THE COMPOSITION AND PALAEOGEOGRAPHICAL SIGNIFICANCE OF THE ORDOVICIAN OSTRACODE FAUNAS OF SOUTHERN BRITAIN, BALTOSCANDIA, AND IBERO-ARMORICA

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ABSTRACT. A review of more than 250 genera has established the taxonomic composition, patterns of geographical and stratigraphical distribution, and faunal links for the Ordovician ostracodes of the British Isles, Ibero-Armorica, and Baltoscandia. Compositional and diversity changes of the faunas can be correlated with tectonic and ecological controls.

Four orders (Beyrichiocopa, Platycopa, Podocopa, and Leperditiocopa), comprising over fifty families and more than 800 species are represented. In the three regions ostracodes show high diversity at all taxonomic levels, especially in Baltoscandia. Palaeocopes and binodicopes represent some 85% of the total number of Ordovician genera in the three regions. Palaeocope dominance increases from Ibero-Armorica to the British Isles and then to Baltoscandia. The same dominant families of palaeocopes and binodicopes (tetradellids, ctenonotellids, bolliids, and circulinids) occur in the three domains. Palaeocope and binodicope diversity increases during the Arenig–Llanvirn and maximum diversity at all taxonomic levels is reached in all three regions during the Llandeilo–early Caradoc interval. The later Ordovician is marked by a general decline of palaeocopes.

Faunal links most clearly occur between Baltoscandia and the British Isles, with twenty-seven genera and some uppermost Ordovician species in common. There is a uniform increase in faunal similarity between Britain and Baltoscandia throughout the Ordovician, whereas British/Ibero-Armorican and Ibero-Armorican/Baltoscandian generic contacts show an irreversible decline (for the Ordovician) after Llanvirn/Llandeilo times.

Faunal composition and diversity vary with environment: binodicope-rich faunas are typically associated with clastic and unstable environments (e.g. Ibero-Armorica); more diversified, palaeocope-rich faunas are typically associated with more stable conditions and carbonate sedimentation (e.g. Baltoscandia). The biological effects of sea-level changes are attested by, for example, a diversity increase during the Llandeilo–early Caradoc (transgression) and a diversity decrease during the later Caradoc–Ashgill (regression).

The evolving pattern of ostracode links support: 1, the northwards movement of the southern part of the British Isles (microcontinent Avalonia) towards Baltica and the consequent closing of Tornquist's Sea by the Caradoc/Ashgill; 2, the development of the Rheic Ocean between Gondwana (including Ibero-Armorica) and Avalonia by the mid-late Ordovician.

FOR more than 130 years taxonomic data have been published on Ordovician ostracodes from Europe, especially on taxa from the erratic boulders of the Baltic regions (see Schallreuter 1964 *et seq.*). During this period no investigation has specifically addressed the nature, comparative composition, and possible palaeogeographic significance of the overall spatial and stratigraphic distribution of the various Ordovician ostracode faunas of Europe. One major problem has been that, until recently, most of the Ordovician ostracodes from the British Isles and western and southern Europe were poorly documented as compared to those of Baltoscandia, a neglect stemming partly from their often relatively unattractive state of preservation (see Siveter 1978). However, the last 10 years have witnessed substantial research on key British (e.g. Siveter 1978; Jones 1986, 1987) and Ibero-Armorican (e.g. Vannier 1986*a*, *b*) Ordovican ostracodes, providing much needed monographic and distributional data. Furthermore, such studies coincided with the

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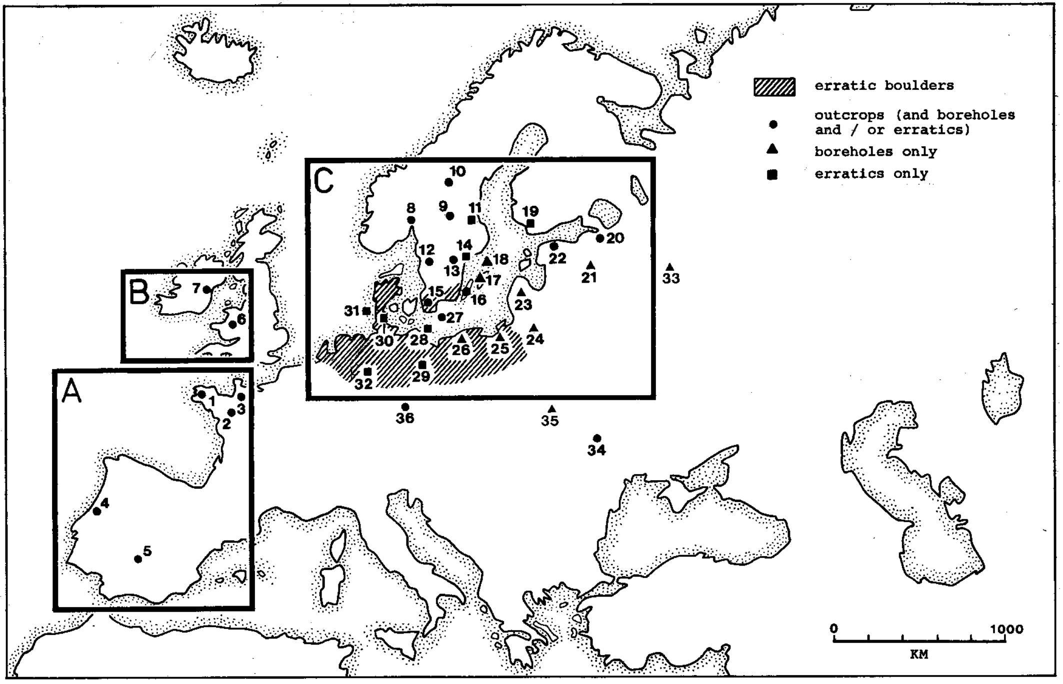

TEXT-FIG. 1. Occurrence of the main Ordovician ostracode faunas from A, Ibero-Armorica; B, British Isles; C, Baltoscandia; and other localities in central and eastern Europe (excluding Czechoslovakia). Key papers from which the main data were collected are as follows:

A, Ibero-Armorica (see Vannier 1983*a*, *b*, *c*, 1984*a*, *b*, *c*, 1986*a*, *b*; Vannier and Schallreuter 1983; Lethiers *et al.* 1985)

1-3. Armorican Massif, western France: 1, Crozon Peninsula; 2, Lavel area and Menez Belair; 3, Domfront area, Normandy.
4. Buçaco syncline, Portugal.
5. Toledo Mountains and Guadalupe, central Spain.

B, British Isles

6. Wales and southern England (Siveter 1978, 1982*a*, *b*, 1983; Schallreuter and Jones 1984; Jones and Siveter 1983; Schallreuter and Siveter 1983; Jones 1984, 1985, 1986, 1987).
7. Ireland (Orr 1985*a*, *b*).

C, Baltoscandia

8. Oslo area (Henningsmoen 1948, 1953, 1954*a*, *b*; Dons and Henningsmoen 1949; Qvale 1980).
9. Siljan district (Thorslund 1940; Hessland 1949; Jaanusson 1957, 1966).
10. Jämtland (Thorslund 1940).
11. South Bothnian area (Jaanusson 1957).
12. Västergötland (Henningsmoen 1948; Thorslund 1948; Jaanusson 1957; Schallreuter 1984*b*).
13. Östergötland (Jaanusson 1957).
14. Tvären area (Thorslund 1940; Jaanusson 1957).
15. Scania (Troedsson 1918; Schallreuter 1980*a*).
16. Öland (Jaanusson 1957; Schallreuter 1977*e*).
17. Gotland (Schallreuter 1969*a*, 1971*b*, 1972, 1984*b*).
18. Gotska Sandon (Jaanusson 1966).
19. Nyland (Martinsson 1956).
20. Leningrad area (Männil 1963).
21. Pskov district (Neckaja 1973).
22. Estonia (Sarv 1959, 1962, 1963; Meidla 1983, 1986).

[*continued opposite*

revision of the major Ordovician ostracode taxa from Baltoscandia (for example, Schallreuter 1976, 1982*a*, 1983*a*) and with a major study (Schallreuter 1978*a*) focusing on problems of classification of Ordovician ostracodes. European Ordovician ostracode faunas are now sufficiently well documented for an assessment of their affinity and palaeogeographical significance to be undertaken.

This study deals with ostracode faunas from Ibero-Armorica, the British Isles, and Baltoscandia (text-fig. 1): domains fundamental to an understanding of the Ordovician palaeogeography of 'Europe'. Faunal and facies distributions (Cocks and Fortey 1982) indicate that in the early Ordovician Baltoscandia was sited in temperate latitudes, Ibero-Armorica was positioned on high latitude Gondwana, together with southern Britain which was later in the Ordovician to form part of a northerly drifting microcontinent, Avalonia (e.g. McKerrow and Cocks 1986; see also text-fig. 38).

Herein we present the stratigraphic range and geographic distribution for nearly all of the recorded Ordovician ostracode genera across Europe (excluding Czechoslovakia), representing over 200 genera belonging to all major lower Palaeozoic ostracode groups. The aim of the paper is to compare such distributions from Baltoscandia, the British Isles, and Ibero-Armorica; to determine possible taxonomic links through the Ordovician; and to correlate any changes in the patterns of ostracode faunal composition and distribution with possible tectonic or other controls. Similar types of syntheses are already published for benthic macrofossil groups such as trilobites (for example, Whittington and Hughes 1972) and brachiopods (for example, Williams 1973, 1976). To what extent do Ordovician ostracode distributions and dynamics confirm or modify the separation of Gondwana, Baltica, and Avalonia (and North America: see Schallreuter and Siveter 1985) by such bodies as the Rheic and Iapetus oceans and Tornquist's Sea (text-fig. 38)?

THE STUDY AREAS: DISTRIBUTION OF ORDOVICIAN OSTRACODES IN EUROPE

Most Ordovician ostracodes known from Europe are recorded either from Baltoscandia, the British Isles, or Ibero-Armorica (text-fig. 1): areas which reflect three Ordovician palaeogeographic domains (see above). Correlation with the British sequence (Atlantic graptolite zones) is given in text-fig. 2. The Estonian sequence (text-fig. 2: 22), zoned on conodonts, chitinozoa, and shelly macrofaunas (e.g. Männil 1966, 1971; Rõõmusoks 1970) is often used as a standard for the Baltic Ordovician succession. For practical reasons, the Ontikan, Viruan, and Harjuan 'Series' of the

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23. Latvia (Gailīte 1971, 1975*a*, *b*; Gailīte *in* Ulst *et al.* 1982).
24. Lithuania (Sidaravičiene 1971, 1975; Pranskev̌icius 1972; Neckaja 1973 and cited papers).
25. North-eastern Poland (Sztejn 1985).
26. Pomerania (Bednarczyk 1974).
27. Bornholm (Poulsen 1978).

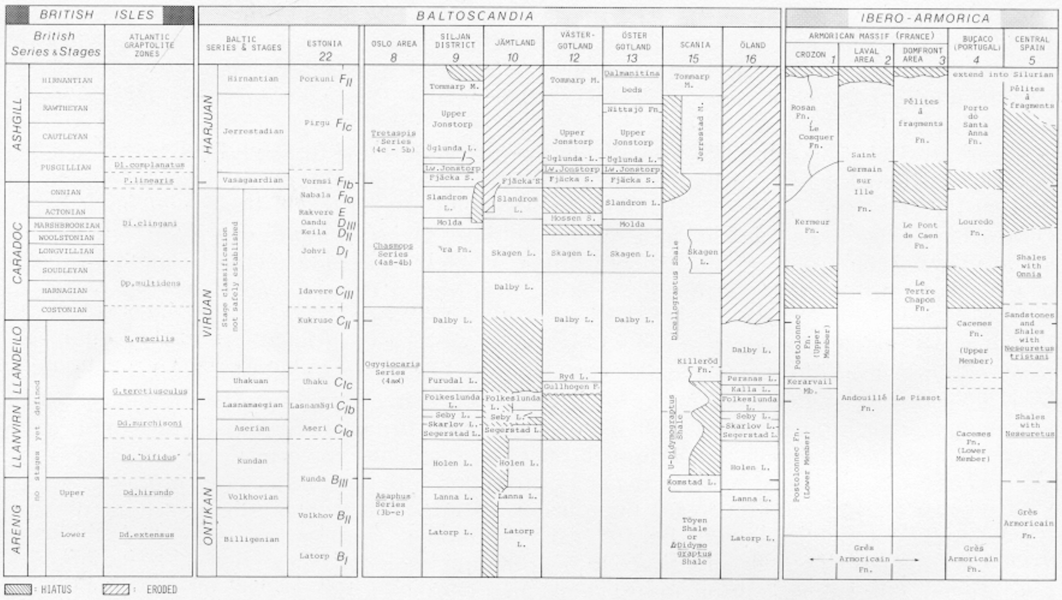
Northern Germany—erratic boulders (see Schallreuter 1984*a* for further references).

28. Hiddensee.
29. Berlin.
30. Schleswig-Holstein.
31. Isle of Sylt (Schallreuter 1984*a*, *b*, 1985*a*, 1986, 1987).
32. Münster area (Schallreuter 1985*b*).

Central and eastern Europe

33. Moscow syneclise (Prokofiev and Kuznetzov 1982).
34. Podolia (Abushik and Sarv 1983; Krandiesky 1969).
35. Volyn (Krandiesky 1975).
36. Thuringia (Blumenstengel 1965; Knüpfer 1968).

Locality 8 is in Norway; 9-18, 27 in Sweden; 19 in Finland; 20-24, 33-35 in USSR; 25, 26 in Poland; 28, 29 in German Democratic Republic; 30-32, 36 in Federal Republic of Germany.



TEXT-FIG. 2. Correlation of Ordovician stratigraphy in Ibero-Armorica and Baltoscandia with the British series and stages, mainly based on the distribution of Atlantic graptolites. All selected localities from Baltoscandia and Ibero-Armorica are numbered as in text-fig. 1. Correlations based on Bruton (1984), Hammann *et al.* (1982), Paris (1981), Williams *et al.* (1972), Bruton and Williams (1982), and further references cited therein. Lw, Lower; L, Limestone; M, Mudstone; Mb, Member; Fn, Formation; S, Shale. Atlantic graptolite genera: Dd, *Didymograptus*; Dl, *Dicellograptus*; Dp, *Diplograptus*; G, *Glyptograptus*; N, *Nemagraptus*.

Baltic are sometimes employed herein. Correlation of the Ibero-Armorican successions particularly uses chitinozoan biostratigraphy (Paris 1981).

Ibero-Armorica (text-fig. 1A)

This area comprises the Armorican Massif of north-west France and Portugal and Spain of the Iberian Peninsula. Faunal data have been collected from most of the Palaeozoic synclines (Vannier 1986*a*, *b*) extending east–west throughout the Armorican Massif (Cogné 1971), from the Alcudian area of central Spain (Hammann *et al.* 1982), and from the Buçaco syncline in Portugal (Paris 1979; Vannier 1986*a*, *b*). Ordovician sequences in Armorica and Iberia (text-fig. 2) show strong similarities. Coeval shallow water deposits occur in both regions: for example, Arenig (Armorican) quartzites; Llanvirn, Llandeilo, and Caradoc siltstones, mudstones, and sandstones; and late Ordovician glacio-marine sediments. Furthermore, except for the Ashgill carbonates of the Rosan Formation (Armorican Massif) and the Porto-do-Santa-Anna Formation (Portugal), there is a general absence of limestone. The types of facies present, extending southwards to Morocco (Destombes 1962, 1971) and presumably to Saudi Arabia (Fortey and Morris 1982; Vannier and Vaslet 1987), correspond to an inner shelf environment probably (in the earlier Ordovician) at relatively high latitudes and forming the northern edge of the Gondwana continent (Cocks and Fortey 1982, text-fig. 4).

Striking faunal resemblances, many at specific level, have been documented between Armorica and Iberia for many Ordovician benthic groups (Henry *et al.* 1976; Paris and Robardet 1978; Henry 1980; Vannier 1986*a*, *b*). Trilobites and ostracodes both show increased diversity during the Llandeilo and scarce, low diversity yet widely distributed Caradoc faunas occur in Armorica and

Iberia. Most Arenig–Caradoc ostracode species from Iberia are also found in Armorica (Vannier 1983*a*, *b*, 1986*a*, *b*).

Trilobite and ostracode associations are not, however, always uniformly distributed over the areas in question. Some specific and generic level differences between the northern and southern part of the Armorican massif are possibly related to sedimentary differences such as grain size and organic content. During the Llandeilo, and to some extent the Llanvirn, Armorican Massif trilobite and ostracode associations (Henry 1980; Vannier 1986*a*, *b*) seem to follow a north–south deepening bathymetric gradient; a possible deep water area occurs from Ancenis to the Montagne Noire in southern France (Dean 1966; Henry 1980; Cocks and Fortey 1982). Comparable coeval differences are also observed between northern and southern trilobite (Henry 1980) and ostracode faunas within the Alcudian zone of central Spain.

All these sedimentological and faunal similarities are presumed to result from similar environmental influences such as clastic and water energy conditions. Together they support the notion that Iberia and Armorica were two geographically closely related areas (on Gondwana) throughout the Ordovician.

Baltoscandia (text-fig. 1c)

Ordovician ostracode faunas are known from central Baltoscandia (outcrops and boreholes in Estonia, Latvia, Lithuania, Leningrad area, Sweden, and Norway) and are also abundantly documented from erratic boulders of Scandinavia and northern central Europe. In contrast with the thick terrigenous Ordovician deposits in Ibero-Armorica (over 1500 m for the Armorican Massif), the epicontinental Ordovician of Baltoscandia rarely exceeds 200 m in total thickness. Jaanusson (1976) distinguished three major facies belts which are geographically fairly constant throughout the Ordovician. The north 'Estonian and Lithuanian' facies belt contains mainly calcarenites (includes areas 22, 23, 24 respectively in text-figs. 1 and 2). The central Baltoscandian facies belt (Jämtland, Siljan district, Östergotland, Öland: text-figs. 1 and 2, areas 9, 10, 13, 16) is characterized by carbonates, calcilutites, and calcarenites during the middle Ordovician. Graptolite shales predominate in the Scanian facies belt (Oslo region, Västergotland, and Scania: text-figs. 1 and 2, areas 8, 12, 15).

General bathymetry can be inferred from these facies belts. Water depth seems to increase from the east and north-east towards the south-western Wendian Basin through successive Estonian, central Baltoscandian, and Scandian facies belts respectively. Contrasting markedly with the epicontinental carbonates are the thick terrigenous deposits of the Wendian Basin running beyond 'Tornquist's line' (Jaanusson 1976, fig. 6) and separating Baltoscandia from other European palaeogeographic units.

Generic and specific faunal differences mainly occur between the different facies belts and apparently relate to sedimentary and bathymetric changes. For example, Arenig cyclopygid trilobites (Poulsen 1965) are closely associated with dark marginal limestones and shales. Except for some widespread faunal changes associated with physical events such as sea-level changes, in many cases Baltoscandian benthic faunas (trilobites, ostracodes) seem at times to change independently in each facies belt. Using ostracode faunal logs Jaanusson (1976, p. 324) suggested that 'each major zone was affected by environmental changes that were specific to the zone'. For example, the dramatic ostracode faunal change at the Kukruse–Idavere boundary (text-fig. 2) in northern Estonia is unknown in corresponding Swedish sequences (Dalby Formation). This change may be related to a major crater-like impact structure, the oldest fill of which is of early Idavere age (Kala *et al.* 1984; Lindström 1987). By contrast, the ostracode faunal change at the base of the Skagen Limestone (Caradoc) occurs throughout the central Baltoscandian facies belt.

The nature of both the (benthic) trilobite and planktonic faunas and the ('temperate') carbonates indicate an intermediate latitudinal position for Baltoscandia during the Arenig (Cocks and Fortey 1982). By the end of the Ordovician the occurrence of bahamitic limestone places Baltoscandia within the tropics (Jaanusson 1973).

The British Isles (text-fig. 1B)

British Ordovician ostracode faunas are known mainly from the Welsh Borderland, Wales, and northern England (Siveter 1978; Jones 1986, 1987). Some Ashgill ostracodes are known from southern Ireland (Orr 1985*a*, *b*). During the early Ordovician, the Welsh Basin is often characterized by possible marginal outer shelf and slope environments, sometimes associated with transgressive facies (e.g. during the Llanvirn) and volcanism (Williams 1980; Fortey 1984). The deeper environments of the Welsh Basin generally occur to the west, as exemplified by the graptolite black mudstones with bathypelagic and blind benthic trilobites in the Arenig of South Wales (Fortey and Owens 1978). Sandstones, siltstones, and various limestones found along an arcuate belt from the Welsh Borders through to South Wales reflect more diversified environments and bottom conditions appearing in the Welsh Basin during the Llandeilo (Williams 1980). Ostracode abundance and diversity both decrease towards the supposed deeper parts of the Welsh Basin (Jones 1986, 1987). The early Caradoc transgression is often followed by environmental conditions (dark graptolite shales) which seem to affect considerably the distribution of the ostracode fauna in Wales. Shelf limestones and breaks in succession are common features of the Ashgill of southern Britain (Williams 1980).

Southern Britain, including the Lake District and southern Ireland, formed part of the Avalonian microcontinent which supposedly drifted northwards, away from its parent plate Gondwana, through the Ordovician (McKerrow and Cocks 1986; Pickering *et al.* 1988). Northern Britain (not considered herein: Ordovician ostracode faunas unrevised) was attached to the low latitude North American plate on the northern margin of the Iapetus Ocean during the Ordovician. In general, the Cambrian to Silurian evolution of this ocean is well documented using sedimentological, structural, tectonic, and faunal evidence. McKerrow and Cocks (1976) argued for a late Ordovician oceanic width of 2000–3000 km. Schallreuter and Siveter (1985) demonstrated mid- and late Ordovician ostracode faunal links across the Iapetus Ocean, between the North American plate and southern Britain—Baltoscandia, and suggested that relevant plates may have been in closer proximity—a notion also proposed by Pickering *et al.* (1988). The position of Avalonia relative to Gondwana, Baltica, and North America during the Ordovician is addressed herein based on ostracode evidence.

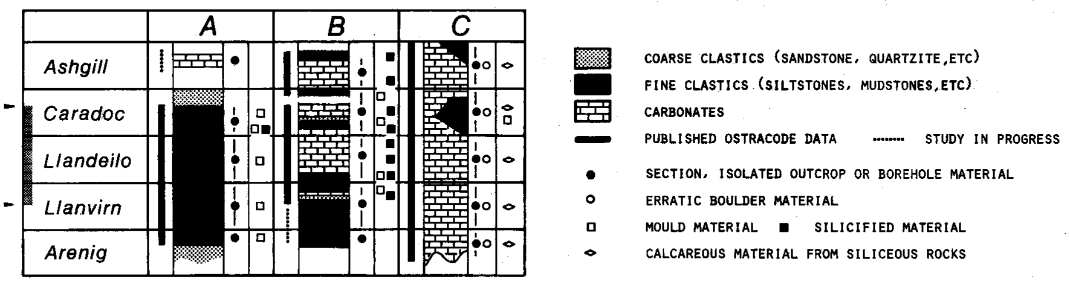
Other European areas

Data are also available from the Moscow syneclise, Podolia, Volyn, and Thuringia (text-fig. 1: 33–36 respectively). The ostracode faunas and (limestone) sediments of Podolia (Abushik and Sarv 1983) suggest that Baltoscandian influences extended to the south-west parts of Europe during the Ordovician. The upper Ordovician ostracodes from Thuringia (Knüpfer 1968) have previously been assumed to be endemic, but in fact also show some Baltic affinities (unpublished information). The Ordovician ostracode faunas of Czechoslovakia (e.g. Přibyl 1975, 1979) will be the subject of another paper.

ORIGIN AND RELATIVE VALUE OF THE OSTRACODE DATA

For faunal comparison it is fundamental to appreciate that documentation of the various European ostracode faunas is not uniform (text-fig. 3). Baltoscandian ostracode faunas are considerably more fully documented compared to those of the relatively more recently monographed British and Ibero-Armorican faunas. Text-figs. 10–17 record some 200 genera from Baltoscandia and about fifty and thirty from the British Isles and Ibero-Armorica respectively. The availability and qualitative and quantitative nature of the data on European ostracode faunas also reflects lithological, preservational, and other factors such as techniques of study.

Most of the Ibero-Armorican ostracode faunas occur in siltstones and mudstones of upper Arenig to Caradoc (Marshbrookian) age (Paris 1981; Vannier 1986*a*, *b*). Lack of information from the upper Caradoc and in the Arenig (Armorican sandstones Formation) seems directly related to lithological factors, ostracodes being virtually absent in coarse-grained deposits. Ostracodes are most abundant in the Llandeilo siltstones and mudstones of the Armorican Massif and Portugal. Ashgill ostracodes are as yet undescribed from Ibero-Armorica but are known to occur within limestones of the Rosan Formation at Lostmarc'h in the Armorican Massif (see Paris 1981). Documented Ibero-Armorican ostracodes were obtained from isolated stratigraphic levels and localities and continuous coastal profiles. They are often strongly distorted tectonically and, except for a poorly silicified fauna in the upper part of the Andouillé Formation (upper Llandeilo and/or early Caradoc), occur exclusively as moulds.



TEXT-FIG. 3. Nature and range of faunal data from the Ordovician of: A, Ibero-Armorica; B, the British Isles; C, Baltoscandia. The vertical line between the arrows indicates the stratigraphic range of possible faunal comparisons between the three regions.

Ordovician ostracodes of southern Britain (Siveter 1978; Jones 1986, 1987) were obtained mostly from frequently silicified calcareous sediments and as mould faunas in clastic deposits. There is a lack of ostracodes particularly from the Arenig and the early Llanvirn (the oldest published fauna comes from the upper Llanvirn Fairfach Group) and from within the Caradoc (the only recorded Actonian–Onnian ostracodes are scarce mid-uppermost Onnian binodicopes). The Ashgill limestones from England (Jones 1986, 1987) and Ireland (Orr 1985*a*, *b*) contain a promising, rich fauna.

Ordovician ostracode faunal data of Baltoscandia are available from the Arenig (BII: Sarv 1959) to the uppermost Ashgill (FII: see Schallreuter 1984*a*). Except for faunas described from the Caradoc of Norway (Qvale 1980) and Sweden (Sularp Shale, Scania: Schallreuter 1976) and from the uppermost Ordovician of Norway (Troedsson 1918), most of the documented Baltoscandian ostracodes were extracted as shells from limestones. Numerous Baltoscandian ostracode faunas are also preserved as calcareous microfossils but within non-calcareous rock matrix: for example, in middle Ordovician 'Backsteinkalk' cherty limestones or upper Ordovician 'Öjlemyrflint' cherts (Schallreuter 1982*b*). In such cases, hydrofluoric acid techniques are needed to recover the ostracodes. The best-preserved Baltoscandian faunas have been recovered from (Arenig to Ashgill) erratic boulders. Unfortunately, many species were first described from boulders for which it is often difficult to determine an exact provenance and age. However, many of the lithologically and faunally distinctive erratic boulders are dated as exactly as the faunal data from the outcrop allow (e.g. see Schallreuter 1969*b*, 1971*a*, 1985*b*) and in many cases the erratic boulder faunas are much more completely known than those of the correlative beds in the Scandinavian-Baltic region generally.

Ostracode faunal data common to Baltoscandia, the British Isles, and Ibero-Armorica currently span an upper Llanvirn to about late Caradoc time interval (text-fig. 3). The present study concentrates on this period though other comparisons, for example between Baltoscandian and British Ashgill faunas, are also made.

So.	Superfamily	Family	Subfamily	A	B	C
1 	PRIMITIOPSACEA	1 Primitiopsidae	1 Ventrygyrinae			
			2 Bubnoffiopsinae			●
			3 Venzavellinae			●
			4 Anisocyaminae			●
			5 Bugariktellinae			
		2 Graviidae	1 Subfam. nov.			●
	EURYCHILINACEA	3 Oepikellidae	1 Oepikellinae			●
			2 Ampletochilininae		●	●
		4 Eurychilinidae	1 Eurychilininae			●
			2 Piretellinae			●
			3 Chilobolbininae			●
		5 Oepikiidae			●	●
	HOLLINACEA	6 Euprimitiidae	1 Euprimitiinae			
			2 Gryphiswaldensiinae			●
		7 Tvaerenellidae	1 Hithinae			●
			2 Tvaerenellinae	●	●	●
			3 Nodambichilininae			●
			4 Martinssonopsinae			●
		8 Ctenonotellidae	1 Tallinnellinae	●	●	●
			2 Steusloffinae		●	●
			3 Wehrliinae	●	●	●
			4 Ctenonotellinae	●		●
			5 Guberellinae			
		9 Tetradellidae	1 Tetradellinae	●	●	●
			2 Sigmoopsinae	●	●	●
			3 Perspicillinae			●
			4 Glossomorphitinae	●	●	●
			5 Dillobellinae			●
			6 Sylthinae			●
			7 Gunnaropsinae		●	
			8 Subfam. nov.	●	●	
		10 Sarvinidae				●
		11 Fam.nov.				
		12 Hollinidae	1 Hollininae			●
			2 Triemilomatellinae			
			3 Tetrasacculinae			●
			4 Nodellinae			
		13 Hollinellidae				
		14 Cherskiellidae				
		15 Egorovellidae				
		16 Soanellidae				

TEXT-FIG. 4. Systematic position and presence of Ordovician palaeocope ostracode families and subfamilies in: A, Ibero-Armorica; B, British Isles; C, Baltoscandia. The drawing represents a typical valve of the suborder Palaeocopa (Order Beyrichiocopa). Systematic classification mainly based on Schallreuter 1978*a*.

