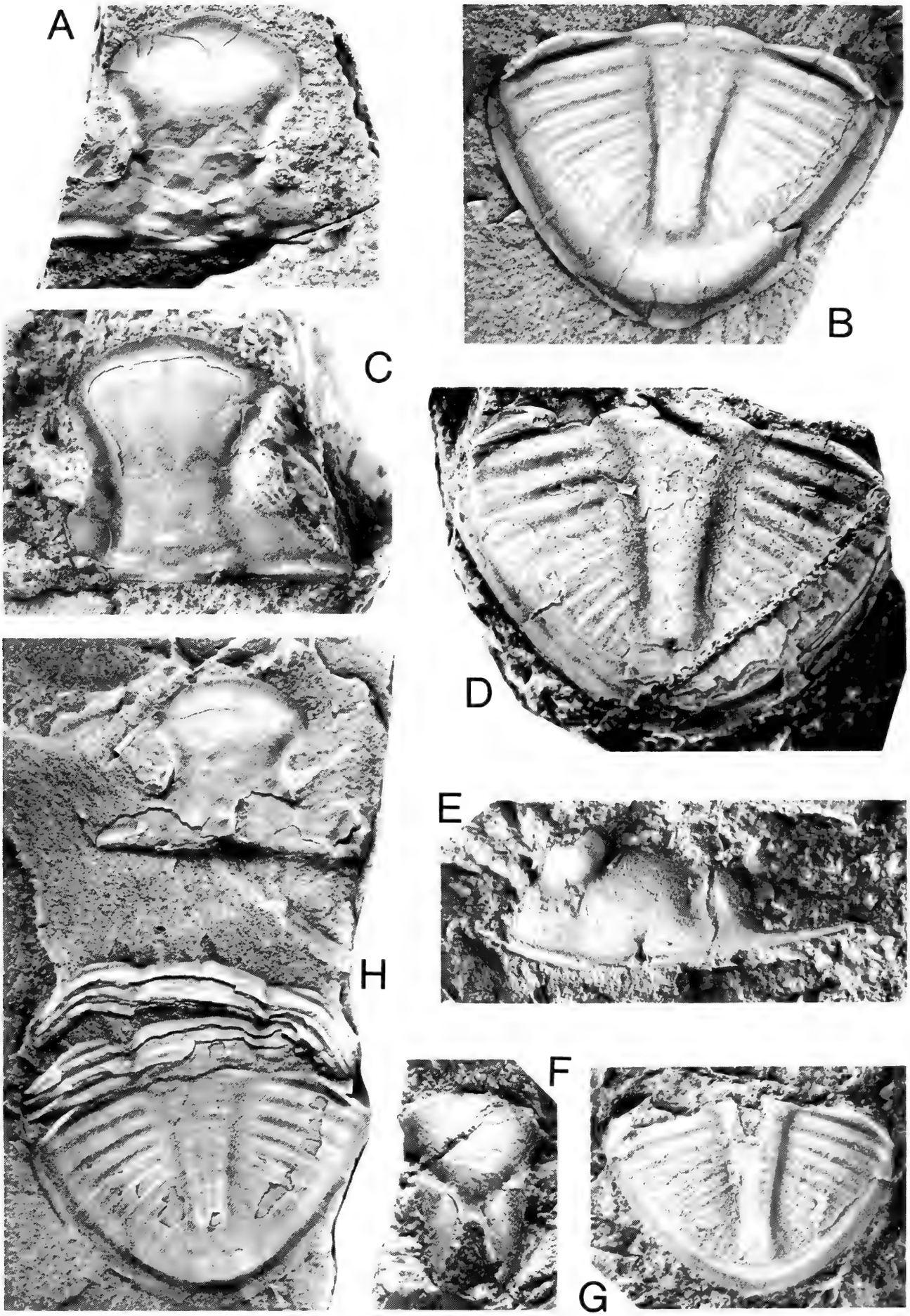
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Pseudogygites akpatokensis n. sp.
Fig. 10E

Pseudogygites sp., Workum, Bolton, and Barnes, 1976:pl. 3, fig. 1.

Diagnosis

A species of *Pseudogygites* with a relatively long preglabellar field (= 19% of sagittal cephalic length) and a subtriangular pygidium with 10 very faint pleurae, well-defined border furrow, and relatively broad border.

Holotype

An external mould of a cranidium (GSC 41187a) from the bituminous limestone unit on the westcentral coast of Akpatok Island, Ungava Bay collected by R.H. Workum (Section II, 9.1 m above sea level; Workum, Bolton, and Barnes, 1976).

Occurrence

AKPATOK ISLAND

Same locality and collector as the holotype.

Age

The graptolites of the bituminous limestone unit on Akpatok Island were assigned to the *Climacograptus manitoulinensis* Zone by Riva (*in* Workum, Bolton, and Barnes, 1976). This zone is herein considered late Maysvillian in age.

Discussion

Pseudogygites akpatokensis n. sp. differs from *P. latimarginatus* (Hall) in having a more waisted glabella, fainter lateral glabellar furrows, eyes located farther back on

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Fig. 9 *Pseudogygites arcticus* n. sp.

A Dorsal view of cranidium, GSC 47518, × 2.1, lower Cape Phillips Formation, Driftwood Bay, Bathurst Island (GSC loc. 67001).

B Dorsal view of pygidium, GSC 47519, × 1.7, lower Cape Phillips Formation, Driftwood Bay, Bathurst Island (GSC loc. 67001).

C Dorsal view of latex impression of external mould of cranidium, holotype, ROM 35388a, × 2.3, Cape Phillips tongue in lower Allen Bay Formation, Grinnell Peninsula, Devon Island.

