

## Nonpalaeocope ostracod biostratigraphy of the type Wenlock Series, Silurian, of the Welsh Borderland.

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**ABSTRACT** - Analysis of distribution, diversity and abundance of nonpalaeocope ostracods from the type Wenlock Series demonstrates that a major faunal change occurs around the Sheinwoodian-Homerian Stage boundary and that significant increases in faunal diversity occur at that boundary and in the late Whitwell Chronozone. Low abundance and low diversity in the late Sheinwoodian is interpreted to represent maximum water depth for the type Wenlock Series whereas the high diversity fauna of the late Homerian represents shallowest water conditions for this sequence. Many late Homerian species range into the Lower Elton Formation (early Ludlow) which suggests gradual ecostratigraphic change across the Wenlock-Ludlow boundary. Ancestor-descendant relationships for several lineages in the type Wenlock Series define lineage zones which essentially coincide with assemblage zones based on nonpalaeocope ostracods.

### INTRODUCTION

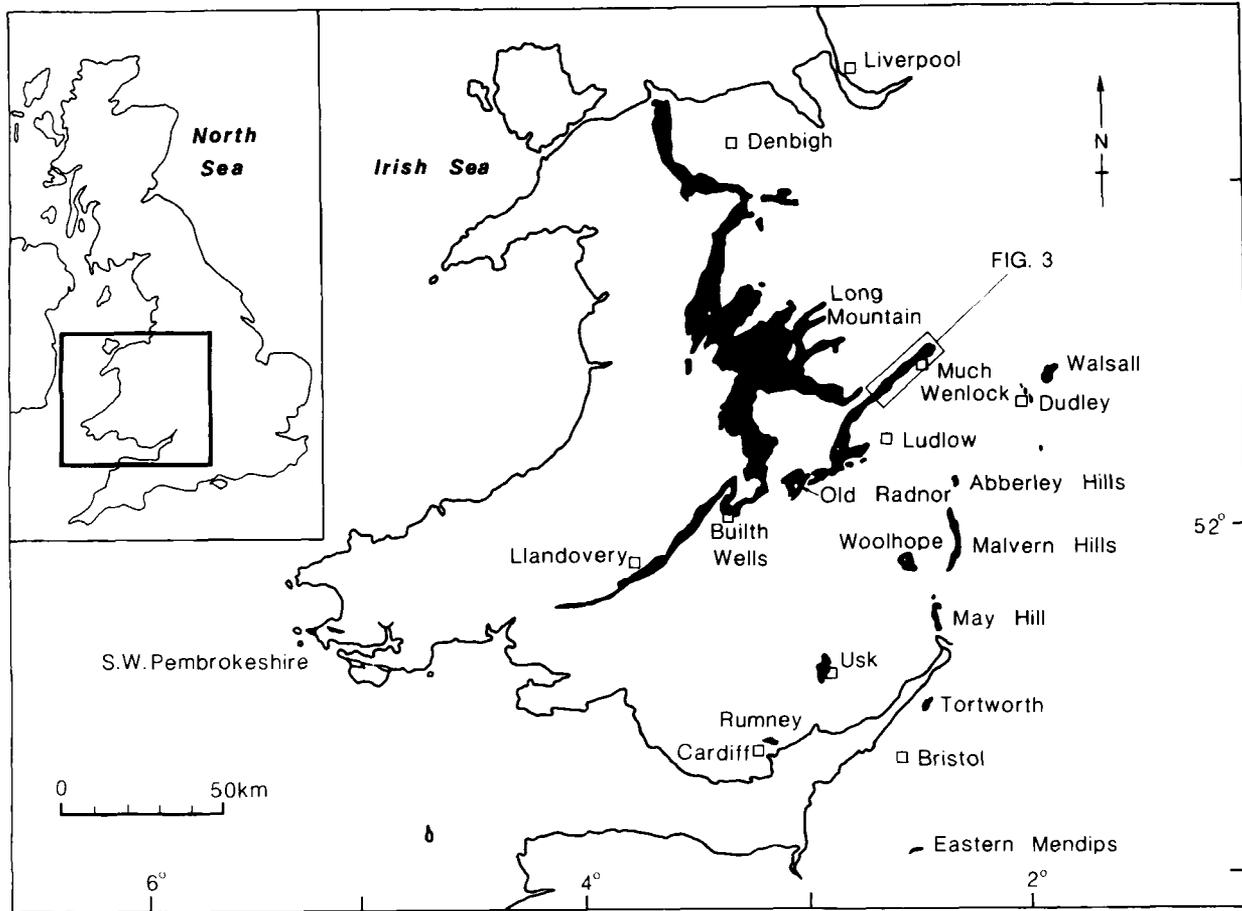
In this paper "nonpalaeocopes" is an informal term used to refer collectively to podocope, metacope and platycope Ostracoda as well as taxa which are not obviously archaeocopes, leperditicopes, palaeocopes or myodocopes. Nonpalaeocope ostracods have been known from the Wenlock strata of the Welsh Borderland and nearby areas (Figs 1-3) since the work of Jones (1887 a,b) and Jones and Holl (1865, 1869, 1886). Many authors have made reference to these early works but, except for revisions of the *Thlipsuridae* by Swartz (1932) and Krandijevsky (1968) and some primary revision of species of *Thlipsura* by Lundin & Petersen (1975), *Octonaria* by Petersen & Lundin (1987) and *Primitia* by Lundin & Siveter (1989), twentieth century reference to these Wenlock nonpalaeocopes has been virtually restricted to specific taxonomic notes. Analysis of the stratigraphic distribution of nonpalaeocopes of the type Wenlock Series has been limited to papers by Siveter (1978, 1988, 1989) and Aldridge *et al.* (1979) in which only a few nonpalaeocope species were treated, studies by Mabillard (1981) and Mabillard & Aldridge (1985) which treated only Llandovery-Wenlock boundary beds, and to preliminary reports on type Wenlock Series nonpalaeocope biostratigraphy by Petersen & Lundin (1981, 1982) and Lundin & Petersen (1982). Finally, Siveter (1984) discussed the habitats and modes of life of Silurian ostracods and made inferences regarding a few nonpalaeocopes from the type Wenlock Series. However, no comprehensive analysis of the stratigraphic distribution of nonpalaeocope ostracods of the type Wenlock Series has been published. This is especially unfortunate because ostracods have been particularly useful components of biostratigraphic

