OSTRACODES ACROSS THE IAPETUS OCEAN

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ABSTRACT. A pilot study comparing ostracode faunas from the North American and European plates dispels the notion that Ordovician ostracodes show strict endemicity. Problems addressed include: how some ostracodes managed to cross the Ordovician Iapetus Ocean estimated at 3,000 + km wide; and why some of their ostracode counterparts in the Silurian show provinciality? It is concluded that, from the point of view of ostracode dispersal, opposing Ordovician plates may have been in closer effective geographical proximity than hitherto supposed. Ostracodes recovered only slowly and with general provincial aspect from global sea level changes at the Ordovician–Silurian boundary.

Ostracode distributions support other biogeographic evidence that Tornquist's Sea, the ocean between the Gondwanan plate (containing southern Britain) and Baltica, had contracted by mid to late Ordovician and that the Rheic Ocean, separating northern and southern Europe, was developing during the Silurian. Much more work on Lower Palaeozoic ostracodes is needed to test these findings further.

MOST of present day Europe and North America were separated by an ocean during the early Palaeozoic. Wilson's (1966) idea that the 'proto-Atlantic' had opened and closed again during the Cambrian to Silurian has been amplified in many accounts which document sedimentological, structural, and tectonic evidence for what has been termed the Iapetus Ocean (e.g. Dewey 1969; Phillips *et al.* 1976; Mitchell 1984). Palaeontologists have independently tested for the existence and distance apart of the plates by comparing Lower Palaeozoic faunas and floras from both sides of the presumed ocean, and assessing their relative provincial or cosmopolitan nature (e.g. Spjeldnaes 1978). Faunal evidence relating to continental separation has been elaborated mainly using trilobites (e.g. Whittington and Hughes 1972; Fortey 1975), brachiopods (Williams 1973, 1976), and graptolites (Skevington 1978). Some microfossil groups (e.g. conodonts; Fortey and Barnes 1977) have been similarly employed but ostracodes have been neglected in this respect.

There is no recognized Lower Palaeozoic equivalent of the ostracode fauna of the later (Tertiary–Recent) deep-sea psychrosphere. Thus, no Lower Palaeozoic (benthic) ostracodes can be regarded as diagnostically 'oceanic'. However, ostracode endemicity can be used as a good independent test for the presence of an ocean recognized from other geological and faunal evidence. Ordovician ostracodes have previously been assumed to be endemic across the Iapetus Ocean: in a paper which provided the standard reference model for progressive faunal migration across the Iapetus Ocean, McKerrow and Cocks (1976, fig. 1) charted ostracodes as the last major animal group, apart from freshwater fish, to migrate (in the middle Silurian) across the former oceanic barrier.

The present paper represents a pilot study to assess the possible occurrence of generic or species level links between pertinent ostracode faunas of the North American and European plates, particularly during Ordovician times, and also to assess what implications such possible links may have for palaeogeography and for the palaeozoology of Lower Palaeozoic Ostracoda. Supporting the model of development of the Iapetus Ocean based on structural and allied evidence (Phillips *et al.* 1976), distributional patterns of trilobites and brachiopods indicate that the discrete lower Ordovician faunal provinces, which help define each plate, had by Caradoc–Ashgill times broken down as the ocean narrowed. Ostracode faunal links between the two plates are herein shown to occur and increase throughout the Ordovician. It is concluded that, bearing in mind the possible dispersal capabilities of Ordovician ostracodes, opposing Ordovician plates may have been in closer effective geographical proximity than hitherto supposed.

According to recent palaeogeographic reconstructions based on facies and faunal analysis (Cocks and Fortey 1982, figs. 2, 3; see text-fig. 1 herein), during the Arenig–early Llanvirn a North American continent straddled the equator, while Baltic and Gondwanan continents were positioned at southerly, relatively temperate and high latitudes respectively. North America included Britain north of the Lake District, Spitzbergen, Greenland, and western Newfoundland, but excluded parts of the present day American Atlantic seaboard. The Baltic continent extended from Scandinavia eastwards to parts of the Russian platform. Gondwana included southern Britain, Africa, South America, Iberia, Bohemia, and eastern Newfoundland. Tornquist's Sea, the proposed ocean (Cocks and Fortey 1982) separating the Baltic and Gondwanan continents, is thought to have closed during mid to late Ordovician times, thus creating a latitudinally more continuous southern continental margin to the Iapetus Ocean. Cocks and Fortey (1982) also document mid to late Silurian faunal evidence supporting the presence of a widening Rheic Ocean between the latter southern continental area and Gondwana–southern Europe (including France, Iberia, and Bohemia) further south.

SILURIAN OSTRACODE FAUNAS OF THE NORTH ATLANTIC REGION

Unusually for Silurian invertebrates, a barrier to geographical dispersal of many characteristic ostracodes apparently still existed along the site of the remnant Iapetus Ocean. Late Silurian (Ludlow–Přídolí) ostracode faunas of the European plate indicate widespread faunal links, particularly in the distribution of kloedeniine beyrichiaceans (Martinsson 1963, 1965, 1967, 1970, 1977; Siveter 1978b). Combinations of the genera *Kloedenia*, *Londinia*, and *Frostiella*, and concomitant beyrichiine and amphitoxotidine taxa define a late Silurian faunal region incorporating parts of Maritime Canada and New England (eastern Maine, southern New Brunswick, eastern Nova Scotia), southern Britain including the Lake District, Scania, subsurface rocks in the Baltic and Poland and extending into Podolia, Ukrainian SSR. Corresponding faunas on the North American plate (Lundin 1971; Berdan 1983) are mostly different, being rare in ostracodes with strong 'Baltic' affinities. Thus, a parallel 'Appalachian belt' is traceable from westernmost Virginia to Gaspé and the Silurian faunas of Anticosti Island, Canada (Berdan 1970; Copeland 1977a; Copeland and Berdan 1977). This belt has an essentially endemic beyrichiacean fauna (Copeland 1980) characterized, for example, by early Silurian zygobolbines and a later Silurian–early Devonian 'false *Kloedenia*' fauna. Silurian faunas from central Europe (Czechoslovakia), dominated by non-palaeocopes (see Bouček 1936), are largely different again from those of northern Europe and eastern North America, and thus could support the notion of a second more southerly barrier (the Rheic Ocean) hindering the dispersal of invertebrates.

These three ostracode regions are broadly defined, largely on the occurrence and type of beyrichiaceans present (a distinctive group of shallow-water benthic ostracodes), and are conspicuous during the late Silurian. Concurring with the faunal migrational patterns proposed by McKerrow and Cocks (1976), Cocks and Fortey (1982, p. 474) concluded that in the Silurian, 'The assumption, from faunal grounds alone, that there was still a Iapetus Ocean is based on continued provinciality of the thelodont fish and ostracods'. This seemed to confirm the migrational pattern one might expect of ostracodes from a knowledge of the life history of extant forms, which lack pelagic larvae.