D Dorsal view of pygidium, ROM 35389, × 2.5, Cape Phillips tongue in lower Allen Bay Formation, Grinnell Peninsula, Devon Island.

E Dorsal view of free cheek, ROM 35391, × 3.0, Cape Phillips tongue in lower Allen Bay Formation, Grinnell Peninsula, Devon Island.

F Ventral view of hypostome, ROM 35392, × 3.0, Cape Phillips tongue in lower Allen Bay Formation, Grinnell Peninsula, Devon Island.

G Dorsal view of exfoliated pygidium, ROM 35393, × 3.0, Cape Phillips tongue in lower Allen Bay Formation, Grinnell Peninsula, Devon Island.

H Dorsal view of dismembered specimen, ROM 35390, × 1.4, Cape Phillips tongue in lower Allen Bay Formation, central Cornwallis Island.

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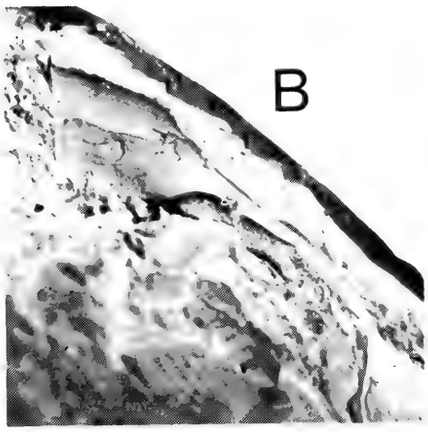

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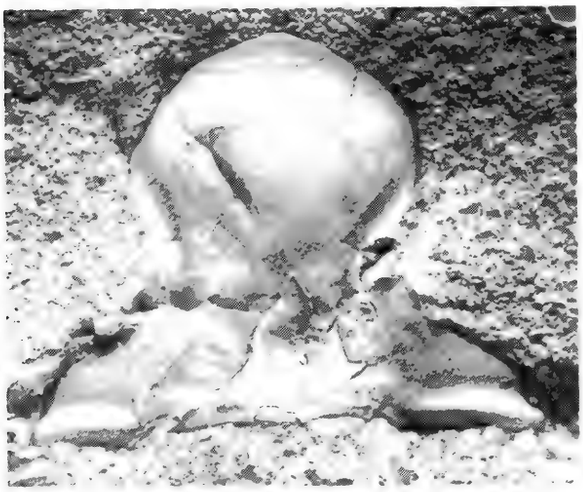

E

the cephalon, stout and bladelike genal spines, and a narrower (tr.) pygidium with very faint pleural, interpleural, and axial ring furrows.

The pygidium of *P. akpatokensis* is most similar to that of *P. arcticus*, but it has a narrower axis, shallower furrows, and a broader border.

Moulting of Pseudogygites latimarginatus

The prevalent occurrence of *Pseudogygites latimarginatus* in the dark brown bituminous shales of the lower Whitby Formation is as disarticulated exoskeletal pieces. Such accumulations often comprise enormous numbers of specimens (see Levi-Setti, 1975, pl. 3 for a typical occurrence). Entire or nearly entire exoskeletons are not uncommon. These do not occur in direct association with the massed specimens mentioned above but, instead, occur in sparsely fossiliferous layers (see Ludvigsen, 1979a, fig. 37 for an unusual concentration of such specimens). Entire specimens are preserved in two main configurations. The first configuration is that shown in Figs. 3A, 4D, 5G, and 7B which consists of the entire exoskeleton preserved intact with no displacement of exoskeletal parts (other than that resulting from compaction). In these specimens the hypostome is attached along the hypostomal suture. In compressed specimens, the crescent-shaped imprint of the upturned portion of the notched posterior margin of the hypostome may be seen in the central part of the glabella between the eyes. In order to verify that this imprint actually represents the hypostome, the glabella and underlying matrix were removed from a few specimens to expose the hypostome on the ventral surface (Fig. 4D). The anterior parts of the facial sutures are slightly opened in some of these specimens. This is not an ecdysal sutural gape (Henningsmoen, 1975), but is merely the result of slight splaying of the cephalic units during compaction. I conclude that this configuration indicates the remains of a dead individual (a carcass). The second configuration is best shown in Figs. 3B, 4B, E, and 5C. This configuration consists of the yoked cheeks lying immediately in front of, and at an angle to, the conjoined thorax and pygidium. In most cases, the posterior edge of one side of the yoked cheeks lies on

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Fig. 10 A *Pseudogygites hudsoni*, n. sp.
Dorsal view of latex impression of external mould of cranidium, GSC 47473, × 2.6, Boas River Shale, Southampton Island (GSC loc. 84653).

B–D *Pseudogygites arcticus* n. sp.

B Ventral view of latex impression of external mould of free cheek (note median connective suture), ROM 35388b, × 2.6, Cape Phillips tongue in lower Allen Bay Formation, Grinnell Peninsula, Devon Island.

C Dorsal view of latex impression of external mould of cranidium, GSC 49475, × 2.6, lower Cape Phillips Formation, Driftwood Bay, Bathurst Island (GSC loc. 67001).

D Dorsal view of crushed cranidium, GSC 49474, × 2.1, lower Cape Phillips Formation, Driftwood Bay, Bathurst Island (GSC loc. 67001).