analysis of Silurian sequences in the Baltic-Podolian region as indicated, for example, by the works of Martinsson (1967), Gailite (1967), Sarv (1968), Abushik (1971, 1979), and Pranskevichius (1972). Although in these works emphasis has been placed on various groups of palaeocope ostracods, it is not uncommon that nonpalaeocopes dominate the faunas. Therefore, it is clear that analysis of the stratigraphic distribution of nonpalaeocope ostracods in the sections in which the Wenlock Series is based will fill a significant gap in our knowledge of Wenlock ostracod biostratigraphy.

In view of the above, the purpose of this paper is to present the stratigraphic distribution of nonpalaeocope ostracod species in the area of the type Wenlock Series and to relate that distribution to the standard graptolite zonation which has been established for that succession of rocks (Bassett *et al.*, 1975). In addition, we consider the reasons for the primary ostracode faunal changes which occur in these strata. The data presented herein have been accumulated during taxonomic studies of the nonpalaeocopes of the type Wenlock Series. It is not the purpose of this paper, however, to describe, redescribe or revise the taxonomy of these ostracods. That has been done partially by Petersen & Lundin (1974, 1987, 1989), Lundin & Petersen (1975, 1989) and Lundin & Siveter (1989), and additional revisions will be published elsewhere. Clarification of the taxonomy used herein is given below (see TAXONOMY).

### MATERIALS AND METHODS

Samples used for this study are primarily from well known localities which have been published by Siveter (1980, 1988). The location of 40 exposures from which point samples of



Text-fig. 1. Map of the outcrop of the Wenlock Series in Wales and the Welsh Borderland. The area of the type Wenlock Series is detailed in Text-fig. 3. Wenlock successions for the type Wenlock Series, The Dudley-Walsall area, the Malvern Hills, the Woolhope inlier, May Hill, and the Tortworth inlier are given in Text-fig. 2.