The regions inevitably have some ostracode genera in common. For example, *Beyrichia*, *Craspedobolbina*, and *Aechmina* are also known from the early Silurian sequence of Anticosti (Copeland 1974a, 1982a). In Britain, where remnants of the North American and European plates are sutured, the rare ostracode species known from the Silurian of Scotland are endemic, although some of the genera (e.g. *Beyrichia*, *Craspedobolbina*) are also known from the prolific faunas of southern Britain (Siveter 1978b). Further afield, other 'European'–'North American' Silurian ostracode contacts are more difficult to explain palaeogeographically, such as those few (pelagic?) podocopid genera from Bohemia and Soviet Asia which are also recorded from the mid to late Silurian of north-western Canada (Copeland 1977b). This part of Canada belongs to the late Silurian–Devonian Cordilleran ostracode province extending from Nevada to Alaska (Berdan 1983)
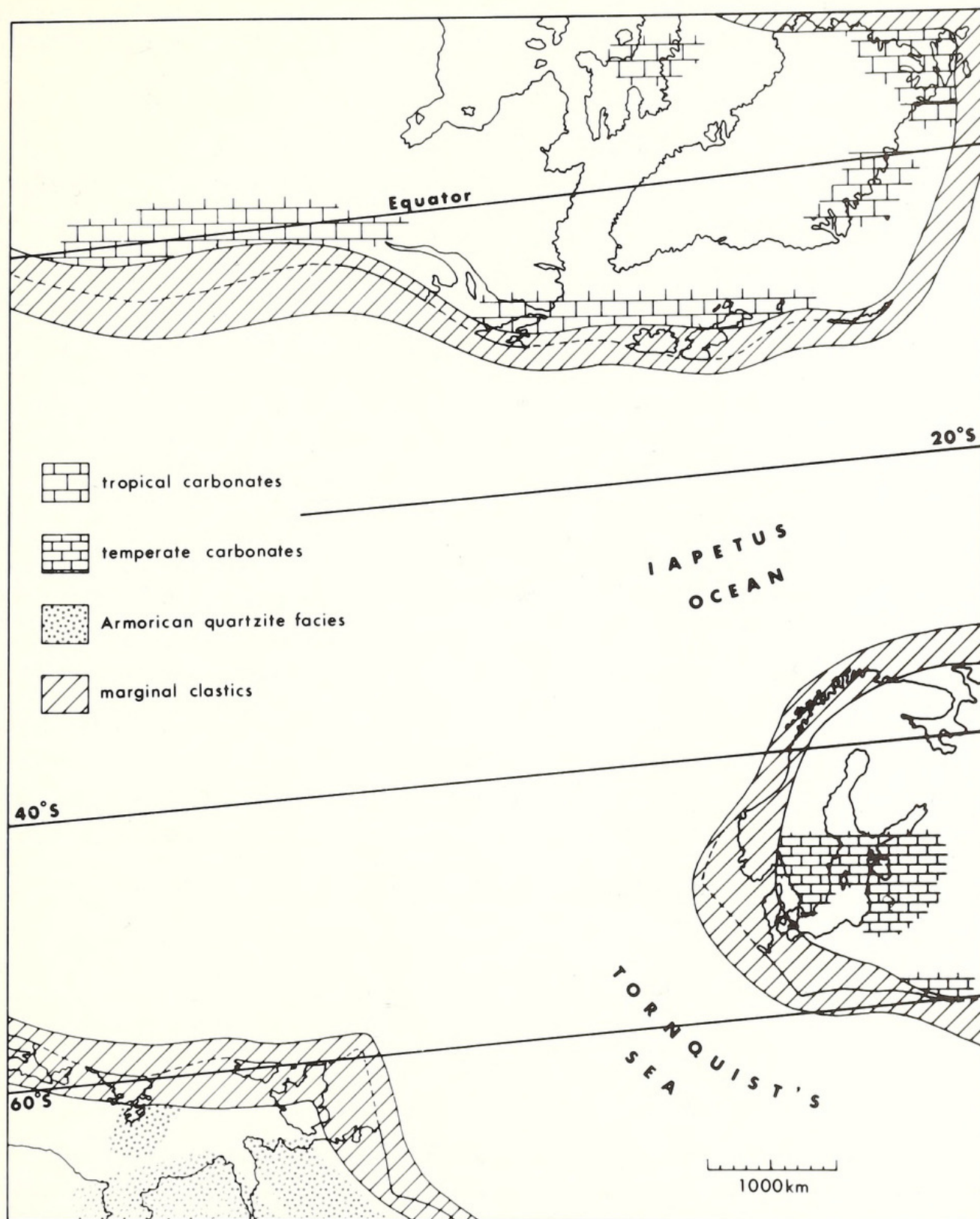
TEXT-FIG. 1. Palaeogeography and chief sedimentary facies of the area surrounding Britain in Arenig times (from Cocks and Fortey 1982).

which, although on the opposite side of the North American plate to the western margin of the Iapetus Ocean, was nevertheless capable of recruiting a few north 'European' type beyrichiacean genera in addition to central European podocopids.

OSTRACODES AS INDICATORS OF ENVIRONMENT

Studies of the life cycle and ecology of modern species (for example Elofson's (1941) classic paper on marine forms from Sweden) indicate that benthic ostracodes have no known pelagic larval stage and that ontogeny normally proceeds within a single biotope. Unaided dispersal across deep oceanic barriers would logically be a formidable task for benthic ostracodes, which generally live on, or sometimes burrow into, the substrate. Although some ostracode groups such as the Myodocopida are pelagic, the overwhelming number of both living and fossil marine forms have, or are thought to have had, a benthic mode of life. The vast majority of extant marine ostracodes live in the typically high diversity littoral and shallow marine zones. By contrast, the present day deep-ocean (psychrospheric) benthic ostracode faunas (those living at depths of about 500–5000 m) are global and cosmopolitan in distribution but relatively poorly diverse (Benson and Sylvester-Bradley 1971; Benson 1979). The junction between the psychrosphere and the shallower, warmer 'thermosphere' represents a fundamental biological frontier (Hessler and Saunders 1967)—an environmental barrier which, if breached, induces amongst ostracodes skeletal and diversity changes in response to the new stresses imposed (Benson 1975c, 1981).

Ostracodes can be good palaeoenvironmental indicators, particularly in post-Palaeozoic rocks where closer taxonomic correlation with modern groups facilitates easier ecological interpretation than for Palaeozoic forms. Ostracodes are opportunistic colonizers, occurring in marine, brackish, freshwater, and even terrestrial environments. Unlike the plankton, extant benthic ostracodes are affected by such environmental factors as the nature of the substrate (Elofson 1941). However, salinity and depth-related factors, such as bottom-water temperatures, exert the most significant control on their overall distribution. As Benson elegantly demonstrated in his studies of Tethys and its Messinian salinity crisis (1972, 1973, 1975a, 1976), and of the early Tertiary origin of the psychrosphere (1975b), the development of a sedimentary basin or the evolution of oceanic systems can be independently charted using ostracode faunal evidence. Ostracodes—often facies controlled—have the capacity to crawl into or out of basins as changing geological and environmental controls dictate. The history of Lower Palaeozoic ostracodes is presumably controlled in like fashion and would similarly betray major events such as the relative movements of plates.

OCCURRENCE OF EUROPEAN AND NORTH AMERICAN ORDOVICIAN OSTRACODES

The occurrence of described Ordovician ostracode faunas is shown in text-figs. 2 and 3. Ostracodes are known from much of Scandinavia, with important faunas from the lower Ordovician of the Siljan district (Hessland 1949) and the Oslo region (Henningsmoen 1954a); from the middle Ordovician of Jämtland and Tvären (Thorslund 1940), central Sweden (Jaanusson 1957), and the Oslo region (Henningsmoen 1953); and from the upper Ordovician of Västergotland (Henningsmoen 1948), the Oslo region (Henningsmoen 1954b), and Scania (Troedsson 1918; Schallreuter 1980). Sarv (e.g. 1959, 1963) has described Estonian Ordovician ostracodes and Schallreuter (1983; full bibliography) has extensively documented faunas from Baltoscandian erratic boulders. Faunas described from eastern Europe embrace the middle and upper Ordovician of Latvia and Lithuania (Gailīte in Ulst et al. 1982; Sidaravičiené 1971, 1975) together with records from the Leningrad region (Männil 1963), Volhyn (Krandievsky 1975), and Podolia (Krandievsky 1969). In central Europe ostracodes are recorded from nearly all Ordovician stages in Bohemia, the late Ordovician of Thuringia, and a borehole in Pomerania (Schmidt 1941; Blumenstengel 1965; Knüpfer 1968; Přibyl 1979).