E *Pseudogygites akpatokensis* n. sp.
Latex impression of slab with fragmentary cranidia, pygidia, and a free cheek, GSC 41187, × 1.3. Holotype cranidium is in the lower third of photograph, marked by white dot. Bituminous limestone and shale unit on westcentral coast of Akpatok Island, Ungava Bay (Section II, 9.1 m above high sea level; Workum, Bolton, and Barnes, 1976).

top of the first few thoracic segments. The cranidium may be present and on one specimen (Fig. 3B) it is displaced laterally and lies at an angle to the yoked cheeks. The hypostome is often attached to the yoked cheeks, but in the specimen described above, it is overturned and shifted sideways relative to the cheeks. In most of these specimens, the thorax is not displaced or distorted, but in a single specimen (Fig. 5C) it is slightly telescoped. Such persistent configurations of exoskeletal units strongly suggest that they are exuviae of *Pseudogygites latimarginatus* and that the exuvial units have not been moved from where they were shed.

With the two end members of the exuvial cycle preserved (that is, a carcass, Fig. 3A, and a complete exuvia, Fig. 3B) it is now possible to make an attempt at reconstruction of the moulting behaviour of *Pseudogygites latimarginatus*. A hypothetical sequence is summarized below (see also Ludvigsen, 1979a: fig. 14).

1. In preparation for moulting, the trilobite severed the connection between the key exuvial units—the cephalic unit and the thoracopygon.
2. Further separation of these two exuvial units occurred as the trilobite anchored one genal spine in the mud and crawled backward. This caused the opposite side of the cephalic unit to rotate back and across the front part of the thoracopygon.
3. When the trilobite had backed up sufficiently so that the front part of the head was behind the facial suture of the cephalic unit, it separated this unit along the facial suture into an upper unit (cranidium) and a lower unit (yoked cheeks plus hypostome) and nudged aside the upper cephalic unit with its head.
4. The trilobite then crawled forward and sideways through the gape of the facial suture while shoving aside the cranidium. The thoracopygon became caught against the edges of the upper and lower cephalic units and slid off the trilobite.
5. The trilobite continued its forward motion until it was clear of the thoracopygon and the upper cephalic unit. The thrashing appendages dislodged and overturned the hypostome.

The preceding is a possible moulting scenario which accounts for the constellation shown in Fig. 3B. The absence of the lower cephalic unit in one specimen (Fig. 4B) seems to indicate that occasionally the moulting trilobite carried away portions of the cephalic unit.

An example of abnormal moulting is possibly shown by the specimen in Fig. 7A. The crescent-shaped bulge between the eyes indicates that the hypostome is still in place and because the sutures are tightly sealed, this specimen is interpreted as a carcass. The first four segments on the left side are sharply bent backward and two of these are broken near the axial furrow. If the moulting sequence outline above is correct, then this specimen appears to represent an individual that perished during an incomplete moult. The deformation is consistent with an unsuccessful attempt by the trilobite at severing the cephalic unit from the thoracopygon.

The ability to complete a moult sequence quickly and without inflicting self-injury was obviously of paramount importance to a trilobite and the inherent functional requirements should be reflected in its morphology. Two features of *Pseudogygites latimarginatus*—the yoked cheeks and the genal spines—may be explained, at least in part, by reference to their role in facilitating ecdysis. The possession of yoked cheeks would allow the trilobite to discharge the lower cephalic unit in one smooth

motion by applying pressure to just one side of the cephalon. In addition, the danger of inflicting self-injury to the ventral surface would be reduced if the sharp edges of the median connective suture were eliminated. Possession of spikelike genal spines appears to have been significant because a rounded genal angle, such as that in mature *Isotelus*, would probably have provided insufficient grip in soft mud.

Origin of Pseudogygites latimarginatus

Pseudogygites is an endemic North American trilobite whose numerical acme is consistently confined to a narrow interval near the base of certain Upper Ordovician bituminous shales where they overlie carbonates in eastcentral and arctic North America (Fig. 11).

Previous workers have suggested that *Pseudogygites* belongs in the Asaphinae (Raymond, 1912), the Ogygiocaridiinae (Whittington, 1966), or the Isotelinae (Jaanusson, 1959). Because the morphology of this taxon clearly indicates an assignment to the Isotelinae, the ancestry of *Pseudogygites* should be sought among members of this typical North American subfamily. The following discussion centres on the origin of *P. latimarginatus* because it is the best known of the four species, and because more is known about the age and stratigraphic setting of the lower Whitby Formation in southern Ontario than about the bituminous shale units in northern Canada.

Isotelus, the most abundant and widely distributed of the Isotelinae in North America, shares a number of general cephalic, pygidial, and hypostomal features with *Pseudogygites latimarginatus* (compare Figs. 12D and 12H). The similarity between mature *Isotelus* and mature *Pseudogygites* is not great, but immature specimens of *Isotelus* (Fig. 12E) are strikingly similar to immature specimens of *Pseudogygites* (Fig. 12A). In addition, many immature specimens of *Isotelus* are very similar to mature specimens of *Pseudogygites* (compare the immature *Isotelus* spp. illustrated by Whittington [1941:pl. 75, figs. 27–29, 34–36], Hu [1975:pl. 4, figs. 12, 13, 20, 28, 29], and Chatterton and Ludvigsen [1976:pl. 2, figs. 38–41] with the mature specimens of *P. latimarginatus* illustrated in this paper).

