The earliest known *Kinnella*, an orthide brachiopod from the Upper Ordovician of Manitoulin Island, Ontario, Canada

CHRISTOPHER A. STOTT and JISUO JIN

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A new species of the orthide brachiopod genus *Kinnella* is described from the Upper Member of the Georgian Bay Formation (Upper Ordovician) of Manitoulin Island, Ontario, Canada. This species, herein designated as *Kinnella laurentiana* sp. nov., occurs in strata of Richmondian (mid-Ashgill; Katian) age, most likely correlative with the eastern North American *Dicellograptus complanatus* Zone. This occurrence extends the known stratigraphic range of *Kinnella* downward considerably from its previously inferred basal Hirnantian inception. The new species is characterized by a moderately convex dorsal valve and an apsacline ventral interarea rarely approaching catacline. This is the third reported occurrence of *Kinnella* in North America, and is the only species known to have inhabited the epicontinental seas of Laurentia. The associated benthic shelly fauna indicates a depositional environment within fair weather wave base (BA 2). The ancestry of *Kinnella* and this species appears most likely to lie among older, morphologically similar members of the Draboviidae which were seemingly confined to higher latitude faunal provinces prior to the Hirnantian glacial event. Thus, the mid-Ashgill occurrence of *Kinnella laurentiana* in the palaeotropically located Manitoulin Island region suggests the mixing of a probable cooler water taxon with the warmer water epicontinental shelly fauna of Laurentia, as well as a possible earlier episode of low-latitude oceanic cooling. Cluster analysis of *Kinnella*-bearing brachiopod faunas reveals a sharp differentiation between the *K. laurentiana*-associated brachiopod fauna and all other known (Hirnantian–lower Rhuddanian) occurrences mainly represented by the type species *K. kielanae*.

Key words: Brachiopoda, Orthida, Enteletoidea, *Kinnella*, Ordovician, Ashgill, Canada.

Christopher A. Stott [castott@uwo.ca] and Jisuo Jin [jjin@uwo.ca], Department of Earth Sciences, The University of Western Ontario, London, Ontario, Canada N6A 5B7.

Introduction

The orthide brachiopod genus *Kinnella*, commonly represented by the species *Kinnella kielanae* (Temple, 1965), is one of the diagnostic components of the *Hirnantia* Fauna, known from highest Ordovician (Hirnantian) strata worldwide. Previously, *Kinnella*, was believed to be restricted to beds of late Ashgill age (Cocks and Price 1975) and more specifically to the Hirnantian Stage, the latter corresponding to the *Normalograptus extraordinarius* and *N. persculptus* graptolite zones (Rong and Harper 1988, 1999; Owen et al. 1991; Chen et al. 1999; Rong et al. 2002). Harper and Williams (2002), however, demonstrated that *Kinnella* also occurs in lowest Rhuddanian (Silurian) strata assignable to the *Parakidograptus acuminatus* Zone. Prior to this study, no pre-Hirnantian representatives of *Kinnella* were known, although it has been long realized that other common or key genera of the *Hirnantia* Fauna originated much earlier in the Ordovician and continued well into the Early Silurian (see Cocks and Price 1975; Rong and Harper 1988, 1999; Bassett 1989; Cocks 1989).

As a characteristic taxon of the Kosov Province *Hirnantia* Fauna, *Kinnella* has been known to occur in cool-water, siliciclastic-dominated depositional settings at the periphery of low-latitude palaeocontinents, as well as a wider range of environments in association with higher latitude Gondwanan and peri-Gondwanan terranes (see Rong and Harper 1988, 1999; Owen et al. 1991; Cocks and Torsvik 2002). Most of the core members of the Kosov Province *Hirnantia* fauna were interpreted to have inhabited relatively low energy settings below fair weather wave base, with fine grained, soft, siliciclastic substrates (Rong and Harper 1988, 1999; Harper and Williams 2002). However, typical and diverse *Hirnantia* faunas are also known from Hirnantian argillaceous micritic limestones deposited under similar depth conditions, such as the Kuanyinchiao Beds of South China (Rong et al. 2002). As such, the composition of the substrate is unlikely to have been the prime factor governing the paleoenvironmental distribution of the *Hirnantia* Fauna. *Kinnella* and other key genera of the *Hirnantia* Fauna are, however, notably absent in a silicified fauna from bioclastic limestones of the Kuanyinchiao Beds in Guizhou (Rong and Li 1999). This was attributed by these authors to deposition of these limestones under somewhat shallower and perhaps warmer water conditions than those typical for the formation.

In light of this, the discovery of *Kinnella* in mid-Ashgill (pre-Hirnantian), shallow-water (higher energy), low-latitude, epicontinental carbonates of Manitoulin Island, Ontario, Can-