MORPHOLOGICAL CHARACTERISTICS OF THE MAJOR ORDOVICIAN OSTRACODE TAXA

The Ordovician ostracode faunas treated herein fall into four orders (Beyrichiocopa, Platycopa, Podocopa, and Leperditiocopa), thirteen suborders, and over fifty families (text-figs. 4 and 5). An outline of the morphological differences between major groups is given in order to appreciate the possible significance that morphology might have in association with particular stratigraphic, spatial, or palaeoecological patterns of distribution.

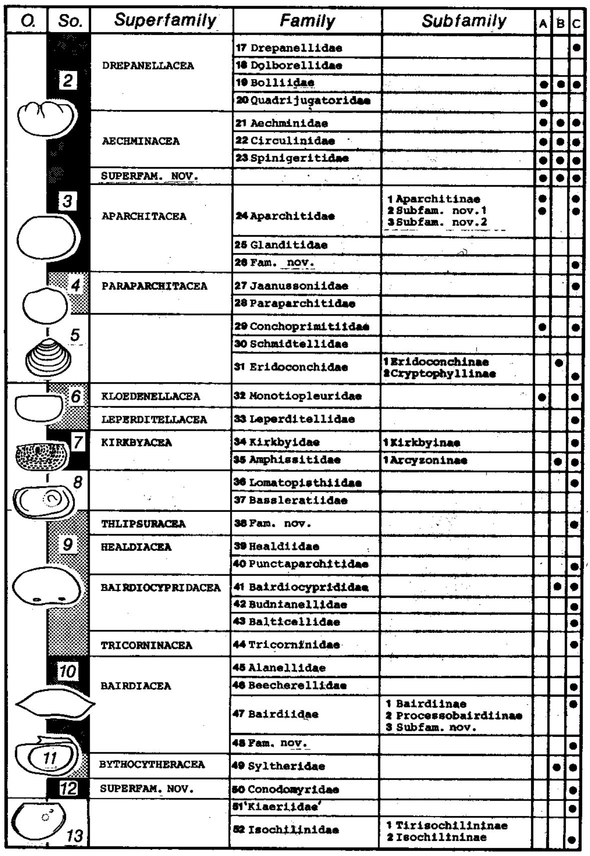
Problems of classification of Ordovician ostracodes have been discussed by Schallreuter (1966*a*, *b*, 1967, 1968*a*, *b*, 1973*a*, 1975, 1978*a*, 1979, 1985*c*). The major taxonomic groups are distinguished on the basis of the overall lobal, sulcal, and dimorphic characteristics of the shell, the presence of an inner lamella, and on valve overlap conditions. These features almost certainly reflect vital aspects of the biology (and ecology) of the ostracode.

Suborder Palaeocopa (text-fig. 6)

Palaeocopes are non-sulcate to quadrilobate, typically 0·5–5·0 mm long (adults), and are the most diversified and prolific Ordovician ostracode group. Their most important lobal-sulcal sculptures are a preadductorial node (L2) and an adductorial sulcus (S2). An anterior lobe (L1), posterior lobe (L4), and posteroventral elevation/lobe (L3) also often occur. Adventral sculptures are closely related to sexual dimorphism and possible brood care; domiciliar dimorphism is rare. Marginal sculptures as well as a slight (usually left) valve overlap often occur (for example, see Schallreuter 1982*a*).

TEXT-FIG. 5. Systematic position and presence of Ordovician non-palaeocope ostracode families and subfamilies in: A, Ibero-Armorica; B, British Isles; C, Baltoscandia. The non-palaeocope Ordovician faunas discussed herein fall into four orders: Order Beyrichiocopa: suborders Binodicopa (2), Leiocopa (3), Paraparchitocopa (4), and Eridostraca (5). Order Platycopa: suborders Cytherelliformes (6), Punciocopa (7), uncertain suborder (8). Order Podocopa: suborders Metacopa (9), Cypridocopa (10), Cytherocopa (11), and Parapodocopa (12). Order Leperditiocopa (13).

Typical forms from all the listed suborders (except 12) are illustrated for general comparison. All drawings are of external views except those for suborders Metacopa and Cytherocopa (9 and 11), whose most significant features are internal (stop-pegs and inner lamella respectively). O., Order; So., Suborder. Numbers given to families follow on from text-fig. 4.



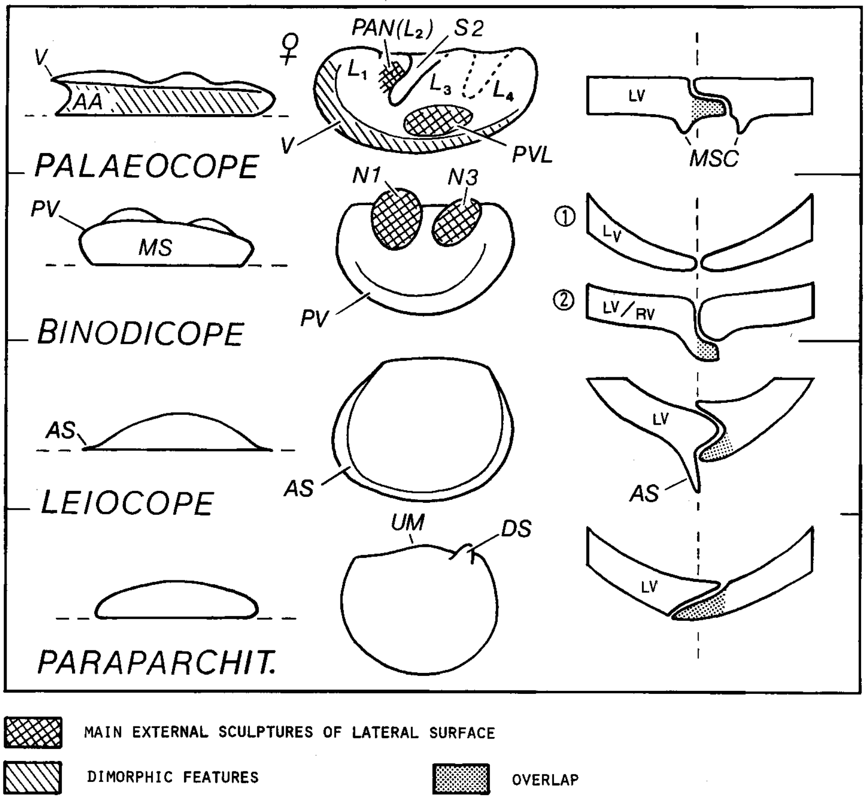
O.	So.	Superfamily	Family	Subfamily	A	B	C
	2	DREPANELLACEA	17 Drepanellidae				●
			18 Dolborellidae				
			19 Bolliidae		●	●	●
			20 Quadrijugatoridae		●		
		AECHMINACEA	21 Aechminidae		●	●	●
			22 Circulinidae		●	●	●
			23 Spinigeritidae		●	●	●
		SUPERFAM. NOV.			●	●	●
	3	APARCHITACEA	24 Aparchitidae	1 Aparchitinae 2 Subfam. nov.1 3 Subfam. nov.2	● ●		● ●
			25 Glanditidae				
			26 Fam. nov.				●
	4	PARAPARCHITACEA	27 Jaanussoniidae				●
			28 Paraparchitidae				
	5		29 Conchoprimitiidae		●		●
			30 Schmidtellidae				
			31 Eridoconchidae	1 Eridoconchinae 2 Cryptophyllinae		●	●
	6	KLOEDENELLACEA	32 Monotiopleuridae		●		●
		LEPERDITELLACEA	33 Leperditellidae				●
	7	KIRKBYACEA	34 Kirkbyidae	1 Kirkbyinae			●
			35 Amphissitidae	1 Arcyzoninae		●	●
	8		36 Lomatopisthiidae				●
			37 Bassleratiidae				
	9	THLIPSURACEA	38 Fam. nov.				●
		HEALDIACEA	39 Healdiidae				
			40 Punctaparchitidae				●
		BAIRDIOCYPRIDACEA	41 Bairdiocyprididae			●	●
			42 Budnianellidae				●
			43 Balticellidae				●
		TRICORNINACEA	44 Tricorninidae				●
	10	BAIRDIACEA	45 Alanellidae				
			46 Beecherellidae				●
			47 Bairdiidae	1 Bairdiinae 2 Processobairdiinae 3 Subfam. nov.			●
			48 Fam. nov.				●
	11	BYTHOCYTHERACEA	49 Syltheridae			●	●
	12	SUPERFAM. NOV.	50 Conodomyridae				●
	13		51 'Kiaeriidae'				●
			52 Isochilinidae	1 Tirisochilininae 2 Isochilininae			●

Palaeocopes may be classified into the infraorders Beyrichimorpha and Primitiopsiomorpha. The latter (comprising only a single superfamily, Primitiopsacea) are non- to bi-sulcate, have posterior antral dimorphism and, in contrast with other palaeocopes, normally have a right valve overlap (text-fig. 9). Beyrichiomorphs (e.g. see Schallreuter 1977*f*, 1978*a*, 1987) typically have either an antrum (Hollinomorpha) or crumina (Cruminata = post-Ordovician) as an egg/brood-care area in heteromorphs (presumed females).

The Hollinomorpha comprises:

a. Superfamily Hollinacea (text-fig. 9). Highly diversified throughout the Ordovician. Non-sulcate to quadrilobate. Velar dimorphism sometimes occurs, as does 'marginal' dimorphism. Antral dimorphism is expressed as a dolonal or admarginal concavity either without (= a botulus) or with loculi. Another adventral dimorphic sculpture, the histium, is present in some groups (e.g. Tetradellidae). Domicilar, egorovellid (see Schallreuter 1978*a*) size and/or proportional dimorphism can also be closely associated with typical antral dimorphism.

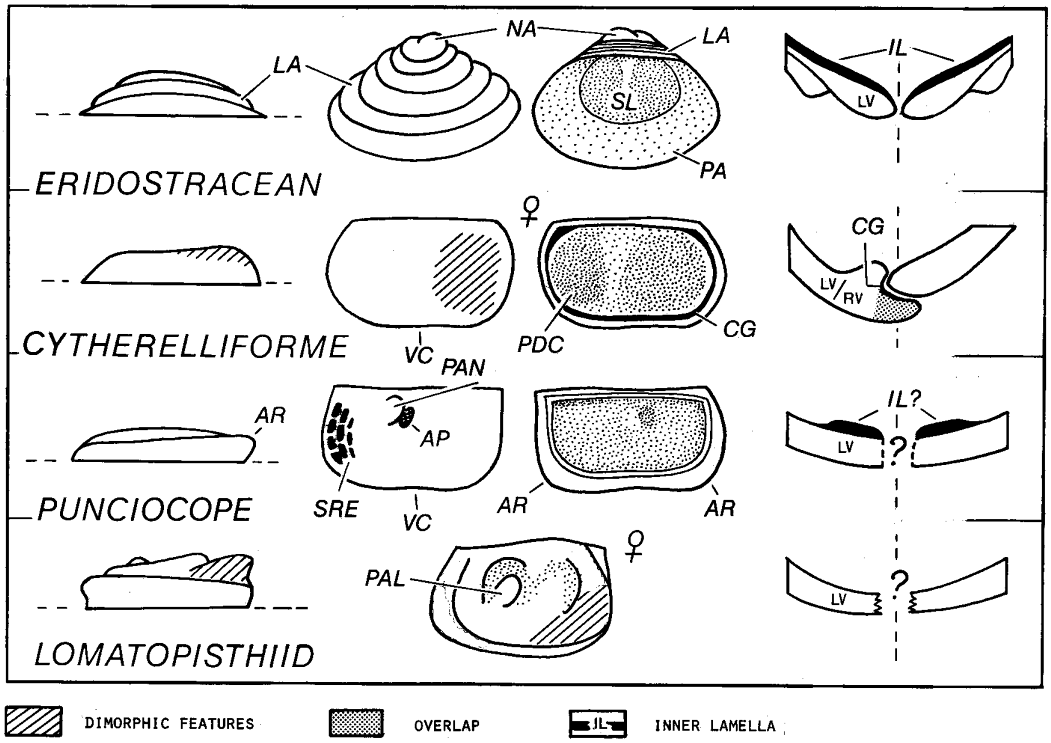
b. Superfamily Eurychilinacea (text-fig. 9). In contrast with Hollinacea the velum of Eurychilinacea is, typically, tubulose. In many cases both velar dimorphism and dimorphism affecting marginal structures occur. A loculate antrum rarely occurs and histial sculptures are unknown.



TEXT-FIG. 6. Main morphological features of palaeocopes, binodicopes, leiocopes, and paraparchitocopes. From left to right: ventral view; left lateral view; and a schematic cross-section of the ventral contact margin. Two types of contact margin occur in binodicopes: 1, no overlap; 2, reverse overlap. The following abbreviations apply to text-figs. 6–9. AA, admarginal antrum; AP, adductorial pit; AMS, adductorial muscle scars; AR, adventral ridge; AS, adventral sculpture; CG, contact groove; DS, dorsal spine; ET, eye tubercle; H, histium; HA, histial antrum; IL, inner lamella; L_1–L_4, lobes 1, 2, 3, 4; LA, lamella; LP, lappet; LV, left valve; MB, marginal brim; MS, marginal surface; MSC, marginal sculpture; N1, anterior node; N3, posterior node; NA, nauplioconch; OP, overlap platform; OSR, outer stop-ridge; PA, paleola; PAL, preadductorial lobe; PAN, preadductorial node; PDC, posterior domiciliar concavity; PV, pseudovelum; PVL, posteroventral lobe; RV, right valve; S, sulcus; S2, adductorial sulcus; SL, sulcament; SP, stop-pit; SR, stop-ridge; SRE, shell reticulation; STP, stop-peg; UM, umbo; V, velum; VC, ventral concavity; VD, velar dolon; VE, vestibulum; VSR, ventral stop-ridge.

Suborder Binodicopa (text-fig. 6)

Compared to palaeocopes, binodicopes have a relatively simple morphology with comparatively few taxonomically useful features. Valve sculpture consists of prominent to obsolescent lateral nodes (N1, N3), one of which often has a marked spine or is sometimes divided into three swellings. Unlike most palaeocopes a velum is absent, though a rounded peripheral ridge (pseudovelum) may occur between lateral and marginal surfaces. The nodes may be completely or incompletely connected by ridges (for example, see Vannier 1986*a*). Possible dimorphism in binodicopes mainly involves slight differences in domicilial shape or in carapace size and outline (e.g. see Schallreuter 1980*a*; Vannier 1986*a*). Intraspecific reversal of valve overlap occurs (Schallreuter 1980*b*).



TEXT-FIG. 7. Main morphological features of eridostracans, cytherelliformes, punciocopes, and lomatopisthiids (suborder uncertain (8); see text-fig. 5). From left to right: ventral view; external left lateral view; internal left lateral view (except for lomatopisthiids); and a schematic cross-section of the ventral contact margin. All abbreviations are listed under text-fig. 6.

Suborder Leiocopa (text-fig. 6)

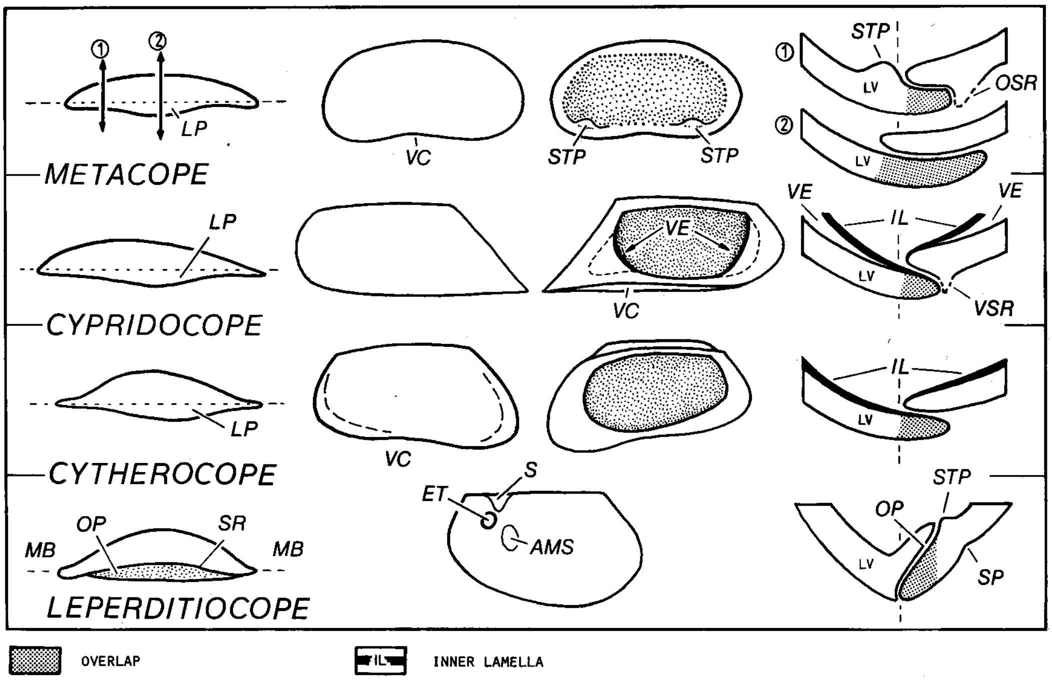
Most leicopes listed herein (text-fig. 16) belong to the family Aparchitidae (see Schallreuter 1973*a*). Most are smooth or punctate, lack any lobal-sulcal sculptures, and are slightly umbonate. Overlapping right valves have a contact ridge and a contact groove running parallel to the margin (Schallreuter 1977*b*). Adventral sculpture may occur (only on the left valve) as a ridge or a row of spines.

Suborder Paraparchitocopa (text-fig. 6)

The paraparchitaceans discussed herein all belong to the Jaanussoniidae (Schallreuter 1971*b*, 1986). They are small to medium-sized, non-sulcate, and inequivalved. The left valve usually bears an umbonate sculpture and/or a dorsal spine of varying shape and position. Right valve overlap; sexual dimorphism may occur (Schallreuter 1971*b*).

Suborder Eridostraca (text-fig. 7)

Compared to palaeocopes, binodicopes, and metacopes, Ordovician eridostracans form a minor group, but uniquely for ostracodes show molt retention (see Schallreuter 1977*a*, 1987). Only the Conchoprimitiidae and Eridoconchidae are represented in the Ordovician of Europe. Adventral sculpture may occur within these groups (Schallreuter 1988). A well-marked umbo usually occurs, as do two dorsal nodes on the nauplioconch (first instar). A broad inner lamella (paleola: see



TEXT-FIG. 8. Main morphological features of metacopes, cypridocopes, and leperditiocopes. Overlap conditions of metacopes are illustrated by transverse sections 1 and 2. From left to right: ventral view; external left lateral view and (except for leperditiocopes) internal left lateral view; and a schematic cross-section of the ventral contact margin. All abbreviations are listed under text-fig. 6.

Gramm 1984) and a sulcament occur internally. Valves connect simply, without overlap (Schallreuter 1977*a*).

Suborder Cytherelliformes (text-fig. 7)

The commonest cytherelliformes are the Monotiopleuridae, which typically have a contact groove, left or right valve overlap, and slight ventral concavity. Dimorphism of the kloedenellid type (Guber and Jaanusson 1964) is expressed as a broad posterior domiciliar concavity in heteromorphs.

Suborder Punciocopa (text-fig. 7)

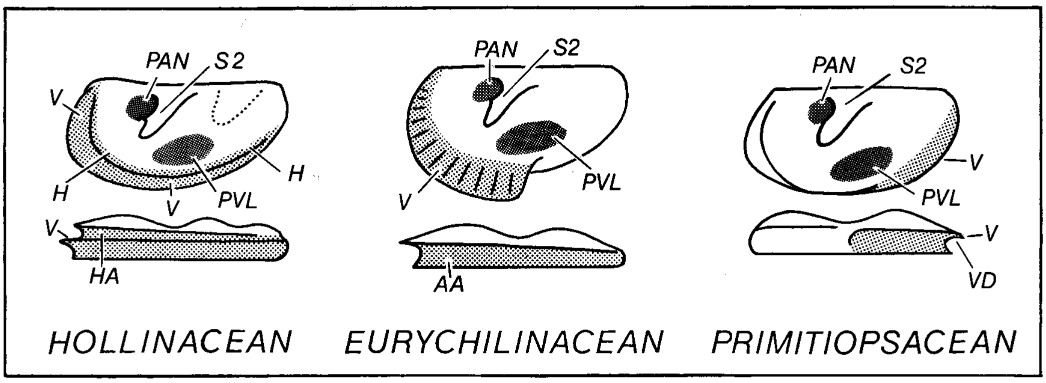
This suborder is essentially represented by the Kirkbyacea (see Schallreuter and Jones 1984), which are non-dimorphic and which typically have an adductorial ('kirkbyan') pit, a ventricular concavity, and reticulation (sensu Schallreuter 1973*b*).

Suborder uncertain, Family Lomatopisthiidae (text-fig. 7)

Lomatopisthiids occur rarely in the Ordovician of Europe (Schallreuter 1978*a*). They have a strong, ridge-like velar sculpture and a special type of posterior domiciliar dimorphism (Guber and Jaanusson 1964).

Suborder Metacopa (text-fig. 8)

Metacopes are abundantly documented from throughout the Ordovician of Baltoscandia. The taxonomy of the Podocopa, including metacopes, is partly based on internal features (Adamczak 1976; Schallreuter 1979). Metacopes are inequivalved, normally lack a calcified inner lamella, and



▨ DIMORPHIC FEATURES ■ MAIN LOBAL SCULPTURES

TEXT-FIG. 9. Main morphological features of three major Ordovician palaeocope superfamilies: primitiopsaceans, eurychilinaceans, and hollinaceans. External lateral and ventral views of a left heteromorphic valve are figured in each case. All abbreviations are listed under text-fig. 6.

typically have a larger left valve bearing a contact groove or internal stop-ridges (stop-pegs) (see Schallreuter 1978*a*, 1979, 1986). Antero- and posteroventral outer stop-ridges may also occur (Schallreuter 1979, pl. 1). Dimorphism is unknown.

Suborder Cypridocopa (text-fig. 8)

Typical Cypridocopa (superfamily Bairdiacea) are mostly very small ($<0{\cdot}5$ mm) to medium-sized (1–2 mm), oblong Ordovician podocopes with a broad inner lamella and often distinct vestibula (Schallreuter 1978*b*, 1979, 1986). Overlap conditions are like those of metacopes: the smaller right valve often has a continuous ventral stop-ridge.

Suborder Cytherocopa (text-fig. 8)

All known European Ordovician Cytherocopa belong to the Syltheridae. Most have a broad inner lamella without vestibula and flattened anterior and posterior external surfaces (Schallreuter 1977*d*, 1978*b*, 1984*a*).

Suborder Parapodocopa

The Conodomyridae and Fam. nov., represented by the single genera *Conodomyra* and *Oejlemyra* respectively, are assigned to this small group (Schallreuter, unpublished). *Conodomyra* (Schallreuter 1977*d*, 1986) has a completely fused inner lamella which, in contrast with most other Ordovician podocopes, is broadest centroventrally.

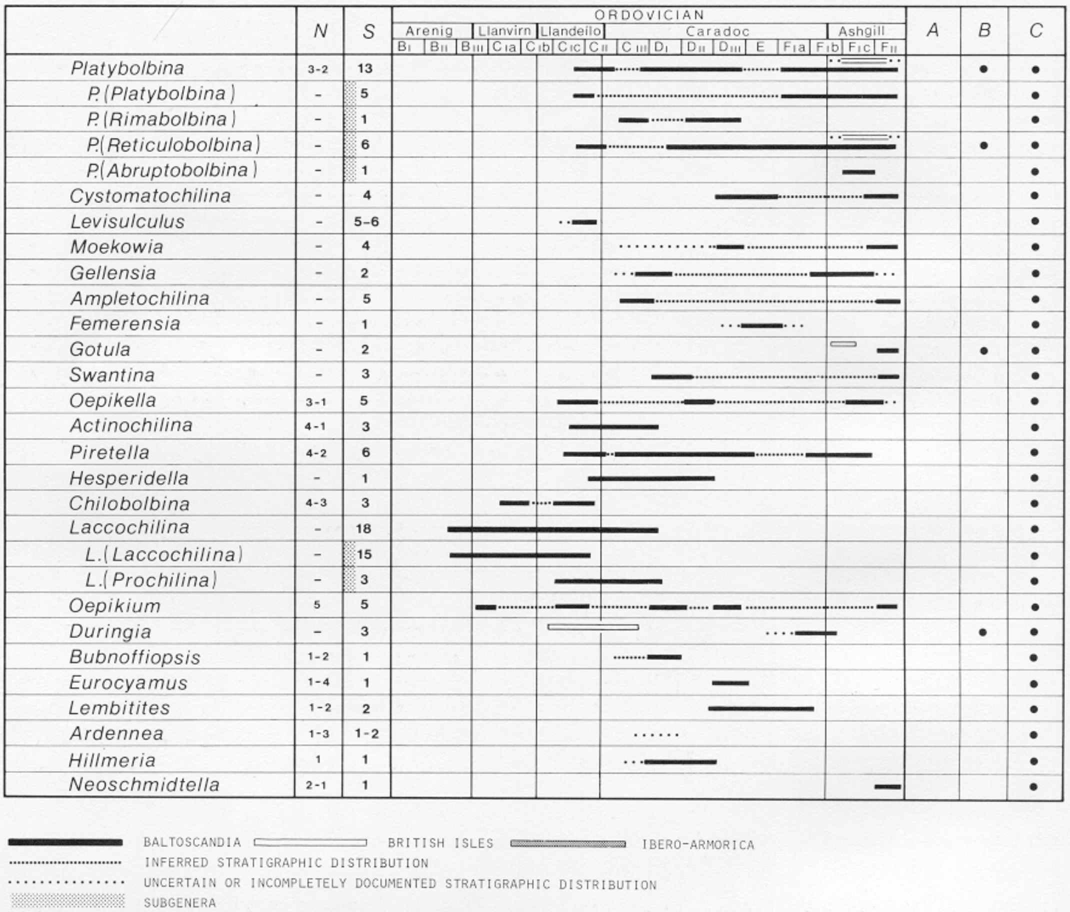
Suborder Leperditiocopa (text-fig. 8)

Ordovician leperditiocopes are extremely rare in Europe. They belong to the families Isochilinidae and Kiaeriidae (Schallreuter 1984*d*). All Baltoscandian forms are kiaeriids (Schallreuter 1984*d*), having an anterior and posterior (centroventral) marginal brim and one of two stop-pegs internally on the overlapping right valve.

STEPS USED IN THE ANALYSIS OF THE OSTRACODE FAUNAS

The occurrence and stratigraphic distribution are given for 223 genera from Baltoscandia, the British Isles, and Ibero-Armorica (text-figs. 10–17). This accounts for some 800 species and subspecies. Taxa from Podolia (text-fig. 1: 34), Thuringia (text-fig. 1: 36), and those of uncertain

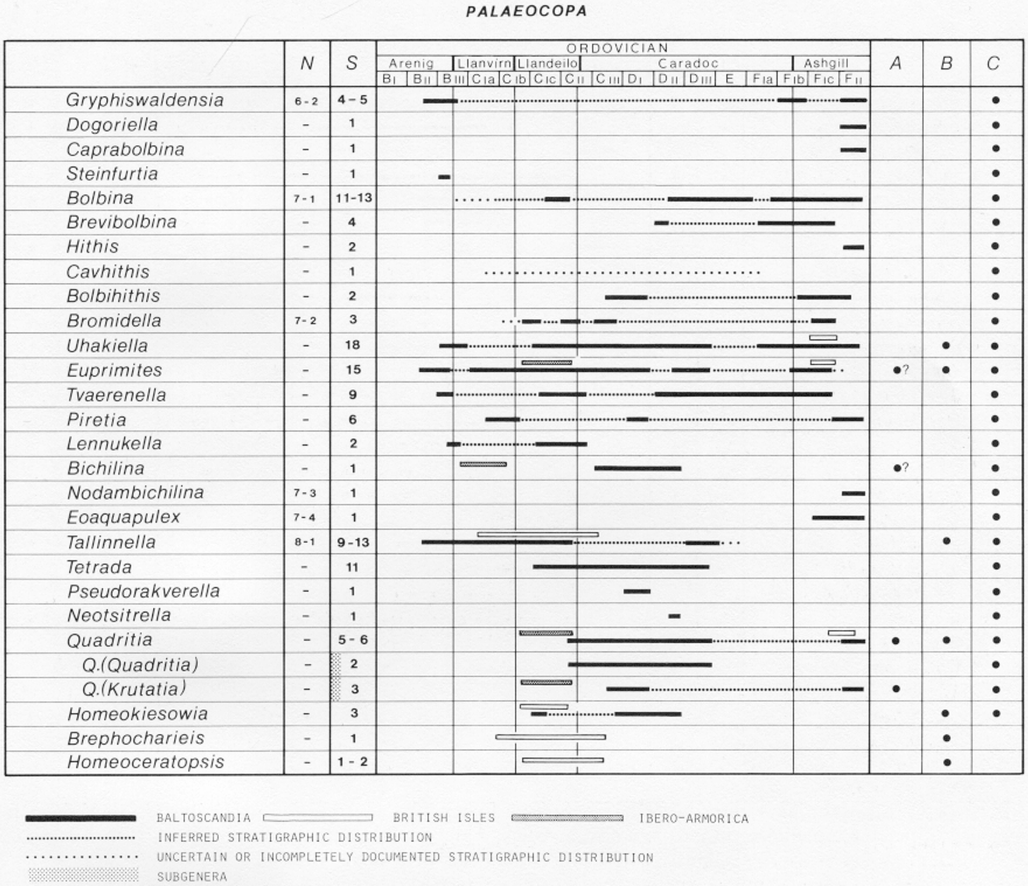
PALAEOCOPA



TEXT-FIG. 10. Stratigraphic range and occurrence of Ordovician palaeocope ostracode genera and subgenera of the superfamilies Eurychilinacea and Primitiopsacea (see text-fig. 4) in: A, Ibero-Armorica; B, British Isles; C, Baltoscandia. Stratigraphy as for the British Series (Arenig to Ashgill) and the main stratigraphic subdivisions of the Baltic Ordovician (B_I to F_{II}; see text-fig. 2). N = taxonomic position of genera and subgenera according to the serial numbers of families and subfamilies as listed in text-fig. 4; – indicates 'taxonomic position as above'; S = total number of species within each genus or subgenus. Occurrences mainly based on papers given in text-fig. 1. All symbols apply to text-figs. 10–17.

systematic position have not been plotted. Occurrences of some (especially the palaeocope) subgenera are included (text-figs. 10–14). The data were drawn from published and (rarely) in press studies.