The evidence seems to indicate a derivation of *P. latimarginatus* from a species of *Isotelus*—which species of *Isotelus* is difficult (or perhaps impossible) to determine. The presence of a novel shared-derived (synapomorphic) character may point to the identity of the *P. latimarginatus* ancestor. The fused median connective suture is, perhaps, such a character. Of the North American species of *Isotelus* and *Pseudogygites*, only *I. gigas* and *P. latimarginatus* definitely possess this character (compare Fig. 6H and 4C). The cranidial microsculpture of the two species is nearly identical (compare Fig. 6D and 6F). Because the remaining morphological characters of the two species are compatible with such a phyletic connection, I suggest that *P. latimarginatus* was derived from *I. gigas* during the early Late Ordovician of eastern North America.

It is now becoming clear that many of the morphological characters that serve to distinguish an immature *Isotelus* from a mature *Isotelus* will equally well serve to distinguish a mature *Pseudogygites* from a mature *Isotelus*. Some of these characters are listed below:

1. Virtually all dorsal furrows are deeper. These include the axial, lateral glabellar, and border furrows on the cephalon and the axial, border, articulatory, axial ring, interpleural, and pleural furrows on the pygidium.
2. The preglabellar field is longer (sag.).
3. The facial suture curves farther laterally in front of the eyes.
4. The eyes are located farther back on the cephalon.
5. The free cheeks are wider (tr.).
6. The cephalon and pygidium are rounded in outline.
7. The glabella is more waisted.
8. The axis is relatively narrower.
9. The median glabellar tubercle is more prominent.
10. Long, slim genal spines are present.
11. Vincular sockets are present.
12. The hypostome is relatively longer.

Such a list of features implies that heterochrony played an important role in the derivation of *Pseudogygites latimarginatus* from *Isotelus gigas*. Although critical data on age and timing of maturation are not available, the juvenilized morphology of *P. latimarginatus*, coupled with its large size, suggest that paedomorphosis by retardation of somatic features (neoteny) was the evolutionary mechanism (see Gould, 1977). *P. latimarginatus* is a large trilobite. In a sample of 79 entire specimens from the lower Whitby Formation of southern Ontario, 20 per cent have lengths exceeding 7 cm (Fig. 13). In a sample of 46 entire specimens of *I. gigas* from the middle Trenton Group at Trenton Falls, New York, only 15 per cent are longer than 7 cm (Fig. 13). *P. latimarginatus*, therefore, is as large and maybe somewhat larger than *I. gigas*.

A comparison of the ontogenies of *Isotelus gigas* and *Pseudogygites latimarginatus* is hampered by the availability of only a few meraspid specimens of either species. Two meraspid specimens of *P. latimarginatus* are known; a degree 3 specimen (Fig. 12A) and a degree 5 specimen (Fig. 12B). Only a single meraspid specimen of indeterminate degree, but probably early meraspid (Fig. 12E), occurs in the large Walcott Collection of entire *I. gigas* from the middle Trenton Group kept in the Museum of Comparative Zoology at Harvard University. The speciment of *I. gigas* in this collection that Raymond (1914:fig. 1) reconstructed as a degree 4 meraspid is probably a small holaspid, as Whittington (1957:445) has already pointed out. Figure 12 summarizes the main points of the ontogenies of the two species and this figure clearly shows that *P. latimarginatus* changes much less during ontogeny than does *I. gigas*. If the morphologic information of early ontogenetic stages available for other

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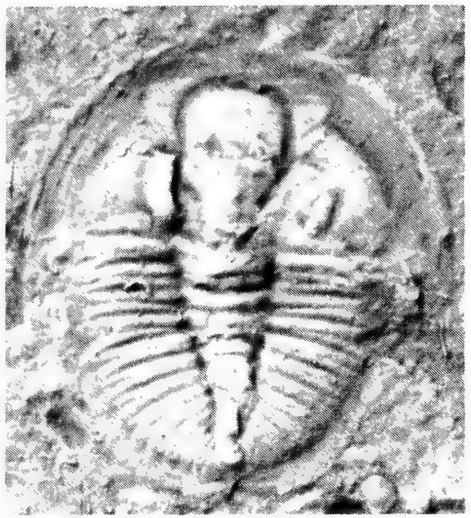
Fig. 11 Correlation chart of Late Ordovician successions in eastern and arctic North America. Stratigraphic intervals with significant amounts of bituminous shale and limestone are indicated by diagonal shading. Occurrences of species of *Pseudogygites* are indicated by circled dots. *P. latimarginatus* (Hall) occurs in northern Michigan, Manitoulin Island, Craigleith, Oshawa, New York, and Ottawa; *P. hudsoni* n. sp. occurs on Southampton Island; *P. akpatokensis* n. sp. occurs on Akpatok Island; and *P. arcticus* n. sp. occurs on Bathurst, Cornwallis, and Devon islands.

British Series	North American Stages	NORTHERN MICHIGAN	MANITOULIN ISLAND	CRAIGLEITH	OSHAWA	NEW YORK (RODMAN)	OTTAWA	SOUTHAMPTON ISLAND	AKPATOK ISLAND	BATHURST, CORNWALLIS, DEVON ISLANDS
ASHGILLIAN	RICHMONDIAN	BIG HILL	KAGAWONG	QUEENSTON	QUEENSTON		QUEENSTON	RED HEAD RAPIDS	UNNAMED LIMESTONE	ALLEN BAY, CAPE PHILLIPS
		STONINGTON	GEORGIAN BAY	GEORGIAN BAY	GEORGIAN BAY		RUSSELL	CHURCHILL RIVER		
							CARLSBAD		?	IRENE BAY
CARADOCIAN	MAYSVILLIAN	BILL'S CREEK	SHEGUIANDAH	upper WHITBY	upper WHITBY	LOWER FRANKFORT		BOAS RIVER	BITUMINOUS SHALE	THUMB MOUNTAIN
			WHITBY	lower WHITBY	lower WHITBY, middle WHITBY	WHITBY	BILLINGS			
							EASTVIEW		UNNAMED LIMESTONE	
	EDENIAN (part)	GROOS QUARRY	COBOURG	COBOURG	COBOURG	HILLIER	COBOURG	BAD CACHE RAPIDS		