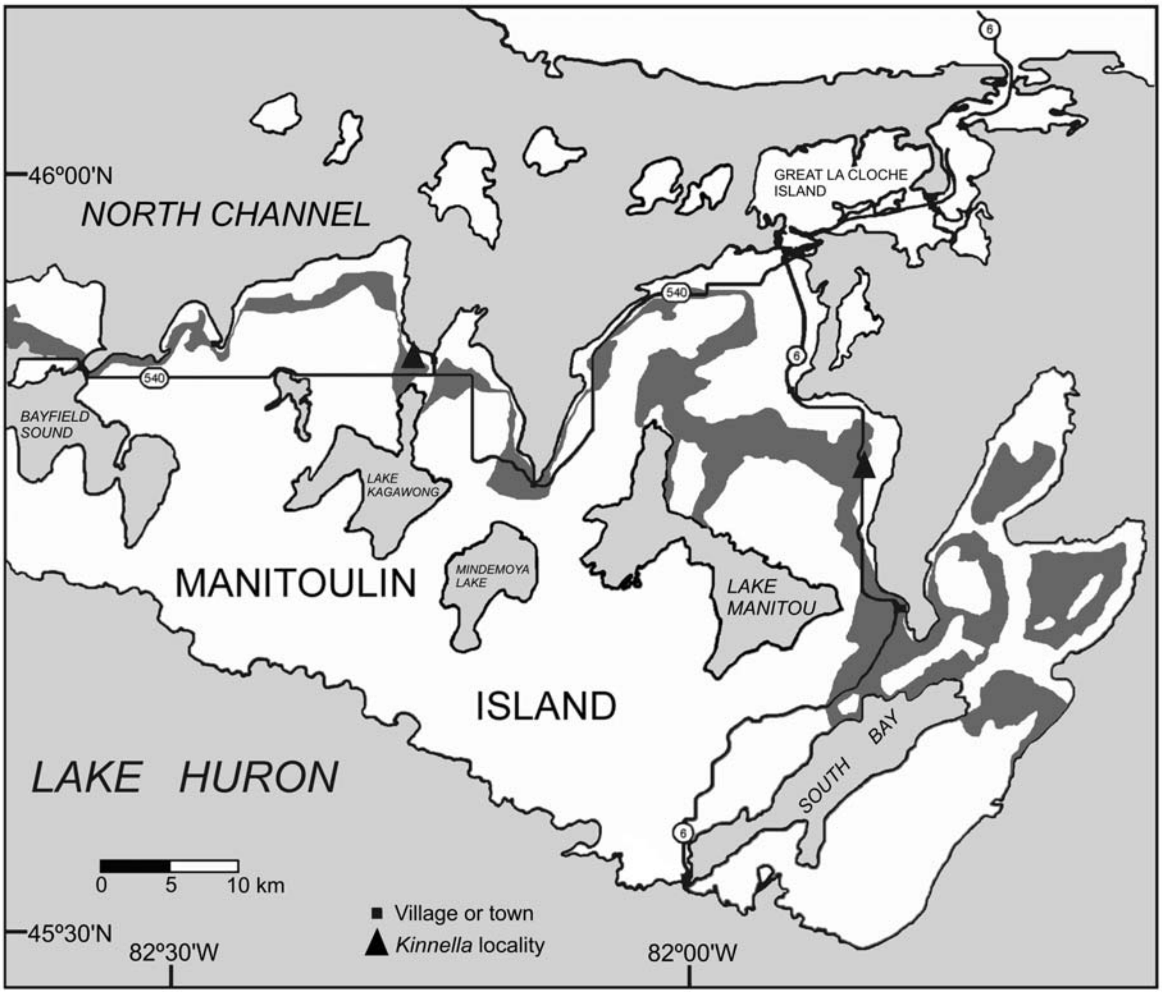

Fig. 1. Map of Manitoulin Island showing the localities of *Kinnella laurentiana* sp. nov. in the lower Kagawong Submember, upper Georgian Bay Formation. Dark shaded region corresponds to the outcrop belt of the Kagawong Submember.

ada (Fig. 1), is of particular significance for our understanding of the palaeoecology, evolution and palaeobiogeography of this genus and, potentially also, the *Hirnantia* Fauna.

On Manitoulin Island, *Kinnella* has been discovered at two localities, all from fine to medium crystalline dolostones of the lower Kagawong Submember (Upper Member), Georgian Bay Formation (Fig. 1). Several hundred silicified specimens have been obtained through acid digestion of bulk samples of dolostone. Associated fossil groups include other brachiopods, corals, bryozoans, bivalves, gastropods and cephalopods. Although some key elements of the *Hirnantia* Fauna are known to appear as low as the sub-Hirnantian *Diceratograptus mirus* Subzone in China (Rong and Harper 1988; Rong et al. 2002), the occurrence of *Kinnella* in the Georgian Bay Formation apparently predates all previously known occurrences of the genus. The main purposes of this study are, therefore, to provide a systematic description of the Manitoulin Island form of *Kinnella*, and to explore the evolutionary and palaeobiogeographic implications of this occurrence.

Institutional abbreviation.—GSC, Geological Survey of Canada, Ottawa.

Geological setting

During the Late Ordovician, the region corresponding to present-day Manitoulin Island was located in the northern Michigan Basin, in south-central Laurentia between 15° and 20° south latitude (see Scotese and McKerrow 1990; Cocks and Torsvik 2002). Apart from sporadic influx of fine-grained siliciclastic sediments from the Taconic Orogeny during the Edenian–early Richmondian (latest Caradoc–early Ashgill), carbonate sedimentation generally prevailed in this region during the mid to late Richmondian (mid-Ashgill). This period of carbonate deposition is represented by the Upper Member of the Georgian Bay Formation, as distinguished from the claystone-rich lithologies of the Lower Member. The Meaford Submember, the lower portion of this carbonate interval, comprises up to 15 m of argillaceous dolostones and dolomitic limestones interbedded with blue-green claystone interbeds (Fig. 2). This unit contains a relatively diverse macrofauna, similar to the mixed brachiopod-bryozoan assemblage of Holland (1996), reflecting substrate conditions below fair weather wave base, most likely corresponding to a mid-shelf, upper