Qualitative and quantitative analysis of these data has been undertaken in four steps (text-fig. 18). First, the taxonomic composition (in % of genera) of the Baltoscandian, British, and Ibero-Armorican ostracode faunas is compared for the Ordovician as a whole. Comparison is made at various taxonomic levels, such as subordinal, familial, and (for tetradellids and ctenonotellids) subfamilial levels. The relative abundance in the Ordovician of palaeocopes and binodicopes is also compared between the three areas. Secondly (text-fig. 18: 2), the changing taxonomic



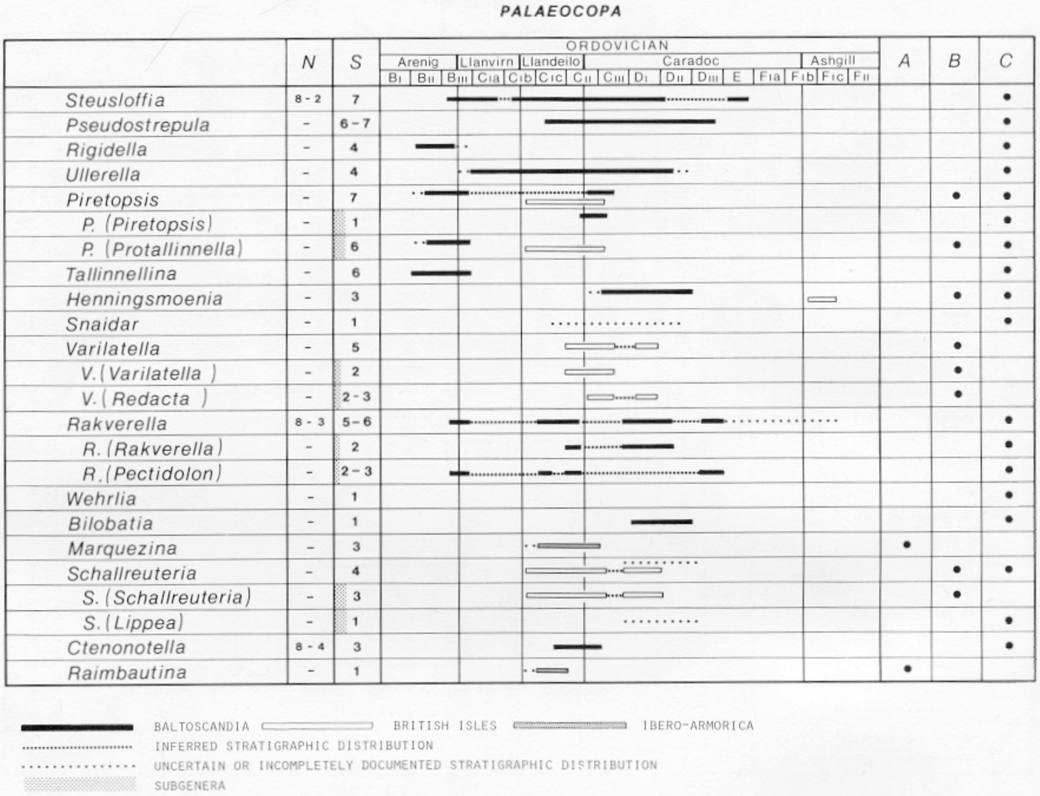
TEXT-FIG. 11. Stratigraphic range and occurrence of Ordovician palaeocope ostracode genera and subgenera of the families Euprimitiidae, Tvaerenellidae, and Ctenonotellidae (in part; see also text-figs. 4 and 12) in: A, Ibero-Armorica; B, British Isles; C, Baltoscandia. All symbols as for text-fig. 10.

composition and diversity of the ostracode faunas through the Ordovician within each area have been examined. Thirdly (text-fig. 18: 3), generic links are identified between the total Ordovician ostracode faunas of Baltoscandia, the British Isles, and Ibero-Armorica (for example, see text-fig. 29). Fourthly (text-fig. 18: 4), the changing pattern of genera common to two or more of the areas is examined through Ordovician time.

COMPARISON OF THE TAXONOMIC COMPOSITION OF BALTOSCANDIAN, BRITISH, AND IBERO-ARMORICAN ORDOVICIAN OSTRACODE FAUNAS

Baltoscandia

The higher taxa. Thirteen suborders are represented in the Ordovician ostracode faunas of Baltoscandia (text-fig. 19). The main groups are the palaeocopes (54% of total genera) and binodicopes (18%); other groups include the metacopes (9%) and a range of minor groups

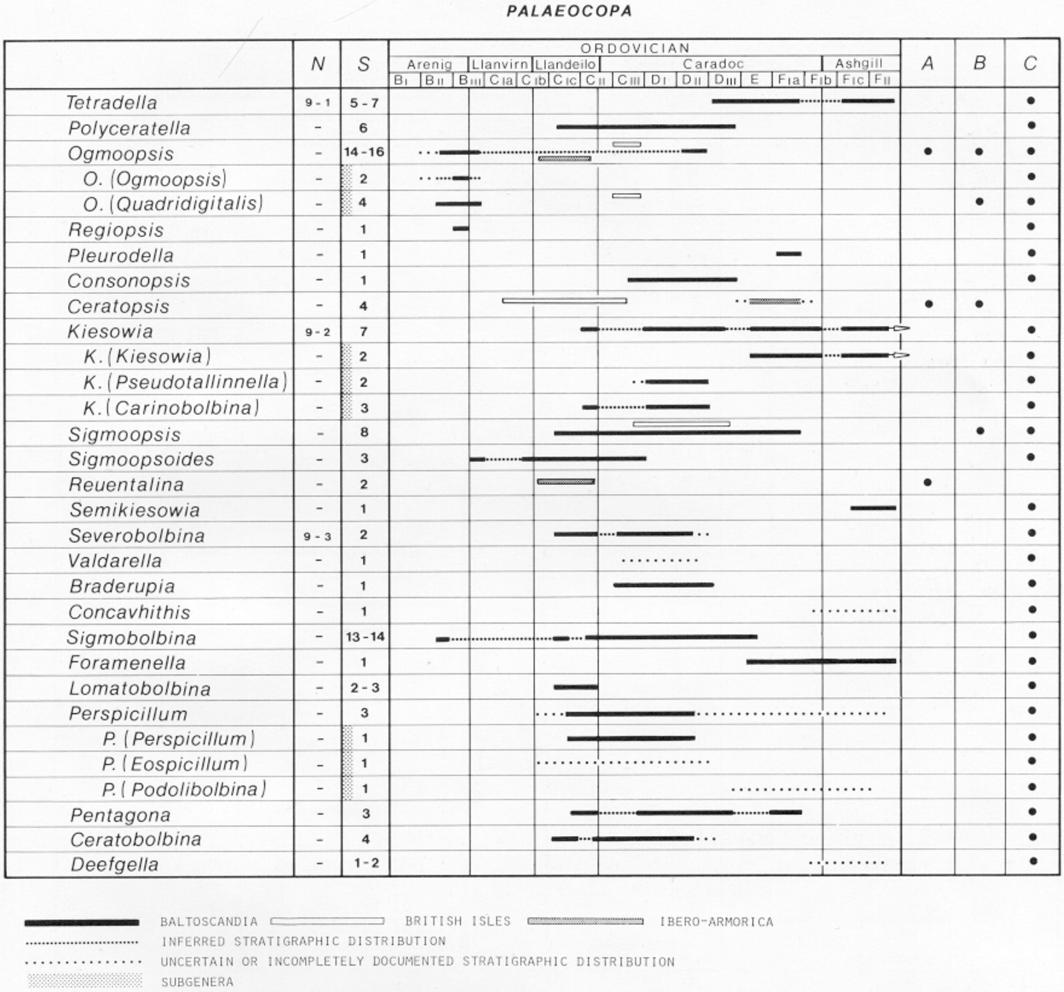


TEXT-FIG. 12. Stratigraphic range and occurrence of Ordovician palaeocope ostracode genera and subgenera of the family Ctenonotellidae (in part; see also text-figs. 4 and 11) in: A, Ibero-Armorica; B, British Isles; C, Baltoscandia. All symbols as for text-fig. 10.

(<1%–4·5%). The total fauna reflects broad morphological diversity: compare, for example, a palaeocope, a leiocope, an eridostracan, and a leperditiocope (text-figs. 6–8). The palaeocope: binodicope ratio is about 3:1 (% genera) and almost 5:1 (% species) (text-fig. 22).

Composition of the palaeocopes. Although primitiopsacean, eurychilinacean, and hollinacean palaeocopes are represented in Baltoscandia (text-figs. 4 and 9), about 75% of the palaeocope genera are hollinaceans (text-fig. 23). Of the six hollinacean families present, tetradellids are dominant (37% genera; 32% species). Typical tetradellids (for example, *Sigmoopsis rostrata*, Pl. 27, fig. 10) have a long sigmoidal adductorial sulcus (S2) and a well-developed dimorphic (botulate or loculate) velum.

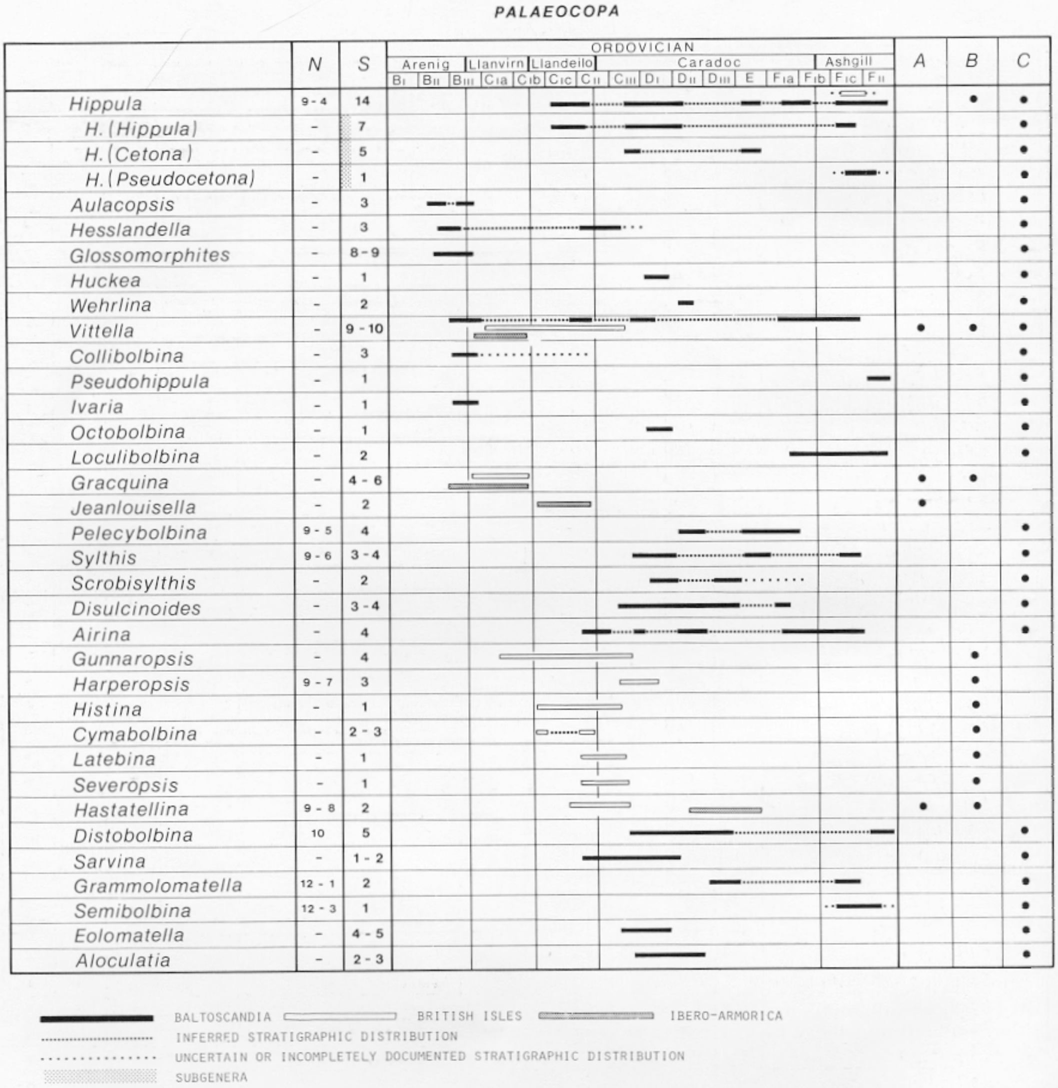
Other important palaeocope groups are the hollinacean ctenonotellids (17% genera; 20% species) and tvaerenellids (13%; 18%), and the eurychilinacean oepikellids (10%; 10%) and eurychilinids (4%; 7%). Ctenonotellids (for example, *Tallinnella*: see Öpik 1937; Sarv 1959) have a long S2, botulate velar dimorphism, and in many cases show a lobal reduction and dissolution into cristae. In tvaerenellids, dimorphism is expressed as a well-marked dolon running up to the dorsal margin (for example, in *Bromidella sarvi*: see Schallreuter 1983*b*). In contrast, oepikellids (for example, *Platybolbina* (*Rimabolbina*) *rima*: see Schallreuter 1983*a*, pl. 13, figs. 5 and 6) and eurychilinids



TEXT-FIG. 13. Stratigraphic range and occurrence of Ordovician palaeocope ostracode genera and subgenera of the family Tetradellidae (in part; see also text-figs. 4 and 14) in: A, Ibero-Armorica; B, British Isles; C, Baltoscandia. All symbols as for text-fig. 10.

(for example, *Piretella triebeli*: see Schallreuter 1983*a*, pl. 13, fig. 1) have a very simple lobal sculpture, a velum consisting mainly of hollow tubules, and velar dimorphism associated with marginal dimorphism.

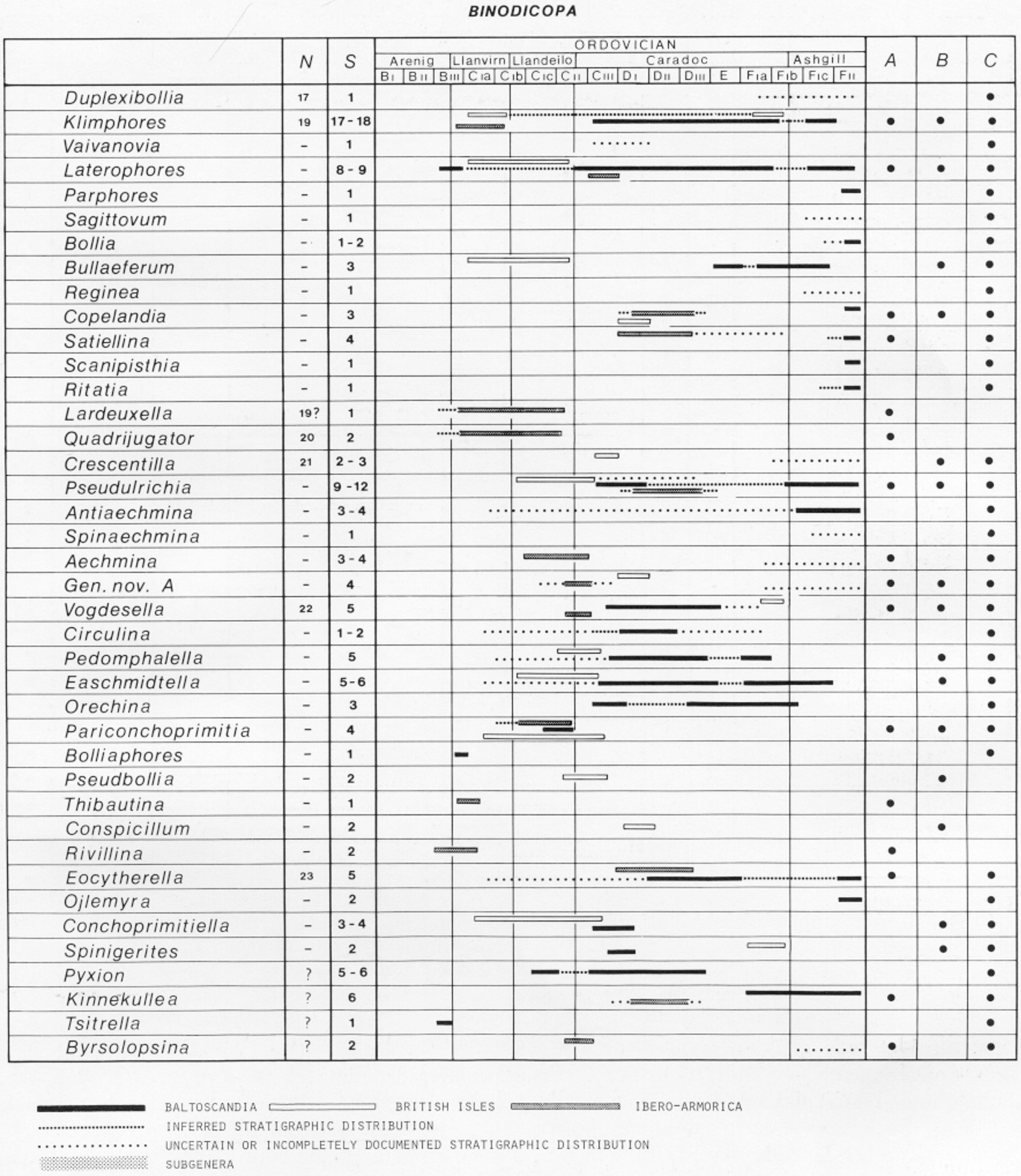
Ordovician tetratellids of Baltoscandia (text-fig. 25) consist of four main subfamilies: Glossomorphitinae (33% of tetradellid genera), Sigmoopsinae (21%), Perspicillinae (18%), and Tetradellinae (15%). The occurrence and morphological variation of a second adventral sculpture (the histium), in addition to the velum, determines the recognition of these subfamilies (see Schallreuter 1978*a*). Sigmoopsines are characterized by both histial and velar dimorphism; in contrast, in tetradellines the histium (present in tecnomorphs and heteromorphs) is not dimorphic. In most perspicillines the histium occurs only in heteromorphs and is connected anteriorly to the velum. Glossomorphitinae have a dimorphic velum and heteromorphs exhibit an adventral sculpture (histio-velum) which



TEXT-FIG. 14. Stratigraphic range and occurrence of Ordovician palaeocope ostracode genera and subgenera of the families Tetradellidae (see also text-fig. 13), Sarvinidae and Hollinidae (see text-fig. 4) in: A, Ibero-Armorica; B, British Isles; C, Baltoscandia. All symbols as for text-fig. 10.

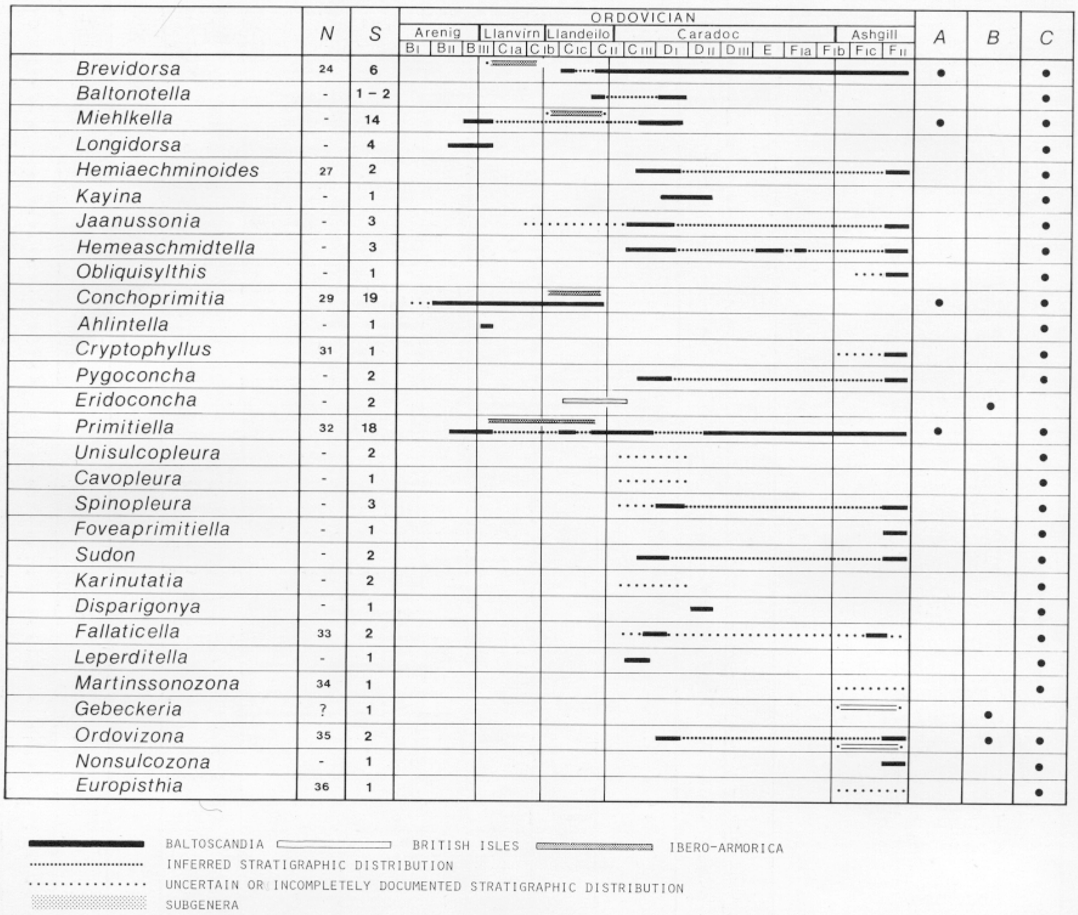
is thought to represent a coalesced velum and histium. The Baltoscandian ctenonotellid fauna (text-fig. 26) is dominated by the subfamilies Steusloffiinae (43% of ctenonotellid genera) and Tallinnellinae (31%). Their distinctive feature is lobal sculpture (Schallreuter 1976, 1978*a*).

Composition of the binodicopes. As dimorphic adventral sculptures are typically lacking in binodicopes, their classification is especially difficult. Lobal and adventral morphology (see text-fig. 6) distinguish binodicope families, of which four are dominant in Baltoscandia: bolliids (35% of binodicope genera), circulinids (22%), aechminids (16%), and spinigeritids (13%) (text-fig. 24).



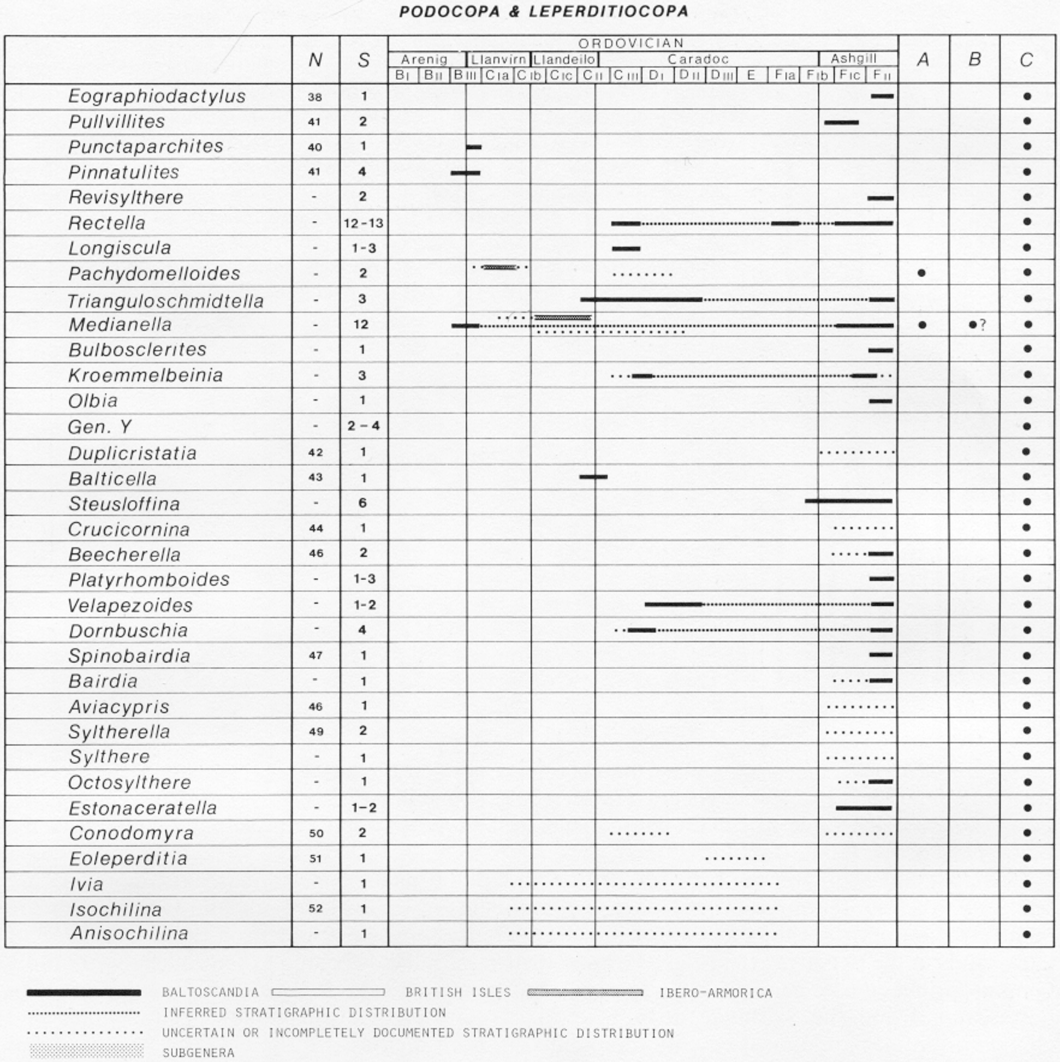
	N	S	A	B	C
Duplexibollia	17	1			●
Klimphores	19	17-18	●	●	●
Vaivanovia	–	1			●
Laterophores	–	8-9	●	●	●
Parphores	–	1			●
Sagittovum	–	1			●
Bollia	–	1-2			●
Bullaeferum	–	3		●	●
Reginea	–	1			●
Copelandia	–	3	●	●	●
Satiellina	–	4	●		●
Scanipisthia	–	1			●
Ritatia	–	1			●
Lardeuxella	19?	1	●		
Quadrijugator	20	2	●		
Crescentilla	21	2-3		●	●
Pseudulrichia	–	9-12	●	●	●
Antiaechmina	–	3-4			●
Spinaechmina	–	1			●
Aechmina	–	3-4	●		●
Gen. nov. A	–	4	●	●	●
Vogdesella	22	5	●	●	●
Circulina	–	1-2			●
Pedomphalella	–	5		●	●
Easchmidtella	–	5-6		●	●
Orechina	–	3			●
Pariconchoprimitia	–	4	●	●	●
Bolliaphores	–	1			●
Pseudbollia	–	2		●	
Thibautina	–	1	●		
Conspicillum	–	2		●	
Rivillina	–	2	●		
Eocytherella	23	5	●		●
Ojlemyra	–	2			●
Conchoprimitiella	–	3-4		●	●
Spinigerites	–	2		●	●
Pyxion	?	5-6			●
Kinnekullea	?	6	●		●
Tsitrella	?	1			●
Byrsolopsina	?	2	●		●

TEXT-FIG. 15. Stratigraphic range and occurrence of Ordovician binodicope ostracode genera (see text-fig. 5) in: A, Ibero-Armorica; B, British Isles; C, Baltoscandia. All symbols as for text-fig. 10. For gen. nov. A: see Vannier 1986*a*.