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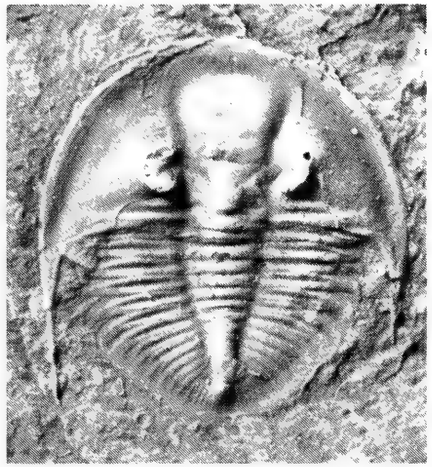

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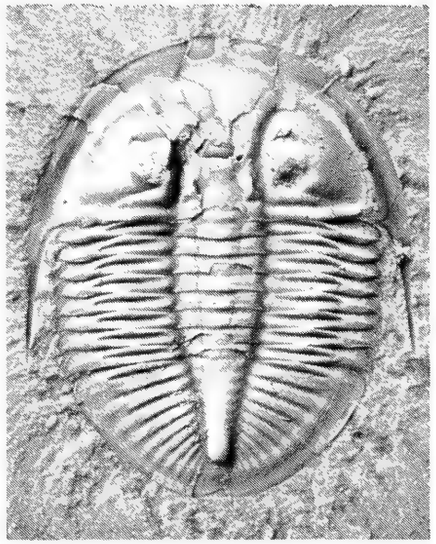

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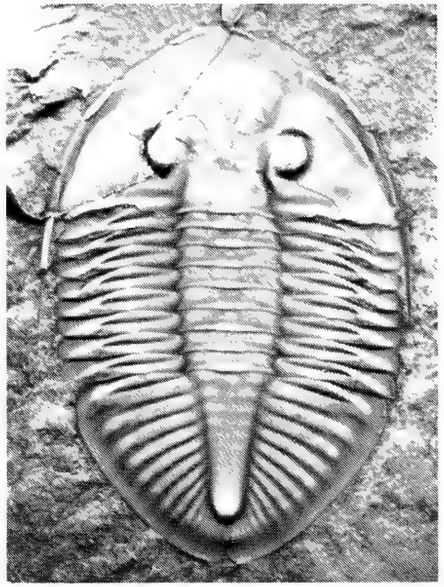

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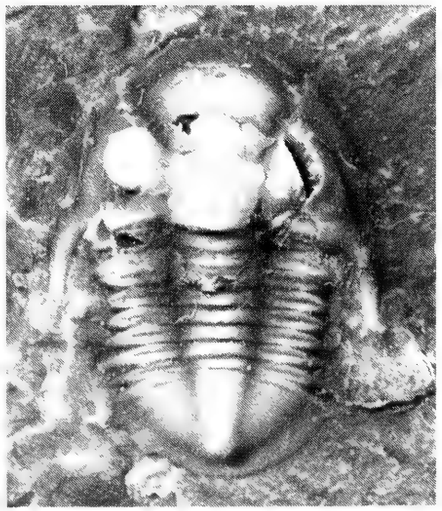

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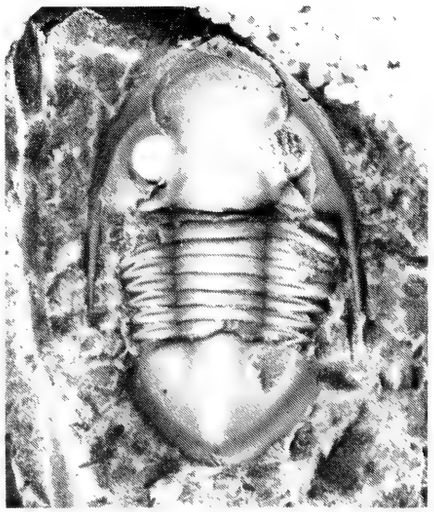

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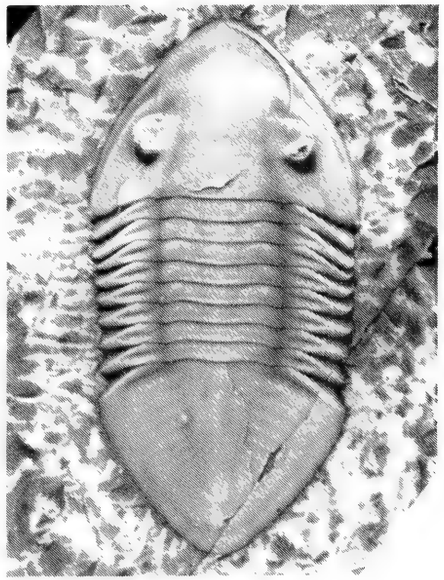

species of *Isotelus* (see Whittington, 1941; Hu, 1975; and Chatterton and Ludvigsen, 1976) is used to augment the meagre data on meraspid ontogeny of *I. gigas*, then tentative shape correlations can be drawn between the meraspid stage of *P. latimarginatus* and the early meraspid stage of *I. gigas* and between the holaspid stage of *P. latimarginatus* and the late meraspid and, possibly, the early holaspid stage of *I. gigas* (Fig. 13).