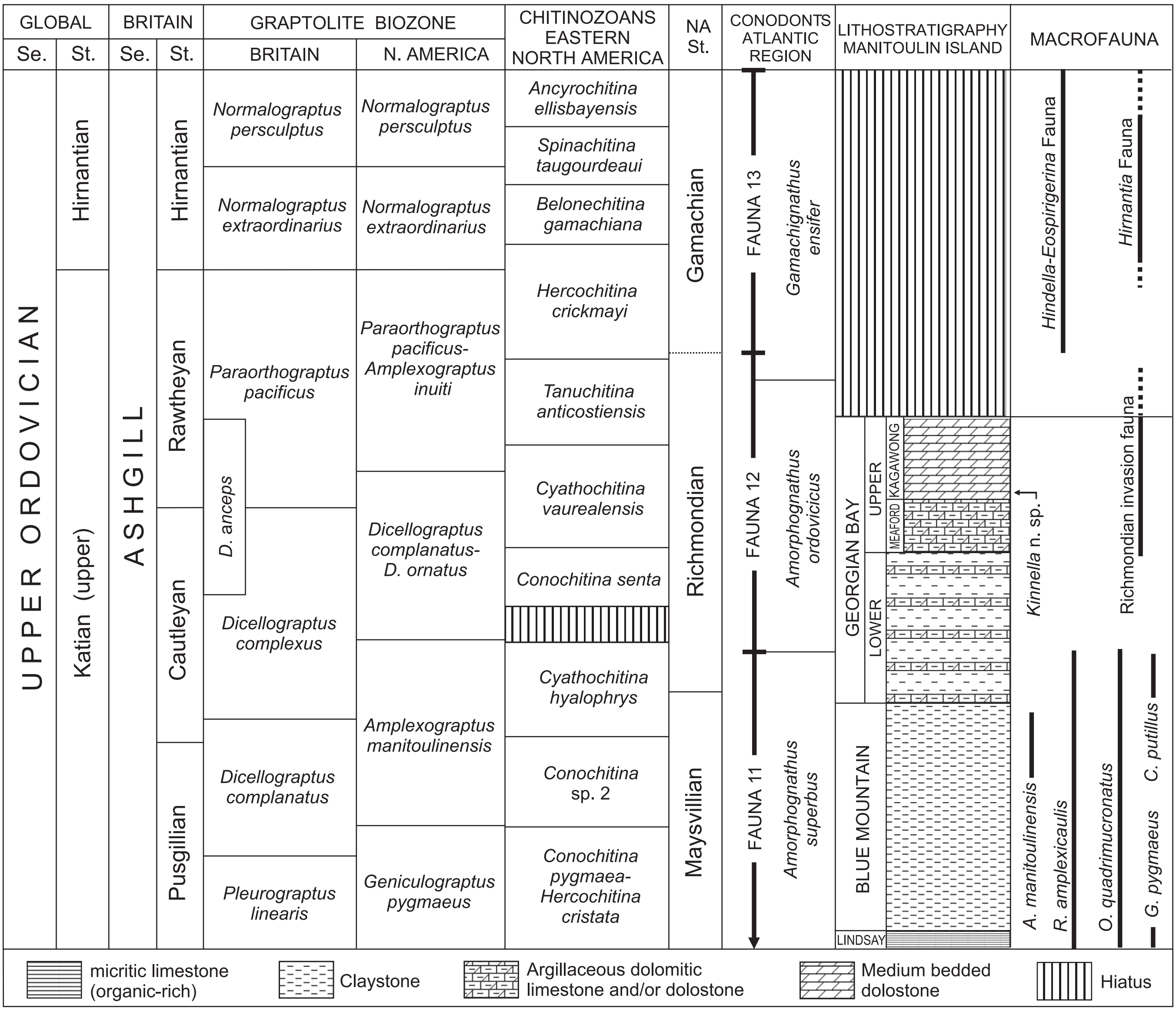

Fig. 2. Stratigraphic position of *Kinnella laurentiana* sp. nov. British graptolite zonation follows Webby, Cooper et al. (2004). North American graptolite and Atlantic faunal region conodont zonations and correlations are based on Bergström and Mitchell (1986), McCracken and Nowlan (1988), Melchin et al. (1991) and Goldman and Bergström (1997). Chitinozoan zonation from Achab (1989) and Asselin et al. (2004). Manitoulin Island graptolite species ranges from Goldman and Bergström (1997). Correlation of Pusgillian–Cautleyan and equivalent graptolite zones is based on the assumption that the *Amorphognathus superbus*–*A. ordovicicus* zonal boundary is not significantly diachronous globally. NA St., North American Stage; Se., Series; St., Stage. Graptolite genera: *A.*, *Amplexograptus*; *C.*, *Climacograptus*; *G.*, *Geniculograptus*; *O.*, *Orthograptus*; *R.*, *Rectograptus*.

BA 3 setting (see Brett et al. 1993). The overlying Kagawong Submember consists of up to 30 m of fine to medium crystalline, sparsely to moderately fossiliferous dolostone with minor claystone interbeds (Fig. 2). Basal biostromal carbonates with a relatively diverse, open marine shelly fauna dominated by corals and brachiopods (BA 2 conditions), change upward to finer grained, sparsely to moderately fossiliferous micrites of probable lagoonal (upper BA 2) origin.

Kinnella, as described herein, is known only from the lowermost part of the Kagawong Submember (Gore Bay Biostrome) (Fig. 2), in association with large, domical, cerioid colonial corals (*Favistina stellata*, *Calapoecia huronensis*, *Foerstephyllum* sp.), small solitary rugose corals (*Grewingkia* sp.), robust ramose bryozoans, thick-shelled, strongly biconvex to globular brachiopods (*Hiscobeccus capax*, *Hebertella occidentalis*, *Platystrophia* sp., and *Zygospira* sp.) and relatively small epifaunal bivalves (*Ortonella* sp., small *Ambonychia* sp.) suggesting a depositional environment within fair weather wave base (see Holland 1993, 1996).

Age of the fauna

The shelly macrofauna of the Upper Member of the Georgian Bay Formation on Manitoulin Island indicate a broad Richmondian age. Taxa characteristic of the Richmondian Stage

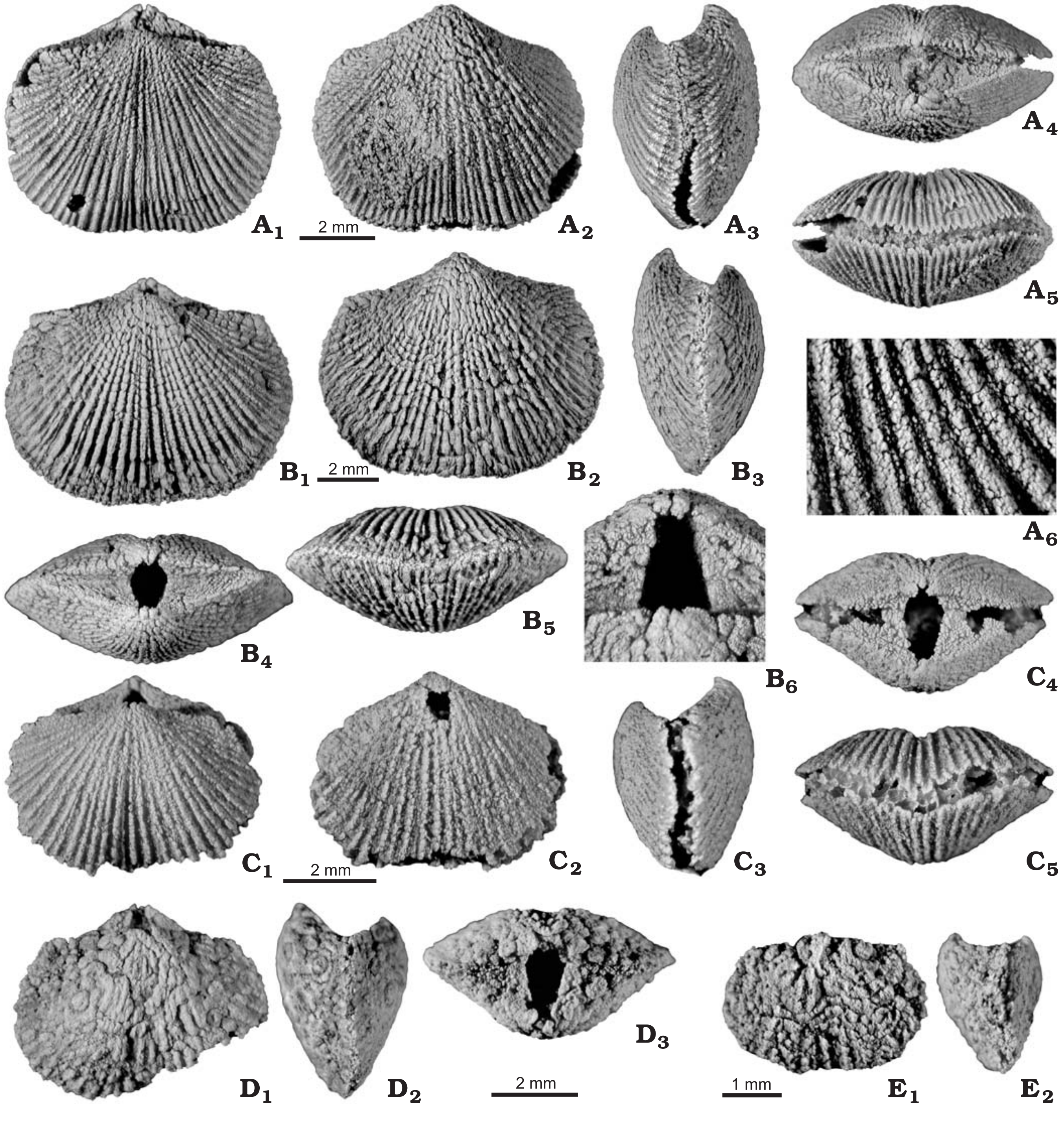

Fig. 3. Orthide brachiopod *Kinnella laurentiana* sp. nov.; Kagawong Submember, upper Georgian Bay Formation, Richmondian (mid-Ashgill), Manitoulin Island. **A**. GSC 117898, paratype, dorsal (A_1), ventral (A_2), lateral (A_3), posterior (A_4), anterior (A_5), and enlarged (A_6) costae. **B**. GSC 117899, holotype, dorsal (B_1), ventral (B_2), lateral (B_3), posterior (B_4), anterior (B_5), and enlarged (B_6) delthyrium. **C**. GSC 117900, paratype, dorsal (C_1), ventral (C_2), lateral (C_3), posterior (C_4), and anterior (C_5) views. **D**. GSC 117901, paratype, dorsal (D_1), lateral (D_2), and posterior (D_3) views of immature shell. **E**. GSC 117902, paratype, dorsal (E_1) and lateral (E_2) views of immature shell, showing nearly catacline ventral interea.