Wenlock strata where this study is described below (see LOCALITIES). Nonpalaeocope ostracods were found in approximately 150 samples at these localities. Most (approximately 75%) of these samples are from localities in the type Wenlock area (Fig. 3). In addition, four samples from two localities in Ludlow strata have been used to confirm the Ludlow occurrence of some species. The data on stratigraphic distribution presented in this paper is based upon identification of 16,000-17,000 nonpalaeocope specimens.

Except for the carbonate-dominated upper part of the type Wenlock Series where quarry exposures are common, most exposures of these rocks are limited in stratigraphic as well as geographic extent. It is not possible to sample stratigraphically-extensive parts of the type Wenlock Series at single sections. Accordingly, this study is based on samples from scattered localities, most of which occur in the type Wenlock area of Wenlock Edge to Ironbridge, Shropshire, England (see Bassett *et al.*, 1975, fig. 8). Other English Wenlock successions sampled for this study include those of the Woolhope and Mayhill inliers and the Malvern Hills in the Welsh Borderland,

the Dudley-Walsall area in the West Midlands, and the Tortworth inlier near Bristol in southwest England (Figs 1, 2). In terms of the palaeogeographic setting, all sampled localities represent the relatively shallow and relatively nearshore parts of the Welsh depositional basin. Most of the samples used in this study have been related to the graptolite zonation established for the type Wenlock area (Bassett *et al.*, 1975) by plotting the localities on the detailed field maps of Dr M.G. Bassett.

Samples used in this study are almost exclusively from soft mudstones and marls. Even samples from the Much Wenlock Limestone Formation have been taken predominantly from argillaceous mudstone beds within the limestone sequence. Accordingly, virtually all of the ostracodes identified in this study have been extracted from washed residues.

Preservation of the ostracodes is variable. In general, however, it is good, and uncertain identification of specimens due to poor preservation generally has not been a problem. Specimens of questionable identity have not been used in defining the limits of the stratigraphic ranges presented in this paper.



## LOCALITIES

This paper is based on specimens from three sources: samples collected by R.F.L. and D.J.S. in 1970, 1983 and 1988; sample washings kindly made available by the late Professor Anders Martinsson; and faunal slides in D.J.S. collections at Leicester University. Most of the sampled localities are listed in Siveter (1980) and, for ease of cross reference, are therefore listed below using the locality number and field designation of that paper. Additional localities which we have used are given, unnumbered, at the end of the list. Information on geographical location (including National Grid Reference), stratigraphical position and relevant references for the locality or area also accompanies each of the localities cited below.

Localities modified from Siveter (1980):

12. Brinkmarsh Quarry, *Pycnactis* Band: SW side of Quarry at Whitfield, Tortworth Inlier, Avon. Shale of *Pycnactis* Band, near base of Brinkmarsh Formation; basal Sheinwoodian. Curtis, 1972; Bassett, 1974. Four localities, a few metres apart along strike. 12a, ST 6737 9128. 12b, ST 6739 9126. 12c, ST 6741 9125. 12d, ST 6744 9124.

15. Hobbs Ridge: Line of old quarries immediately N of old road across crest of Hobbs Ridge, c. 0.7km NE of Longhope, May Hill inlier, Gloucestershire. Much Wenlock Limestone Formation (lower part); upper half of Homeric. Lawson, 1955, p.89; Bassett, 1974, p.761; 1976. Three localities, c. 10m apart and approximately same horizon. 15a, SO6946 1952. 15b, SO 6946 1953. 15c, SO 6946 1954.

18. Croft Farm: Line of old quarries along ridge between Cother Wood and Croft Farm, 0.5km W of Malvern, Hereford & Worcester. Much Wenlock Limestone Formation: upper half of Homeric. Phipps & Reeve, 1967, p.344; Bassett, 1974, p.760; 1976. Several closely spread localities; all pathside exposures. 18a, SO 7527 4650 (W side of middle path). 18b, SO 7574 4646 (W side of middle path). 18c, SO 7577 4627 (W side of upper path). 18d, SO 7579 4623 (W side of upper path).