In terms of Gould's (1977:fig. 35) clock model of heterochrony, the neoteny of *P. latimarginatus* is expressed by shape remaining in the juvenile domain of the ancestor, size being slightly increased, and, possibly, maturation being delayed.

This is not the first heterochronous interpretation of *Isotelus gigas* and *Pseudogygites latimarginatus*. Raymond (1914) presented an account of the ontogeny of *I. gigas* which, in the spirit of the times, he interpreted in a recapitulatory framework. That is, in the course of its development *I. gigas* passes through stages which represent the adults of its ancestors and that this sequence of stages constitutes a phylogeny. Raymond named these stages, a *Basilicus* stage (for *Basiliella barrandei*), an *Ogygites* stage (for *Pseudogygites latimarginatus*), an *Isotelus maximus* stage, an *I. iowensis* stage, and an *I. gigas* stage. The first two stages are meraspids, the last three are holaspids. Raymond's phylogeny finds little support in modern stratigraphic palaeontology. It is difficult to accept *P. latimarginatus* as an ancestor of *I. gigas* because the "ancestor" appeared much later (early Maysvillian) than the "descendant" (Blackriveran; Ludvigsen, 1978). Although Raymond's observations and heterochronic correlations appear to be valid, the similarity between juvenile *I. gigas* and adult *P. latimarginatus* is better explained as the result of paedomorphosis (by retardation) than of recapitulation (by acceleration).

A question remains. Why should *P. latimarginatus* suddenly become so abundant immediately above the unconformable Cobourg-Whitby contact? The answer, I believe, lies in chance preadaptation. The neotenous features of this trilobite became advantageous in the new ecologic setting above the base of the Whitby Formation.

Isotelus gigas is one of the most abundant trilobites in the Trenton Group and, in the upper Cobourg Formation and its correlatives, it is associated with relatively rare *Pseudogygites latimarginatus*. The reverse is the case in the lower Whitby Formation and its correlatives. Here, *P. latimarginatus* is by far the most common trilobite and *Isotelus* (including *I. gigas*) follows distantly, well behind *Triarthrus* and *Flexicalymene*. It seems reasonable to suggest that the environmental shift associated

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Fig. 12 Comparative ontogeny of *Pseudogygites latimarginatus* (Hall) from the lower Whitby Formation, southern Ontario and *Isotelus gigas* DeKay from the middle Trenton Group, Trenton Falls, New York.

A–D *Pseudogygites latimarginatus* (Hall)

A Meraspid (M.3), ROM 27759, × 11.5, Craigleith.

B Meraspid (M.5), ROM 37829, × 5.5, Bowmanville.

C Holaspid, ROM 37830, × 3.3, Bowmanville.

D Holaspid, ROM 35029, × 1.5, Craigleith.

E–H *Isotelus gigas* DeKay

E Meraspid (degree indeterminate), MCZ 45, × 10.8 (original of Raymond, 1914:pl. 1, fig. 1).

F Holaspid, MCZ 48, × 5.3 (original of Raymond, 1914:pl. 1, fig. 2).

G Holaspid, MCZ 38, × 2.6 (original of Raymond, 1914:pl. 2, fig. 3).

H Holaspid, MCZ 41, × 1.0 (original of Raymond, 1914:pl. 3, fig. 3).

Note that *P. latimarginatus* changes less during ontogeny than does *I. gigas*.