in the eastern North American midcontinent (e.g., *Glyptorthis insculpta, Catazyga headi*, *Hebertella occidentalis*, *Hiscobeccus capax*, *Grewingkia canadensis*, and *Cyclonema bilix*) appear conspicuously at, or just above, the base of the Upper Member (Foerste 1916, 1924). This appearance coincides with the major Richmondian faunal invasion of eastern North America, correlated with rocks of the lower to middle Richmondian Stage in the type area of the Cincinnatian Series (see Foerste 1924; Holland 1996; Patzkowsky and Holland 1996; Bergström 2003).

Although dominated by relatively long-ranging representatives of the midcontinent faunal region, conodonts of the

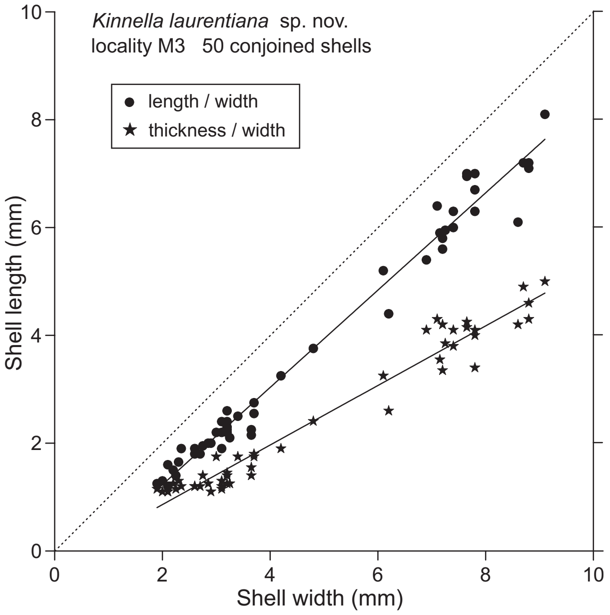

Fig. 4. Plot of measurements of 50 conjoined shells of *Kinnella laurentiana* sp. nov.; Kagawong Submember, upper Georgian Bay Formation, Richmondian (mid-Ashgill), Manitoulin Island. Note the largely isometric shell outline (consistent length/width ratio) and convexity (thickness/width ratio) with ontogeny.

Upper Member studied by Tarrant (1977), Barnes et al. (1978), and Nowlan (2001) correspond broadly to Fauna 12 of Sweet et al. (1971) (Fig. 2). The occurrence of several species of *Pseudobelodina* in the Upper Member of the Georgian Bay Formation (Nowlan 2001) is of particular biostratigraphical and palaeoecological significance. *Pseudobelodina inclinata* was identified as key member of Fauna 12 by Sweet et al. (1971). Similarly *P. vulgaris vulgaris* is commonly associated with Richmondian rocks (Fauna 12) in eastern North America, although it is also known from Edenian and Maysvillian strata of the western midcontinent (Sweet 1979). As a genus common in the Red River Faunal Province of the central and western American midcontinent, *Pseudobelodina* has been regarded as an indicator of relatively shallow, clean, warm, and slightly hypersaline waters (Sweet and Bergström 1984).

Regional conodont biostratigraphy suggests that the Upper Member of the Georgian Bay Formation is assignable to the *Amorphognathus ordovicicus* Biozone (Fig. 2; Goldman and Bergström 1997). The absence of indicators of conodont Fauna 13 of late Richmondian to Gamachian age (McCracken and Barnes 1981; McCracken and Nowlan 1988) in the Georgian Bay Formation allows only a general Richmondian age to be inferred for the Upper Member on the basis of conodonts.

The Upper Member coral fauna, including that of the Gore Bay Biostrome, is also suggestive of a general Richmondian age. The most commonly recognized coral genera (*Grewingkia*, *Favistina*, *Foerstephyllum*) are characteristic of the Richmond Province, and are clearly different from those typical of the Gamachian Edgewood Province (see Elias 1982; Webby, Elias et al. 2004). Similarly, brachiopod genera characteristic of the Upper Member fauna, most notably *Hiscobeccus* and *Zygospira*, appear to be absent in Gamachian and Hirnantian strata (Jin 2001; Harper et al. 2004).

A chitinozoan fauna recovered from the Meaford Submember (Gishler 1976) is similar to those from middle Richmondian strata of Anticosti Island (Achab 1977a, b), the Gaspé Peninsula (Martin 1980), and the Restigouche area of northern New Brunswick (Asselin et al. 2004), correlated with the *Dicellograptus complanatus* and lower *Climacograptus prominens elongatus* (= *Amplexograptus inuiti*; lower *Paraorthograptus pacificus*) graptolite zones. This indirectly supports a mid-late Richmondian age for the overlying Kagawong Submember.

These various lines of evidence point to a mid-Ashgillian (probable *Dicellograptus complanatus* Zone) age for the *Kinnella* fauna described herein.

Systematic palaeontology

Phylum Brachiopoda Duméril, 1806

Order Orthida Schuchert and Cooper, 1932

Superfamily Enteletoidea Waagen, 1884

Family Draboviidae Havlíček, 1950

Genus *Kinnella* Bergström, 1968

Type species: *Hirnantia*? *kielanae* Temple, 1965, *Dalmanitina* Beds (Hirnantian), Holy Cross Mountains, Poland.

Discussion.—In external morphology, *Kinnella* has a certain degree of resemblance to the Late Ordovician *Fascifera* Ulrich and Cooper, 1942, especially in its small, ventribiconvex shell, multicostellae, and a high, weakly curved, apsacline ventral interarea. Internally, however, the North American *Fascifera* has high, basomedially inclined brachiophore plates, which are basolaterally divergent in *Kinnella*. The delthyrium is high and trapezoidal in *Kinnella* but sharply triangular in *Fascifera*. The Manitoulin Island form of *Kinnella* described in this paper has all the diagnostic characters of *Kinnella* and is the only species currently known from pre-Hirnantian strata. In typical *Kinnella*, the ventral interarea tends to be strongly apsacline approaching catacline (Bergström 1968; Rong 1984). Among the shells described as *K. kielanae* by Lespérance and Sheehan (1976) from Percé, Québec, some ventral valves have an apsacline ventral interarea forming an angle of 60° with the commissural plane; these do not approach a catacline orientation. Consequently it is important to note that even within the type species the orientation of the ventral interarea appears to be variable. As will be discussed below, there is also considerable ontogenetic variation in the tilting angle in *Kinnella* ventral valves from Manitoulin Island.