Ostracodes occur in many Ordovician areas in Britain; Siveter (1978a) has reviewed all known
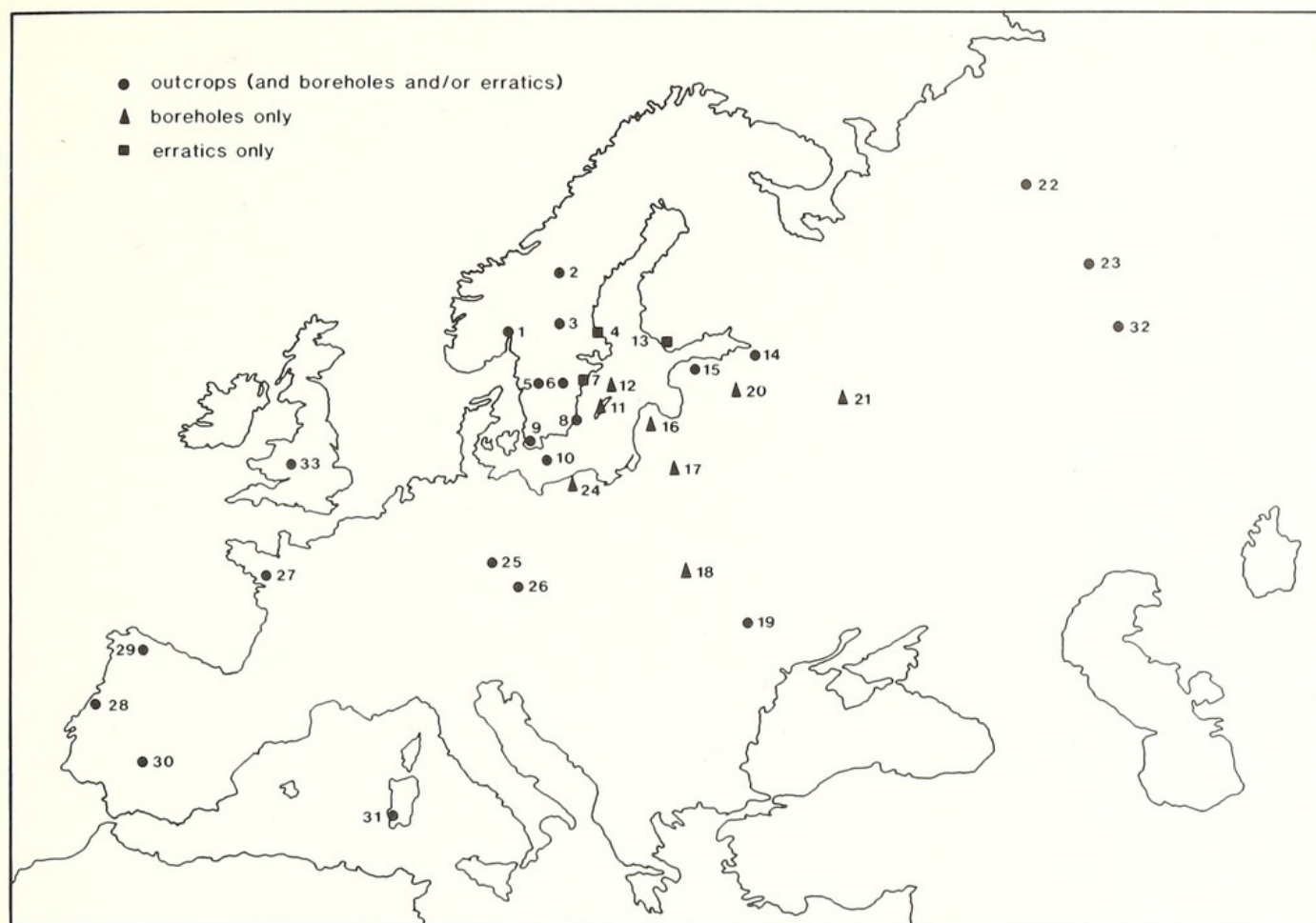
TEXT-FIG. 2. Occurrence and key papers of the main Ordovician ostracode faunas from Europe: 1, Oslo Region (Henningsmoen 1953, 1954a, b; Qvale 1980); 2, Jämtland (Thorslund 1940); 3, Siljan district (Hessland 1949; Jaanusson 1957); 4, South Bothnian area (Jaanusson 1957); 5, Västergotland (Henningsmoen 1948; Jaanusson 1957); 6, Östergotland (Jaanusson 1957); 7, Tvären area (Thorslund 1940; Jaanusson 1957); 8, Öland (Jaanusson 1957; Schallreuter 1977c); 9, Scania (Troedsson 1918; Schallreuter 1980); 10, Bornholm (Poulson 1978); 11, Gotland and Baltic erratics in general (e.g. see Schallreuter 1983, and references therein); 12, Gotska Sandön (Jaanusson 1966); 13, Nyland (Martinsson 1956); 14, Leningrad district (Männil 1963); 15, Estonia (Sarv 1959, 1963); 16, Latvia (Gailīte *in* Ulst *et al.* 1982); 17, Lithuania (Sidaravičiené 1971, 1975); 18, Volyn (Krandievsky 1975); 19, Podolia (Krandievsky 1969); 20, Pskov district (Neckaja 1973); 21, Moscow syneclise (Prokofiev and Kuznetzov 1982); 22, Pečorskian Urals (Zenkova 1977); 23, Central Urals (Peršina *et al.* 1971); 24, Pomerania (Bednarczyk 1974); 25, Thuringia (Knüpfer 1968); 26, Bohemia (Přibyl 1979); 27, Armoricain Massif (Vannier 1984); 28, Portugal (Vannier 1984); 29, Cantabrian Mountains (Bassler and Kellett 1934); 30, Almaden (Bassler and Kellett 1934); 31, Sardinia (Bassler and Kellett 1934); 32, Central Urals (Varganov *et al.* 1970); 33, Great Britain (Siveter 1978a, 1982b, c, 1983; Jones and Siveter 1983; Schallreuter and Siveter 1983a).

faunal associations and revised key taxa. Vannier (1984) has recently provided comprehensive faunal records from the Armoricain Massif, France, and a comparison with Ordovician ostracodes from Iberia.

The better known faunas from the North American plate include those from Oklahoma (Harris 1957), Kentucky (Warshauer and Berdan 1982), Virginia (Kraft 1962), Michigan (Kesling 1960; Kesling *et al.* 1962), Missouri (Keenan 1951), Iowa and Ontario (Kay 1934, 1940), Minnesota and Iowa (Swain *et al.* 1961; Burr and Swain 1965), and various eastern states (e.g. Swain 1957, 1962). Many faunas, particularly of middle and upper Ordovician age, have been described from Canada by Copeland (e.g. 1962, 1965, 1966, 1970, 1973, 1974b, 1977a, b, c, 1978, 1982b, 1983). Unrevised faunas
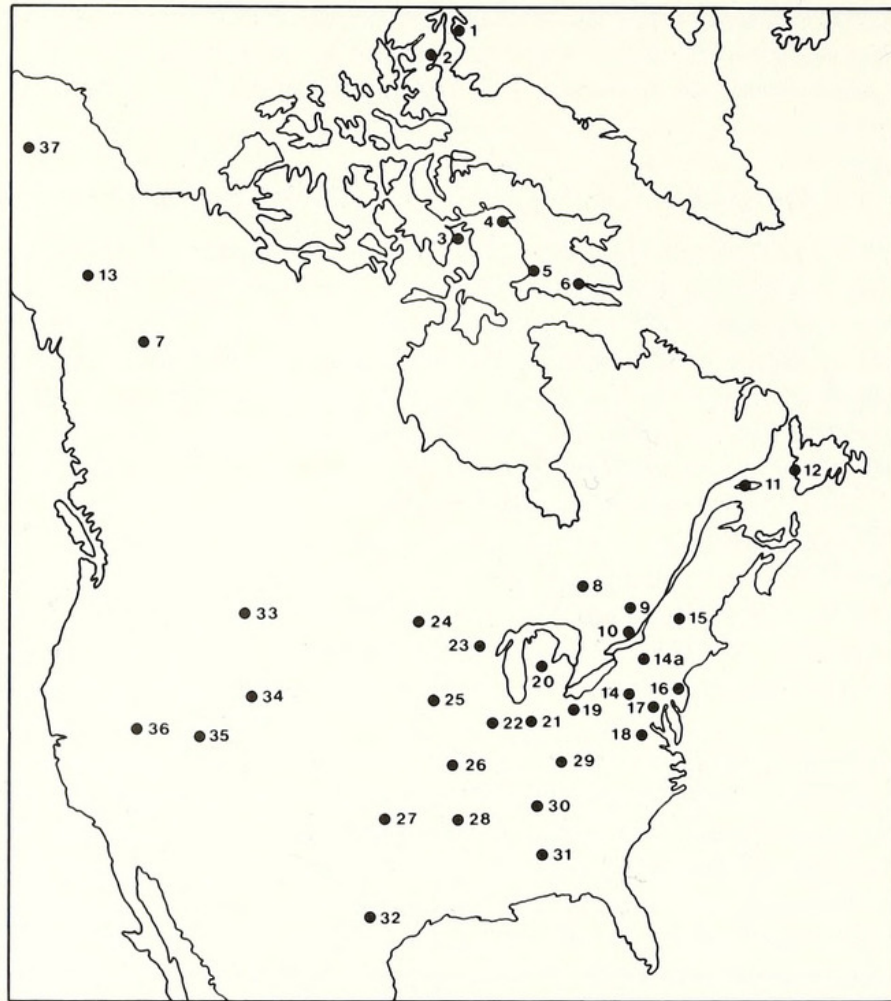
TEXT-FIG. 3. Occurrence and key papers of the main Ordovician ostracode faunas from United States, Canada, and Greenland. 1, Greenland (Teichert 1937a, b); 2, Ellesmere Island (Teichert 1937a, b); 3-6, Melville Peninsula and Baffin Island (Copeland 1977c); 7, District of McKenzie (Copeland 1974b, 1977b, 1982b); 8, Lake Timiskaming and vicinity (Copeland 1965); 9, Ottawa Valley (Copeland in Steele and Sinclair 1971); 10, Napanee, Ontario (Copeland 1962); 11, Anticosti Island (Copeland 1970, 1973); 12, Newfoundland (Copeland and Bolton 1977; Whittington and Kindle 1963); 13, Yukon (Copeland 1966, 1977b, 1978); 14, 14a, Pennsylvania and New York (Swain 1957, 1962); 15, Vermont (Creath and Shaw 1966); 16, 17, New Jersey and Maryland (Bassler and Kellett 1934); 18, Virginia (Kraft 1962); 19, Ohio (Warshauer 1975; Guber 1971); 20, Michigan (Kesling 1960; Kesling et al. 1962); 21, Indiana (Guber 1971); 22, Illinois (Bassler and Kellett 1934); 23, Wisconsin (Kay 1940); 24, Minnesota (Burr and Swain 1965; Swain et al. 1961); 25, Iowa (Burr and Swain 1965); 26, Missouri (Keenan 1951); 27, Oklahoma (Harris 1957); 28, Arkansas (Harris 1957); 29, Kentucky (Warshauer and Berdan 1982); 30, 31, Tennessee and Alabama (Bassler and Kellett 1934); 32, 33, Texas and Montana (Harris 1957); 34, Wyoming (Guber and Jaanusson 1964; Berdan 1976); 35, 36, Utah and Nevada (Berdan 1976); 37, Alaska (Copeland 1983).

occur in Greenland (Teichert 1937b) and Scotland (see Siveter 1978a), and ostracodes are also known to occur in the Arenig of Spitsbergen (Fortey 1975).