LEIOCOPA, PARAPARCHITOCOPA, ERIDOSTRACA & PLATYCOPA

TEXT-FIG. 16. Stratigraphic range and occurrence of Ordovician leiocope, paraparchitocope, eridostracan, and platycope ostracode genera (see text-fig. 5) in: A, Ibero-Armorica; B, British Isles; C, Baltoscandia. All symbols as for text-fig. 10.

Characteristically, bolliids have two prominent lateral nodes (as in *Klimpores planus*: see Schallreuter 1980*b*) and an adventral sculpture (pseudovelum) separating lateral and steep marginal surfaces. Such nodes occur as spine-like structures in most aechminids (as in *Antiaechmina pseudovelata:* see Schallreuter 1977*c*), which also have an acute angle between the ventral surface and contact plane. Circulinids (for example, *Vogdesella subovata*: see Schallreuter 1980*a*) have rather obsolete nodes, a very convex domicilium, and a more or less complete pseudo-velum; the marginal surface (mainly flattened) forms an acute angle with the contact plane (as in most aechminids). Spinigeritids differ from circulinids by their more elongate carapace and slight swellings anteriorly and posteriorly (for example, *Spinigerites spiniger:* see Schallreuter 1980*a*). Baltic spinigeritids provide a rare example of dimorphism (merely involving valve size) within the binodicopes.



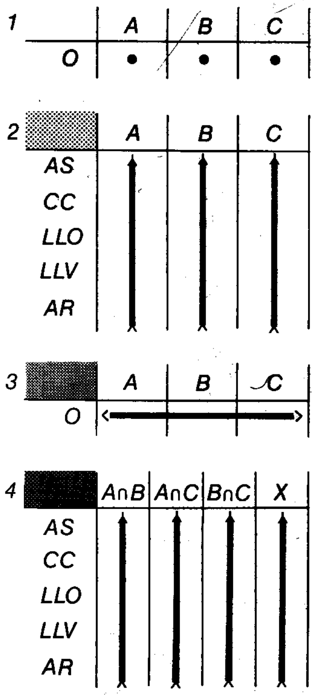
	N	S	A	B	C
Eographiodactylus	38	1			●
Pullvillites	41	2			●
Punctaparchites	40	1			●
Pinnatulites	41	4			●
Revisylthere	-	2			●
Rectella	-	12-13			●
Longiscula	-	1-3			●
Pachydomelloides	-	2	●		●
Trianguloschmidtella	-	3			●
Medianella	-	12	●	●?	●
Bulbosclerites	-	1			●
Kroemmelbeinia	-	3			●
Olbia	-	1			●
Gen. Y	-	2 – 4			●
Duplicristatia	42	1			●
Balticella	43	1			●
Steusloffina	-	6			●
Crucicornina	44	1			●
Beecherella	46	2			●
Platyrhomboides	-	1-3			●
Velapezoides	-	1-2			●
Dornbuschia	-	4			●
Spinobairdia	47	1			●
Bairdia	-	1			●
Aviacypris	46	1			●
Syltherella	49	2			●
Sylthere	-	1			●
Octosylthere	-	1			●
Estonaceratella	-	1–2			●
Conodomyra	50	2			●
Eoleperditia	51	1			●
Ivia	-	1			●
Isochilina	52	1			●
Anisochilina	-	1			●

TEXT-FIG. 17. Stratigraphic range and occurrence of Ordovician podocope and leperditiocope ostracode genera (see text-fig. 5) in; A, Ibero-Armorica; B, British Isles; C, Baltoscandia. For genus Y: see Schallreuter 1979. All symbols as for text-fig. 10.

In summary, Baltic Ordovician ostracode faunas are dominated by palaeocopes (especially tetradellids and ctenonotellids) and binodicopes (especially bolliids).

The British Isles

The higher taxa. Though the database on British Ordovician ostracode faunas is not as complete as that for Baltoscandia, palaeocopes and binodicopes again represent the dominant components. Minor groups (also found in Baltoscandia) include metacopes, eridostracans, and cytherelliformes. The palaeocope : binodicope ratio (text-fig. 22) is about 1·5 : 1 (% genera) and 1·8 : 1 (% species). Palaeocope dominance over binodicopes is somewhat less marked than in Baltoscandia.



TEXT-FIG. 18. Schematic illustration of successive steps followed in the present study. Faunal data from: A, Ibero-Armorica; B, British Isles; C, Baltoscandia. 1, comparison of the taxonomic composition of the ostracode faunas of the three regions for the entire Ordovician (O); 2, the changing taxonomic composition and diversity of ostracode faunas within each area through the Ordovician from the Arenig (AR) to Llanvirn (LLV), Llandeilo (LLO), Caradoc (CC), and Ashgill (AS) series; 3, faunal similarities between Ibero-Armorica, the British Isles, and Baltoscandia for the whole Ordovician (O); 4, changes in the nature and amount of taxa common to two regions (AnB = Ibero-Armorica/British Isles; AnC = Ibero-Armorica/Baltoscandia; BnC = British Isles/Baltoscandia) and between the three regions (X = AnBnC) from the Arenig to the Ashgill.

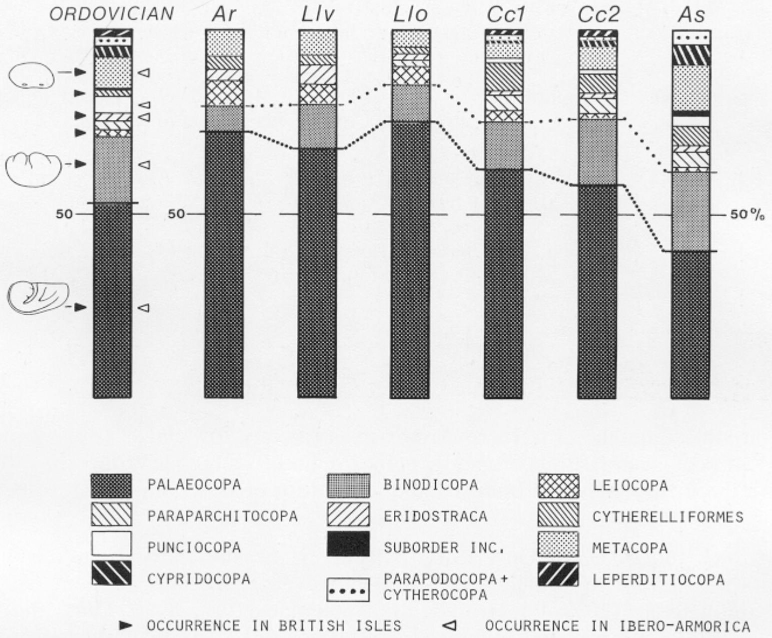
Composition of the palaeocopes. The main families are tetradellids (48% genera; 53% species), ctenonotellids (33%; 36%), tvaerenellids (7·5%; 4·5%), oepikellids (7·5%; 4·5%), and oepikiids (3·5%; 2%). These are the same five main components and show the same relative abundance as in the Baltic palaeocope fauna (text-fig. 23).

There are some differences between British and Baltic palaeocope faunas: ctenonotellids are relatively much more important palaeocope components in the British Isles, and tvaerenellids are relatively less important than in Baltoscandia. Differences are also apparent in the composition of tetradellids in the two areas (text-fig. 25): most British tetradellids belong to the endemic subfamily Gunnaropsinae (46% genera; 52% species), but perspicillines (18% of tetradellid genera in Baltoscandia) and the Sylthinae do not seem to occur in the British Isles. Tetradellines and glossomorphitines are almost equally represented in both regions: 15·5% and 23% and 15% and 33% of total tetradellid genera and species in the British Isles and Baltoscandia respectively (text-fig. 25). Gunnaropsines typically show well-developed quadrilobation occasionally associated with cristae, an inclined histial ridge uniting anteroventrally with the velum, and a dolonal antrum. As for the ctenonotellids (text-fig. 26), the tallinnellines and (then) the steusloffines are the two major components of the second most generically abundant family in both regions.

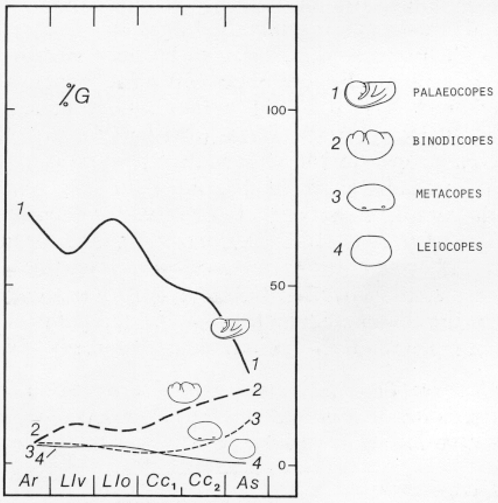
Composition of the binodicopes. The British and Baltic binodicope faunas show strong similarities, consisting of bollids (34% and 35% respectively of total binodicope genera), circulinids (40%; 22%), aechminids (13%; 14%), and spinigeritids (11%; 13%) (text-fig. 24).

Ibero-Armorica

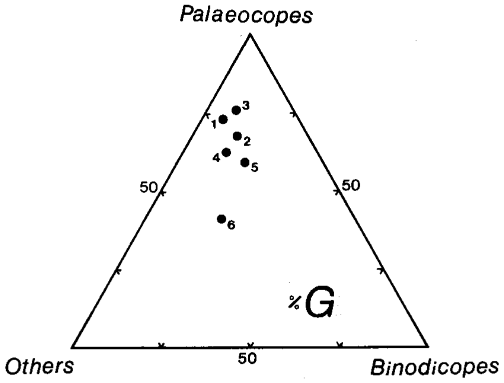
The higher taxa. The overall taxonomic composition of the Ibero-Armorican fauna (Vannier 1986*a*, *b*) is not fundamentally different from Baltoscandia or Britain, mainly consisting of palaeocopes and binodicopes with minor proportions of metacopes, eridostracans, and leiocopes (text-fig. 19).



TEXT-FIG. 19. Generic percentage abundance of ostracode suborders for the Ordovician and its series in Baltoscandia. Data for the Caradoc is particularly abundant and well dated and is divided into two parts at the D_{II}/D_{III} boundary (see text-fig. 2).



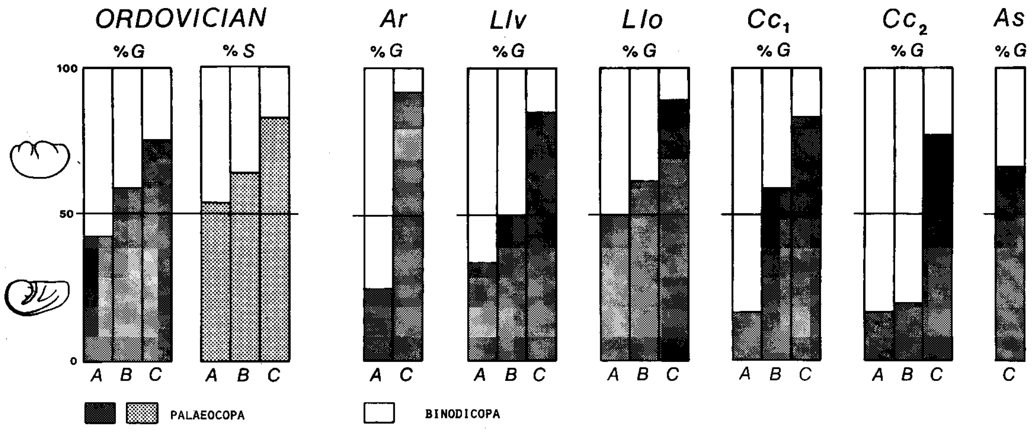
TEXT-FIG. 20. Changes in generic abundance of the four major ostracode suborders (given in % of the total fauna) known throughout the Ordovician of Baltoscandia. Lower and upper part of Caradoc as defined in text-fig. 19.



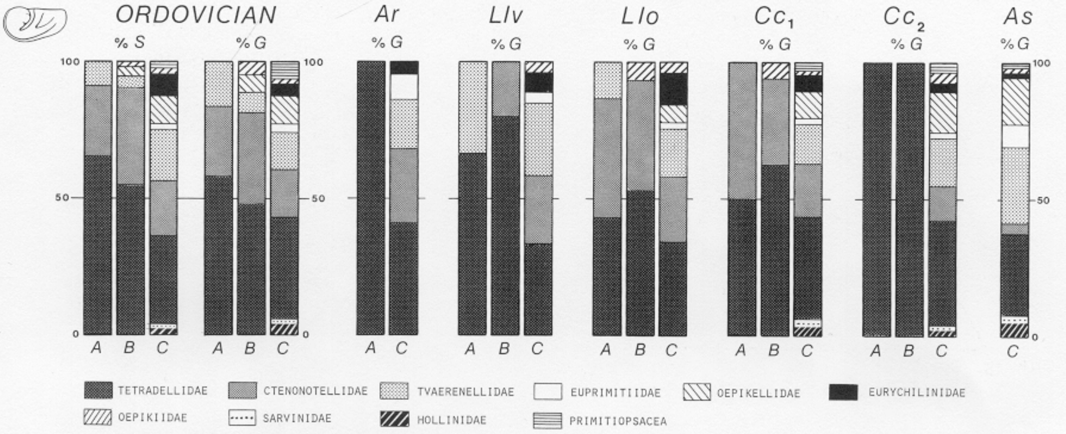
TEXT-FIG. 21. Changes in the composition of the ostracode fauna from Baltoscandia through the Ordovician, given in % of genera of palaeocopes, binodicopes, and 'other groups'. 1, Arenig; 2, Llanvirn; 3, Llandeilo; 4, 5, lower part and upper part of the Caradoc (as defined in text-fig. 19); 6, Ashgill.

However, a notable difference for Ibero-Armorica is its very low palaeocope : binodicope ratio (0·7 : 1, based on % of genera). Binodicopes form the dominant ostracode group, thereby contrasting markedly with the British Isles and Baltoscandia with ratios of 1·5 : 1 and 3·1 : 1, respectively (text-fig. 22).

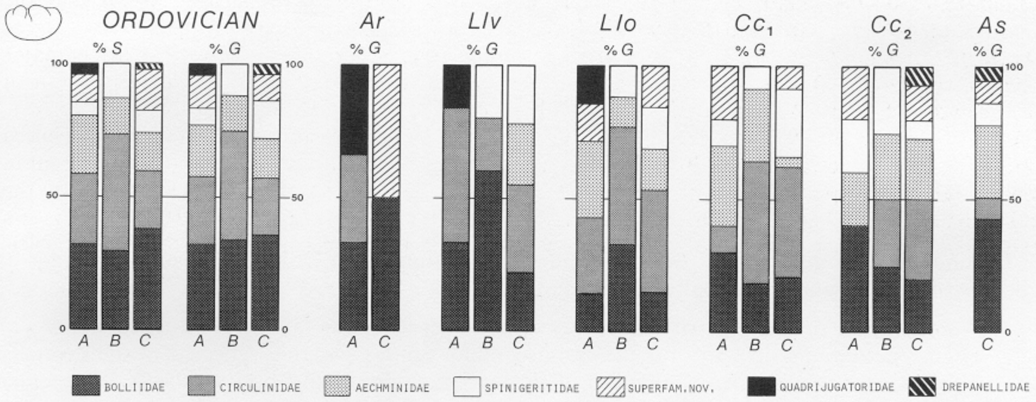
Composition of the palaeocopes. Only three palaeocope families have been recognized in the Ordovician of Ibero-Armorica (text-fig. 23): Tetradellidae (58% palaeocope genera; 66% palaeocope species), Ctenonotellidae (26%; 24%), and Tvaerenellidae (16%; 8%). Thus, the three major components of the British and Baltic faunas also occur (with a particularly high proportion of tetradellids) in Ibero-Armorica. Detailed analysis of each family shows additional similarities. Ibero-Armorican tetradellids (text-fig. 25) consist of glossomorphitines (44% of tetradellid genera and 55% species), tetradellines (30%; 22·5%), and sigmoopsines (13·5%; 15·5%), groups present in similar relative proportions within the two other regions. Differences are mainly expressed by the absence of ('British') gunnaropsines and ('Baltic') perspicillines and sylthines. The Ibero-Armorican ctenonotellid fauna (text-fig. 26), in common with those in Baltoscandia and the British Isles,



TEXT-FIG. 22. Generic (and specific) percentage abundance to palaeocope of binodicope ostracodes for the Ordovician and its series in: A, Ibero-Armorica; B, British Isles; C, Baltoscandia. The Caradoc is divided into two, at the D_{II}/D_{III} boundary (see text-fig. 2). All data from text-figs. 10–15.



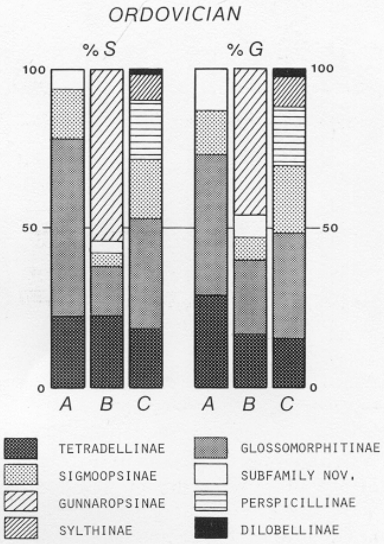
TEXT-FIG. 23. Generic (and specific) percentage abundance of palaeocope families for the Ordovician and its series in: A, Ibero-Armorica; B, British Isles; C, Baltoscandia. The Caradoc is divided as in text-fig. 22. All data from text-figs. 10–14.

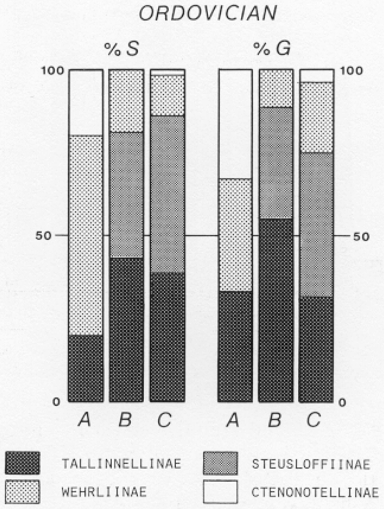


TEXT-FIG. 24. Generic (and specific) percentage abundance of binodicope families for the Ordovician and its series in: A, Ibero-Armorica; B, British Isles; C, Baltoscandia. The Caradoc is divided as in text-fig. 22. All data from text-fig. 15.

contains a high proportion of wehrliines and tallinnellines (both 33% of total ctenonotellid genera). In contrast with the other regions, steusloffines are apparently unknown in Ibero-Armorica, while ctenonotellines reach a comparatively high proportion (33% of ctenonotillid genera).

Composition of the binodicopes. Ordovician binodicopes of Ibero-Armorica are remarkably similar in general composition to those of the British Isles and Baltoscandia (text-fig. 24). For example, the relative importance of bolliids (the dominant binodicope group in Ibero-Armorica) is almost exactly the same in the three regions (32%, 34%, 35%, respectively, of genera); this is also true for aechminids (19%, 13%, 16%) and to a lesser extent for circulinids (26%, 40%, 22%). The only significant faunal anomaly of Ibero-Armorican binodicopes is the presence of the Quadrijugatoridae, a superfamily otherwise known only from North America.





TEXT-FIG. 25 (*left*). Generic (and specific) percentage abundance of tetradellid (hollinacean) subfamilies for the Ordovician (Arenig to Ashgill) in: A, Ibero-Armorica; B, British Isles; C, Baltoscandia. All data from text-figs. 13 and 14.

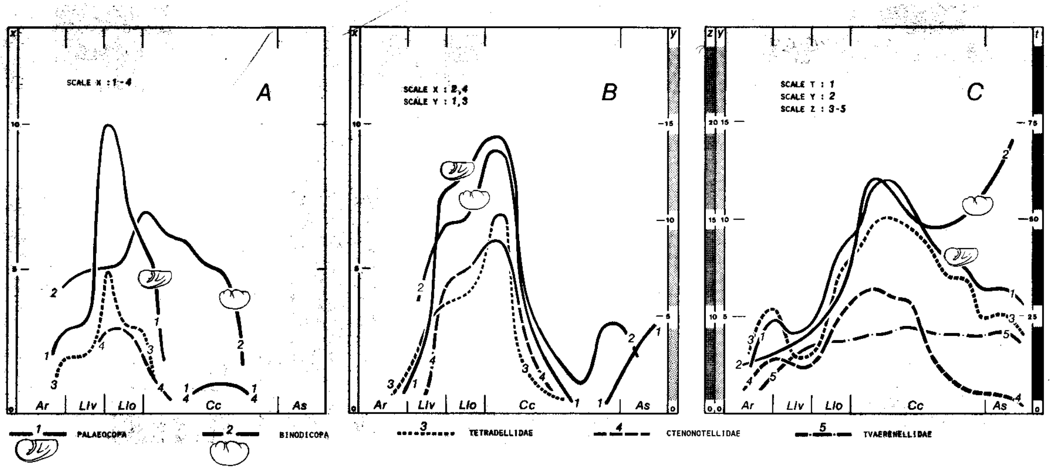
TEXT-FIG. 26 (*right*). Generic (and specific) percentage abundance of ctenonotellid (hollinacean) subfamilies for the Ordovician (Arenig to Ashgill) in: A, Ibero-Armorica; B, British Isles; C, Baltoscandia. All data from text-figs. 11 and 12.

In summary, a comparison of the taxonomic composition of the Ordovician ostracod faunas of Ibero-Armorica, Britain, and Baltoscandia shows:

1. A remarkable diversity at virtually all taxonomic levels of the faunas in all three areas.
2. Higher taxonomic diversity for the Baltoscandian faunas—mainly reflected in the diversity of suborders and of palaeocope families. This feature undoubtedly partly reflects the greater amount of taxonomic work undertaken on Ordovician ostracodes from the Baltic compared to those from the other two areas.
3. Close similarities, between each domain, in the occurrence and relative proportions of all the dominant taxonomic groups of palaeocopes (tetradellids, ctenonotellids) and binodicopes (bolliids, circulinids, aechminids).
4. Differences in the palaeocope : binodicope ratio show a gradually increasing dominance of palaeocopes from Ibero-Armorica to the British Isles and then to Baltoscandia.
5. Other, minor differences occur in the composition of the Tetradellidae and Ctenonotellidae. At the subfamily level each area may display unique characteristics, such as the occurrence of gunnaropsines in the British Isles and the absence of steusloffines in Ibero-Armorica.

GENERIC ABUNDANCE OF ORDOVICIAN PALAEOCOPES AND BINODICOPES IN BALTOSCANDIA, BRITAIN, AND IBERO-ARMORICA

Changes in generic abundances of palaeocopes and binodicopes, from Arenig to Ashgill, in the three regions investigated are given in text-fig. 27.



TEXT-FIG. 27. Total numbers of genera, through the Ordovician, of palaeocope and binodicope ostracodes and of selected palaeocope families (Tetradellidae, Ctenonotellidae, and Tvaerenellidae) from: A, Ibero-Armorica; B, British Isles; C, Baltoscandia. Ar = Arenig; Llv = Llanvirn; Llo = Llandeilo; Cc = Caradoc; As = Ashgill. All data from text-figs. 10–17. Four different scales are used to enable comparison of abundant and minor groups.

Baltoscandia (text-fig. 27C)

Palaeocopes in general (for example, major families Tetradellidae, Ctenonotellidae), form a relatively poor late Arenig–early Llanvirn fauna (maximum 23 genera), slightly decrease in abundance during the Llanvirn and are marked by a steep increase in numbers of genera (from 25 to 50) during the Llandeilo. Maximum numbers of palaeocope genera (about 60) occur during the early Caradoc; this is followed by a gradual reduction into the Ashgill (about 30 genera). Interestingly, although similar variations in numbers of genera are also observed in binodicopes up to the mid-Caradoc, their maximum abundance is reached during the Ashgill (14 genera) and coincides with a marked reduction in numbers of palaeocope genera.

British Isles (text-fig. 27B)

Generic abundance in the British Isles shows a similar pattern to that of Baltoscandia. Highest generic abundance of palaeocopes (for example, tetradellids, ctenonotellids) and binodicopes occurs during the early Caradoc. However, a later Caradoc reduction in numbers of genera in both groups is more dramatic than that seen in Baltoscandia and, moreover, the British faunas show a more marked increase during the late Llanvirn–Llandeilo. As for Baltoscandia, British late Caradoc ostracode faunas are dominated by binodicope genera. Ashgill ostracode faunas from Britain are still insufficiently documented to place significance on its numbers of genera plotted in text-fig. 27.

Ibero-Armorica (text-fig. 27A)

Variations in generic abundance of Ibero-Armorican palaeocopes and binodicopes differ slightly from those of British and Baltic faunas by having a palaeocope (e.g. tetradellid and ctenonotellid) maximum (lower–middle Llandeilo) and subsequent decrease (late Llandeilo) which is earlier, and a binodicope pattern whose maximum (late Llandeilo–early Caradoc) does not coincide with that of palaeocopes and which thereafter (during the later Caradoc) shows a more gradual decrease and greater numbers of genera compared to palaeocopes.

VARIATION OF OSTRACODE FAUNAL COMPOSITION, THROUGH THE ORDOVICIAN, IN BALTOSCANDIA, BRITAIN, AND IBERO-ARMORICA

Baltoscandia

Faunal diversity at subordinal level increases notably between the lower and upper Ordovician: the Arenig, Llandeilo, Caradoc, and Ashgill having six, seven, eleven, and twelve suborders respectively (text-fig. 19).

During the Arenig to Llandeilo, palaeocopes predominate, comprising 73%, 68%, and 75% of the Arenig, Llanvirn, and Llandeilo ostracode genera, respectively. Other higher taxa, such as binodicopes (e.g. 12% in the Llanvirn), metacopes (e.g. 7% in the Arenig), or leiocopes (e.g. 6% in the Llanvirn), are minor faunal components. No significant changes occur during this period (text-fig. 19).

During the Caradoc to Ashgill, newly introduced ostracode groups or groups previously forming minor faunal components become relatively more important; they include metacopes (4% of lower Caradoc genera; 6% in upper Caradoc; 12% in Ashgill), binodicopes (13% in lower Caradoc; 18% in upper Caradoc; 21% in Ashgill), and cytherelliformes (7% in lower Caradoc). Palaeocopes consequently show a marked drop in relative importance from the lower Caradoc through to the Ashgill, where they comprise some 40% of ostracode genera. A similar, though less important, trend also affects leiocopes, which form 5% of genera in the Llandeilo and 1% in the Ashgill. Cypridocopes, parapodocopes, cytherocopes, punciocopes, and leperditiocopes seem to appear first during the early Caradoc.

To reinforce these points, the generic percentage abundance (of the total ostracode fauna) of the four major suborders (Palaeocopa, Binodicopa, Metacopa, Leiocopa) known from throughout the Ordovician of Baltoscandia are given in text-fig. 20. It is again seen that the late Llandeilo–early Caradoc is a period of significant faunal changes, when both palaeocopes and leiocopes begin to decrease, and binodicopes and metacopes start to increase in relative abundance (see also text-fig. 21).

Palaeocopes dominate binodicopes throughout the Ordovician of Baltoscandia, though the palaeocope : binodicope generic ratio (see text-fig. 22) decreases gradually from about 11·5 : 1 in the Arenig to 2 : 1 for the Ashgill. Ratios for the Llanvirn, Llandeilo, and upper and lower Caradoc are 6, 8·5, 5·5, and 3·5 : 1 respectively.

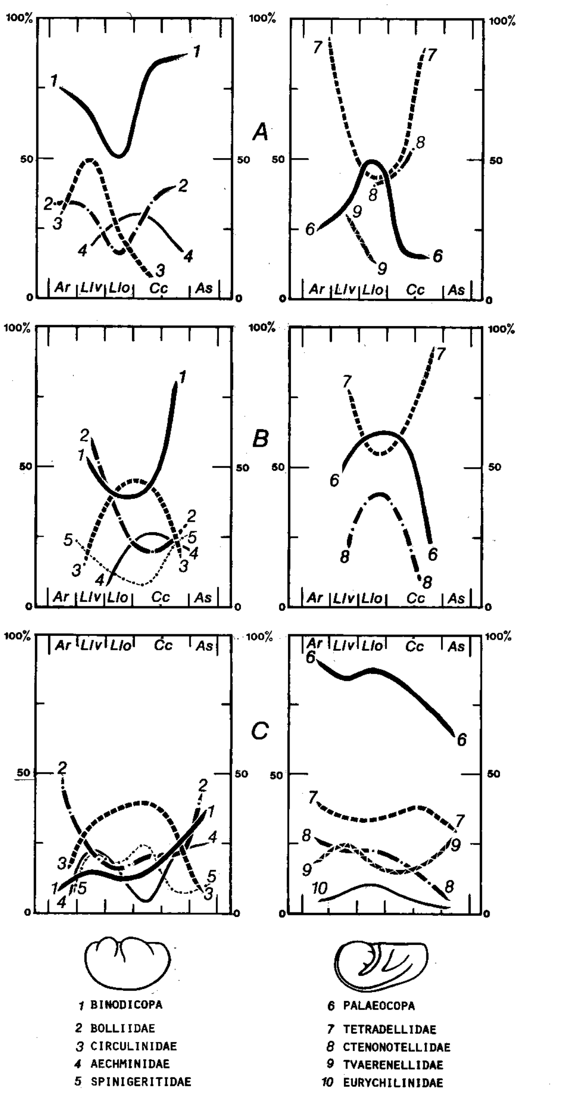
Diversity of palaeocope families (text-fig. 23) reaches a maximum during the Caradoc and Ashgill (ten families), thus contrasting with the Arenig–Llandeilo interval (five to seven families). The late Llandeilo–early Caradoc interval is characterized by the appearance of new palaeocope taxa such as Oepikellidae, Sarvinidae, Hollinidae, and Primitiopsacea. Text-figs. 23 and 28C clearly show:

a. The relatively stable importance of tvaerenellid and tetradellid palaeocopes throughout the Ordovician, comprising 18–25% and 31–37% respectively, of the total palaeocope genera.

b. A gradual decrease of the relative abundance of ctenonotellids from the Arenig to the Ashgill (25% and 5% respectively, of the total palaeocope genera).

c. In contrast to euprimitiids, a maximum relative abundance of eurychilinid genera during the Llandeilo.