Kinnella laurentiana sp. nov.

Figs. 3–5.

Derivation of the name: After Laurentia, the tectonic plate of North America.

Type material: Holotype, GSC 117899 (Fig. 3B), and ten figured paratypes, GSC 117898 (conjoined shell), GSC 117900–117902 (con-

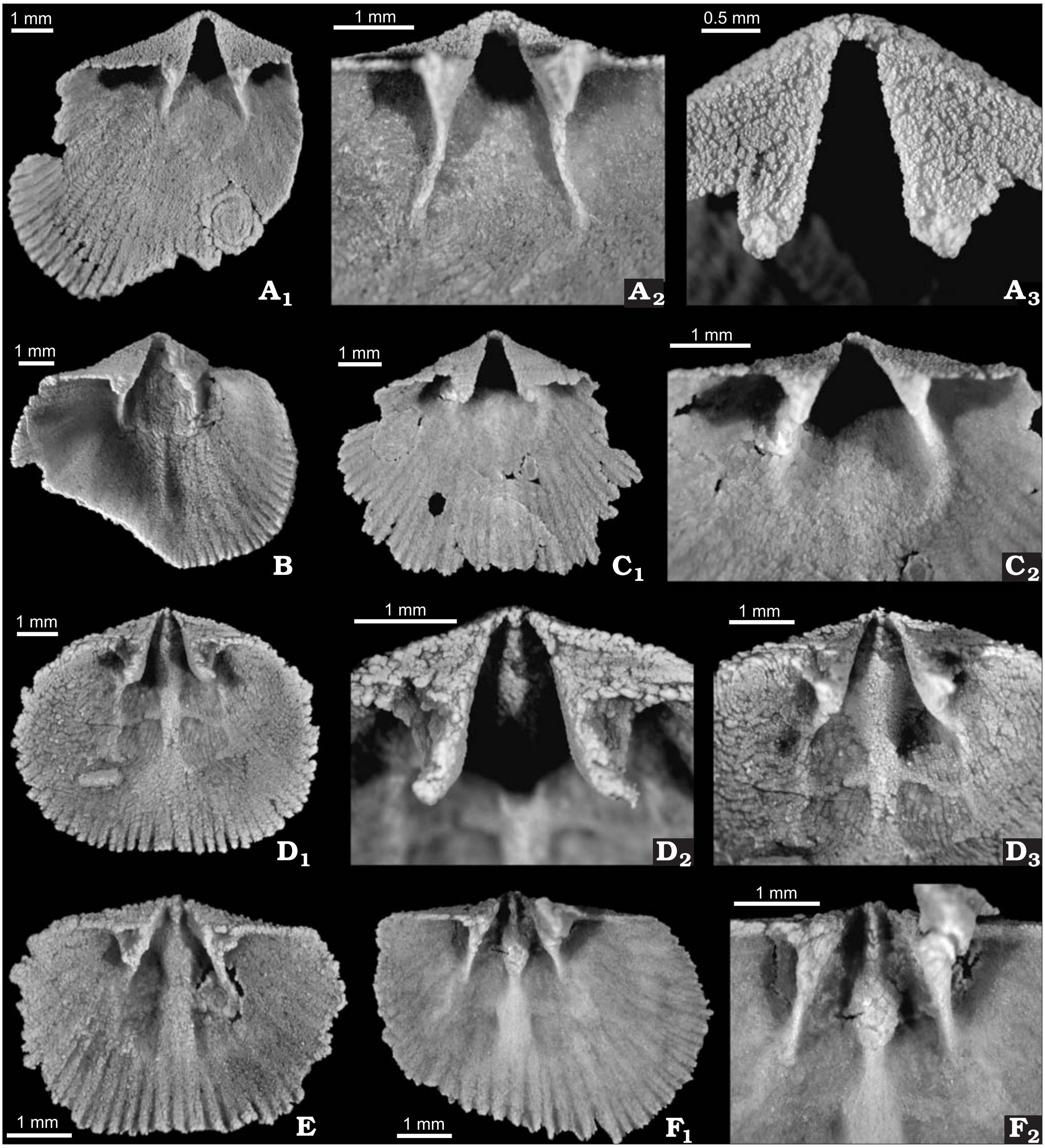

Fig. 5. Orthide brachiopod *Kinnella laurentiana* sp. nov.; Kagawong Submember, upper Georgian Bay Formation, Richmondian (mid-Ashgill), Manitoulin Island. **A**. GSC 117903, paratype, various views of interior of ventral valve (A_1) showing dental plates (A_2) and large interarea (A_3). **B**. GSC 117904, paratype, interior of ventral valve. **C**. GSC 117905, paratype, interior of ventral valve (C_1) showing dental plates and muscle field (C_2). **D**. GSC 117906, paratype, interior of dorsal valve (D_1), with details of cardinalia and adductor muscle scars (D_2 and D_3). **E**. GSC 117907, paratype, interior of dorsal valve, with relatively strong median ridge. **F**. GSC 117908, paratype, interior of dorsal valve (F_1), with crenulated, anteriorly swollen cardinal process (F_2).

joined shells; Fig. 3C–E), GSC 117903–117905 (ventral valves; Fig. 5A–C), GSC 117906–117908 (dorsal valves; Fig. 5D–F).

Type locality: Roadside section 2 km west of Kagawong, Manitoulin Island, Ontario, Canada. Coordinates: 45°54'54.5"N Latitude, 82°16' 41.7"W Longitude; UTM 0400871 easting, 5085414 northing.

Type horizon: Lower Kagawong Submember (Gore Bay Biostrome), upper Georgian Bay Formation, Richmondian (mid-Ashgill; upper Katian).

Material.—About 750 silicified specimens, mostly disarticulated valves; all from the Lower Kagawong Submember of the Georgian Bay Formation, Manitoulin Island.

Diagnosis.—Shell small, transversely subelliptical to subquadrate, subequally biconvex with moderately convex dorsal valve; ventral interarea high, apsacline (60–65° with commissual plane) in adult shells, catacline in juveniles; cardinal process swollen anteriorly in larger shells.

Description.—Shell small, transversely subelliptical to subquadrate in outline, strongly and subequally biconvex with ventral valve slightly deeper (Figs. 3A–E, 4); average length 3.76 mm (max = 8.1 mm), width 4.8 mm (max = 9.1 mm), and thickness 2.4 mm (max = 5.0 mm). Hinge line straight, about four-fifths of maximum width of shell, with rounded to obtusely angular cardinal extremities. Ventral valve with moderately convex umbo and suberect beak, lacking fold or sulcus; ventral interarea high, strongly apsacline at 60–65° angles with commissural plane; with largely planar surface becoming weakly curved in apical portion (Fig. 3A_3, B_3, C_3, D_2), catacline only in immature shells (Fig. 3E_2); delthyrium open, long, narrow, trapezoidal in outline, with two sides nearly parallel in portions near hinge line. Dorsal valve gently sulcate from umbo to anterior margin; dorsal interarea anacline, notably lower than ventral, with open notothyrium. Multicostellae fine, 18–20 per 5 mm at 5 mm arc from apex, increasing in number anteriorly by bifurcation or intercalation; capillae and fine growth lines present; coarser growth lamellae irregularly developed.