AFFINITIES BETWEEN EUROPEAN AND NORTH AMERICAN ORDOVICIAN OSTRACODES

Ordovician ostracodes have previously been assumed to be endemic across the North Atlantic region (McKerrow and Cocks 1976; Cocks and Fortey 1982), but the evidence indicates that this is not the case.

Rader (1965), Copeland (1977a, p. 5; 1978, p. 97; 1981, p. 185; 1983), Copeland and Berdan (1977, p. 22), Swain (1977, p. 39), Siveter (1978a), and Schallreuter and Siveter (1982, 1983b) indicate some Ordovician genera common to Europe and North America but no comprehensive comparison of Ordovician faunas from opposite sides of the Iapetus Ocean has been made, partly because of inherent difficulties. Most Ordovician faunas are incompletely known and taxonomic revision is required for several major faunas, especially those described from North America. In general, early Ordovician ostracode faunas are poorly represented or are less well documented than those of the middle and late Ordovician. In addition, within the Palaeocopa, homeomorphy, misidentification, and classificatory difficulties are widespread. Nevertheless, as Ordovician ostracodes are documented from virtually all North American states and relevant western European countries, a faunal comparison is possible.

Plates 68–70 illustrate just a few of the Ordovician ostracode genera common to two or more relevant continents. They embrace a wide variety of both palaeocopes (Pls. 68, 70) and non-palaeocopes such as Eridostraca (Pl. 69, figs. 1, 2), Metacopa (Pl. 69, figs. 3, 4), Leiocopa (Pl. 69, figs. 5, 6), Binodicopa (Pl. 69, figs. 7, 8), and Leperditiocopa (Pl. 69, figs. 9, 10). Taxonomic revision and improved documentation (of, for example, British faunas) will undoubtedly produce an extended list of cosmopolitan genera (and possibly some conspecific taxa) from opposite sides of the Iapetus Ocean.

Earliest contacts

Ostracode faunas of the North American and European plates reveal elements in common from at least the later part of early Ordovician times. *Eobromidella* provides an early link, occurring in the lower Ordovician of Sweden (Hessland 1949) and the Tulip Creek Formation (early Champlanian), Simpson Group of Oklahoma (Harris 1957); differences between the two forms appear minimal (Pl. 68, figs. 5, 6). This early ostracode contact across the Iapetus Ocean confirms the migrational pattern defined from palaeogeography: an equatorial North America opposed a southerly, approaching Baltica, with the Gondwanan continent further to the south beyond a contracting Tornquist Sea.

Other initial links would possibly be recognized if early Ordovician faunas were better known, particularly from North America. Moreover, compared with the Scandinavian limestone-and-shale successions in which Ordovician palaeocopes flourished from Arenig to Ashgill, known British faunas are notably deficient in the Arenig and early Llanvirn. For instance, the oldest known ostracode faunas of significance from Wales and the Welsh Borderland are from the Llandeilo of South Wales (Siveter 1978a). In the strongly contrasted facies of the British Ordovician, representative ostracode assemblages belong mostly to the shelly associations and not to the alternative basin facies; it seems a valid generalization to group Ordovician ostracodes with trilobites and brachiopods as shelf-sea benthos. It may be significant, therefore, that British ostracode faunas largely come from post-Llanvirn sequences when the contrast between shelly and graptolitic facies was strongest, and lithologies similar to 'Llandeilo Flags' prevailed.

Middle Ordovician

Most of the genera with supposed European affinities mentioned by Swain (1962, 1977) we consider misidentified. Nevertheless, in the middle Ordovician clearly increased affinities exist between opposing Iapetus Ocean ostracode faunas, presumably reflecting a closer proximity of plates than in earlier times. Many middle Ordovician ostracode genera are common to both North American and European plates; there is ample evidence also of contemporaneous ostracode contact between Baltica and part of the old Gondwanan continent, as represented by southern Britain. The notion that Gondwana moved north, so that Tornquist's Sea had virtually ceased to exist by mid to late Ordovician (Cocks and Fortey 1982), is corroborated in as much as any remnant of this ocean evidently failed to provide an effective barrier to ostracode dispersal. Whittington and Hughes (1972) and Williams (1973, 1976) showed that, by the late Caradoc, certain trilobite and brachiopod faunas of southern Britain and Scandinavia respectively were very similar; generic links between the ostracode faunas of the two areas, and between Britain and North America, can be traced somewhat

earlier to the Llandeilo Series of Wales. Additionally, the presence in the Caradoc and possibly the Ashgill of southern Britain (Siveter 1978a, pl. 3, fig. 5 and p. 46 respectively) of the Bohemian genus *Crescentilla* suggests that, unless the ostracode was pelagic, the postulated developing Rheic Ocean was not yet a formidable obstacle to migration. Obviously many middle Ordovician ostracode genera are endemic to one particular plate, but the fact that ostracode faunal links between the plates were firmly established by mid Ordovician is also clear and requires explanation.

Homeokiesowia, Vittella, Klimphores, Pseudulrichia, and *Tallinnellina* are amongst many ostracode genera occurring in the Llandeilo Series of South Wales and the middle Ordovician of Baltoscandia (Siveter 1978a, 1982b, 1983; Schallreuter and Siveter 1983a). For example, the Llandeilo material includes a form close to *Pseudulrichia bucera*, a species recorded from middle Ordovician Backsteinkalk boulders of North Germany and Gotland and from the higher part of the Idavere Stage (C$_3$) (= early Caradoc) in the Pskov district, Russia (Siveter 1978a). *Cryptophyllus* (Pl. 69, figs. 1, 2) is one of the rare ostracodes to show moult retention and occurs as far afield as the Llandeilo Series of South Wales (Siveter 1978a), the Öjlemyrflint erratics of the Baltic (Schallreuter 1977a), the early to mid Ordovician of Oklahoma (Harris 1957), and the Whiterockian Sunblood Formation of north-western Canada (Copeland 1978). *Ceratopsis* is equally as distinctive morphologically and characteristic of mid to late Ordovician sequences in the United States (e.g. Kentucky: Warshauer and Berdan 1982; Ohio: Warshauer 1975) and north-western and eastern Canada (Copeland 1974b, 1977a); it is represented by *C. britannica, C. duftonensis,* and undescribed species variously from the

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EXPLANATION OF PLATE 68

Palaeocopes from the lower and middle Ordovician of both sides of the Iapetus Ocean (*left* North America, *right* Europe).

Fig. 1. *Platybolbina (Rimabolbina) omphalota* Kesling, 1960, middle Ordovician (Bony Falls Limestone, Blackriverian), Bony Falls on the Escanaba River, Deltay County, Michigan, U.S.A.; right valve (holotype, UMMP 37355), × 34 (from Kesling 1960, pl. 8, fig. 4 *left*).

Fig. 2. *P. (Rimabolbina) rima* Schallreuter, 1964, middle Ordovician (Skagen Formation, Upper Viruan), Backsteinkalk erratic boulder (no. Sta1, 1B1 type), Staberhuk, Isle of Fehmarn (Baltic Sea), Germany; right valve (GPIMH 2717), × 47.

Fig. 3. *Hesperidella michiganensis* Kesling, Hall and Melik, 1962, same bed and locality as fig. 1; immature female right valve (paratype, UMMP 37225), × 87 (from Kesling *et al.* 1962, pl. 2, fig. 2 *left*).

Fig. 4. *H. esthonica* (Bonnema, 1909), same boulder as fig. 2; tecnomorphic right valve (GPIMH 2718), × 48.

Fig. 5. *Laccochilina [Eobromidella] eurychilinoides* (Harris, 1957), middle Ordovician (Tulip Creek horizon, Blackriverian), Sycamore Creek Simpson section, Oklahoma, U.S.A.; left valve (holotype, Museum of Comparative Zoology, Harvard University, Boston, no. 4631), × 29 (from Harris 1957, pl. 8, fig. 1a).

Fig. 6. *L. dorsoplicata* Hessland, 1949, lower Ordovician (Upper Oelandian, Kundan), Silverberg II, Eastern Siljan District, Dalecarlia, Sweden; right valve (holotype, Museum of the Palaeontological Institute, University of Uppsala, no. ar.os.398), × 42 (from Hessland 1949, pl. 6, fig. 6).

Fig. 7. *Hithis colonus* Schallreuter and Siveter, 1982, middle Ordovician (lower part of Edinburg Formation), section in field on south side of road, 0·2 km south-east of Strasburg Junction, just west of Strasburg, Shenandoah County, Virginia, U.S.A.; female right valve (paratype, GPIMH 2675; valve tilted 10°), × 45.