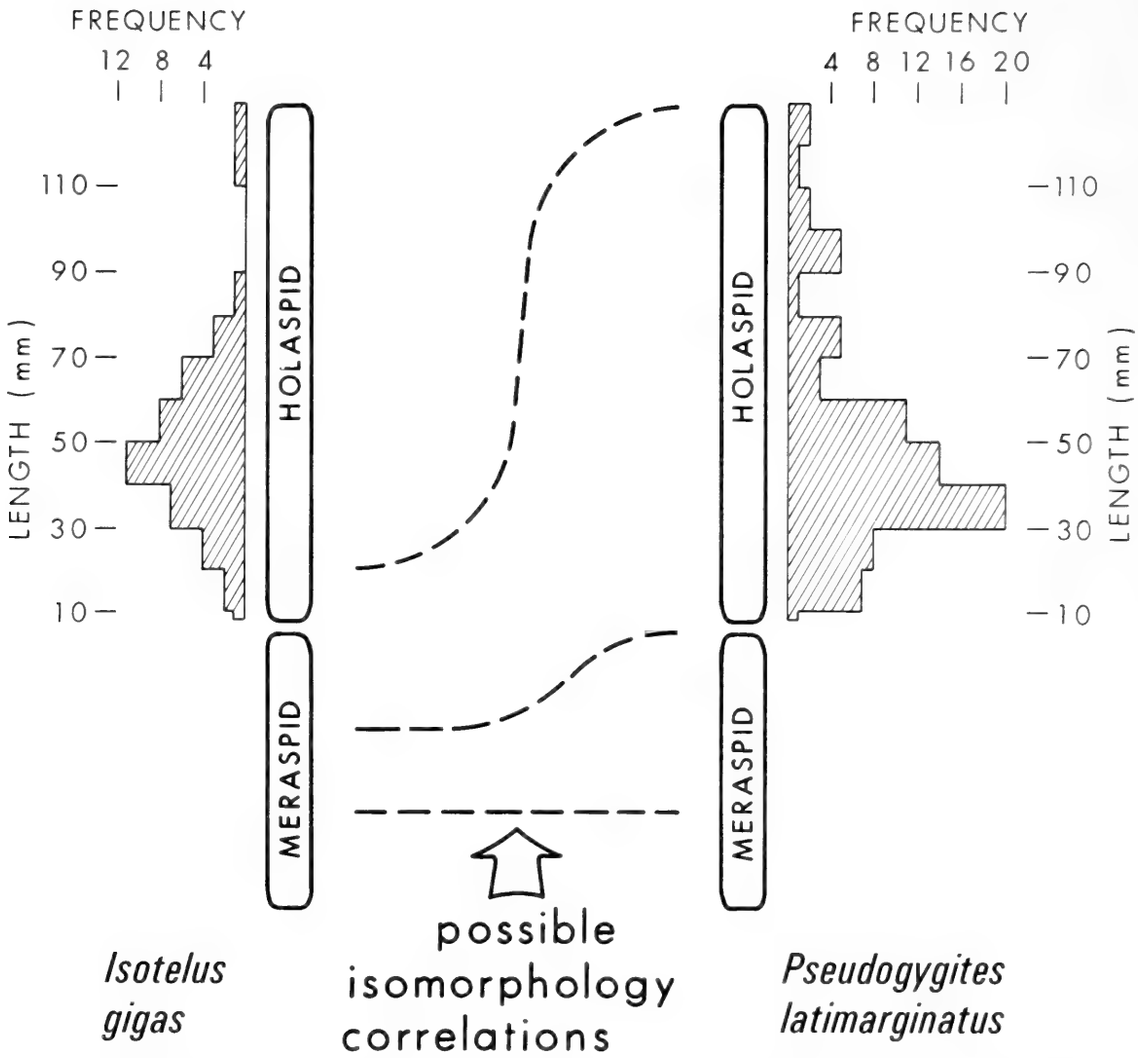

Fig. 13 Model of neotenous derivation of *Pseudogygites latimarginatus*. Tentative shape correlations are drawn with its ancestor, *Isotelus gigas*. Also shown are frequency distributions of sagittal lengths of entire holaspid specimens of *I. gigas* (46 specimens from the middle Trenton Group, Trenton Falls, New York; data extracted from Whittington's [1957] fig. 25; a single large specimen measuring 180 mm is not shown) and *P. latimarginatus* (79 specimens from the lower Whitby Formation, Craigleith; Royal Ontario Museum and University of Toronto collections). Both species become holaspids at length of 8 or 9 mm. Compare with Fig. 12 and see discussion in text.

with the change of sedimentary regime from predominantly carbonate mud deposition in the Cobourg, to predominantly organic-rich mud deposition in the lower Whitby was also responsible for the change in relative dominance of *I. gigas* and its neotenate.

The lithologic and faunal attributes of the upper Cobourg Formation point to a shallow, well-lit, well-oxygenated, and warm shelf environment. This environment is clearly indicated by the abundance of organisms with thick calcareous shells (notably bryozoans, gastropods, brachiopods, cephalopods, and echinoderms), the ubiquity of carbonate mud, and the common occurrence of lingulid brachiopods in burrowing position. The total species diversity is moderately high; Liberty (1969) tallied 93 species from the Cobourg Formation (his Lindsey Formation) in the Craigleith area.

The lower Whitby Formation, which disconformably overlies the Cobourg

Formation, is lithologically and faunally unique. The outstanding and most obvious feature of the lower Whitby is its bituminous nature. The petroleum content of this unit is considerable and Logan (1863) reported that in the 1860s condensate was distilled from these shales near Craigleith (yields were 7 gallons of petroleum per ton of shale). Pyrite is very common throughout the lower Whitby, occurring both as finely disseminated crystals and as partial replacement of many of the fossils. The fauna of the lower Whitby differs markedly from that of the Cobourg, even though many of the same genera and some species occur in both units. Trilobites (*P. latimarginatus* and *Triarthrus eatoni*); graptolites (climacograptids); small smooth ostracods; cephalopods (*Geisonoceras*); and strophomenid, zygospirid, and lingulid brachiopods dominate the fauna. Most of the calcareous fossils of the lower Whitby possess thin shells.

Liberty (1969:72) suggested that "the lower member [of the Whitby Formation] was probably deposited under reducing conditions in stagnant, non-aerated water". The significant organic carbon content of the lower Whitby and the presence of iron in reduced form are clearly indicative of the "oxygen debt" of these sediments (Fischer and Arthur, 1977), but some faunal and lithologic aspects suggest that other factors besides reducing conditions were important. Byers (1977:8) predicted that when dissolved oxygen is lowered, "the benthos becomes less diverse, less abundant, smaller in body size, less heavily calcified, and dominated by infauna". The lower Whitby fauna is, by no means, impoverished or stunted and the fine continuous laminae of the shales demonstrate that it lacks a burrowing infaunal component. Furthermore, faunal lists compiled by Liberty (1969) show a total diversity of 54 species for the lower Whitby in the Craigleith area.

The abrupt appearance of the olenid trilobite *Triarthrus* in the lower Whitby (Ludvigsen, 1979a: figs. 38, 39) suggests that water temperature was an important contributory factor governing the structure and composition of these black shale communities. Olenids are characteristic trilobites of the slope biofacies that occupied relatively deep and cold settings around the North American continent during the Ordovician (Titus and Cameron, 1976; Ludvigsen, 1979b) and their abundance in the lower Whitby suggests the influence of low water temperatures as well as low oxygen levels. There is no evidence to suggest that the lower Whitby represents an environment that is significantly deeper than that of the underlying Cobourg (Liberty, 1969:72) even though the deposition of these shales did coincide with the near maximum extent of the late Ordovician transgressing seas.