Ventral interior: Teeth knobby to wedge-shaped; dental plates strong, extending to level of hinge line or slightly beyond, divergent from each other basolaterally and anteriorly, forming lateral bounding ridges of muscle field (Fig. 5A_1, A_2, B, C_2). Muscle field subrhomboidal to cordate in outline, occupying 40% length and 28% width of valve, with low myophragm and lateral ridges on floor; anterior bounding ridge present in some specimens. Low median ridge originating from midpoint of anterior margin of muscle field, terminating shortly before anterior margin of valve (Fig. 5B). Crenulations strong around periphery of inner surface in both valves.

Dorsal interior: Hinge sockets open antero-laterally, with well-developed fulcral plates. Cardinal process blade-like, with chevron-crenulated myophore, resting directly on valve floor, with inflated anterior end in some specimens (Fig. 5D–F). Notothyrial cavity simple, lacking notothyrial platform. Low, thick myophragm continuous posteriorly with shaft of cardinal process disappearing towards anterior margin of muscle field. Dorsal adductor muscle field large, subrectangular in outline, extending anteriorly for three-fifths length of valve; anterior adductor scars separated by transverse ridge from nearly equal-sized posterior pair (Fig. 5D_1, D_3); lateral bounding ridges low but well defined.

Discussion.—The new species is assigned to *Kinnella* on the basis of its small size (rarely exceeding 7 mm in length), fine costellae, high and strongly apsacline ventral interarea, and long, narrow delthyrium with an apical callist. Internally, the crenulated cardinal process merges anteriorly into a thick median septum, and there is no notothyrial platform so that the cardinal process and the median septum are sitting directly on the valve floor. These characters, together with the large, quadrilobate dorsal adductor muscle scars, are typical of *Kinnella*. *Kinnella laurentiana* can be distinguished from the widely reported Hirnantian species, *K. kielanae*, in having a more convex dorsal valve and a less strongly apsacline ventral interarea, which typically approach catacline in the adult shells of the type species (Lespérance and Sheehan 1976; Williams and Harper 2000). In over one hundred specimens examined, there is a notable range of ontogenetic variation in the tilting angles of the ventral interarea: the immature shells tend to have a nearly catacline ventral interarea, which changes gradually to more typically apsacline in increasingly larger shells (compare Fig. 3A–D with Fig. 3E). A similar ontogenetic variation in the orientation of ventral interarea from catacline to apsacline has also been shown by Lespérance and Sheehan (1976) for *K. kielanae* from the White Head Formation of Percé, Québec. Another species of *Kinnella*, *K. medlicotti* (Reed, 1915) was recently described by Cocks and Fortey (2002) from Hirnantian strata of Burma. This species is distinguished from *K. kielanae* only by a slightly more transverse shell outline and a larger ventral interarea and may be conspecific with the type species (Cocks and Fortey 2002). These authors further suggested that the form of *Kinnella* known from South China, treated so far as *K. kielanae* (e.g., Rong 1984), more closely resembles *K. medlicotti* than *K. kielanae* as known from Europe; they consequently proposed that use of *K. medlicotti* be extended to South China. With respect to its length/width ratio, *K. laurentiana* is more similar to *K. medlicotti* than to typical *K. kielanae* (see Cocks and Fortey 2002). *K. laurentiana* can be distinguished from these other species by its commonly apsacline ventral interarea and the anteriorly inflated cardinal process identified in some specimens. Also, observation of the available material indicates that the dorsal median ridge (myophragm) is lower in *K. laurentiana* than in the type species, although it is not clear whether or not this has been partly due to the generally coarse silicification of the internal structures.

Fig. 6. Cluster analysis of *Kinnella*-bearing brachiopod faunas worldwide. Software: PAST (Hammer et al. 2001; Hammer and Harper 2005); algorithm: unweighted pair-group; Raup-Crick similarity coefficient. Refer to Appendix 1 for identification of assemblage localities, published sources and taxa employed in the analysis.

Comparison with other *Kinnella*-bearing brachiopod faunas

In this study, *Kinnella*-bearing brachiopod faunas from various regions were compiled as a binary (genus-level presence/absence) dataset, which was then subjected to a Q-mode cluster analysis using the PAST software (Hammer et al. 2001; Hammer and Harper 2005). These data were analyzed employing the unweighted pair-group average algorithm and the Raup-Crick similarity coefficient. As is shown in Fig. 6, the *Kinnella*-bearing fauna of Manitoulin Island is clearly different from the typical, Kosov Province *Hirnantia* faunas of China, Britain, Poland, the Czech Republic, Austria, Tibet, Burma, Sweden, Norway, Sardinia, northern Maine (USA), and the Gaspé Peninsula (eastern Canada). All of these, with the exception of the fauna described by Harper and Williams (2002), are of Hirnantian age (see Rong and Harper 1988; Rong et al. 2002, 2006). Most faunas of the Kosov Province cluster together at a high level of similarity (Raup-Crick similarity coefficient >0.75). The assemblage reported by Rong et al. (2006) from northern Maine, USA is unusual in this regard as it clusters with the other Kosov Province assemblages at a comparatively low level of similarity (~0.55), the latter being most likely due to the small number of genera reported in this assemblage.

Kinnella-bearing faunas of the Gorny Altai region of Siberia (Kulkov and Severgina 1987, 1989) are also shown to be highly distinct in composition from the Manitoulin Island assemblage; no genera other than *Kinnella* are common to the Siberian and Manitoulin Island faunas. The Gorny Altai assemblages contain diagnostic elements of the Kosov Province *Hirnantia* Fauna (*Cliftonia oxoplecioides*, *Eostropheodonta hirnantensis*, *Kinnella kielanae*), as well as genera characteristic of the low-latitude Edgewood Province (*Brevilamnulella*, *Eospirigerina*, *Rostricellula*) (Rong and Harper 1988), accounting for their low level of similarity (~0.21) with the typical Kosov Province faunas.

Clear dissimilarity between the Manitoulin Island assemblage and a post-extinction (Rhuddanian) fauna purportedly containing *Kinnella* (Baarli and Harper 1986) is also suggested. The latter is also shown to be highly distinct in composition from the compiled Hirnantian assemblages, as well as that of Harper and Williams (2002), lacking several of the genera common to these faunas, and including a number of novel Silurian genera, or holdover genera which were not common constituents of the typical *Hirnantia* Fauna.