Fig. 8. *H. hithis* Schallreuter, 1964, middle Ordovician (Skagen Formation, Upper Viruan), Backsteinkalk erratic boulder (no. 1B16, 1B1 type), beach at Dornbusch, Isle of Hiddensee (Baltic Sea), Germany; female right valve (holotype, SGWG 3/3; Schallreuter 1964b, pl. 12, fig. 2), × 80.

Fig. 9. *Hippula (Hippula) varicata* (Harris, 1957), middle Ordovician (Lower Esbataottine Formation, Chazyan), Sunblood Mountain, southwestern District of Mackenzie, Canada; female right valve (GSC 49378), × 67 (from Copeland 1982b, pl. 1, fig. 2).

Fig. 10. *H. (H.) latonoda* (Schallreuter, 1964), middle Ordovician (Skagen Formation, Upper Viruan), Backsteinkalk erratic boulder (no. 1B4, 1B1 type), beach at Dornbusch, Isle of Hiddensee (Baltic Sea), Germany; female right valve (holotype, SGWG 2/3; Schallreuter 1964a, pl. 10, fig. 1), × 60.
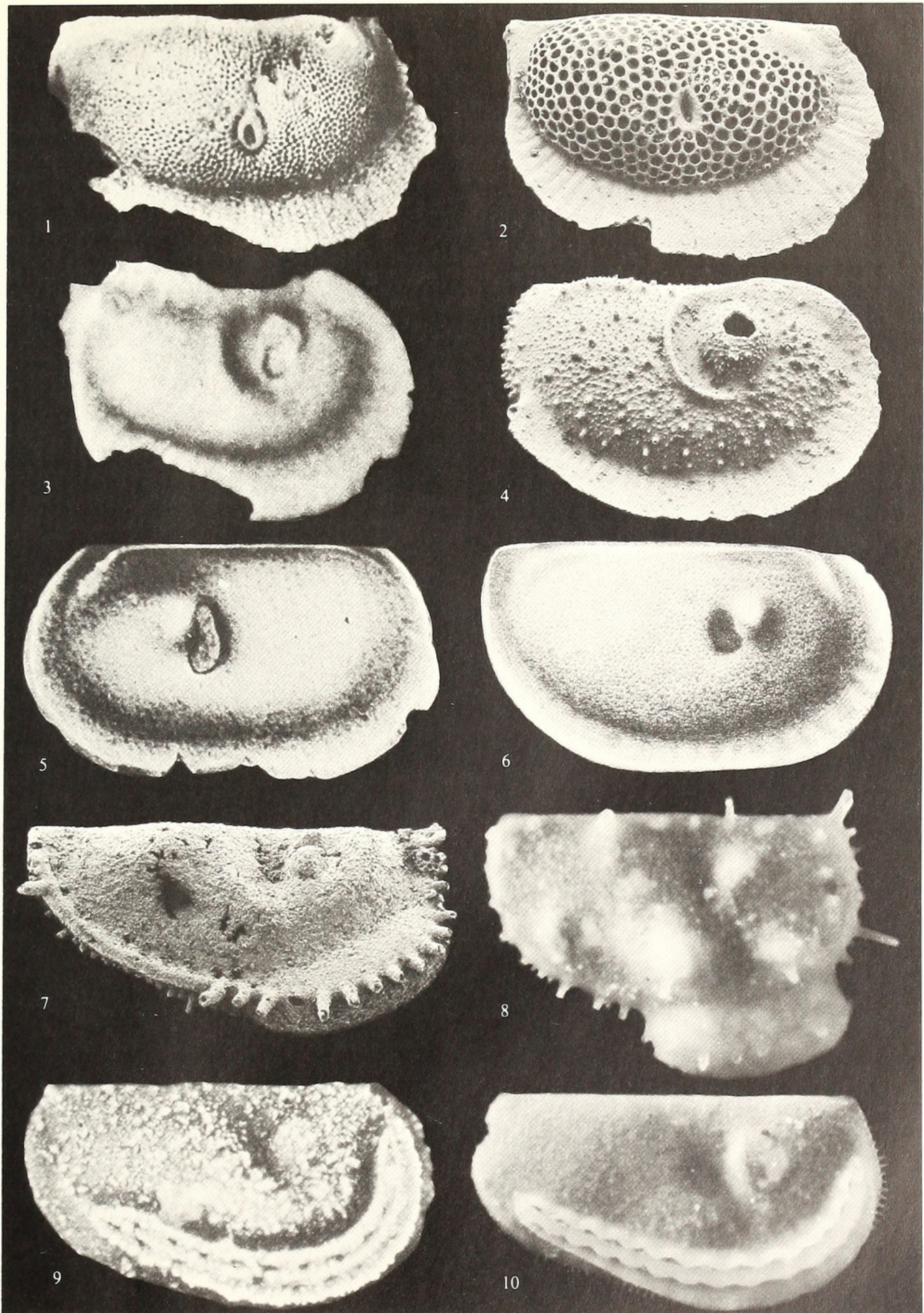
PLATE 68

SCHALLREUTER and SIVETER, palaeocopes from the lower and middle Ordovician of
North America (*left*) and Europe (*right*)

Llandeilo, Caradoc, and Ashgill of South Wales, the Welsh Borders, and Cross Fell in southern Britain (Siveter 1978a). *Hithis* (Pl. 68, figs. 7, 8) is present in the mid and late Ordovician of Baltoscandia and the Edinburg Formation of Virginia (Schallreuter and Siveter 1982), while *Hippula* (Pl. 68, figs. 9, 10) occurs in the mid Ordovician of Baltoscandia, Thuringia, Bohemia, Siberia, and Oklahoma (Schallreuter and Krůta 1980), and in the District of Mackenzie, Canada (= *Oecematobolbina* of Copeland 1982b).

Later Ordovician

Many ostracode genera from the late Ordovician of the North American continent are typical of the fairly homogeneous coeval faunas of the Baltic regions (see Pl. 70) and also occur to a varying extent in Scandinavian and southern British faunas. On Anticosti Island alone, the late Ashgill Ellis Bay and underlying Vaureal formations (Copeland 1970, 1973) have the following genera in common with the Baltic: *Moeckowia, Anticostiella, Caprabolbina, Platybolbina, Tetradella, Eoaquapulex, Pseudulrichia, Antiaechmina, Cryptophyllus, Eographiodactylus, Hemeaschmidtella, Triangulo-schmidtella, Warthinia, Byrsolopsina, Monotiopleura, Brevibolbina, Pseudohippula* (Pl. 70, figs. 3, 4), *Rectella,* and *Brevidorsa. Distobolbina warthini* Copeland, 1977, from the late Mohawkian of Baffin Island, Canada, and *D. grekoffi* Schallreuter, 1977, from upper Ordovician Baltic erratics, may be conspecific (Pl. 70, figs. 1, 2). Furthermore, Copeland (1983) has recently reported the typical circum-Baltic species *Steusloffina cuneata* from the latest Ordovician/earliest Silurian of Anticosti Island. The ostracode fauna of the Ashgill Brachiopodskiffer of Scania (Troedsson 1918) includes the characteristic American genus *Quadrijugator,* whilst that of the late Ordovician Maquoketa Shale of Missouri (Keenan 1951) contains many genera also found in the Baltic, exemplified *inter alia* by the species *Eoaquapulex barbatus, Byrsolopsina irregularis, Deefgella? septinoda, Spinaechmina taura,* and *Antiaechmina maquoketensis.*

EXPLANATION OF PLATE 69

Non-palaeocopes from the middle Ordovician of both sides of the Iapetus Ocean (*left* North America, *right* Europe).

Figs. 1, 2. Eridostraca. 1, *Cryptophyllus magnus* (Harris, 1931), middle Ordovician (Sunblood Formation, Whiterockian, Chazyan), Esbataottine Mountain, southwestern District of Mackenzie, Canada; left valve (GSC 38417), × 36 (from Copeland 1978, pl. 1, fig. 7). 2, *Cryptophyllus?* sp. of Siveter 1978, middle Ordovician ('Llandeilo Flags'), old quarry 300 m north of Big House, Lampeter Velfrey, east of Narberth Dyfed, Wales; right valve (BM(NH) no. OS 6676), × 76 (from Siveter 1978a, pl. 1, fig. 1).

Figs. 3, 4. Metacopa. 3, *Balticella deckeri* (Harris, 1931), middle Ordovician (lower part of Edinburg Formation, Blackriverian), Strasburg Junction, Virginia, U.S.A.; left valve (GPIMH 2719), × 45. 4, *B. binodis* (Krause, 1897) (= *B. oblonga* Thorslund, 1940), middle Ordovician [Idavere- (C₃) or Johvi-Stage (D₁), Upper Viruan], Backsteinkalk erratic boulder (type and no. 14B2), Teschenhagen near Stralsund, Pomerania, Germany; juvenile left valve (SGWG 28/9; Schallreuter 1968, fig. 10.4), × 64.

Figs. 5, 6. Leiocopa. 5, *Brevidorsa fimbriata* (Ulrich, 1892), from same bed and locality as fig. 3; left valve (GPIMH 2720), × 32. 6, *B. crassispinosa* (Schallreuter, 1973), from same bed and locality as Plate 68, fig. 2; left valve (GPIMH 2721), × 67.