Binodicope higher taxa diversity increases reasonably uniformly from lower to upper Ordovician (text-fig. 24), four families occurring during the Llanvirn and six in the Ashgill. The Llandeilo to early Caradoc again appears as a period of significant faunal change (text-fig. 28C). For example, the percentage of circulinid genera (of the total binodicope fauna) drops from a 40% maximum during the late Llandeilo–early Caradoc to 8% in the Ashgill. Similar variations are observed for the Spinigeritidae (text-fig. 28C, graph 5). The zenith of the circulinids apparently coincides with a period of reduction of bolliids (minimum in the Llandeilo) and of aechminids (early Caradoc).



TEXT-FIG. 28. Generic percentage abundance of palaeocopes and binodicopes and of some of their important families through the Ordovician from: A, Ibero-Armorica; B, British Isles; C, Baltoscandia.

1. Percentage of binodicope genera of the total palaeocope-binodicope fauna.

2, 3, 4, 5. Percentage of bolliid, circulinid, aechminid, and spinigeritid genera, respectively, of the total binodicope fauna.

6. Percentage of palaeocope genera of the total palaeocope-binodicope fauna.

7, 8, 9, 10. Percentage of tetradellid, ctenonotellid, tvaerenellid, and eurychilinid genera, respectively, of the total palaeocope fauna.

Ar = Arenig; Llv = Llanvirn; Llo = Llandeilo; Cc = Caradoc; As = Ashgill.

British Isles

There is a lack of data from the Arenig, where ostracodes are rare, and the Ashgill data are unpublished. Comparisons will thus be restricted to Llanvirn-late Caradoc faunas and will consider only the (well-documented) palaeocopes and binodicopes.

Palaeocopes are most dominant during the Llandeilo (palaeocope : binodicope generic ratio = 1·6 : 1) and early Caradoc (1·4 : 1), but show a substantial reduction in the upper Caradoc (0·25 : 1), when binodicopes become the most important ostracode group (text-fig. 22). A similar, though less marked, trend was noted for Baltoscandia.

Analysis of important groups of palaeocopes and binodicopes (text-figs. 23, 24, 28B) show diametrically opposite trends during the Llandeilo-early Caradoc. This interval witnesses a maximum development of ctenonotellids (40% of Llandeilo palaeocopes), circulinids (45% of Llandeilo binodicopes), and aechminids (26% of early Caradoc binodicopes) and coincides with an important reduction of tetradellids (55% of Llandeilo palaeocopes), bolliids, and spinigeritids (18% and 8% respectively, of early Caradoc binodicopes).

The most important differences in trends compared to Baltoscandia (text-fig. 28) affect the palaeocope faunas, especially tetradellids, whose significance to palaeocope faunas is much more constant in Baltoscandia than in Britain. The reduced importance of British ctenonotellids from Llandeilo to late Caradoc contrasts with their gradual decrease throughout the Ordovician of Baltoscandia. On the other hand, the two major binodicope groups in both Baltoscandia and the British Isles, circulinids and bolliids, have comparable percentage values (in relation to their respective binodicope faunas) and trends throughout the Ordovician (text-fig. 28).

Ibero-Armorica

The palaeocope: binodicope generic ratio through the Ordovician in Ibero-Armorica (text-fig. 22) indicates two major phases: a gradual increase in relative abundance of palaeocopes from the Arenig (0·3 : 1) to a Llandeilo maximum (1 : 1), followed by a marked palaeocope reduction beginning in the Caradoc (0·2 : 1). The same general trend was noted for both Baltoscandia and the British Isles. The trend in Ibero-Armorica is distinctive in that the faunal changes seem to occur earlier in the Caradoc than in the British Isles and is much more abruptly expressed than in Baltoscandia.

The only really significant trend observed within the palaeocope fauna of Ibero-Armorica is provided by the tetradellids, whose parabolic graph is exactly the same as for the British tetradellids, with minimum relative generic abundance in the Llandeilo (text-fig. 28).

As with the palaeocopes, the most diversified binodicope faunas in Ibero-Armorica are known during the Llandeilo and early Caradoc (text-fig. 24), a period marked by an increase in aechminids (28% of Llandeilo binodicope genera) and spinigeritids (10% of early Caradoc binodicope genera) as well as by the presence of circulinids (28% and 10% of Llandeilo and early Caradoc binodicope genera, respectively) and bolliids (14% and 30%, respectively). Apparently, circulinids are not represented within the late Caradoc faunas.

Ratios of bolliid, circulinid, and aechminid genera with respect to the total binodicope fauna of Ibero-Armorica are comparable to those for the British Isles and Baltoscandia. Thus, the bolliid : binodicope ratio reaches a minimum almost simultaneously in all three regions, during the late Llandeilo–early Caradoc. However, the maximum value of the circulinid : binodicope ratio occurs during the Llanvirn in Ibero-Armorica compared to the Llandeilo–Caradoc for the British Isles and the early Caradoc for Baltoscandia.

In summary, variations in generic abundance and faunal composition of Baltic, British, and Ibero-Armorican ostracode faunas show:

1. General common trends throughout the Ordovician:
   - *a.* An increasing importance (% of genera) of palaeocopes over binodicopes during the Arenig–Llanvirn to a Llandeilo peak followed by a general decrease (marked in Ibero-Armorica and the British Isles) of palaeocopes during the Caradoc.
   - *b.* Except for Baltic binodicopes, palaeocopes and binodicopes reach maximum generic diversity during the Llandeilo–early Caradoc, a trend confirmed at a higher taxonomic level with a particularly steep increase in numbers of suborders recorded in Baltoscandia in the Llandeilo.
   - *c.* Comparable variations in the relative percentage of major binodicope families (Bolliidae and Circulinidae), and a peak of binodicope generic abundance during the early Caradoc.
2. Each domain has its own faunal characteristics, which include:
   - *a.* Persistent high diversity of families and genera of palaeocopes and binodicopes in Baltoscandia up to the Ashgill.
   - *b.* Similar parabolic graph trends of British and Ibero-Armorican tetradellids through the

Ordovician (Llandeilo minimum), thus contrasting with only minor variations in generic abundance of the group in Baltoscandia.

c. A uniform decline of Baltoscandian ctenonotellids, a trend not observed in the British Isles or Ibero-Armorica.

d. A marked reduction in generic abundance of palaeocopes in Britain and Ibero-Armorica during the Caradoc, compared to a more gradual decrease in Baltoscandia.

3. Faunal events suggested by variations of generic abundance of ostracode faunas seem to be diachronous in the three domains. The maximum abundance of palaeocopes occurs during the early Llandeilo, the late Llandeilo–early Caradoc and the early Caradoc in Ibero-Armorica, the British Isles and Baltoscandia, respectively. Diachronism is similarly observed for the rise and decline of this group.

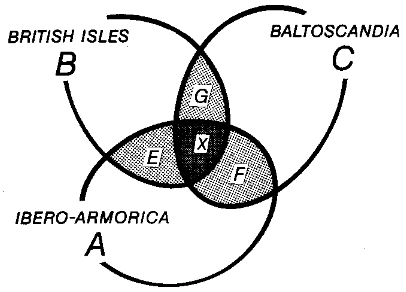
OSTRACODE GENERIC LINKS BETWEEN IBERO-ARMORICA, THE BRITISH ISLES, AND BALTOSCANDIA FOR THE ORDOVICIAN

The four palaeocopes *Platybolbina* (*Reticulobolbina*) *spongiosoreticulata* and *Uhakiella magnifica* (see Jones 1985, 1986), and *Sylthere vonhachti* (R. Orr, pers. comm.) and *Quadritia* (*Krutatia*) *iunior* (see Pl. 30, fig. 8), known from the Ashgill of the British Isles and Baltoscandia, represent the species-level contacts between the Ordovician of the three regions in question. Numerous links exist at generic and subgeneric level (text-figs. 10–17, 29–35). Text-fig. 29 names genera common to pairs of areas (E, Ibero-Armorica/British Isles; F, Ibero-Armorica/Baltoscandia; G, British Isles/Baltoscandia), and to all three regions (X). As for the data on faunal composition, comparisons will essentially focus on palaeocopes and binodicopes, which represent about 85% of the total common genera listed (text-fig. 29). The total number of genera of palaeocopes and binodicopes recorded herein from the Ordovician of each area is 12 and 16, respectively, in Ibero-Armorica; 27 and 15 in the British Isles; and 104 and 34 in Baltoscandia (text-fig. 30).

Generic affinities between Ibero-Armorica and the British Isles

These two regions have fifteen ostracode genera in common in the Ordovician (text-fig. 29): one metacope (*Medianella*), and seven palaeocopes and seven binodicopes belonging to several

	E	F	G	X
 1	Hastatellina Ceratopsis Gracquina	Bichilina	Duringia Homeokiesowia Tallinnella Piretopsis Schallreuteria Sigmoopsis Gotula Henningsmoenia Platybolbina Uhakiella Hippula	Ogmoopsis Vittella Euprimites Quadritia
 2	Copelandia	Satiellina Aechmina Eocytherella Kinnekullea Byrsolopsina	Bullaeferum Crescentilla Easchmidtella Pedomphalella Conchoprimitiella Spinigerites	Klimphores Laterophores Gen.nov. A Pseudulrichia Vogdesella Pariconchoprimitia
3		Miehlkella Brevidorsa Pachydomelloides Conchoprimitia Primitiella	Ordovizona	Medianella



TEXT-FIG. 29. Ordovician (Arenig–Ashgill) genera of Palaeocopa (1), Binodicopa (2), and other groups (3) occurring in two or more of the following regions: A, Ibero-Armorica; B, British Isles; C, Baltoscandia. E = genera common between A and B only; F = between A and C only; G = between B and C only; X = between all three regions (A, B, C). In further text-figs. A, B, C, E, F, G, and X will indicate corresponding number or percentages of genera.

	A	B	C	E	F	G	X	E+X	F+X	G+X	$\frac{E+X}{A+B-(E+X)}=R1$	$\frac{F+X}{A+C-(F+X)}=R2$	$\frac{G+X}{B+C-(G+X)}=R3$
PAL	12	27	104	3	1	11	4	7	5	15	0.22	0.04	0.13
BIN	16	15	34	1	5	6	6	7	11	12	0.29	0.28	0.44
PAL+BIN	28	42	138	4	6	17	10	14	16	27	0.25	0.10	0.19

TEXT-FIG. 30. Similarity indices for the Ordovician palaeocope (PAL), binodicope (BIN), and combined palaeocope-binodicope faunas variously between Ibero-Armorica, British Isles, and Baltoscandia. A, B, C: total number of genera known from Ibero-Armorica, British Isles, and Baltoscandia, respectively. E, F, G, X: number of genera common between Ibero-Armorica/British Isles, Ibero-Armorica/Baltoscandia, British Isles/Baltoscandia, and between all three areas, respectively. R1, R2, R3: similarity indices for Ibero-Armorica/British Isles, Ibero-Armorica/Baltoscandia, and British Isles/Baltoscandia, respectively.

families including the Tvaerenellidae, Ctenonotellidae, Tetradellidae, Bolliidae, Aechminidae, and Circulinidae.

In order to illustrate the relative importance of cosmopolitan palaeocope and binodicope genera, both graphical representation of results (e.g. text-figs. 29, 31, 32) and a similarity index (text-fig. 30) are used. The similarity index is defined as the ratio between the total number of genera in common between two areas (e.g. Ibero-Armorica and the British Isles = E + X: see text-figs. 29 and 30) and the total 'endemic' fauna (in this case A + B—(E + X)) from the two areas in question. The similarity indices (R1) for Ibero-Armorican and southern British Ordovician palaeocopes, binodicopes, and combined palaeocope-binodicope faunas are 0·22, 0·29, and 0·25, respectively.

Generic affinities between Ibero-Armorica and Baltoscandia

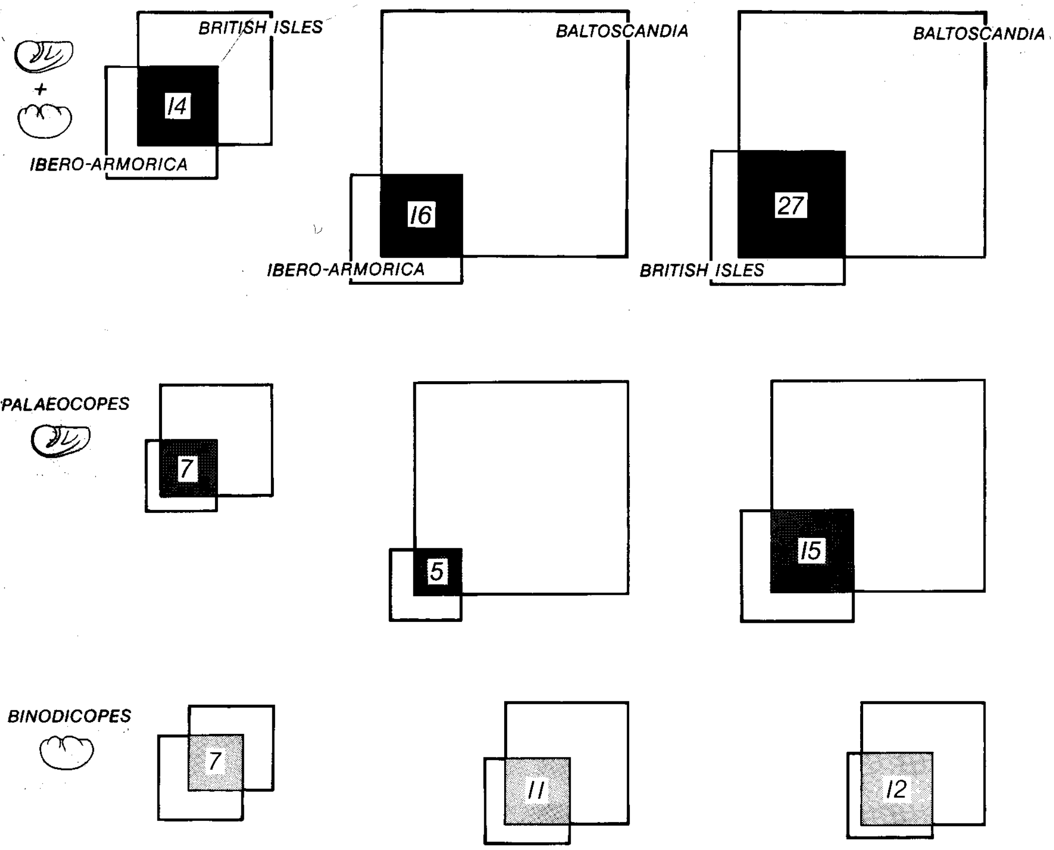
These two regions have a high number of binodicope (11) compared to palaeocope (5) genera in common (text-figs. 29, 31, 32). The binodicopes include bolliids (3), aechminids (3), circulinids (2), and spinigeritids (1). The palaeocopes are tvaerenellids (2), tetradellids (2), and ctenonotellids (1). The relevant similarity index (R2: text-fig. 30) is very low for palaeocopes (0·04) and very high for binodicopes (0·28). Although similarity indices R1 (Ibero-Armorica/British Isles) and R2 reach almost identical figures for binodicopes (0·29 and 0·28, respectively), they differ markedly for palaeocopes (0·22 and 0·04, respectively). Metacope genera (2), leiocopes (2), eridostracans (1), and cytherelliformes (1) are also common to Ibero-Armorica and Baltoscandia.

Generic affinities between the British Isles and Baltoscandia

A list of twenty-nine ostracode genera in common (text-fig. 29) indicates close ostracode faunal affinities between the British Isles and Baltoscandia in the Ordovician. Fifteen palaeocope and twelve binodicope genera occur in common (text-figs. 31 and 32), consisting of Ctenonotellidae (6), Tetradellidae (4), Oepikellidae (2), Tvaerenellidae (2), Oepikiidae (1), Circulinidae (4), Bolliidae (3), Aechminidae (3), and Spinigeritidae (2). Metacope (1) and punciocope (1) genera are also common to both regions. The British Isles/Baltoscandia similarity index, R3 (text-fig. 30), consequently reaches high values, especially for binodicopes (0·44). R1 and R2 for binodicopes are only 0·29 and 0·28, respectively. Nevertheless, despite a high number of palaeocope genera in common, the R3 palaeocope value (0·13) is less than the equivalent palaeocope similarly index for the British Isles and Ibero-Armorica (= 0·22; R1, text-fig. 30).

Ostracode genera common between the three regions

A substantial proportion (25%) of the genera in common between the regions in fact occur within all three areas (text-fig. 29); they comprise binodicopes (six genera), palaeocopes (four), and

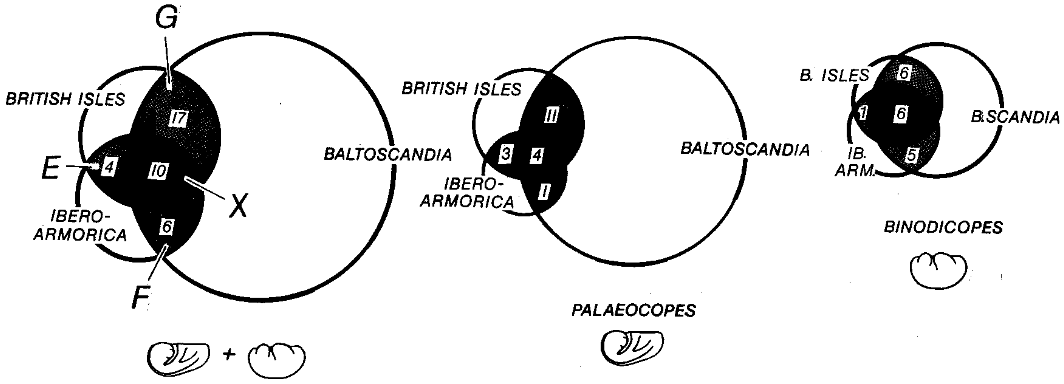


TEXT-FIG. 31. Number of Ordovician (Arenig to Ashgill) palaeocope, binodicope, and palaeocope + binodicope genera common between Ibero-Armorica, British Isles, and Baltoscandia. The size of each area is proportional to the number of genera. Number of genera in common are indicated within the shaded areas.

metacopes (one). Moreover, apart from occurring in Baltoscandia, Ibero-Armorica, and the British Isles, *Quadritia* and *Ogmoopsis* are also known from Czechoslovakia (unpublished data). Interestingly, genera common to the three regions are mainly binodicopes (text-figs. 29 and 32). This characteristic is also observed in the higher binodicope similarity index for each of the three faunal comparisons made compared to the equivalent index for palaeocopes (R1, R2, R3: text-fig. 30). This cosmopolitan character amongst the binodicopes recorded here can be extended geographically: for example, *Laterophores*, *Pseudulrichia*, *Vogdesella*, and *Pariconchoprimitia* are also present in the Ordovician of North America (see Schallreuter 1980*a*; Schallreuter and Siveter 1985; Jones 1986, 1987). *Klimphores* and *Pariconchoprimitia* also apparently occur in the Ordovician of Saudia Arabia (Vannier and Vaslet 1987).

VARIATIONS IN OSTRACODE GENERIC LINKS BETWEEN IBERO-ARMORICA, THE BRITISH ISLES, AND BALTOSCANDIA THROUGH THE ORDOVICIAN

How ostracode faunal similarities between the three areas may have changed through the Ordovician (text-figs. 33–35) is clearly important because of its possible palaeogeographical implications.



TEXT-FIG. 32. Number of Ordovician (Arenig to Ashgill) palaeocope, binodicope, and palaeocope + binodicope genera common between Ibero-Armorica, British Isles, and Baltoscandia. The size of each area is proportional to the number of genera. Number of genera in common are indicated within the shaded areas (E, F, G, X, as defined in text-fig. 29).

Ibero-Armorican–British relationships (text-fig. 35, graphs 1 and 4)

It is during the Llanvirn that British and Ibero-Armorican ostracode faunas show closest affinity, as noted by the relatively high percentage of binodicope, and particularly palaeocope, genera in common. Palaeocopes and binodicopes both show a drop to a minimum percentage of genera in common between Ibero-Armorica and Britain during the Llandeilo, and thereafter show a recovery of the numbers of genera in common into the early Caradoc. The later Caradoc is characterized by very low percentages of binodicope, and particularly of palaeocope, genera in common between the two regions.

Ibero-Armorican–Baltoscandian relationships (text-fig. 35, graph 2)

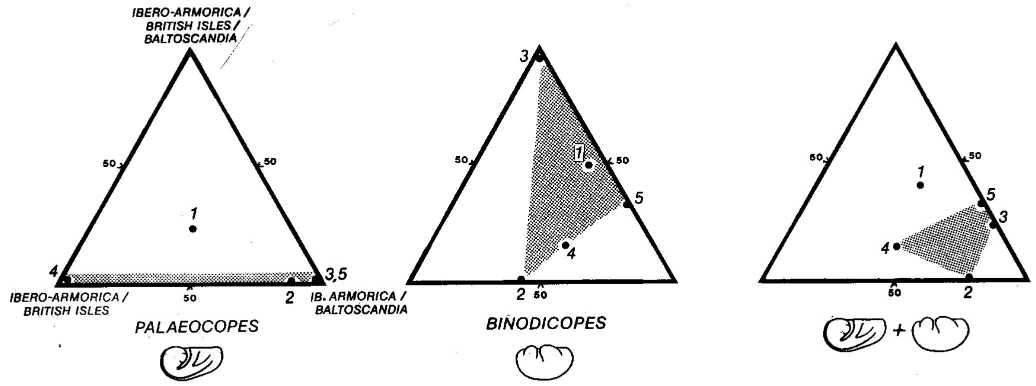
In contrast to the uniform palaeocope and binodicope links between Ibero-Armorica and Britain, the palaeocopes and binodicopes common to Ibero-Armorica and Baltoscandia clearly exhibit mutually opposite trends. The uniform Llanvirn–Caradoc percentage increase of binodicope genera in common contrasts markedly with an irreversible decrease of palaeocopes in common during the Llandeilo–Caradoc interval.

British–Baltoscandian relationships (text-fig. 35, graph 3)

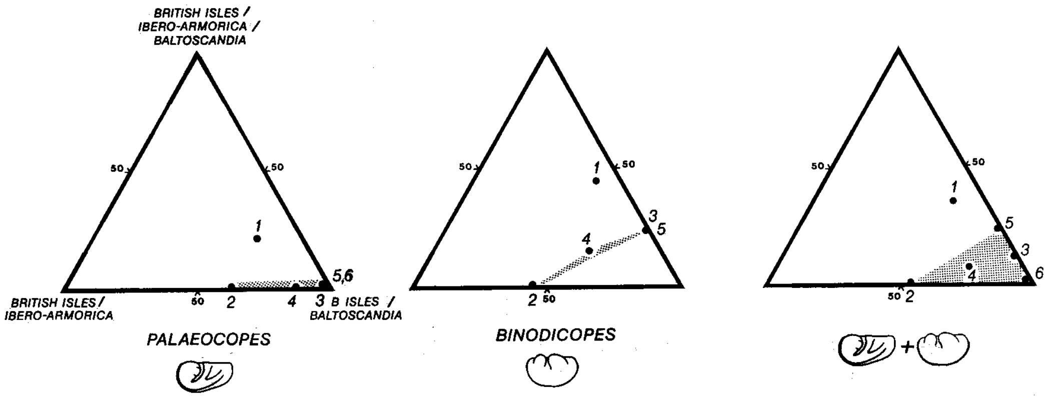
The evolving pattern of ostracode links between these two regions shows: first, very similar variations in the percentage of genera in common for both palaeocope and binodicope faunas, from the Llanvirn through to the Ashgill. Secondly, ostracode faunal contact steadily enhances for both groups during this period, the only difference being a slightly lower increase in the percentage of cosmopolitan binodicope genera during the Llandeilo. Even though faunal data from the Ashgill of the British Isles are still incompletely known or published, it is important to note that all documented British Ashgill palaeocope genera also occur in contemporaneous Baltoscandian sediments. These striking late Ordovician faunal affinities also exist at the subgeneric level and, to some extent (see above), even at the specific level.

Ibero-Armorican–British–Baltoscandian relationships (text-fig. 35, graphs 5 and 6)

The percentages of binodicopes and palaeocopes which are common to all three areas at given times through the Ordovician are clearly very different. No subdivision of the Ordovician (as



TEXT-FIG. 33. Percentage change in geographical affinity, through the Ordovician, of cosmopolitan Ibero-Armorican palaeocope, binodicope, and palaeocope + binodicope genera, respectively. Percentage of Ibero-Armorican genera common with: the British Isles; Baltoscandia; and both the British Isles and Baltoscandia. 1, Llanvirn to Caradoc inclusive; 2, Llanvirn; 3, Llandeilo; 4, 5, Caradoc Cc1 and Cc2, respectively (as defined in text-fig. 22). The shaded area in each case encompasses the plots for the time periods 2-5 inclusive.

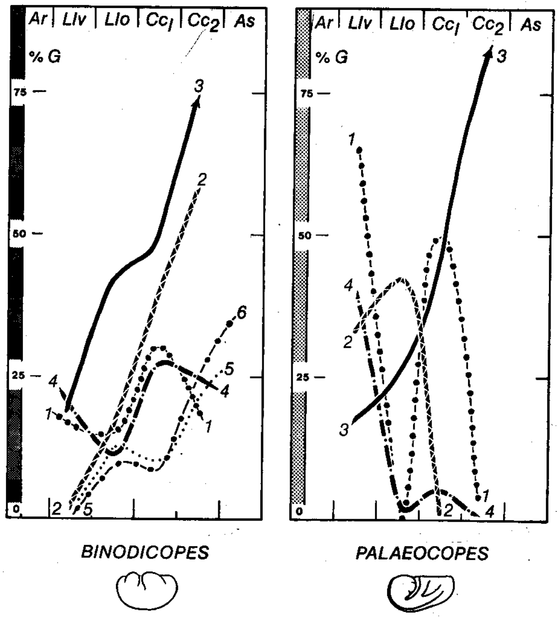


TEXT-FIG. 34. Percentage change in geographical affinity, through the Ordovician, of cosmopolitan British palaeocope, binodicope, and palaeocope + binodicope genera, respectively. Percentage of British genera common with: Ibero-Armorica; Baltoscandia; and both Ibero-Armorica and Baltoscandia. 1, Llanvirn to Ashgill inclusive; 2, Llanvirn; 3, Llandeilo; 4, 5, Caradoc Cc1 and Cc2, respectively (as defined in text-fig. 22). The shaded area in each case encompasses the plots for the time periods 2-5 inclusive.

defined in text-fig. 35) contains palaeocope genera common to the three regions. By contrast, binodicope generic similarities between the three areas exist in each Ordovician time period (text-fig. 35) and, moreover, gradually increase overall through the Ordovician.

Affinities of Ibero-Armorican faunas (text-fig. 33)

The affinities of cosmopolitan Ordovician palaeocope and binodicope genera of Ibero-Armorica are given in a triangular diagram (text-fig. 33). Taking the data for palaeocopes and binodicopes together, the cluster points suggest that, in general through the Ordovician, cosmopolitan Ibero-



TEXT-FIG. 35. The percentage of Ibero-Armorican, British, or Baltoscandian palaeocope or binodicope genera, respectively, common to one or both of the other areas for each of the given time periods of the Ordovician.

1, 2, 5. Percentage of Ibero-Armorican genera common to: the British Isles only (graph 1); Baltoscandia only (2); and to both the British Isles and Baltoscandia (5).

3, 4, 6. Percentage of British genera common to: Baltoscandia only (graph 3); Ibero-Armorica only (4); and to both Ibero-Armorica and Baltoscandia (6).

Armorican Ordovician ostracode faunas have a Baltic character and a relatively poorly marked British influence. However, this signature is less sharp in the early Caradoc (text-fig. 33). Differences between the geographical affinity of cosmopolitan Ibero-Armorican palaeocopes and binodicopes are illustrated by the position of the shaded areas within their respective triangular diagrams; the binodicopes are somewhat more widespread in their distribution.