Palaeobiogeographic implications of *Kinnella laurentiana*

Prior to this study, *Kinnella* was known from North America at only two localities, these being in the White Head Formation of the Percé region, Gaspé Peninsula, Québec (Lespérance and Sheehan 1976; Lespérance 1985), and in unnamed Hirnantian strata of the Penobscot River, Penobscot County, northern Maine (Rong et al. 2006). On the Gaspé Peninsula, specimens assigned to *K. kielanae* are associated with a typical Hirnantian brachiopod and trilobite fauna in calcareous mudstones comprising Unit 5 of that formation (Lespérance and Sheehan 1976; Lespérance 1985). There is no direct graptolite or conodont evidence to confirm the age of this occurrence, although its stratigraphic position lies considerably above the lowest occurrence of *Gamachignathus ensifer* and significantly below the first occurrence of diagnostic Silurian conodont taxa, most notably *Distomodus kentuckyensis* (Nowlan 1981; Lespérance 1985), thus constraining a reasonable Hirnantian age. The specific designation and precise age of the Maine occurrence of *Kinnella* are not identified by Rong et al. (2006), however, its association with key generic elements of the typical *Hirnantia* brachiopod fauna (*Hirnantia*, *Eostropheodonta*, and *Plectothyrella*), genera also present in the White Head Formation, suggests that it is also of Hirnantian age, although this carries the risk of circular reasoning. As in many other regions, these representatives of *Kinnella* occur stratigraphically above a deeper, cool-water *Foliomena* Fauna (Sheehan and Lespérance 1978; Neuman 1994; Zhan and Jin 2005), the latter appearing in strata of probable late Rawtheyan age in the Gaspé region (see Sheehan and Lespérance 1979).

These other occurrences of *Kinnella* in North America are thus consistent with the known spatial and temporal distribution of the Kosov Province *Hirnantia* Fauna (see Rong et al. 1999; Rong et al. 2002), further highlighting the significance of the species described herein.

The occurrence of *Kinnella* in Richmondian strata of the North American midcontinent points to a considerably earlier origin for the genus than known previously (see Rong and Harper 1999) and demonstrates its presence in low-latitude epicontinental settings of Laurentia by the mid-Ashgillian.

Among enteletoid orthides, *Kinnella* is morphologically most similar to *Hirnantia*, as is reflected by the initial description of the type species of *Kinnella* as a form of *Hirnantia* (Temple 1965; Marek and Havlíček 1967). In some internal structures, *Kinnella* closely resembles some older (late Darriwilian–Caradoc) representatives of the Draboviidae, most notably *Drabovia*, which also exhibits a well-developed pedicle callist (Williams and Harper 2000). Prior to the Hirnantian, *Drabovia*, and most closely allied draboviid genera were apparently confined to higher latitude Gondwanan and peri-Gondwanan terranes (Havlíček 1950, 1977, 1989; Bassett et al. 1999, 2004; Boucot et al. 2003). It is thus reasonable to assume that these draboviid orthides were primarily adapted to cooler water conditions.

The occurrence of *Kinnella* in the Richmondian strata of Manitoulin Island can be interpreted in two ways:

(1) *Kinnella* first appeared at low latitudes, possibly in relatively shallow, warmer water epicontinental environments and subsequently migrated to cooler water settings to become a common element of the *Hirnantia* Fauna. The later wide-

spread distribution of *Kinnella* in marginal or cooler water epicontinental seas within the Kosov Province suggests that we can not exclude the possibility that *Kinnella* was established in low-latitude pericratonic settings considerably before the Hirnantian. It is, however, unknown to occur in any assemblage typical of the marginal Scoto-Appalachian (late Llanvirn–early Caradoc), or *Foliomena* (early Cardoc–mid-Ashgill) faunas, although it is likely to have preferred considerably shallower and more energetic settings than those occupied by the thin-shelled, soft-substrate-adapted *Foliomena* faunas (see Rong and Harper 1988; Rong et al. 1999; Zhan and Jin, 2005). As much of the Late Ordovician epicontinental brachiopod fauna of Laurentia and other low-latitude palaeo-plates originated immediately following the early Caradoc (*Nemagraptus gracilus* Zone) transgression from marginal (Scoto-Appalachian) stocks (Jin 1999, 2001), it is possible that the origin of *Kinnella* extends back at least that far. Incomplete sampling, and/or a failure to recognize the genus among a diversity of similar orthides also can not be ruled out as possible reasons for the Richmondian first appearance of the genus. As an example, we note that this species was apparently overlooked by Foerste (1912, 1916, 1924), who conducted extensive faunal surveys of the Upper Ordovician of Manitoulin Island during the early part of the twentieth century.

(2) The appearance of *Kinnella* in the Richmondian indicates an expansion of environmental conditions favourable for cooler water faunas in response to the cooling of low-latitude oceans during the pre-Hirnantian Late Ordovician. Although the main phase of Late Ordovician glaciation is generally regarded to be confined to the Hirnantian (Brenchley et al. 1994; Brenchley 2004), a growing body of evidence suggests that relatively cool and/or glacial conditions occurred episodically during Caradoc–Ashgill times (Havlíček 1989; Frakes et al. 1992; Hannigan and Basu 1997; Dzik 1998a, 1998b; Tobin et al. 2003). Despite the lack of significant carbon or oxygen isotopic excursions in strata of Richmondian, or equivalent age (*Dicellograptus complanatus*/*D. ornatus*, lower *Paraorthograptus pacificus* zones; Brenchley et al. 1994; Berry et al. 2002), evidence of increased thermohaline circulation (see Sheehan 2001) and generally increasing $\delta^{18}O$ values (Veizer et al. 1999) in global oceans during the Late Ordovician suggests that cooler water and nutrient-enriched conditions likely became more common in low-latitude surface waters. The influence of this apparent trend on low-latitude epeiric seas is uncertain, though it undoubtedly would be affected by the level of communication between these seas and the open ocean, as well as the predominant climatic conditions at low latitudes. The persistence of normal marine conditions in the epicontinental seas of eastern North America during a significant part of the Richmondian is suggested by the relatively diverse fossil record of the Richmondian Stage in this region and the absence of significant evidence for widespread subaerial exposure or faunal restriction prior to the end of the interval (see Foerste 1916, 1924; Fox 1962, 1968; Elias 1982; Holland 1996; Goldman and Bergström 1997).

This interpretation is apparently at odds with the conclusion of Fortey and Cocks (2005) that the mid-Ashgill (Cautleyan–Rawtheyan) was an interval of global warming, as suggested by the apparent migration of faunas previously characteristic of low-latitude biogeographic provinces to mid- and high-latitude Gondwanan and peri-Gondwanan terranes at this time. Similar evidence of poleward faunal migration and higher palaeotemperatures in the high (southern) latitude Mediterranean Province is presented by Boucot et al. (2003). During this time it appears that most of the typically "cool-water" brachiopod faunas endemic to the high-latitude Mediterranean Province were augmented and possibly partially replaced by a number of brachiopod taxa previously known from low-latitude, ostensibly warm-water settings. If this does indeed reflect a prominent climatic change, and/or alteration of oceanic temperature or other variables, the presence of *Kinnella* in Richmondian strata of eastern North American may suggest that there was a contemporaneous shift of some high-latitude endemics to low latitudes. Many of the endemic Mediterranean genera (see Boucot et al. 2003) that survived the first phase of the Late Ordovician extinction (see Rong et al. 2006) returned to prominence in the Mediterranean Province during the Hirnantian glaciation, thus suggesting that if they were significantly displaced from higher latitudes during the mid-Ashgill warming event, that they continued to exist in suitable environments elsewhere. As such, the proposed warming event may have not been global in scale, but perhaps was confined solely, or largely, to mid to high southern latitudes. Mean annual temperatures in the tropics may have remained relatively stable or perhaps declined through the mid-Ashgill interval, although no precise event or mechanism leading to such changes can be identified at present.