Figs. 7, 8. Binodicopa. 7, *Pedomphalella intermedia* Swain and Cornell *in* Swain *et al.* 1961, middle Ordovician (Decorah Shale), 3 miles east of Rochester, Minnesota, U.S.A.; imperfect left valve (paratype, Univ. Minnesota), × 115 (from Swain *et al.* 1961, pl. 48, fig. 7a). 8, *P. jonesii* (Krause, 1897) (= *Schmidtella egregia* Sarv, 1963), same boulder as fig. 4; left valve (GPIMH 2722), × 99.

Figs. 9, 10. Leperditiocopa. 9, *Bivia duncanae* Berdan, 1976, middle Ordovician (Llanvirn–Llandeilo; upper part of Kanosh Shale, Pogonip Group, Chazyan), Crystal Peak section, Ibex Area, Millard County, Western Utah, U.S.A.; right valve (paratype, USNM 235540), × 8 (from Berdan 1976, pl. 5, fig. 4). 10, *B.? ordoviciana* (Kummerow, 1924), middle Ordovician light grey limestone erratic boulder corresponding in age to the Echinosphäritenkalk (Lower Viruan), Voigtsdorf, Mecklenburg, Germany; right valve (lectotype, Museum für Naturkunde der Humboldt-Universität Berlin, MB.O.65), × 4 (from Kummerow 1924, pl. 20 [numbered 21], fig. 1).

PLATE 69
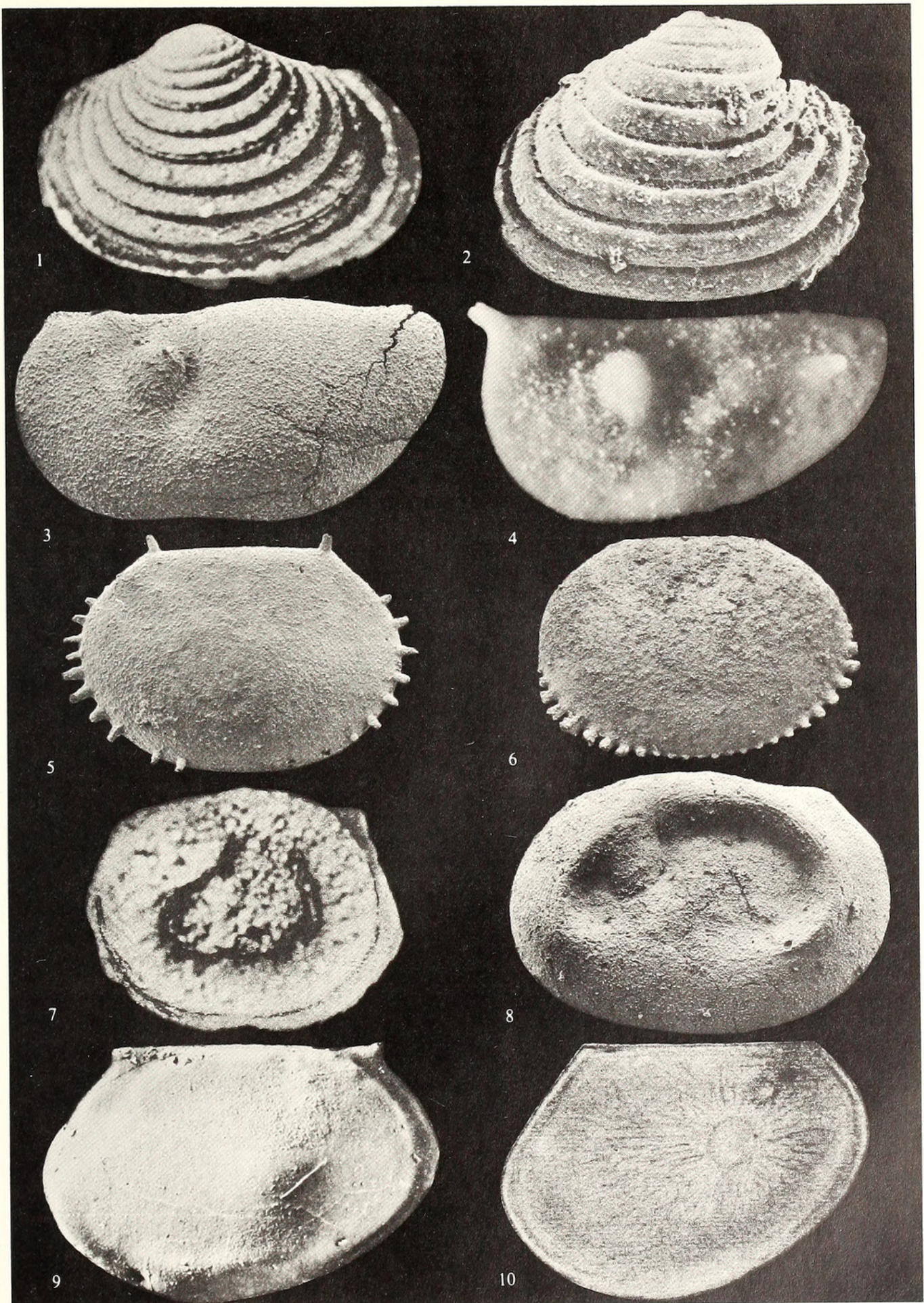
SCHALLREUTER and SIVETER, non-palaeocopes from the middle Ordovician of
North America (*left*) and Europe (*right*)

By contrast the faunas of the Maquoketa Shale in Iowa (Burr and Swain 1965) bear more resemblance to those from Scania. Ostracoda in common with the upper Viru (Caradoc) Sularp Shale fauna (Schallreuter 1980) include *Pariconchoprimitia*, *Vogdesella*, *Orechina*, *Conchoprimitiella*, and *Klimphores*; the last two genera also occur in the mid to late Ordovician of southern Britain.

While the appearance of ostracode genera in common is often broadly contemporaneous between continents, the origins of many ostracode groups apparently lie on the North American plate with subsequent migration to 'Europe'. The Leperditiocopa (e.g. Pl. 69, figs. 9, 10), for example, occurs in North America throughout the Ordovician whereas in Europe only four species are known, including one from the middle Ordovician of Norway. Other groups, such as the Lomatopisthiidae, the Nodambichilinae, and genera such as *Eoaquapulex* (Pl. 70, figs. 9, 10), *Tetradella* (Pl. 70, figs. 5, 6), and *Eographiodactylus* (Pl. 70, figs. 7, 8) occur in North America by the middle Ordovician but not in Baltoscandia until the end of the Ordovician.

In summary, ostracodes display progressively increasing faunal connections between the North American and Baltica/Gondwanan continents throughout the Ordovician. The earliest known connections occur in the late early Ordovician; there are many genera in common in the middle Ordovician; and by the late Ordovician the ostracode faunas of the two areas show even greater similarity, including possibly conspecific material. There are correspondingly increasing ostracode links between the Gondwanan and Baltic continents as the intervening ocean waned. The pattern of ostracode distribution across the Iapetus Ocean seems to mirror that shown by Ordovician brachiopods and trilobites, with progressively increasing contacts associated with the approaching continents.

EXPLANATION OF PLATE 70

Palaeocopes from the middle and upper Ordovician of both sides of the Iapetus Ocean (*left* North America, *right* Europe).

Fig. 1. *Distobolbina warthini* Copeland, 1977, middle Ordovician (late Mohawkian), Silliman's Fossil Mount, southern Baffin Island, Canada; female left valve (paratype, USNM 216133), × 82 (from Copeland 1977c, pl. 6, fig. 9).

Fig. 2. *D. grekoffi* Schallreuter, 1977, upper Ordovician (Upper Harjuan), Öjlemyrflint erratic boulder (no. G8), beach at Gnisvärds, Isle of Gotland (Baltic Sea), Sweden; female left valve (holotype, GPIMH 1926; Schallreuter 1977b, pl. 4.26, fig. 1a), × 63.

Fig. 3. *Pseudohippula castorensis* (Copeland, 1970), upper Ordovician (Vauréal Formation), Anticosti Island, Quebec, Canada; posteriorly incomplete right valve (paratype, GSC 24004) with spines broken away, × 68 (from Copeland 1970, pl. 4, fig. 21).

Fig. 4. *P. pseudopokornina* Schallreuter, 1975, upper Ordovician (Upper Harjuan), Öjlemyrflint erratic boulder (no. Wie2), Wielen, west of Uelsen, Emsland, Niedersachsen, Germany; right valve (GPIMH 2723), × 97.

Fig. 5. *Tetradella scotti* Guber, 1971, upper Ordovician (Elkhorn Formation), Fairhaven, Preble County, Ohio, U.S.A.; female left valve (GPIMH 2724, valve tilted 20°), × 70.

Fig. 6. *T. separata* Sidaravičienė, 1971, upper Ordovician (Upper Harjuan), Öjlemyrflint erratic boulder (no. G16), beach north of Lickershamn, Isle of Gotland (Baltic Sea), Sweden; female left valve (GPIMH 1992, valve tilted 20°), × 59.