Affinities of British faunas (text-fig. 34)

The British cosmopolitan palaeocope and binodicope ostracodes together show mainly Baltic and only minor Ibero-Armorican influences throughout the Ordovician. Again, the cosmopolitan palaeocopes and binodicopes differ by the same characteristic as previously noted for Ibero-Armorican faunas (text-fig. 33), binodicopes being somewhat more cosmopolitan in their distribution (compare respective shaded areas in text-fig. 34).

PALAEOECOLOGICAL IMPLICATIONS OF THE OSTRACODE DISTRIBUTIONAL PATTERNS

The general composition, diversity, distributional patterns, and faunal dynamics of Baltoscandian, southern British, and Ibero-Armorican Ordovician ostracodes can be broadly related to palaeoecological and palaeogeographical factors. In particular, some of their major compositional and distributional characteristics may be interpreted in the light of two palaeobiological models. According to the ecological model of Bretsky and Lorenz (1970), species diversity within communities is correlatable with environmental conditions, especially environmental stability. They see faunal diversity as a result of speciation processes which probably occur, *in situ*, preferentially more often in stable, offshore areas, a notion Eldredge (1974) considered valid and applicable to benthic Palaeozoic faunas. Fortey (1984) stressed that major physical processes such as eustatic sea-level changes are partly the trigger for important faunal events, such as speciation and diversity shifts, observed in the Ordovician. Both these models can be tested using the patterns of Ordovician ostracode distribution in our study areas.

1. *The influence of environmental conditions*

The Bretsky and Lorenz model (1970; Eldredge 1974) recognizes two types of faunal communities and related environmental conditions. Communities in unstable environments (and low spatial heterogeneity) are expected to show low faunal diversities; large numbers of individuals per specific population; significant morphological variations within species; low rates of evolution and hence persistence of stable community structures; and are less severely affected by sudden environmental change. Communities of stable environments (and high spatial heterogeneity) are expected to be characterized by high faunal diversities; relatively small numbers of individuals per species population; limited morphological variation; high rates of evolution and hence frequent faunal reorganizations and changes in community structure; and are normally adversely affected by sudden environmental changes and are thus subject to widespread extinctions. Unstable environments are considered to be basically near-shore areas and stable environments are more off-shore areas (Bretsky and Lorenz 1970).

Within our study areas, two main types of Ordovician ostracode faunas are recognized, based on the relative abundance of palaeocope and binodicope genera (text-fig. 36). Faunas characterized by a low palaeocope : binodicope ratio (<1) seem to be related to predominantly fine-grained detrital environments (e.g. Ibero-Armorica), whereas palaeocope-dominated faunas (palaeocope : binodicope ratio >1) appear to be related to carbonate-dominated environments (e.g. Baltoscandia). This bifaunal distinction is supported by the following evidence:

a. Binodicopes are the dominant ostracode group throughout the Ordovician within Ibero-Armorica (text-fig. 22) where their associated sediments are essentially fine-grained clastics (siltstones and mudstones) with intercalations of sandstones; there is an absence of limestone deposition from Arenig to Caradoc inclusive (text-fig. 3). In the Ordovician of the British Isles, where both clastic and carbonate facies occur, the palaeocope : binodicope ratio is substantially higher (>1) than in Ibero-Armorica for each major interval of Ordovician time. The highest palaeocope : binodicope values are reached in the palaeocope-rich faunas in Baltoscandia, in association with carbonate-dominant sedimentation.

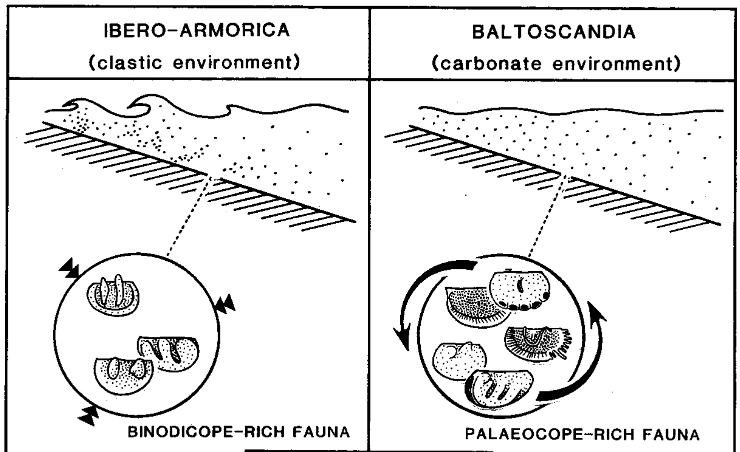
b. In a well-documented, rare example of a Baltic Ordovician ostracode fauna from detrital sediments, from the middle Ordovician Sularp Shale of Scania, Sweden (Schallreuter 1980*a*), binodicopes are relatively abundant (palaeocope : binodicope ratio = 0·4) and its two commonest species are binodicopes. Comparisons with Scandinavian faunas from calcareous sediments are particularly significant. For example, the middle Ordovician Upper Dalby Limestone (Schallreuter 1984*b*) is clearly dominated by palaeocopes (palaeocope : binodocope ratio = 3).

c. Similar observations are made in the British Isles, from the Ordovician of the Welsh Borderland. Although incomplete, the Ordovician (Caradoc) succession in the Welshpool District (Pen-y-Garnedd Shale and Phosphorite: see Williams *et al.* 1972) consists exclusively of shales in which the only ostracodes recorded are binodicopes (Jones 1986, 1987).

d. Ostracode assemblages from the middle Ordovician of Saudi Arabia (Vannier and Vaslet 1987) also seem to confirm a close relationship between clastics (in this case siltstones) and binodicopes, with palaeocopes apparently being absent.

The two, broad and taxonomically based types of ostracode generic faunas correlated above with carbonate and detrital-dominated environments, respectively, have many of the distinctive characteristics (text-fig. 36) of the two types of faunal communities distinguished by Bretsky and Lorenz (1970):

a. *Stability of environmental conditions*. During the middle Ordovician the Baltoscandian shelf environment consisted of a wide carbonate platform (Jaanusson 1976) bordering the Baltic



unstable	*conditions*	stable
low	*diversity (all taxonomic levels)*	high
high	*number of individuals/population*	low
low	*rates of evolution*	high
high	*persistence of stable community structure*	low (frequent faunal reorganizations)
low	*spatial heterogeneity*	high (intense niche partitioning)

TEXT-FIG. 36. Schematic representation of the two major types of ostracode assemblages recognized in the regions studied, as related to their characteristic environmental conditions and exemplified by Ibero-Armorican and Baltoscandian faunas respectively. The arrows around the circle indicate rare (Ibero-Armorica) and frequent (Baltoscandia) faunal reorganization.

continent and extending to both near-shore marginal and deeper water clastic facies. Ostracode faunas, dominated by palaeocopes, occupied a wide range of platform habitats across a bathymetric gradient (Jaanusson 1976). Binodicope-rich faunas seem to be restricted to more detrital-influenced and unstable environments.

Middle Ordovician Ibero-Armorican environments are placed within the context of a widespread platform bordering the Gondwanan continent, with dominant silts and coarser sedimentation. Throughout the middle Ordovician of the Armorican Massif, tempestites (Guillocheau 1983) indicate persistent unstable, storm-related conditions across the bathymetric profile. Distribution of the Llandeilo ostracode fauna in the Armorican Massif seems to be depth-related (Vannier 1986*b*).

b. Diversity. Considering the Ordovician as a whole, the lowest faunal diversity occurs in Ibero-

Armorica. Even during the Llandeilo and early Caradoc, when Ibero-Armorican ostracode faunas seem to be particularly prolific, diversity at all taxonomic levels is much lower than that of equivalent Baltic faunas and is apparently also slightly lower than that of British faunas. The fact that during the Ordovician the Baltic was always nearest to, and Ibero-Armorica always the furthest from, the equator is also an important possible reason to account for the observed levels of diversity.

c. *Number of individuals per population.* Assemblages poor in numbers of species and genera, but very rich in individuals, are most frequently observed throughout all the detrital successions of Ibero-Armorica. Typical examples are the Llandeilo siltstones and mudstones of the Armorican medio-syncline (Vannier 1986*a*, *b*), or the Armorican Caradoc assemblages dominated by a few species of the palaeocope *Hastatellina* and the binodicope *Satiellina.* Similar observations have been made about the Baltic ostracode faunas from detrital horizons. For example, the siliceous Sularp Shales of Sweden (see above: Schallreuter 1980*a*) contain a relatively small number of species in which the only two abundantly represented belong to the binodicope genera *Pariconchoprimitia* and *Spinigerites.* This contrasts markedly with the highly diversified ostracode assemblages of most Baltic carbonate horizons.

d. *Rates of speciation.* Evolutionary trends amongst the ostracode species of the areas studied are still too poorly documented to attempt a comparative evaluation of the rates of speciation. Nevertheless, detailed information on the stratigraphical range and specific diversity of genera (text-figs. 10–17) would suggest that the rate of speciation amongst Baltic ostracode faunas during the Ordovician was relatively high compared to those of Ibero-Armorica or the British Isles. The large number of species within Baltic genera such as *Sigmobolbina*, *Tetrada*, *Tetradella*, *Laccochilina*, *Bolbina*, or the subgenus *Hippula* (*Hippula*) (text-figs. 10–14) apparently has no equivalent amongst British (if we exclude Ashgill faunas: Jones 1986, 1987, Orr (unpublished)) or Ibero-Armorican faunas.

e. *Persistence of community structure.* Some evidence for the nature of this factor can be deduced, at least for the middle Ordovician of Baltoscandia where thorough documentation of its palaeocope-dominant ostracode faunas has recognized high faunal turnover (Jaanusson 1976) and associated frequent rearrangement of species communities. In these stable environments the persistence of a stable community structure is apparently low.

f. *Spatial heterogeneity.* Though it is difficult to assess the degree of spatial heterogeneity and niche-partitioning in the fossil record, the occurrence of high diversity, at all taxonomic levels, of a wide range of macrofossil (e.g. trilobites, brachiopods, bivalves, echinoderms, bryozoans, etc.) and microfossil groups suggest that both factors had relatively high values on the carbonate platform of Baltoscandia. By contrast, the relatively poor benthic faunas of Ibero-Armorica (e.g. trilobites: see Henry 1980) would indicate that the reverse was the case there.

In summary, in the middle Ordovician we have a diverse, frequently reorganized, palaeocope-dominant fauna in relatively stable, carbonate-rich environments in Baltoscandia and a low diversity but relatively longer-lived series of binodicope-rich faunal communities adjusted to often unstable conditions in Ibero-Armorica. In Britain, both aspects of this bimodal pattern can be expected to be represented.

2. *The influence of sea-level changes*

As emphasized by many authors (see Fortey 1984), major sea-level variations during the Ordovician may have induced faunal and diversity changes within various fossil groups such as trilobites (Shaw and Fortey 1977), graptolites, condonts, and shelly faunas (Jaanusson and Bergström 1980) Thus, 'faunal changes which occur at (Ordovician) Series boundaries are as much a product of environmental shift as of evolutionary novelty' (Fortey 1984, p. 39). Fortey has predicted that the biological effects of a eustatic transgressive event will, depending on local circumstances, encompass: the promotion of high speciation rates and diversity in shelf areas (because of spatial heterogeneity and the species area effect: Eldredge 1974; Ludvigsen 1982); high endemism in shelf areas; the diachronous, shelfwards displacement of previously extra-cratonic facies and faunas and a possible associated apparent breakdown of faunal provinciality; an on-shelf migration of tropical 'mound' faunas and a relative scarcity of island faunas. The faunal signatures from a regressive pulse are predicted (Fortey 1984) to be: the occurrence on interior cratonic sites of shallow water deposits whose fossil content is poor and/or which shows taxonomic jumps; a peripheral site location for 'ancestors' of later on-shelf faunas; a higher incidence of both island faunas themselves and of the shelf edge siting of tropical mound faunas and their associated debris slides.

Analysis of the ostracode faunas and facies of Ibero-Armorica, Baltoscandia, and the British Isles for a time interval of one of the major eustatic cycles recognized for the Ordovician, the Llandeilo to Ashgill, reveals features consistent with Fortey's model:

a. The ostracode faunal events recorded from all three areas during the Llandeilo-early Caradoc, a time of major transgression (Fortey 1984, text-figs. 3–5), include a steep increase in the generic diversity of both binodicopes and palaeocopes, culminating in the maximum Ordovician generic diversity for the palaeocopes (text-fig. 27A–C).

By contrast, the later Caradoc is a period of regression (Fortey 1984), an event which continued into the Ashgill with its well-documented glacial episode. Late Caradoc times are marked by the decline of binodicope (except for Baltoscandia) and palaeocope diversity in all three areas (text-fig. 27A–C).

b. In general, the percentage of ostracode genera in common between the British Isles and Ibero-Armorica decreases through the early Ordovician, but this trend is somewhat (and temporarily) reversed for both palaeocopes and binodicopes for the late Llandeilo–early Caradoc (text-fig. 35, graphs 1 and 4). The latter time interval is a period of transgression and, irrespective of plate motion, separated faunas might be expected to show increased contact during such events (Fortey 1984).

c. In the Dalby Formation of Västergötland, Sweden (text-figs. 1 and 2), a significant change in the ostracode fauna is associated with a change from calcilutites to dark mudstones (Jaanusson 1976, p. 323). The appearance of new ostracodes, known previously only from the deeper water areas of Scania, is the kind of local faunal shift associated with the on-shelf migration of facies belts, in response to a transgressive pulse, as predicted by Fortey (1984).

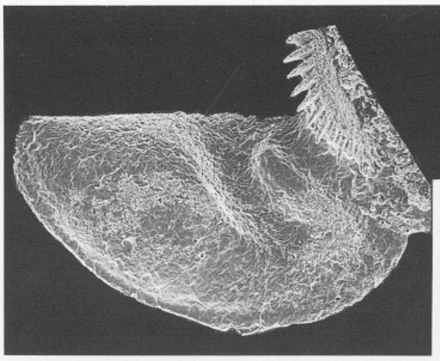
EXPLANATION OF PLATE 24

Palaeocope and binodicope ostracodes from the Ordovician of Ibero-Armorica (*left*) and British Isles (*right*).

Figs. 1–6. Palaeocopa. 1, *Ceratopsis* sp. nov., upper part of Caradoc Series, Corral de Calatrava, Ciudad Real district, Spain; heteromorphic right valve (IGR 32000), × 30. 2, *Ceratopsis inflata* Jones, 1986, upper part of Llandeilo Series, Dryslwyn, Dyfed, Wales; tecnomorphic left valve (BM OS 12647), × 56 (Jones 1986, pl. 11, fig. 13). 3, *Hastatellina normandiensis* Přibyl, 1975, Caradoc Series, Louredo Formation, near Cacemes, Buçaco syncline, Portugal; heteromorphic right valve (IGR 30560/1A), × 28 (Vannier 1986*b*, pl. 1, fig. 5). 4, *Hastatellina*? sp., Llandeilo Series, Dryslwyn Castell, Dyfed, Wales; tecnomorphic left valve (BM OS 12663), × 50 (Jones 1986, pl. 14, fig. 12). 5, *Gracquina hispanica* (Born, 1918), Llanvirn Series, Alisedas, near Almaden, Ciudad Real district, Spain; heteromorphic right valve (SMF X/E 371*b*/1), × 36 (Vannier 1986*b*, pl. 4, fig. 1). 6, *Gracquina vannieri* Jones, 1986, Llanvirn Series, Huntingdon, Cambridgeshire, England; heteromorphic right valve (GSM 8589), × 35 (Jones 1986, pl. 14, fig. 11).

Figs. 7–10. Binodicopa. 7, *Copelandia kerfornei* Vannier, 1986*a*, Grès de Kermeur Formation, Caradoc Series, Raguenez, near Crozon, Finistère, France; right valve (IGR 7052/2), × 35 (Vannier 1986*a*, pl. 5, fig. 3). 8, *Copelandia melmerbyensis* Jones 1987, Woolstonian Stage, Caradoc Series, Melmerby, Cumbria, England; right valve (GSM 2546B), × 51 (Jones 1987, pl. 2, fig. 11). 9, *Thibautina rorei* Vannier, 1984*b*, Le Pissot Formation, Llanvirn Series, Domfront, Orne, France; right valve (IGR 5184C), × 71 (Vannier 1986*a*, pl. 11, fig. 4). 10, *Conspicillum bipunctatum* (Jones and Holl, 1869), middle part of the Llandeilo Series, Builth, Powys, Wales; right valve (NMW 8416G), × 35 (Jones 1987, pl. 4, fig. 3).

All scanning electron micrographs of external lateral views. Figs. 1, 3, 5–8, 10 are cast from external moulds.



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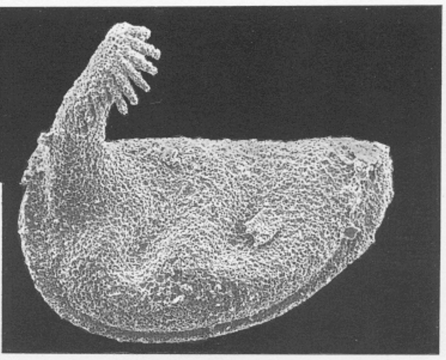

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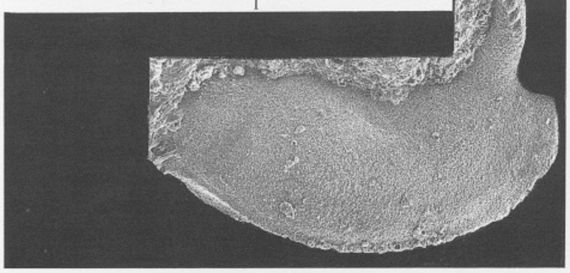

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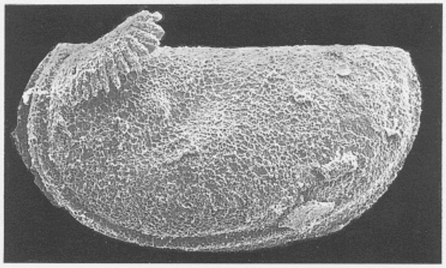

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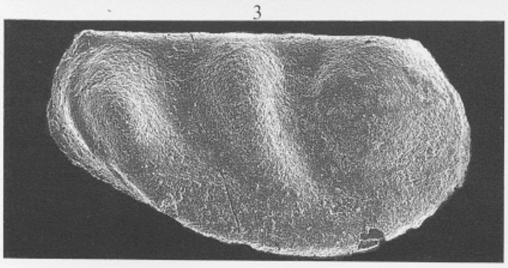

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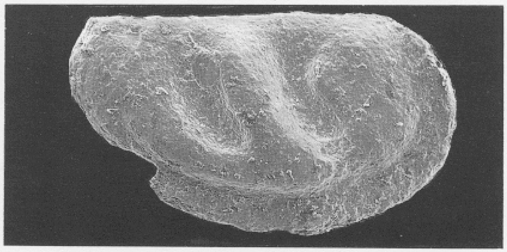

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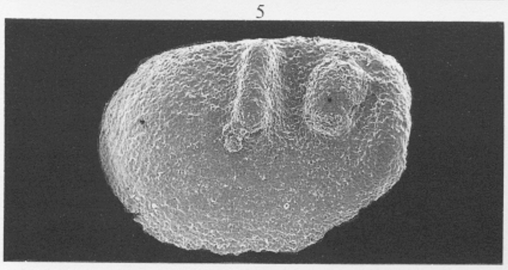

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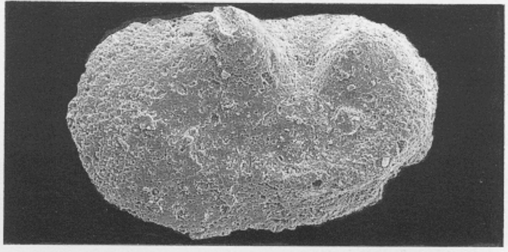

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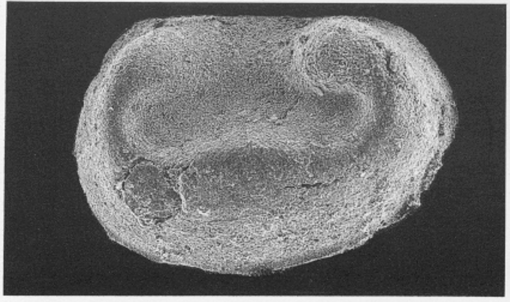

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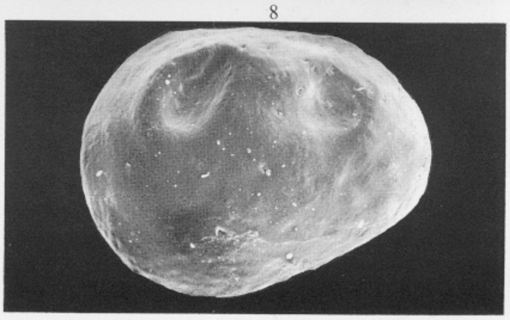

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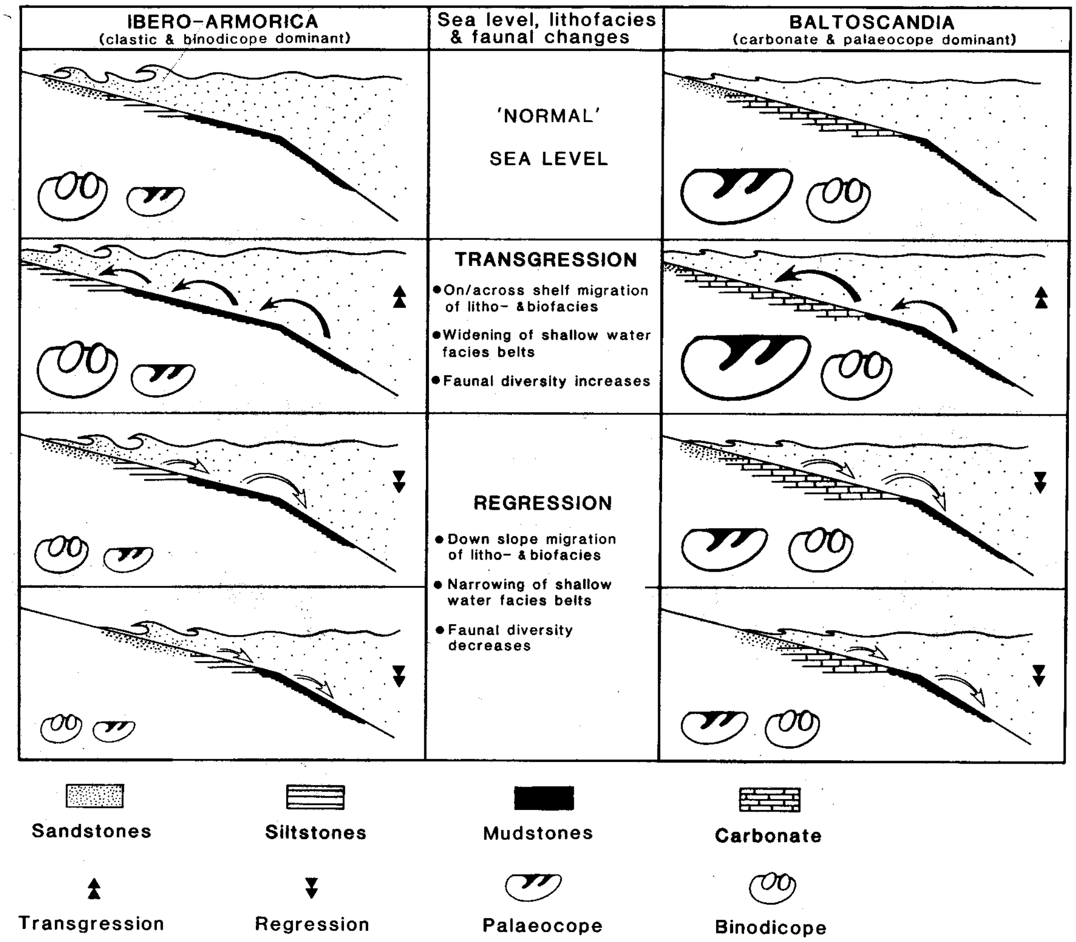
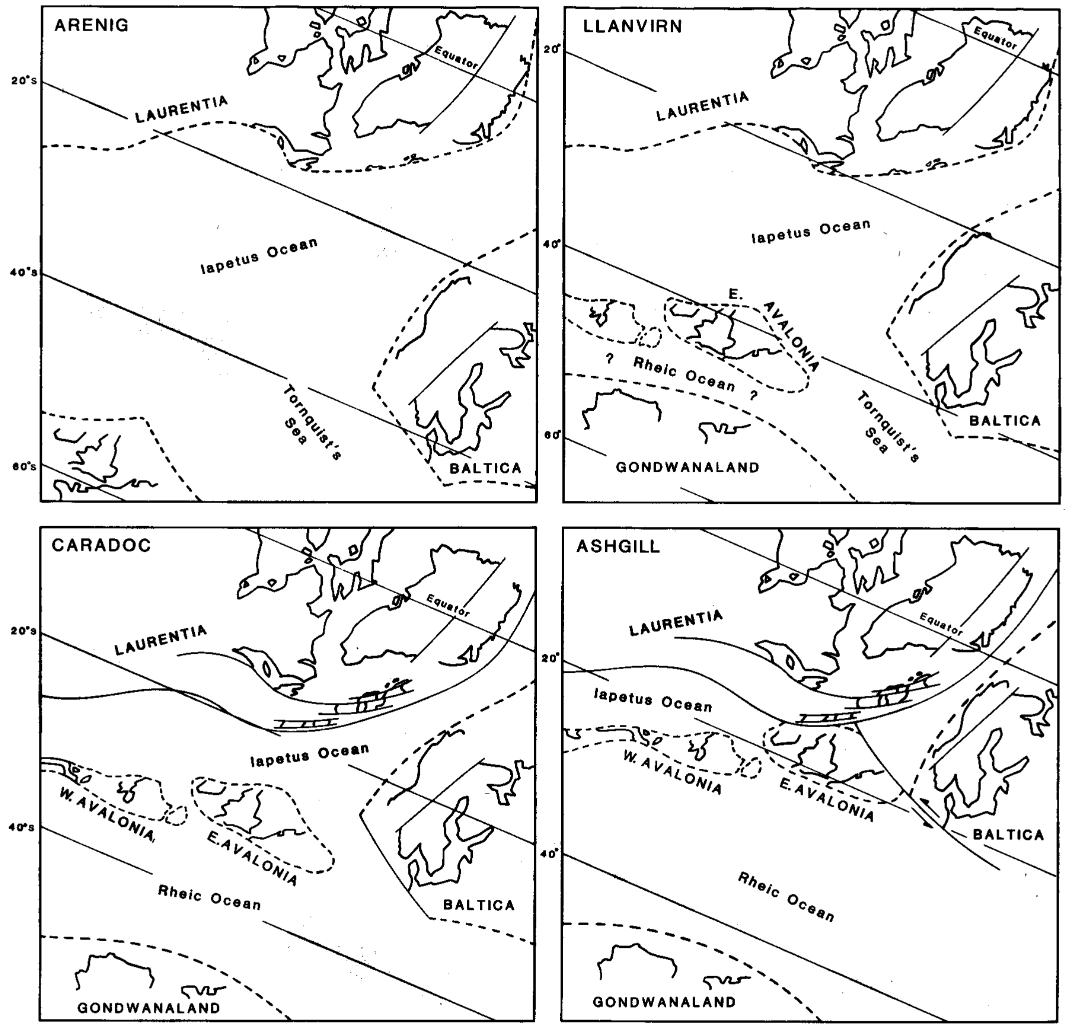


TEXT-FIG. 37. Generalized interpretation of lithofacies and ostracode faunal changes in Ibero-Armorica and Baltoscandia related to a transgressive (e.g. late Llandeilo-early Caradoc) and a regressive (e.g. late Caradoc-Ashgill) cycle. The type of changes listed are those predicted in the model of Fortey (1984). The size of the ostracodes illustrated is proportional to the diversity of the respective palaeocope- or binodicope-dominated ostracode fauna.

PALAEOGEOGRAPHICAL SIGNIFICANCE OF THE OSTRACODE DISTRIBUTIONAL PATTERNS

Cocks and Fortey (1982) have focused on the nature and reliability of employing various types of faunal evidence for oceanic separation in the Lower Palaeozoic. Similarly, the composition, affinity, and faunal dynamics of European Ordovician ostracode faunas can be used to test models of the existence and demise of contemporaneous oceans (e.g. Schallreuter and Siveter 1985).

The typical Lower Palaeozoic ostracode species (e.g. a palaeocope) is benthic, has no known pelagic larval stage, and a distributional pattern often encoding the developmental history of its sedimentary basin (Siveter 1984; Schallreuter and Siveter 1985). The distribution of continents is best defined using shallow water 'endemics', as deep water forms of benthic groups potentially



TEXT-FIG. 38. Ordovician palaeogeographic evolution of the 'North Atlantic' region. Arenig reconstruction is modified after Cocks and Fortey (1982). Later Ordovician reconstructions are modified in part after McKerrow and Cocks (1986) (for the Caradoc) and follow Pickering *et al.* (1988). The reconstructions also concur with the data on ostracode faunal dynamics described herein.

have a wider dispersal capacity which precludes their effective use as tools in palaeogeographical reconstruction (Cocks and Fortey 1982). Bathymetric/community analysis has been undertaken and persuasively argued to account for Ordovician trilobite distributions (e.g. Fortey 1975; Fortey and Owen 1978), but no equivalent detailed analyses have yet been undertaken of facies and any associated ostracode communities, and lie outside the scope of the present study. Nevertheless, virtually all the ostracode genera cited herein can be judged to belong broadly to shelf rather than deep water environments and their use as general indicators of palaeogeography is considered valid.