The association of the *Hiscobeccus*–*Grewingkia* macrofauna (also known as the "Arctic Fauna") with the epicontinental carbonate facies of Laurentia, especially along its palaeoequatorial belt, during the mid-Ashgill generally indicates that these organisms were adapted to relatively warm, shallow, low turbidity and possibly oligotrophic marine environments occurring in areas removed from cooler (deeper) marginal waters and the effects of the Taconic Orogeny (see Patzkowsky and Holland 1996; Jin 2001; Fortey and Cocks 2005). On Manitoulin Island, the association of several key taxa of this epicontinental shelly fauna with *Kinnella laurentiana* suggests at least episodic oceanic cooling when a faunal mixing of cooler water taxa with low-latitude faunas was facilitated. Meter-scale lithological cyclicity as well as faunal evidence of short-lived, small-scale deepening events within the overall regressive Upper Member of the Georgian Bay Formation may be evidence of a significant climatic influence on relative sea-level through thermoeustatic, or potentially glacioeustatic mechanisms. Within this context, the relatively shallow depositional setting of basal Kagawong Submember strata bearing *Kinnella laurentiana* may point to a period of climatic cooling and relative sea level fall as they are immediately underlain and overlain by strata with faunas suggestive of slightly deeper and less turbulent marine conditions. Glacioeustatic cyclicity was earlier proposed by Copper and Grawbarger (1978) as a possible means to explain recurrent benthic successions leading to the development of coral-stromatoporoid biostromes at several levels within the Upper Member.

The appearance of *Kinnella* in Richmondian strata of eastern North America may thus represent an actual case of faunal dispersal and evolution in response to contemporary climatic and environmental changes. Marginal seas of Laurentia during the early to mid-Ashgill are likely to have been too deep to accommodate the environmental preferences (as suggested by its Hirnantian facies distribution) of *Kinnella* at this time, hence possibly explaining its occurrence in shallow epicontinental settings.

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Appendix 1

The binary dataset of *Kinnella*-bearing brachiopod faunas worldwide, used for cluster analysis in Fig. 6, is available from the authors. Below is a list of the faunal localities and the genera used in the analysis.

Kinnella-bearing localities

1. Holy Cross Mountains, Poland (Temple 1965);
2. Aber Hirnant, northern Wales (Temple 1965);
3. Hol Beck, Lake District, England (Temple 1965);
4. Bohemia, Czech Republic (Marek and Havlíček 1967);
5. Västergötland, Sweden (Bergström 1968);
6. Carnic Alps, Austria (Jaeger et al. 1975);
7. Percé, Québec, Canada (Lespérance and Sheehan 1976);
8. Penobscot County, Maine, U.S.A. (Rong et al. 2006);
9. Northern Shan States, Burma (Cocks and Fortey 2002);
10. Northern Tibet (Rong and Xu 1983);
11. Changning, southwest Sichuan, China (Rong 1979);
12. Hanjiadian, northern Guizhou, China (Rong 1979);
13. Liangfenya, northern Guizhou, China (Rong 1979, 1984);
14. Yichang, western Hubei, China (Rong 1979, 1984);
15. Yichang, western Hubei, China (Chang 1981);
16. Ganxi, northeastern Guizhou, China (Rong et al. 2002);
17. Gusong, southern Sichuan, China (Rong et al. 2002);
18. Shuanghe, southern Sichuan, China (Rong et al. 2002);
19. Shichang, northeastern Guizhou, China (Rong et al. 2002);
20. Yangliugou, northwestern Guizhou, China (Rong et al. 2002);
21. Wangjiawan, western Hubei, China (Rong et al. 2002);
22. Southwestern Sardinia (Leone et al. 1991);
23. Yewdale Beck, Lake District, England (Harper and Williams 2002);
24. Oslo Region, Norway (Brenchley and Cocks 1982);
25. Oslo Region, Norway (Baarli and Harper 1986);
26. Gorny Altai, Siberia, Russia (Kulkov and Severgina 1987);
27. Gorny Altai, Siberia, Russia (Kulkov and Severgina 1989);
28. Manitoulin Island, Ontario, Canada (present study).

Genera of *Kinnella*-bearing brachiopod faunas used in cluster analysis (row 1)

1, *Acanthocrania*; 2, *Aegiromena*; 3, *Aphanomena*; 4, *Brevilamnulella*; 5, *Casquella*; 6, *Clarkeia*; 7, *Cliftonia*; 8, *Clorinda*; 9, *Comatopoma*; 10, *Coolinia*; 11, *Cyclospira*; 12, *Dalmanella*; 13, *Dicoelosia*; 14, *Dolerorthis*; 15, *Dorytreta*; 16, *Draborthis*; 17, *Drabovia*; 18, *Dysprosorthis*; 19, *Eoplectodonta*; 20, *Eospirigerina*; 21, *Eostropheodonta*; 22, *Epitomyonia*; 23, *Fardenia*; 24, *Fascifera*; 25, *Garibaldibella*; 26, *Hebertella*; 27, *Hindella*; 28, *Hirnantia*; 29, *Hiscobeccus*; 30, *Horderleyella*; 31, *Howellites*; 32, *Idiospira*; 33, *Isorthis*; 34, *Jezercia*; 35, *Templeella*; 36, *Leganella*; 37, *Leptaena*; 38, *Leptaenopoma*; 39, *Meifodia*; 40, *Mirorthis*; 41, *Onniella*; 42, *Onychoplecia*; 43, *Orbiculoidea*; 44, *Paromalomena*; 45, *Philhedra*; 46, *Philhedrella*; 47, *Pionodema*; 48, *Platystrophia*; 49, *Plectatrypa*; 50, *Plectothyrella*; 51, *Protatrypa*; 52, *Protozyga*; 53, *Pseudopholidops*; 54, *Rafinesquina*; 55, *Ravozetina*; 56, *Reuschella*; 57, *Rostricellula*; 58, *Salopina*; 59, *Sanxiella*; 60, *Schizonema*; 61, *Skenidioides*; 62, *Sowerbyella*; 63, *Sphenotreta*; 64, *Stegerhynchus*; 65, *Streptis*; 66, *Stricklandia*; 67, *Toxorthis*; 68, *Triplesia*; 69, *Trucizetina*; 70, *Zygospira*; 71, *Zygospiraella*.