If the Cobourg Formation represents a shallow, well-oxygenated, and warm epicontinental shelf environment and the overlying lower Whitby Formation a moderately shallow, oxygen-poor, and cold epicontinental shelf environment, then the Cobourg-Whitby contact should indicate the time when a permanent thermocline became established on the shelf seas. The establishment of a thermocline over the epicontinental sea would have resulted in the spread of cold and oxygen-poor oceanic waters well into shallow sites (Heckel, 1977: fig. 5). The biota inhabiting this new ecologic setting would have been a mixture of those elements of the slope biofacies that were able to follow the shifting oceanic water masses into shallow settings, certain eurytopic elements of the shelf biofacies, and a few shelf taxa that, by chance, happened to have been preadapted for the new conditions. *Pseudogygites latimarginatus* could well fall into the third category.

Gould (1977:289, 290) emphasized that although the adaptive significance of

heterochrony has most commonly been expressed in terms of morphologic advantage alone, certain life history strategies such as timing of reproduction, fecundity, and longevity are adaptations in themselves and because such strategies are the very processes of heterochrony, they provide additional and highly significant indications of the expression of heterochrony in ecologic contexts.

Temperature profoundly affects most marine invertebrates, influencing their morphology, distribution, physiology, growth, and reproduction. Valentine (1973:123) has noted that growth tends to be slower, the onset of reproduction later, and death later among cold-water marine invertebrates than among warm-water marine invertebrates. Despite their slower growth, animals in cold water often attain larger dimensions than those in warm water because of postponed reproduction and increased longevity.

The twin pathways of paedomorphism, that is progenesis (precocious sexual development of an organism in a juvenile state) and neoteny (retention of juvenile characters of ancestor by adult descendant) (Gould, 1977), and their possible macroevolutionary roles should be examined in terms of temperature because temperature is known to influence the timing of sexual maturation in insects (Gould, 1977:305) and, of course, timing of maturation is the very core of paedomorphism.

McNamara (1978) suggested that the Early Cambrian trilobite *Olenellus* (*Olenelloides*) *armatus* was derived from *Olenellus* (*Olenellus*) by progenesis and that the paedomorphic derivation may have been triggered by elevated water temperatures in shallow sites.

I have here suggested that *Pseudogygites latimarginatus* was derived from *Isotelus gigas* by neoteny. It is possible that this paedomorphic derivation was triggered by low water temperatures in deeper sites near the facies edge of the upper Trenton Group, but such a theory presupposes that the relatively rare specimens of *P. latimarginatus* that are known to occur in warm and shallow settings in the upper Cobourg Formation of southern Ontario are merely peripheral members of larger populations occupying deeper and colder environments during deposition of the upper Cobourg. There is no evidence that such populations existed in the deeper water Cobourg equivalents, such as the Utica and upper Canajoharie Shales of New York State, and the first appearance of *P. latimarginatus* in this area is synchronous with its abundant appearance in the lower Whitby in Ontario (Fig. 11). One must conclude, therefore, that the neotenous derivation of *P. latimarginatus* took place in the shallow and warm Cobourg environment and that *Isotelus gigas* was sympatric with the initial members of its neotenate.

Water temperature cannot be used to explain the paedomorphic derivation of *Pseudogygites latimarginatus*, but it may offer an explanation for the great abundance of this trilobite in the lower Whitby Formation. The convergence of the suite of characteristics of cold-water invertebrates and the heterochronous characteristics of *P. latimarginatus* is significant and suggests that this species was equipped with the developmental and ecologic features of a cold-water species as a direct result of its neotenous derivation. It remained relatively rare during deposition of the Cobourg, but its preadaptation permitted explosive increase at the onset of declining water temperatures in the lower Whitby.

The lower Whitby Formation may be viewed as a slope litho- and biotope that has been shifted to a shelf position. This shift certainly necessitated a number of lithologic and biotic changes, but the basic ecologic attributes of the predictable and

stable slope environment probably remained intact. In terms of the environmental spectrum associated with a continuum of *r* to *K* selection strategies (Pianka, 1970), the lower Whitby environment should fall closer to the *K* end member. The abundance of *Pseudogygites latimarginatus* in this setting thereby supports Gould's (1977:293) prediction that "progenesis will be associated with *r* strategies and neoteny with *K* strategies".

The preceding is a possible explanation for the origin and localized abundance of *Pseudogygites latimarginatus*. It originated as a neotenate of *Isotelus gigas* and its great abundance in the lower Whitby is attributed to a fortuitous preadaptation to a new ecologic setting. The origin of the remaining three species of *Pseudogygites* is unclear. Each is somewhat younger than *P. latimarginatus* and each occurs in a separate bituminous unit where it directly overlies a carbonate unit (Fig. 11). The establishment of a uniform lithotope (brown bituminous shales and limestones) and biotope (the *Leptobolus-Triarthrus-Pseudogygites-Geisonoceras* fauna of Workum, Bolton and Barnes, 1976) over vast areas of eastern and arctic North America is one result of the extensive Late Ordovician transgression (Sanford, *in* Bolton et al., 1977). These shales and limestones apparently record the flooding of large parts of the craton by cold and oxygen-poor waters. It is possible that the four species of *Pseudogygites* constitute a single phyletic sequence (that is, *P. latimarginatus* to *P. hudsoni* to *P. akpatokensis* to *P. arcticus*), but because the similarity between these species of *Pseudogygites* are those features that could well indicate separate neotenous derivations, it is equally possible that they are iterative paedomorphs of different species of *Isotelus*. The possible *Isotelus* ancestors of the northern species of *Pseudogygites*, however, have not been studied.

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