Faunal and facies distributions indicate the existence of two major early Ordovician continents (Cocks and Fortey 1982) relevant to the present study (see text-fig. 38): Gondwana, which included Ibero-Armorica; and Baltica, embracing the Baltic regions and adjacent parts of Scandinavia and the Russian platform. Southern Britain is thought to have been part of a microcontinent, Avalonia (e.g. McKerrow and Cocks 1986), which after the early Ordovician broke away from high latitude Gondwana to drift northwards towards lower latitude Baltica and the North American continent (Laurentia) which lay astride the equator on the other side of the Iapetus Ocean.

Schallreuter and Siveter (1985) have already addressed the nature and palaeogeographical significance of ostracode faunal contracts across the Ordovician Iapetus Ocean between North America and 'Europe'. Our ostracode data presented herein (e.g. text-fig. 35) endorse the Ordovician oceanic separation of Baltica, Avalonia, and Gondwana and the nature of the development of the Rheic and Tornquist tracts (text-fig. 38). Particularly important is the fact that the ostracode faunal dynamics indicate an Ordovician development for the Rheic Ocean.

1. *Iapetus Ocean*

An assessment of the ostracode faunal connections across the Iapetus Ocean (Schallreuter and Siveter 1985), between Europe (southern Britain and Baltoscandia) and North America, dispelled notions that Ordovician ostracodes showed strict endemicity (thirty middle-late Ordovician genera are common to both sides) and concluded that by the late Ordovician the two plates may have been in closer 'effective' proximity than previously supposed (e.g. McKerrow and Cocks (1976) suggested a minimal 2000-3000 km width for Iapetus even by the late Ashgill). Indeed, Pickering (1987) and Pickering *et al.* (1988; also Hutton 1987) argue that the available tectonic, stratigraphical, palaeontological, palaeomagnetic, igneous, and sedimentological data from Newfoundland, the British Isles, and Scandinavia suggest that by the late Ordovician-early Silurian the Iapetus Ocean separating Laurentia from eastern Avalonia (southern Britain) and Baltica had closed, at least in part, with the consumption of intervening oceanic crust, although marine seaways clearly persisted until the late Silurian.

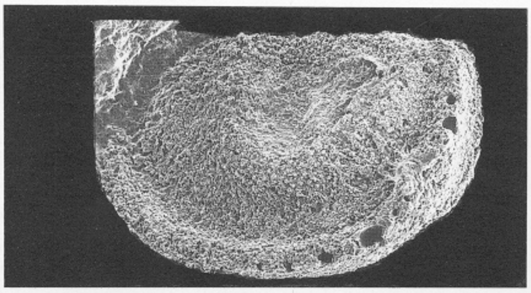
EXPLANATION OF PLATE 25

Palaeocope and binodicope ostracodes from the Ordovician of Ibero-Armorica (*left*) and Baltoscandia (*right*).

Figs. 1-4. Palaeocopa. 1, *Bichilina* sp., Llanvirn Series, Ligné, Loire-Atlantique, France; tecnomorphic (?)left valve (IGR 5610), × 39. 2, *Bichilina prima* Sarv, 1959, middle Ordovician Backsteinkalk erratic boulder, Northern Germany; heteromorphic left valve (GPIMH 2600), × 56 (Schallreuter 1983*a*, pl. 12, fig. 3). 3, *Euprimites* sp., Llandeilo Series, Guichen, Ille-et-Vilaine, France; left valve (IGR 5611), × 65. 4, *Euprimites minor* (Thorslund, 1940), middle Ordovician Backsteinkalk erratic boulder, Northern Germany; heteromorphic right valve (GPIMH 2628), × 47 (Schallreuter 1983*a*, pl. 12, fig. 6).

Figs. 5-10. Binodicopa. 5, *Vogdesella ngakoi* Vannier 1986*a*, Andouillé Formation, Caradoc Series, Andouillé, Mayenne, France; right valve (holotype, IGR 30415/1), × 37 (Vannier 1986*a*, pl. 9, fig. 1). 6, *Vogdesella subovata* (Thorslund, 1948), Sularp Shale, Caradoc Series, Gislövshammar, Scania, Sweden; right valve (GPIMH 2291), × 37 (Schallreuter 1980*a*, pl. 5, fig. 4). 7, *Satiellina henningsmoeni* (Nion, 1972), Pont-de-Caen Formation, Caradoc Series, Domfront, Orne, France; left valve (IGR 7086/1), × 40 (Vannier 1986*a*, pl. 7, fig. 1). 8, *Satiellina biloba* (Troedsson, 1918), uppermost part of Ordovician, Röstanga, Scania, Sweden; left valve (LO 2885), × 37 (Troedsson 1918, pl. 2, fig. 21). 9, *Aechmina* sp., Andouillé Formation, Caradoc Series, La Touche, Andouillé, Mayenne, France; right valve (IGR 30502/1), × 66 (Vannier 1986*a*, pl. 8, fig. 5). 10, *Spinaechmina keitumensis* Schallreuter, 1984*a*, Öjlemyrflint erratic boulder, upper part of the Ordovician, Isle of Sylt, North Sea, Germany; right valve (holotype, GPIMH 2915), × 90 (Schallreuter 1984*a*, pl. 1, fig. 5).

All external lateral views; all scanning electron micrographs except fig. 8. Figs. 1, 3, 5, 7, 9 are casts from external moulds.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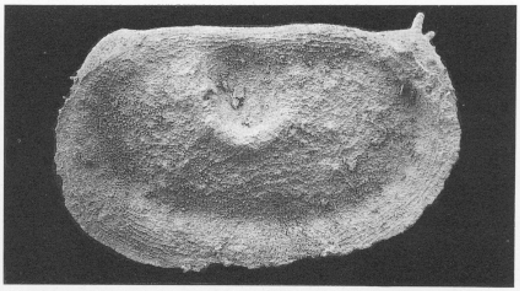
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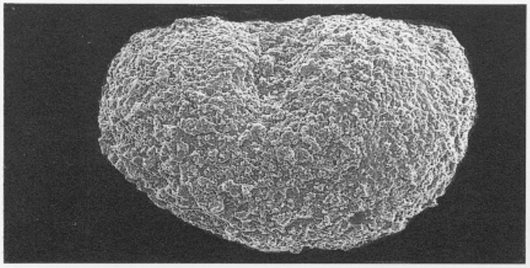
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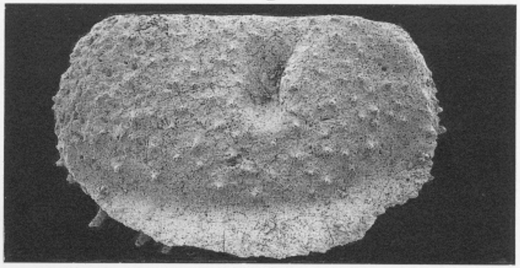
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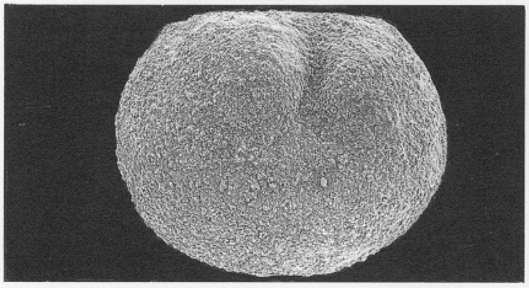
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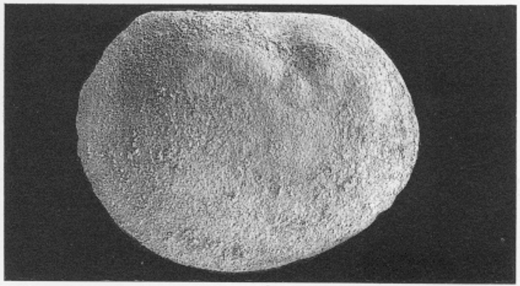
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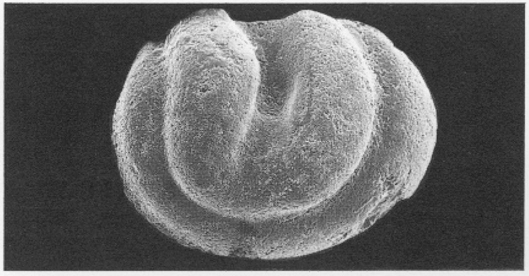
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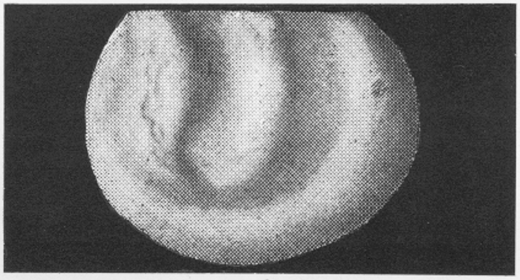
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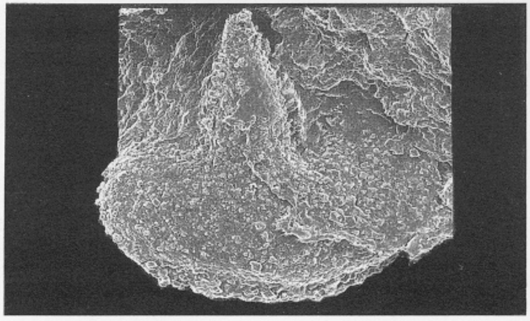
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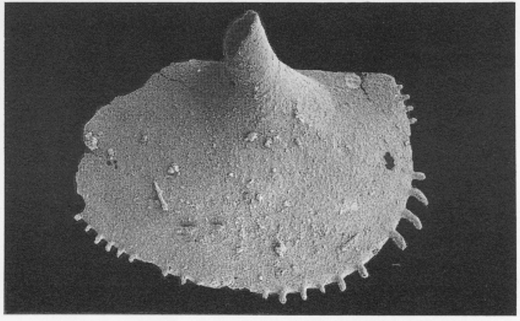
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2. *Tornquist's Sea*

Late Ordovician trilobite and other faunas demonstrate that Tornquist's Sea, the ocean which had earlier separated Baltica from Gondwana, had effectively closed at least to the extent that it no longer provided a barrier to faunal migration (Cocks and Fortey 1982).

As noted in our data, both palaeocope and binodicope ostracodes show an impressive continuous steep increase in the percentage of common genera between southern Britain (Avalonia) and Baltoscandia (Baltica) throughout the Ordovician (text-fig. 35, plot 3). This generic faunal similarity is particularly marked in the Caradoc and is enhanced in the Ashgill with the occurrence of species in common (see above). Thus, the ostracode evidence concurs with other faunal and geological evidence (Cocks and Fortey 1982; McKerrow and Cocks 1986; Pickering *et al.* 1988) that Avalonia and Baltica were probably in close proximity by the late Ordovician. McKerrow and Cocks (1986) in fact propose a possible early Ashgill collision between the two plates.

3. *Rheic Ocean*

By contrast with the Iapetus Ocean or Tornquist's Sea, the timing and nature of the development of the Rheic Ocean has not been so well documented faunally. It has been recognized to exist by lower Silurian times based, for example, on brachiopod and phytoplankton evidence (Cocks and Fortey 1982, fig. 6 and p. 475), when it appears to have separated subtropical northern Europe (e.g. Baltoscandia–southern Britain) from Gondwana (containing e.g. Ibero-Armorica and Bohemia) positioned at higher latitudes to the south. Cocks and Fortey (1982, p. 472) also note that by the Caradoc the trilobite faunas of Scandinavia and Britain were distinctively different from those of the impoverished (typically high latitude) faunas of Bohemia and Morocco (= on Gondwana) and that the palaeogeography of the respective plates probably had a 'configuration

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EXPLANATION OF PLATE 26

Binodicope, leiocope, eridostracan, and metacope ostracodes from the Ordovician of Ibero-Armorica (*left*) and Baltoscandia (*right*).

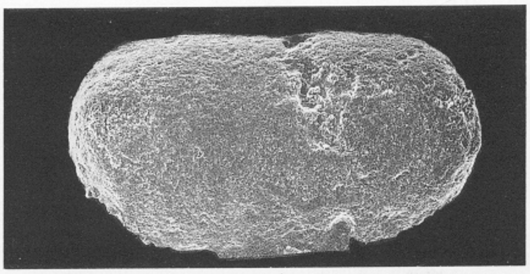
Figs. 1–4. Binodicopa. 1, *Eocytherella nioni* Vannier, 1986*a*, Pont-de-Caen Formation, Caradoc Series, Domfront, Orne, France; right valve (holotype, IGR 7103*b*/1), ×69 (Vannier 1986*a*, pl. 13, fig. 4). 2, *Eocytherella troedssoni* Bonnema, 1931, uppermost part of Ordovician, Röstanga, Scania, Sweden; left valve (LO 2888), ×65. 3, *Kinnekullea morzadeci* Vannier, 1986*a*, La Sangsurière Formation, Caradoc Series, Saint-Germain-sur-Ay, Manche, France; right valve (holotype, IGR 7052/4), ×35 (Vannier 1986*a*, pl. 12, fig. 2). 4, *Kinnekullae hesslandi* Henningsmoen, 1948, Black *Tretaspis* Shale, upper part of the Ordovician, Kinnekulle, Västergötland, Sweden; left valve (UM no. ar. os. 95), ×59 (Henningsmoen 1948, pl. 25, fig. 5).

Figs. 5 and 6. Leiocopa. 5, *Brevidorsa* sp., Le Pissot Formation, Llanvirn Series, Domfront, Orne, France; right valve (IGR 5613), ×62. 6, *Brevidorsa limbata* (Sidaravičiene, 1975), Öjlemyrflint erratic boulder, upper part of the Ordovician, Isle of Sylt, North Sea, Germany; left valve (GPIMH 3412), ×59 (Schallreuter 1986, pl. 5, fig. 9).

Figs. 7 and 8. Eridostraca. 7, *Conchoprimitia* sp., Cacemes Formation, Llandeilo Series, near Cacemes, Buçaco syncline, Portugal; right valve (IGR 5613), ×25. 8, *Conchoprimitia leperditioidea* Thorslund, 1940, '*Ludibundus* Limestone', middle part of the Ordovician (lower Viruan; see text-fig. 2), Bödahamn boring, Öland, Baltic Sea, Sweden; right valve (UM no. ol. 831), ×22 (Jaanusson 1957, pl. 15, fig. 4).

Figs. 9 and 10. Metacopa. 9, *Medianella* sp., Le Pissot Formation, Llanvirn Series, Domfront, Orne, France; left valve (IGR 5612), ×94. 10, *Medianella robusta* (Kummerow, 1924). Öjlemyrflint erratic boulder, upper part of the Ordovician, Isle of Gotland, Baltic Sea, Sweden; left valve (GPIMH AG G21/4), ×35.

All scanning electron micrographs except figs. 4 and 8. All external lateral views, except fig. 10 (internal view). Figs. 1, 3, 5, 7 are casts from external moulds. Fig. 9 is a cast from an internal mould.



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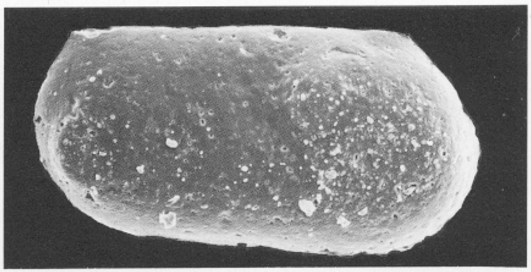

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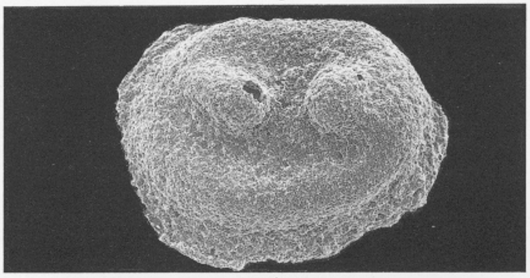

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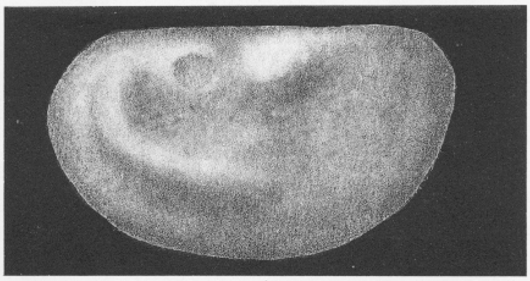

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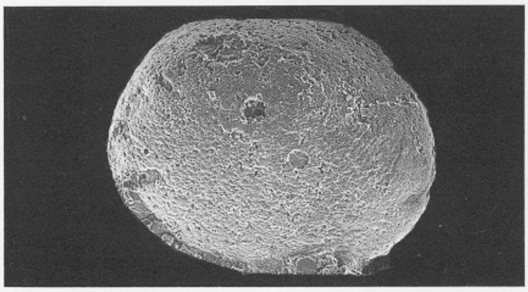

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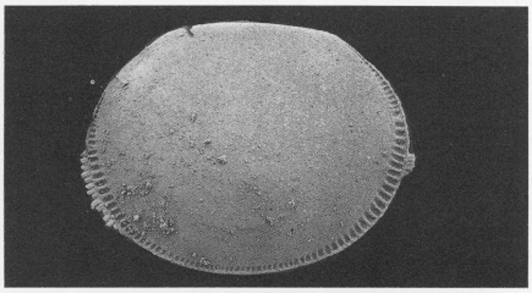

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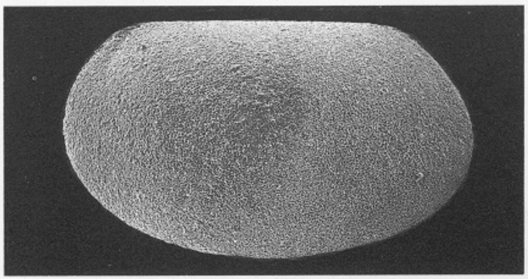

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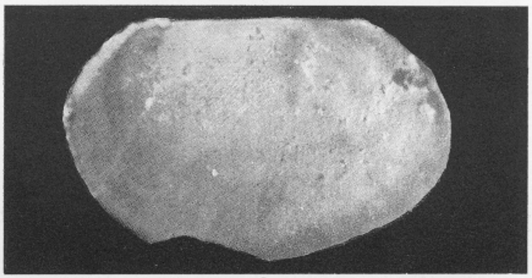

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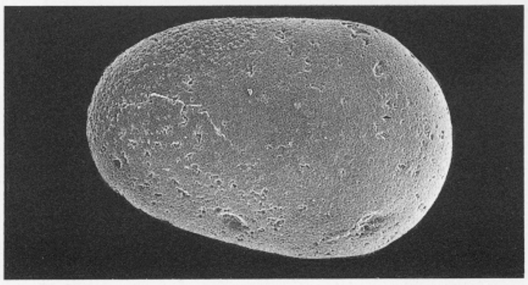

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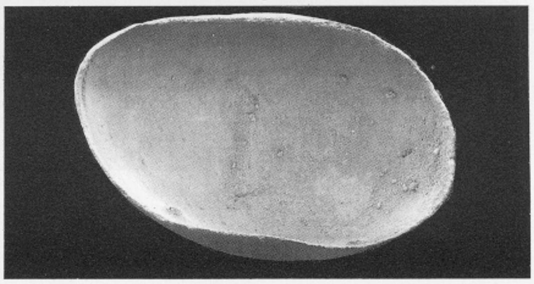

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not unlike that given for the early Silurian by the later Ordovician'. Indeed, a corollary of the general northern drift of Avalonia (southern Britain) to close with Baltica (see above) and a low latitudinal position for Gondwana in the late Ordovician (accounting for the Ashgill glaciation) would be a widening Rheic Ocean throughout the Ordovician. McKerrow and Cocks (1986) speculate that this ocean may have been initiated as early as the Cambrian.

Ostracode evidence suggests the presence and widening of the Rheic Ocean from as early as the Llanvirn–Llandeilo and throughout the upper Ordovician (e.g. text-fig. 35). For example, the percentage of palaeocope genera common to the British Isles and Ibero-Armorica shows a distinctive overall drop during the Llanvirn to upper Caradoc time interval (text-fig. 35, graphs 1 and 4). Punctuating this overall decrease is a slight reversion towards somewhat increased faunal similarity during the late Llandeilo–early Caradoc, which may be due to the coeval transgressive event (see above). A decrease is also evident in the percentage of palaeocope genera common to Ibero-Armorica and Baltoscandia, which shows a sharp uninterrupted drop from the Llandeilo to early Caradoc (text-fig. 35, graph 2). These trends are consistent with the notion of the middle–late Ordovician opening of the Rheic Ocean and the coeval closing of the Tornquist's Sea.

Somewhat different trends are observed for the non-dimorphic, binodicope ostracodes which, through the Ordovician, show: a picture of fairly consistent generic links between the British Isles and Ibero-Armorica (text-fig. 35, graphs 1 and 4; the late Llandeilo–early Caradoc enhancement of generic similarity may, again, be due to the coeval transgression); and a regular increase of the percentage of genera in common between Ibero-Armorica and Baltoscandia. These binodicope faunal contacts, apparently inconsistent with the picture obtained from palaeocopes, have no immediately obvious explanation. Binodicopes may have had wider dispersal capacities than

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EXPLANATION OF PLATE 27

Palaeocope ostracodes from the Ordovician of the British Isles (*left*) and Baltoscandia (*right*).

Fig. 1. *Duringia triformosa* Jones, 1984, upper part of the Llandeilo Series, Dryslwyn, Dyfed, Wales; tecnomorphic left valve (paratype, BM OS 12260), × 63 (Jones 1986, pl. 1, fig. 3).

Fig. 2. *Duringia spinosa* (Knüpfer, 1968), uppermost part of the Caradoc Series, Gebersdorf, Thuringia, Germany; tecnomorphic right valve (GPIMH 2730), × 87 (Schallreuter 1984*a*, pl. 11 (10), fig. 1).

Fig. 3. *Homeokiesowia epicopa* Siveter, 1982*a*, Llandeilo Series, near Llandeilo, Dyfed, Wales; heteromorphic left valve (BM OS 6670), × 28 (Siveter 1982*a*, pl. 9 (90), fig. 4).

Fig. 4. *Homeokiesowia frigida* (Sarv, 1959), Backsteinkalk erratic boulder, middle part of the Ordovician (Idavere (C_{III}) to Keila (D_{II}) stage; see text-fig. 2), Klein-Horst, Pomerania, Poland; heteromorphic right valve (GPIMH 2023*a*), × 53 (Schallreuter 1979, pl. 6 (76), fig. 3).

Fig. 5. *Schallreuteria* (*Schallreuteria*) *superciliata* (Reed, 1910), Longvillian Stage, Caradoc Series, Melmerby, Cumbria, England; heteromorphic right valve (paralectotype, SM A 10983*b*), × 23 (Siveter 1982*b*, pl. 9 (96), fig. 2).

Fig. 6. *Schallreuteria* (*Schallreuteria*) *lippensis* Schallreuter, 1984*a*, Backsteinkalk erratic boulder, middle part of the Ordovician (lower upper Viruan; see text-fig. 2), Lippe, Hohwacht Bay, Baltic Sea, Germany; heteromorphic right valve (GPIMH 2902), × 39 (Schallreuter 1984*a*, pl. 11 (8), fig. 1).

Fig. 7. *Tallinnella*? *tomacina* Jones, 1986, middle part of the Llandeilo Series, Carmarthen, Dyfed, Wales; tecnomorphic right valve (paratype, BM OS 12595), × 22 (Jones 1986, pl. 3, fig. 10).

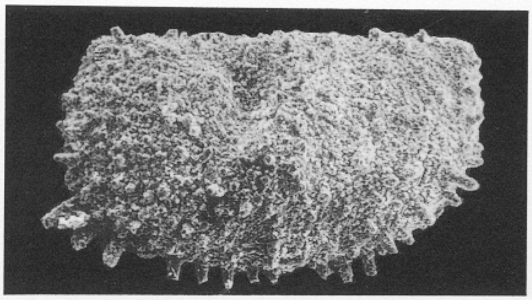
Fig. 8. *Tallinnella sebyensis* Jaanusson, 1957, erratic boulder, Upper grey Orthoceras Limestone, middle part of the Ordovician (lower Viruan ($C_{I}b$)), Linauer Moor, near Trittau, East of Hamburg, Germany; tecnomorphic left valve (GPIMH AG G21/3), × 45.

Fig. 9. *Sigmoopsis duftonensis* (Reed, 1910), Longvillian Stage, Caradoc Series, Melmerby, Cumbria, England; tecnomorphic left valve (paralectotype, SM A 29974*b*), × 24 (Jones 1986, pl. 13, fig. 4).

Fig. 10. *Sigmoopsis rostrata* (Krause, 1892), Backsteinkalk erratic boulder, middle part of the Ordovician, Northern Germany; heteromorphic left valve (GPIMH 2583), × 43 (Schallreuter 1983*a*, pl. 10, fig. 1).

All scanning electron micrographs of external lateral views. Figs. 5 and 9 are casts from external moulds.

PLATE 27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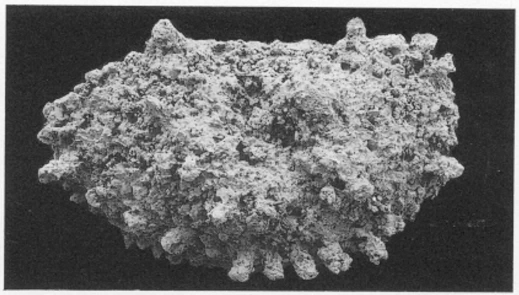
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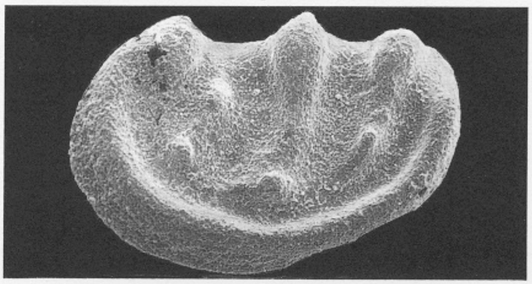
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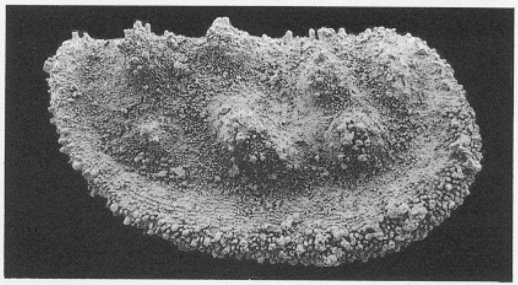
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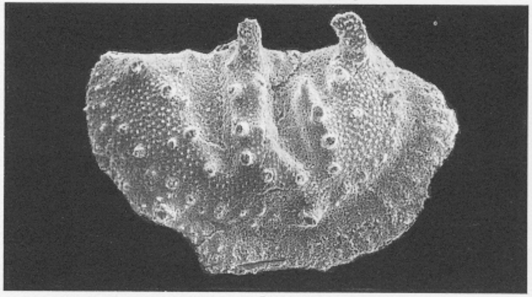
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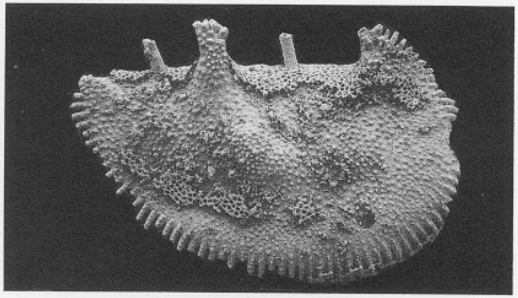
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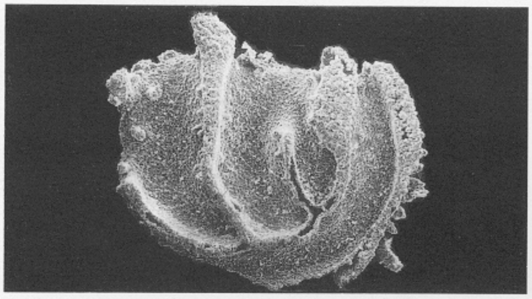
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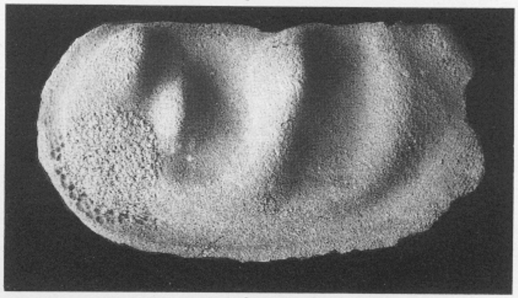
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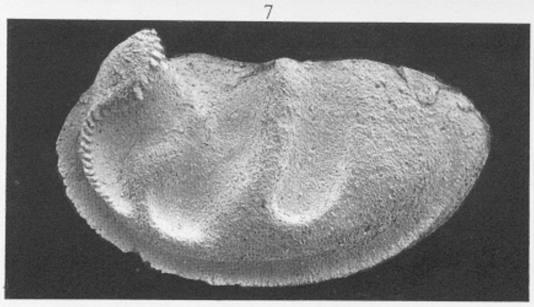
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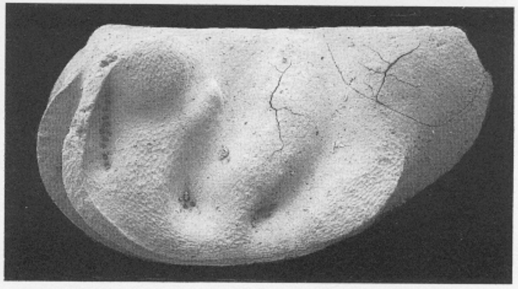
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palaeocopes, or even peculiar substrate preferences. Moreover, it must always be borne in mind that binodicopes are generally less well documented than palaeocopes and would benefit from a thorough taxonomic reappraisal.