Fig. 7. *Eographiodactylus eos* Kraft, 1962, middle Ordovician (Edinburg Formation, Blackriverian), Tumbling Run section, Virginia, U.S.A.; left valve (paratype, USNM 136637), × 71 (from Kraft 1962, pl. 16, fig. 9).

Fig. 8. *E. sulcatus* Schallreuter, 1975, same boulder as fig. 4; left valve (GPIMH 2725), × 100.

Fig. 9. *Eoaquapulex* sp. (= *Oepikella frequens* of Kraft, 1962), same bed and locality as Plate 69, fig. 3; female right valve (GPIMH 2726), × 30.

Fig. 10. *E. frequens* (Steusloff, 1895), upper Ordovician (Upper Harjuan), Leptaenakalk erratic boulder, Neu-Brandenburg, Mecklenburg, Germany; female right valve (lectotype, SGWG 114/37), × 27.

PLATE 70
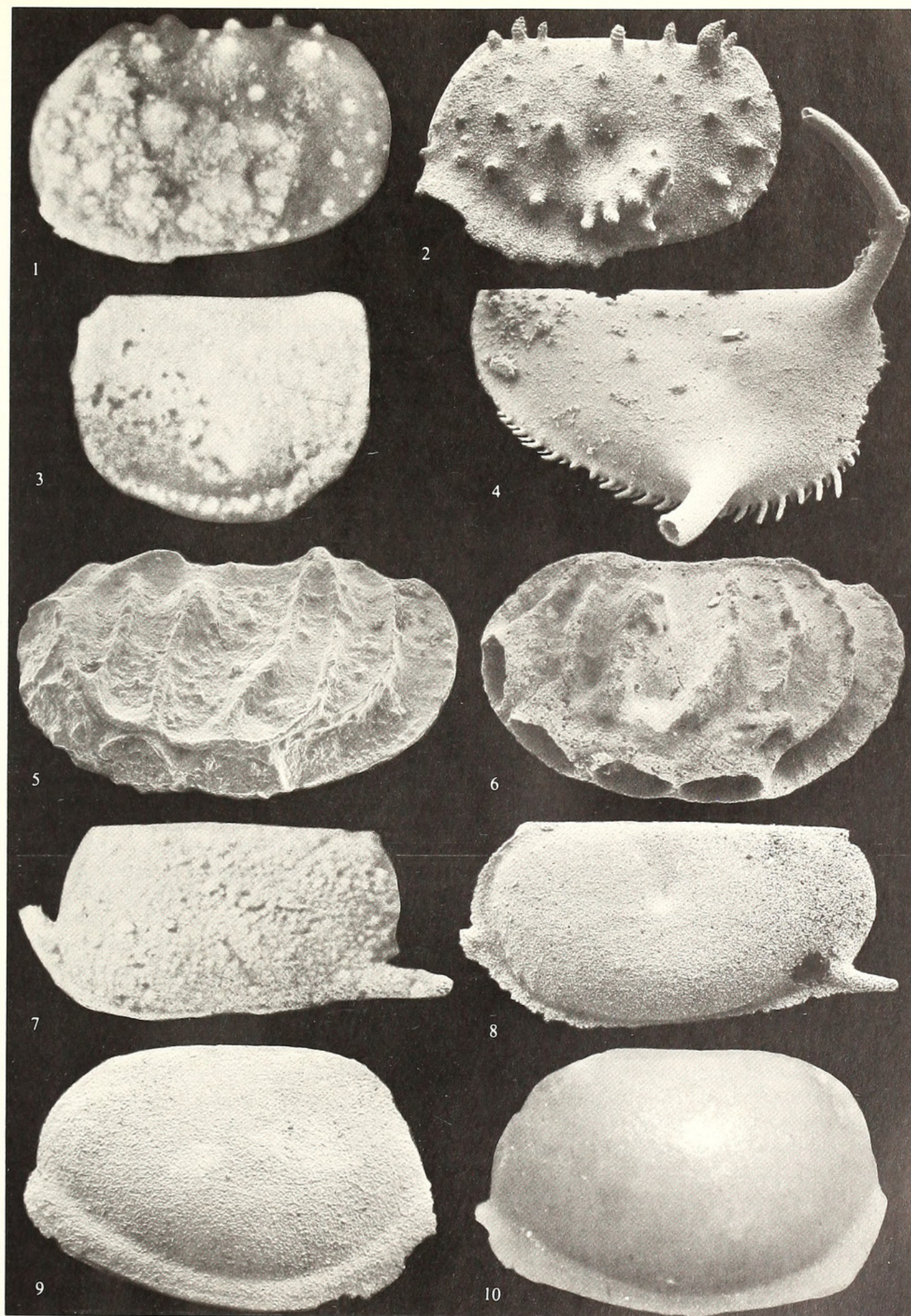
SCHALLREUTER and SIVETER, palaeocopes from the middle and upper Ordovician of
North America (*left*) and Europe (*right*)

SIGNIFICANCE OF THE PATTERNS OF OSTRACODE DISTRIBUTIONS

How did many ostracode genera manage to cross the Iapetus Ocean in the Ordovician and why were some corresponding ostracodes still provincial during the Silurian?

Width of the Iapetus Ocean

Estimated widths of the Iapetus Ocean pose problems in explaining the pattern of ostracode migration. Based on structural and stratigraphic palinspastic restoration of Iapetus, Williams (1980) estimated a minimum width of 2000 km at its maximum development. He concluded (1980, p. 435) that it was unlikely that such a geographically continuous orogen (10,000 km) 'which included equally continuous tectonic-stratigraphic facies belts related to ancient continental margins and an ocean basin, could have been produced by the opening of a narrow rift, a marginal ocean, or even a narrow major ocean'. Analysis of structural telescoping and palinspastic restoration of coeval sedimentary facies across the western margin of Iapetus implies a continental slope/rise of at least 200 km width; modern continental margins of comparable width and length border major oceans (Williams 1980, p. 421).

Cocks and Fortey (1982, p. 474) noted that ostracodes would have been unable to cross an ocean barrier, even one quite narrow. Cocks *et al.* (1980) estimated an ocean 900 km wide by the early Silurian. By analogy with modern subduction rates and with the survival periods and dispersal rates of modern pelagic larvae, McKerrow and Cocks (1976) suggested a minimal 2000–3000 km width, even during late Ashgill, with the first closure occurring in the north-east by the Silurian collision of Greenland and the Baltic. They believed that a mid Silurian trans-Iapetus migration of benthic ostracodes demonstrated closure of the ocean along part of its length.

Pelagic larvae?

One can speculate that ostracodes crossed the Ordovician Iapetus Ocean because, unlike modern forms, they had pelagic larvae. This is improbable, a conclusion supported by the fact that many Ordovician ostracodes apparently brooded their young (dimorphism believed to be associated with egg/brood care dominates palaeocope morphology) and thus would be unlikely to also have had widely dispersed larvae.

Benthic migration?

Fortey (1975) and Fortey and Owens (1978) have demonstrated shelf to slope related Iapetus trilobite communities showing increasing cosmopolitanism with depth. Could the trans-Iapetus ostracodes possibly represent deeper water assemblages, or did they perhaps migrate stepwise down shelf and across the ocean? Alternatively, is the trans-Iapetus ostracode mixing due in part to transgressive events in the manner recently modelled and persuasively tested by Fortey (1984) when assessing biological effects of Ordovician eustatic events? The biological implications of a transgressive pulse include not only generation of endemic taxa on flooded cratonic areas but also migration shelf-wards of previously extra-cratonic, deep-water faunas, thereby giving a false impression of provincial breakdown in response to tectonic events (Fortey 1984, p. 39). Thus, the pronounced Llandeilo–Caradoc transgression augments tectonic explanations for the late Ordovician trilobite mixing across Iapetus (Fortey 1984, pp. 46–47, fig. 4).

That some ostracode faunal mixing may be explained either by trans-oceanic migration or by cratonic migration during transgressions undoubtedly justifies detailed investigation, but this lies beyond the scope of the present study. As noted above, however, depth barriers are generally formidable for ostracodes and, even though community and detailed facies related analyses of Ordovician ostracode faunas have not yet been attempted, in broad terms they belong to the relatively shallow-water shelf/platform environment and not to the outer slope (e.g. Copeland 1982*b*). The existence of a Lower Palaeozoic pyschrospheric (deep-sea) ostracode fauna is not documented, but a controlling inflow of the cold polar waters necessary to create a more universal pyschrosphere (Benson 1979) within a two-layer ocean model (Bruun 1957), similar to that determining global

distribution of extant oceanic ostracodes, was apparently a possibility during the Ordovician. Late Ordovician glaciation is amply attested and Fortey (1984, p. 48, fig. 10) has suggested that a possible early Ordovician South Polar ice sheet was twice as large as Antarctica today. We need to search the right kind of deposits for possible Ordovician pyschrospheric ostracodes; the oceanic deposits of the Ordovician of the Southern Uplands of Scotland (Leggett 1979) are an example, but from which ostracodes are so far unknown.

Chance dispersal?

Dispersal of larvae (or even eggs or adults) by the passive transport of ocean currents is another possibility, as with many other marine invertebrates (Scheltema 1977). The ostracode dispersal patterns noted above suggest that, if current action was a factor, the significant current direction may have been from the North American to the European plate. Rafting on 'floats' (of, for example, marine algae) is yet another viable method of dispersal of modern marine animals, but is less effective (Scheltema 1977) because most benthic invertebrates are not well-adapted to survive long periods as epiplankton in the open sea.

The eggs of freshwater ostracodes are quite hardy; they are able to tolerate cold (Sohn and Kornicker 1979) and, in the case of some (though not all: McKenzie and Hussainy 1968), to withstand decades of desiccation (Van Morkhoven 1962, p. 139). Freshwater ostracode eggs can also possibly survive transport by high altitude winds (Sohn and Kornicker 1979) and have been found viable after ingestion and defecation by aquatic animals such as fish (Kornicker and Sohn 1971). The same has not been demonstrated for marine ostracodes, but they themselves form part of the diet of marine fish (Kornicker and Sohn 1971) and their eggs, when laid (outside the carapace), are usually deposited as clusters on bottom sediment or vegetation—an obvious potential food for many marine invertebrates.

Even though their dispersal mechanism is not in many cases understood, some modern ostracode faunas (from such island sites as Hawaii, for example) combine genera from distant regions separated by deep and in some cases almost 'barren' ocean floors (R. H. Benson, pers. comm.). It is thus possible that Ordovician ostracode dispersal was the result of nothing more than chance rafting or passive transport by other animals. Against this argument, however, is the fact that the ostracode migrational pattern copies that of trilobites and brachiopods, indicating that it reflects something more tangible than chance. Moreover, as noted above, there is reason to believe that in palaeocope ostracodes the well-being of possibly eggs and young depends to some degree on parental care. Potential Ordovician conveyors would also have been limited to cephalopods and possibly early fish, whereas modern ostracodes have many other passive dispersal mechanisms, including carriage by birds (e.g. De Deckker 1977) and man (Van Morkhoven 1962, p. 139).

Pelagic ostracodes?

Another solution is to reinterpret the palaeoecology of palaeocopes, but their shape, centre of gravity, and ventral and adventral structures favour the notion that most were benthic crawlers (or maybe bottom swimmers) and not pelagic; swimmers possibly included, for example, those forms with ventrally open (unprotected) antra, like *Foramenella* (Henningsmoen 1965). Pelagic ostracodes are characteristically planktonic forms and free-swimmers belonging to the Order Myodocopida; they are typically poorly calcified with a limited potential for preservation and have a scant fossil record. The origins of a free-swimming mode of life in Ostracoda is an untackled question but we know of no convincing pelagic myodocopid earlier than the Silurian. The bolbozoids and associates, known from basinal facies of the Ludlow Series of the Welsh Borderland and from coeval horizons of France, Sardinia, and Czechoslovakia, are possibly amongst the pioneer ostracodes adapted to a life off the bottom (Siveter 1984).

Closer geographical proximity?

Unless Ordovician ostracodes had some elusive mechanism of dispersal, their crossing of the Iapetus Ocean may have been aided by geographical proximity of opposing plates, which were possibly much

closer together and the ocean shallower at some point along the 10 000 km length of the Appalachian–Caledonides tract than estimates and palaeogeographical reconstructions have indicated. Bearing in mind the contacts demonstrated above (for example, by the ostracode fauna of South Wales as early as the early Llandeilo), the separation distance of 60° latitude between Britain and North America proposed by Cocks and Fortey (1982) (text-fig. 1 herein) appears to be an overestimate. This argument supports the tectonic model of Phillips *et al.* (1976) of oblique collision as early as the late Ordovician. Likewise the occurrence of only major-sized plates is possibly too simplistic; geographically intermediate 'islands' (microplates?) (e.g. see Neuman 1972) would obviously have provided easier pathways for the long distance oceanic migration of ostracodes. A number of extra-cratonic island faunas occur, for example, in the Llandeilo of the mobile belt of Newfoundland, in sites which concur with both regressive conditions and models, and which might engender speciation events imprinted on later transgressions (Fortey 1984, pp. 40, 45, 47–48). The Llandeilo marks approximately the initial, extensive mixing of trans-Iapetus ostracodes, though no ostracode faunas are as yet documented from supposed island sites.

Effects of late Ordovician eustatic changes

Animals on both the American and European plates, as typified by benthic brachiopods and planktic graptolites, suffered a marked decline during the latest Ordovician—a time of eustatic regression associated with the Gondwanan glaciation centred on North Africa (McKerrow 1979; Leggett *et al.* 1981). Ostracodes are no exception: the late Ordovician in eastern North America marks a period of extinction of, for example, many hollinomorphs, followed by the re-establishment of new ostracode faunas (Copeland 1977*a*); similar changes can be recognized in Europe (e.g. Siveter 1982*a*). In one of the best known and conformable Ordovician–Silurian ostracode successions, that from Anticosti Island, Quebec, about 15 m of strata across the boundary are barren of diagnostic ostracode faunas (Copeland 1970, 1973, 1981). In the Welsh basin of Britain, latest Ordovician and particularly earliest Silurian (early Llandovery) ostracodes are notably few. New Silurian stock in many of these regions is characterized by the occurrence of pioneer representatives of beyrichiacean palaeocopes. The faunal differences between Silurian beyrichiacean ostracodes across the Iapetus Ocean (see above) resulted possibly from the Llandovery, post-glacial transgression which isolated the shelf-living ostracodes into two stocks (Copeland 1977*a*; Copeland and Berdan 1977). Fortey (1984) has indeed predicted that one of the biological implications of a transgressive episode is the generation of high diversity and endemism on separated cratonic areas. The recovery of the shelf benthos was apparently slow (Leggett *et al.* 1981) but, ecological conditions being generally similar on both sides of the remnant Iapetus Ocean, this does not explain why some ostracodes display an endemicity which is particularly marked during the Ludlovian, and at the level of the Ludlow–Přídolí transition (and which is atypical of Silurian animals in general; Holland 1971).

CONCLUSIONS

1. Evidence from ostracode distributions can be used to test independently other faunal and geological data which indicate the site of oceans. As no psychrospheric-type ostracodes are yet documented from the Lower Palaeozoic, ostracodes *alone* cannot be used to diagnose the presence of oceans.

2. A pilot study comparing ostracode faunas from the North American and European plates dispels the notion of McKerrow and Cocks (1976) that Ordovician ostracodes show strict endemicity. Many middle and late Ordovician ostracode genera are common to both sides of an ocean which is recognized from the weight of geological and other faunal evidence.

3. In order for ostracodes to migrate across a mid Ordovician Iapetus Ocean which is estimated, from independent geological evidence, to have been at least several thousands of kilometres wide, it is concluded that opposing plates were at some point possibly in much closer proximity, or the ocean shallower, than hitherto supposed. Alternatively, the existence of intermediately placed islands or microplates may have aided animal dispersal.

4. The provincial aspect of some Silurian ostracodes may be related back to global changes in sea level at the Ordovician–Silurian boundary.

5. Ostracode distributions support other biogeographic evidence for the contraction of Tornquist's Sea by mid to late Ordovician, and for the development of the Rheic Ocean during the Silurian.

6. The use of ostracodes to help solve Lower Palaeozoic biogeographic problems is at a rather crude stage compared with equivalent trilobite or brachiopod studies. The data base is nowhere as comprehensive and there has been no sophisticated analyses of, for example, facies and any associated ostracode 'communities'. A few specialists are fully engaged documenting the ostracode faunas. Much remains to be done, for example, on the taxonomy of North American Ordovician ostracodes. Detailed studies on the autecology of palaeocope species also need to be undertaken to elucidate modes of life. Nevertheless, previous assumptions concerning the timing of ostracode contacts across the Iapetus Ocean must now change and their implications be reappraised. The more we examine the record, the more contacts emerge, even during the Silurian. Endemism is often a reflection of the current state of knowledge.

Plates 68–70. The plates are designed to demonstrate congeneric ostracode occurrence across the Iapetus Ocean in the middle and upper Ordovician, using examples from a variety of major taxa. The figures include scanning electron micrographs of our own material and pertinent illustrations after previous authors. Restrictions on the availability of several relevant specimens have prevented their illustration by scanning electron microscopy. Abbreviations used in plate explanations: GPIMH, Geologisch-Paläontologisches Institut und Museum der Universität Hamburg, Federal Republic of Germany; SGWG, Sektion Geologische Wissenschaften der Universität Greifswald, German Democratic Republic; USNM, United States National Museum, Washington, D.C., U.S.A.; UMMP, University of Michigan Museum of Paleontology, Ann Arbor, Michigan, U.S.A.; GSC, Geological Survey of Canada, Ottawa, Canada.

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