THE PLATES

Plates 24–30 are designed to demonstrate congeneric ostracode occurrence between the three domains treated in the text. The figures include scanning electron micrographs of our own material and pertinent illustrations after previous authors. Restrictions on the availablity of some specimens have prevented their illustration by scanning electron microscopy.

Abbreviations of repositories used in plate explanations: BM, British Museum (Natural History), London; GSM, British Geological Survey, Keyworth (*ex* London); GPIG, Geologisches Institut der Universität Greifswald; GPIMH, Geologisch-Paläontologisches Institut und Museum der Universität, Hamburg (AG = Archiv für Geschiebekunde); IGR, Institut de Géologie de l'Université de Rennes; K, Ulster Museum, Belfast; LO, Geological and Mineralogical Institute, Lund University; NMW, National Museum of Wales, Cardiff; SM, Sedgwick Museum, Cambridge University; SMF, Senckenberg Museum, Frankfurt am Main; UM, Museum of the Palaeontological Institute, University of Uppsala.

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EXPLANATION OF PLATE 28

Palaeocope, binodicope, platycope (kirkbyacean), and eridostracan ostracodes from the Ordovician of the British Isles (*left*) and Baltoscandia (*right*).

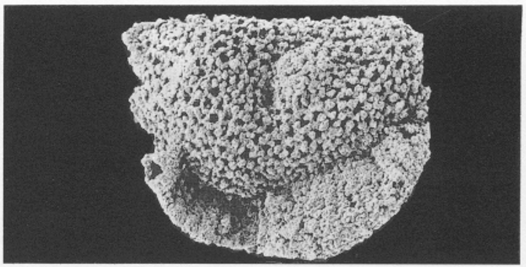
Figs. 1–4. Palaeocopa. 1 and 2, *Gotula gotlandica* (Schallreuter, 1967). 1. Lower Limestones Member, Portrane Limestone, Ashgill Series, near Dublin, Eire; incomplete heteromorphic right valve (K 10022), × 35 (Schallreuter and Orr 1985, pl. 12 (152), fig. 2). 2. Öjlemyrflint erratic boulder, upper part of the Ordovician (upper Harjuan; see text-fig. 2), Vale, Gotland, Sweden; tecnomorphic left valve (GPIMH 3258), × 37 (Schallreuter and Orr 1985, pl. 12 (154), fig. 1). 3, *Henningsmoenia costa* Orr, 1985*b*, Portrane Limestones, Cautleyan Stage, Ashgill Series, Dublin, Eire; tecnomorphic left valve (K 10029), × 48 (Orr 1985*b*, pl. 12 (64), fig. 1). 4, *Henningsmoenia gunnari* (Thorslund, 1948), erratic boulder, middle part of the Ordovician (Idavere (C_{III}) or Johvi (D_{I}) Stage; see text-fig. 2), Northern Germany; heteromorphic right valve (GPIMH 2596), × 51 (Schallreuter 1983*a*, pl. 11, fig. 7).

Figs. 5 and 6. Binodicopa. 5, *Spinigerites hadros* Jones, 1987, Onnian Stage, Caradoc Series, Welshpool, Powys, Wales; left valve (holotype, BM OS 12567), × 36 (Jones 1987, pl. 8, fig. 7). 6, *Spinigerites spiniger* (Lindström, 1953), Sularp Shale, Caradoc Series, Gislövshammar, Scania, Sweden; right valve (GPIMH 2314), × 58 (Schallreuter 1980*a*, pl. 9, fig. 2).

Fig. 7 and 8. Platycopa (Kirkbyacea). 7, *Gebeckeria dryslwynensis* Schallreuter and Jones, 1984, Ashgill Series, Dryslwyn Castell, near Llandeilo, Dyfed, Wales; left valve (paratype, BM OS 12282), × 68 (Schallreuter and Jones 1984, figs. 1 and 2). 8, *Martinssonozona ordoviciana* Schallreuter, 1968, Öjlemyrflint erratic boulder, upper part of the Ordovician, Isle of Sylt, Northern Germany; left valve (GPIMH 3417), × 105 (Schallreuter 1986, pl. 6, fig. 6).

Figs. 9 and 10. Eridostraca. 9, *Eridoconcha plerilamella* Jones, 1987, Costonian Stage, Caradoc Series, Lampeter-Velfrey, Dyfed, Wales; right valve (BM OS 12818), × 60 (Jones 1987, pl. 9, fig. 15). 10, *Cryptophyllus gutta* Schallreuter, 1968*b*, Öjlemyrflint erratic boulder, upper part of the Ordovician, Gotland, Sweden; left valve (GPIMH AG G21/1), × 68.

All scanning electron micrographs of external lateral views.



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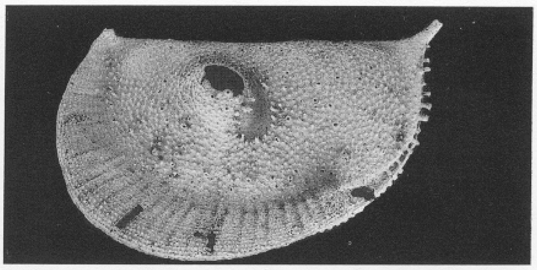

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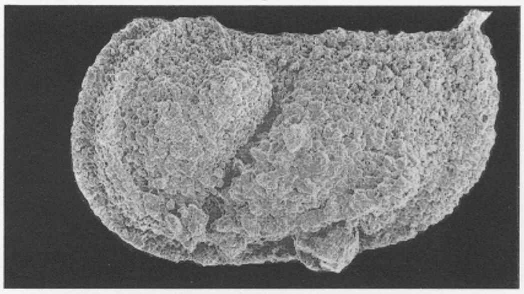

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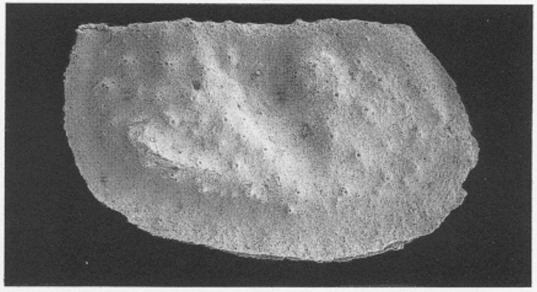

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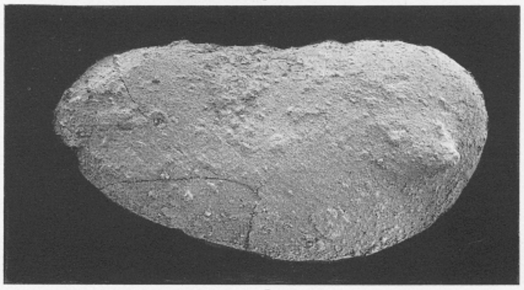

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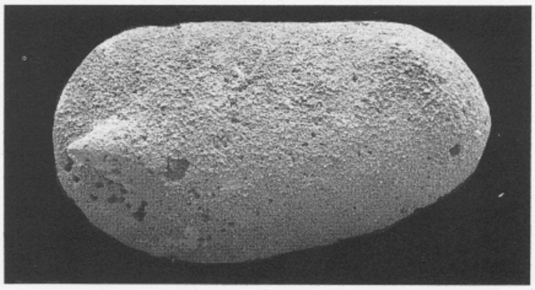

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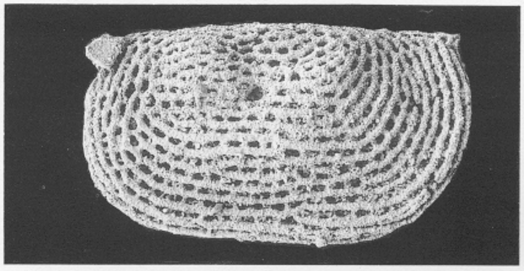

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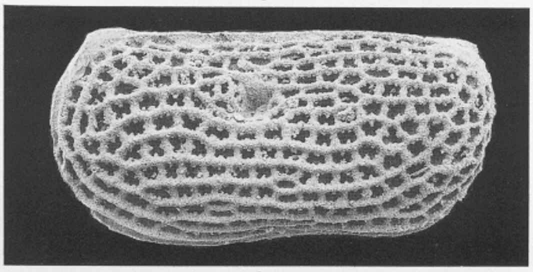

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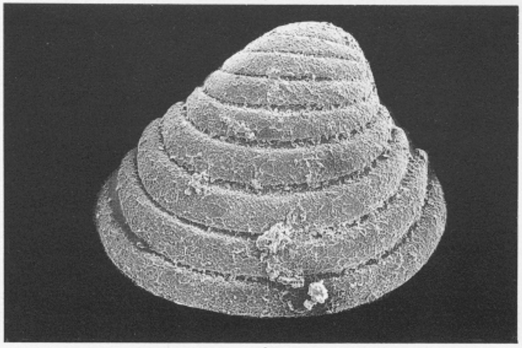

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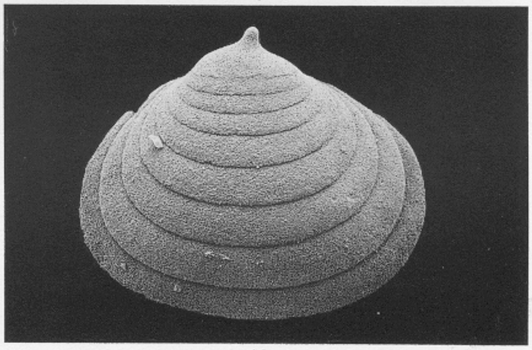

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EXPLANATION OF PLATE 29

Binodicope ostracodes from the Ordovician of the British Isles (*left*) and Baltoscandia (*right*).

Fig. 1. *Bullaeferum llandeiloensis* Jones, 1987, upper part of the Llanvirn Series, Llandeilo, Dyfed, Wales; right valve (holotype, BM OS 12743), × 59 (Jones 1987, pl. 1, fig. 1).

Fig. 2. *Bullaeferum tapaensis* (Sarv, 1959), Öjlemyrflint erratic boulder, upper part of the Ordovician, Isle of Sylt, North Sea, Germany; left valve (GPIMH 3409), × 78 (Schallreuter 1986, pl. 5, fig. 4).

Fig. 3. *Pariconchoprimitia improba* Jones, 1987, upper part of the Llanvirn Series, Llandeilo, Dyfed, Wales; left valve (BM OS 12777), × 65 (Jones 1987, pl. 5, fig. 17).

Fig. 4. *Pariconchoprimitia conchoides* (Hadding, 1913), Sularp Shale, Caradoc Series, Gislövshammar, Scania, Sweden; right valve (GPIMH 2299), × 39 (Schallreuter 1976, pl. 6, fig. 1).

Fig. 5. *Easchmidtella elementa* Jones, 1987, upper part of the Llandeilo Series, Dryslwyn, Dyfed, Wales; right valve (holotype, BM OS 12767), × 66 (Jones 1987, pl. 5, fig. 1).

Fig. 6. *Easchmidtella fragosa* (Neckaja *in* Abushik *et al.*, 1960), Bachsteinkalk erratic boulder, middle part of the Ordovician (Idavere ($\mathrm{C_{III}}$) or Johvi ($\mathrm{D_{I}}$) stage, upper Viruan; see text-fig. 2), Kammin, near Greifswald, Germany; left(?) valve (GPIMH AG G21/5), × 80.

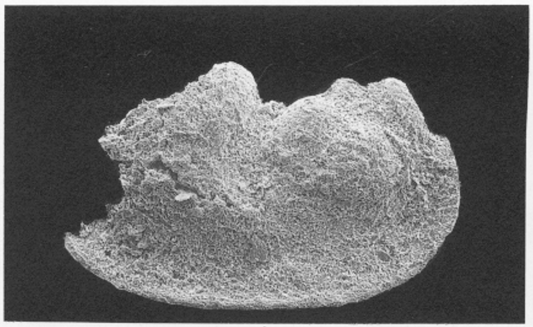
Fig. 7. *Pedomphalella expraeputia* Jones, 1987, Costonian Stage, Caradoc Series, Lampeter-Velfrey, Dyfed, Wales; right valve (BM OS 1278*b*), × 69 (Jones 1987, pl. 6, fig. 1).

Fig. 8. *Pedomphalella jonesii* (Krause, 1897), Backsteinkalk erratic boulder, middle part of the Ordovician (Idavere ($\mathrm{C_{III}}$) or Johvi ($\mathrm{D_{I}}$) Stage, upper Viruan; see text-fig. 2), near Stralsund, Pomerania, Germany; left valve (GPIMH 2722), × 82 (Schallreuter and Siveter 1985, pl. 69, fig. 8).

Fig. 9. *Conchoprimitiella dyfedensis* Jones, 1987, upper part of the Llandeilo Series, Dryslwyn, Dyfed, Wales; right valve (BM OS 12805), × 43 (Jones 1987, pl. 7, fig. 1).

Fig. 10. *Conchoprimitiella eremita* Schallreuter, 1980*a*, Sularp Shale, Caradoc Series, Gislövshammar, Scania, Sweden; left valve (holotype, GPIMH 2292), × 65 (Schallreuter 1976, pl. 4, fig. 4).

All scanning electron micrographs of external lateral views.



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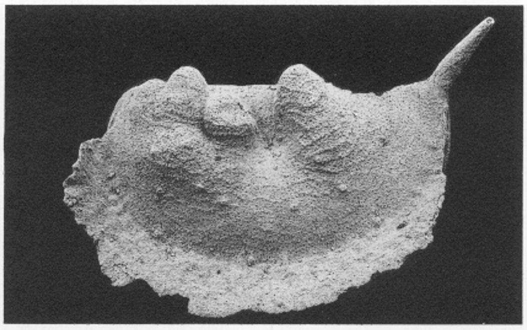

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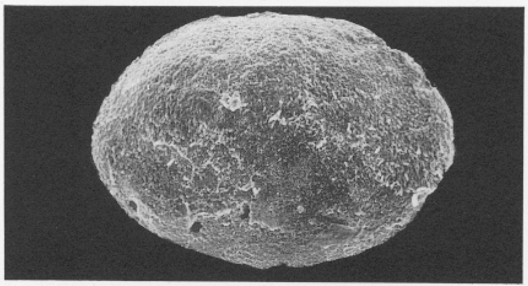

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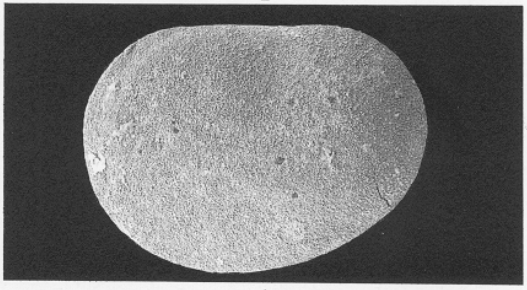

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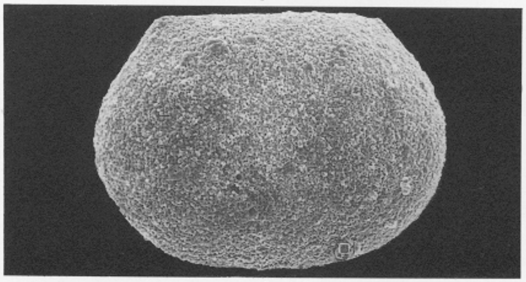

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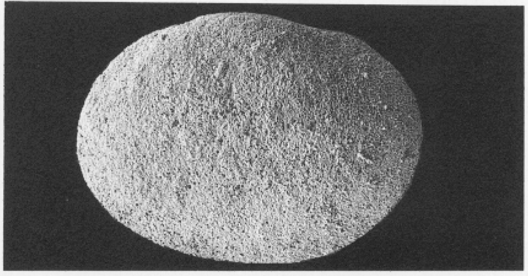

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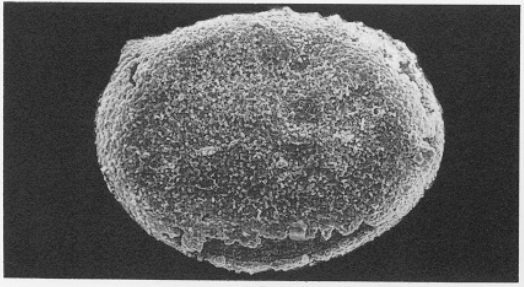

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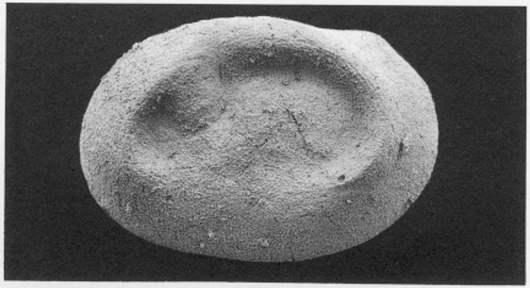

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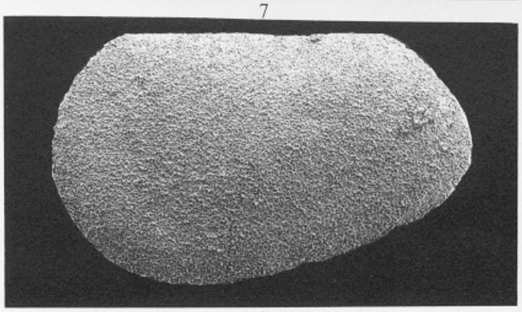

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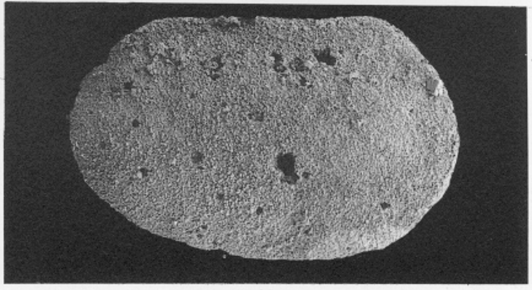

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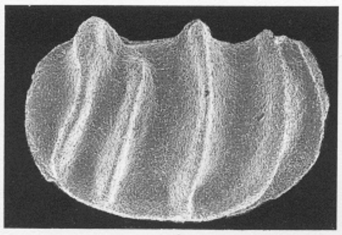
EXPLANATION OF PLATE 30

Palaeocope and binodicope ostracodes from the Ordovician of Ibero-Armorica (*left*), the British Isles (*middle*), and Baltoscandia (*right*).

Figs. 1–9. Palaeocopa. 1, *Ogmoopsis arcadelti* Vannier, 1986*b*, Llandeilo Series, Traveusot, Guichen, Ille-et-Vilaine, France; tecnomorphic left valve (holotype, IGR 5307/1), ×23 (Vannier 1986*b*, pl. 8, fig. 1). 2, *Ogmoopsis* (*Quadridigitalis*) *siveteri* Jones, 1986, Harnagian Stage, Caradoc Series, Cressage, Shropshire, England; heteromorphic left valve (holotype, BM OS 12654), ×16 (Jones 1986, pl. 12, fig. 1). 3, *Ogmoopsis alata* Sarv, 1959, erratic boulder, lower part of the Ordovician (Kunda Stage ($\mathrm{B_{III}}$); see text-fig. 2), Ahlintel, near Münster, Germany; tecnomorphic left valve (Westfälisches Museum fur Naturkunde in Münster, WMN no. A15), ×61 (Schallreuter 1985*b*, pl. 4, fig. 2). 4, *Vittella* sp., Schistes du Fresne Formation, Llanvirn Series, Ligné, Loire-Atlantique, France; tecnomorphic left valve (IGR 5290/1), ×32 (Vannier 1986*b*, pl. 3, fig. 1). 5, *Vittella fecunda* Siveter, 1983, upper part of the Llandeilo Series, Dryslwyn, near Llandeilo, Dyfed, Wales; heteromorphic left valve (holotype, BM OS 7777), ×32 (Siveter 1983, pl. 10 (14), fig. 1). 6, *Vittella vittensis* Schallreuter, 1964, erratic boulder, middle part of the Ordovician (lower upper Viruan; see text-fig. 2), Isle of Hiddensee, Baltic Sea, Germany; heteromorphic left valve (holotype, GPIG no. Os 289), ×40 (Schallreuter 1964, pl. 11, fig. 3). 7, *Quadritia* (*Krutatia*) *tromelini* Vannier and Schallreuter, 1983, Cacemes Formation, Llandeilo Series, Cacemes section, near Cacemes, Buçaco syncline, Portugal; right valve (paratype, IGR 5101/A1), ×46 (Vannier and Schallreuter 1983, pl. 9, fig. 5). 8, *Quadritia* (*Krutatia*) *iunior* Schallreuter, 1981, Ashgill Series, Dryslwyn Castell, near Llandeilo, Dyfed, Wales; right valve (BM OS 13372), ×43. 9, *Quadritia* (*Krutatia*) *krausei* Schallreuter, 1976, Backsteinkalk erratic boulder, middle part of the Ordovician (Idavere ($\mathrm{C_{III}}$) or Johvi ($\mathrm{D_I}$) Stage; see text-fig. 2), Northern Germany; left valve (GPIMH 2591), ×47 (Schallreuter 1983*a*, pl. 11, fig. 1).

Figs. 10–18. Binodicopa. 10, *Klimphores vogelweidei* Vannier, 1986*a*, Traveusot Formation, Llanvirn Series, Laille, Ille-et-Vilaine, France; right valve (holotype, IGR 5255A/8), ×61 (Vannier 1986*a*, pl. 1, fig. 1). 11, *Klimphores morgani* (Jones, 1890), Onnian Stage, Caradoc Series, Welshpool, Powys, Wales; left valve (specimen now broken), ×79 (Jones 1987, pl. 1, fig. 14). 12, *Klimphores planus* Schallreuter, 1966*c*, erratic boulder, middle part of the Ordovician (lower upper Viruan; see text-fig. 2), Isle of Hiddensee, Baltic Sea, Germany; right valve (GPIMH 2230), ×65 (Schallreuter 1980*b*, pl. 7 (10), fig. 4). 13, *Laterophores varesei* Vannier, 1986*a*, Andouillé Formation, Caradoc Series, Andouillé, Mayenne, France; left valve (holotype, IGR 30415/2), ×77 (Vannier 1986*a*, pl. 2, fig. 1). 14, *Laterophores elevatus* Jones, 1987, upper part of the Llanvirn Series, Llandeilo, Dyfed, Wales; right valve (holotype, BM OS 12751), ×64 (Jones 1987, pl. 2, fig. 1). 15, *Laterophores lateris* Schallreuter, 1968*a*, Backsteinkalk erratic boulder, middle part of the Ordovician (lower upper Viruan; see text-fig. 2), Isle of Hiddensee, Baltic Sea, Germany; right valve (GPIMH AG G21/2), ×75. 16, *Pseudulrichia raguenezensis* Vannier, 1986*a*, Grès de Kermeur Formation, Caradoc Series, Raguenez, Crozon, Finistère, France; right valve (holotype, IGR 30576/1), ×32 (Vannier 1986*a*, pl. 5, fig. 2). 17, *Pseudulrichia conispina* Jones, 1987, upper part of the Llandeilo Series, Dryslwyn, Dyfed, Wales; right valve (BM OS 12762), ×59 (Jones 1987, pl. 3, fig. 5). 18, *Pseudulrichia ullehmanni* Schallreuter, 1981, Öjlemyrflint erratic boulder, upper part of the Ordovician (Harjuan Series; see text-fig. 2), Isle of Sylt, North Sea, Germany; right valve (paratype, GPIMH 2151), ×74 (Schallreuter 1981, fig. 9).

All external lateral views; all scanning electron micrographs except fig. 6. Figs. 1, 2, 4, 7, 10, 11, 13, 16 are casts from external moulds.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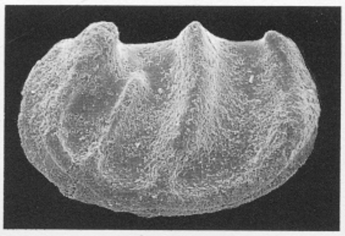
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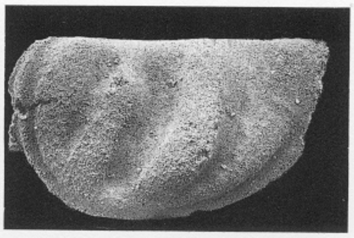
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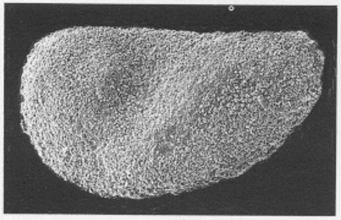
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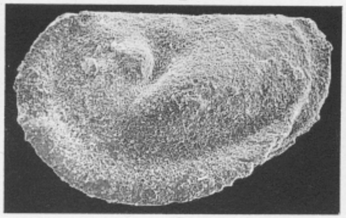
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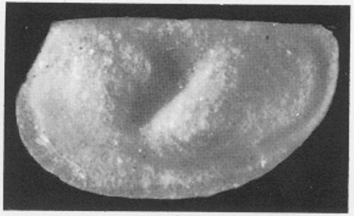
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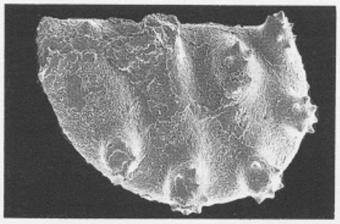
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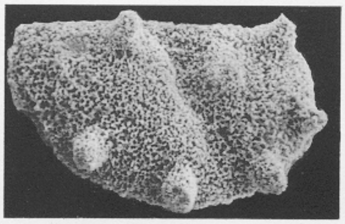
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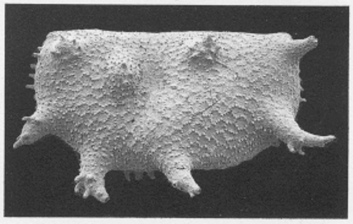
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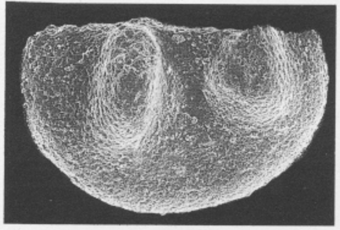
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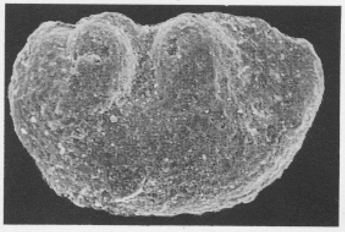
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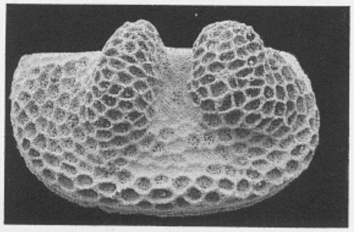
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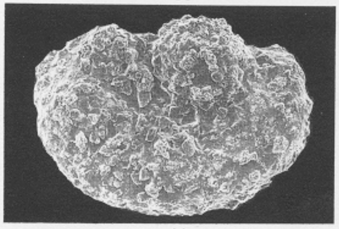
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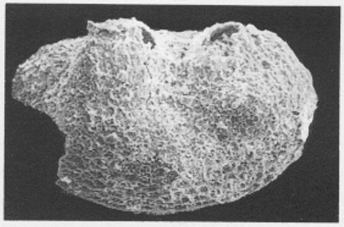
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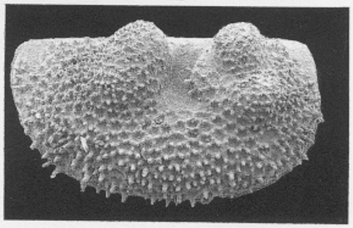
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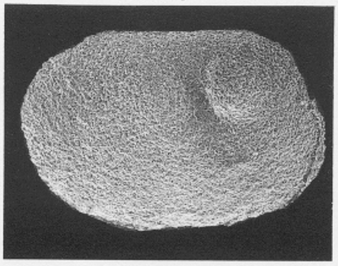
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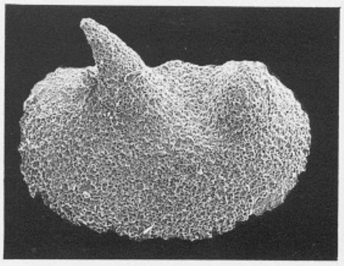
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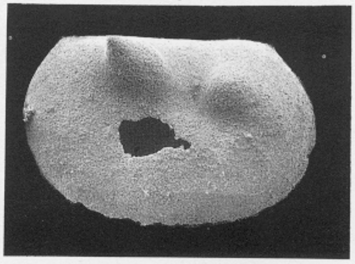
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