19. Whitman's Hill: Quarry c. 300m S of church on A4103 road at Storrige, Malverns area, Hereford & Worcester. Horizon and references as loc.18. 19a, SO 74855 4831. 19b, SO 7485 4833.

20. Storrige: Road section c. 300m SW of church on A4103 road at Storrige, Malverns area, Hereford & Worcester; SO 4758 4853. Uppermost part of Coalbrookdale Formation; Homeric. References as loc.18.

23. Ledbury: Quarry, E side of A449 road, 0.5km NE of Ledbury, Hereford & Worcester; SO 7162 3775. Horizon and references as loc.18.

25. Hay Head Farm: Old workings NE and SE of Hay Head Farm, near Walsall, West Midlands; SP 0492 9890; SP 0475 9845; SP 0485 9879; SP 0489 9888; SP 0513 9902. Barr Limestone Member of Coalbrookdale Formation; probably all of *M. riccartonensis* Biozone age; middle Sheinwoodian. Bassett, 1974, p.756.

26. Daw End: Railway cutting at Rushall, near Walsall, West Midlands; SO 0360 0030. Coalbrookdale Formation; lower half of Homeric. Butler, 1939, p.54; Bassett, 1974, p.757.

27. Wren's Nest: Dudley, West Midlands. Wenlock Series. Localities 27c, f, g, of Siveter (1980). Nodular Member, Much Wenlock Limestone Formation; Homeric. Butler, 1939; Bassett, 1974, p.757; 1976, p.211. 27c, ridge crest, W side; SO 9357 9195. 27f, ridge, W side; SO 9357 9199. 27g, W flank of W side. SO 9394 9184.

28. Hurst Hill: Cutting on A463 road at Sedgley, 4km N of Dudley, West Midlands; SO 9280 9405. Nodular Member, Much Wenlock Limestone Formation; Homeric. Butler, 1939; Bassett, 1974, p.757;

1976, p.212.

34. Buildwas Bridge. The N bed and bank of River Severn, c. 15m upstream from road bridge at Buildwas, Shropshire; SJ 6451 0445. Apedale Member, Coalbrookdale Formation (lower part); middle Sheinwoodian. Bassett *et al.*, 1975; Bassett, 1989.

37. Buildwas Abbey: N bank of River Severn, c. 130m upstream from road bridge and opposite Buildwas Abbey, Shropshire; approximately SJ 643 045. Buildwas Formation (upper part); lower to middle Sheinwoodian. References as loc. 34.

38. Birches Coppice: Slope above N side of B4380 road at S end of Birches Coppice, c. 700m E of Buildwas Bridge, Shropshire; SJ 6523 0460. Apedale Member, Coalbrookdale Formation (lower part); very late Sheinwoodian. References as loc. 34.

39. Benthall Edge, Severnside: S bank of River Severn, opposite Coalbrookdale valley and c. 700m W of bridge at Ironbridge, Shropshire; SJ 6657 0359. Apedale Member, Coalbrookdale Formation (upper part); c. top of lower half of Homeric. References as loc. 34.

40. Coalbrookdale: Small exposure near cottage immediately N of railway bridge, W side of Coalbrookdale, Shropshire; SJ 6555 0400. Apedale Member, Coalbrookdale Formation (upper part); lower half of Homeric. References as loc. 34.

41. Longville: On the road between Longville in the Dale and Stanway, Wenlock Edge, Shropshire; SO 5398 9272. Farley Member (uppermost part) of Coalbrookdale Formation; upper half of Homeric. References as loc. 34.

42. Acklands Coppice: Section along old railway track, NW side of Acklands Coppice, between Buildwas and Much Wenlock, Shropshire; Farley Member of Coalbrookdale Formation; upper half of Homeric. Bassett *et al.*, 1975, p.4; Bassett, 1989. Two localities, approximately same horizon. 42a, SJ 6379 0269. 42b, SJ 6378 0267.

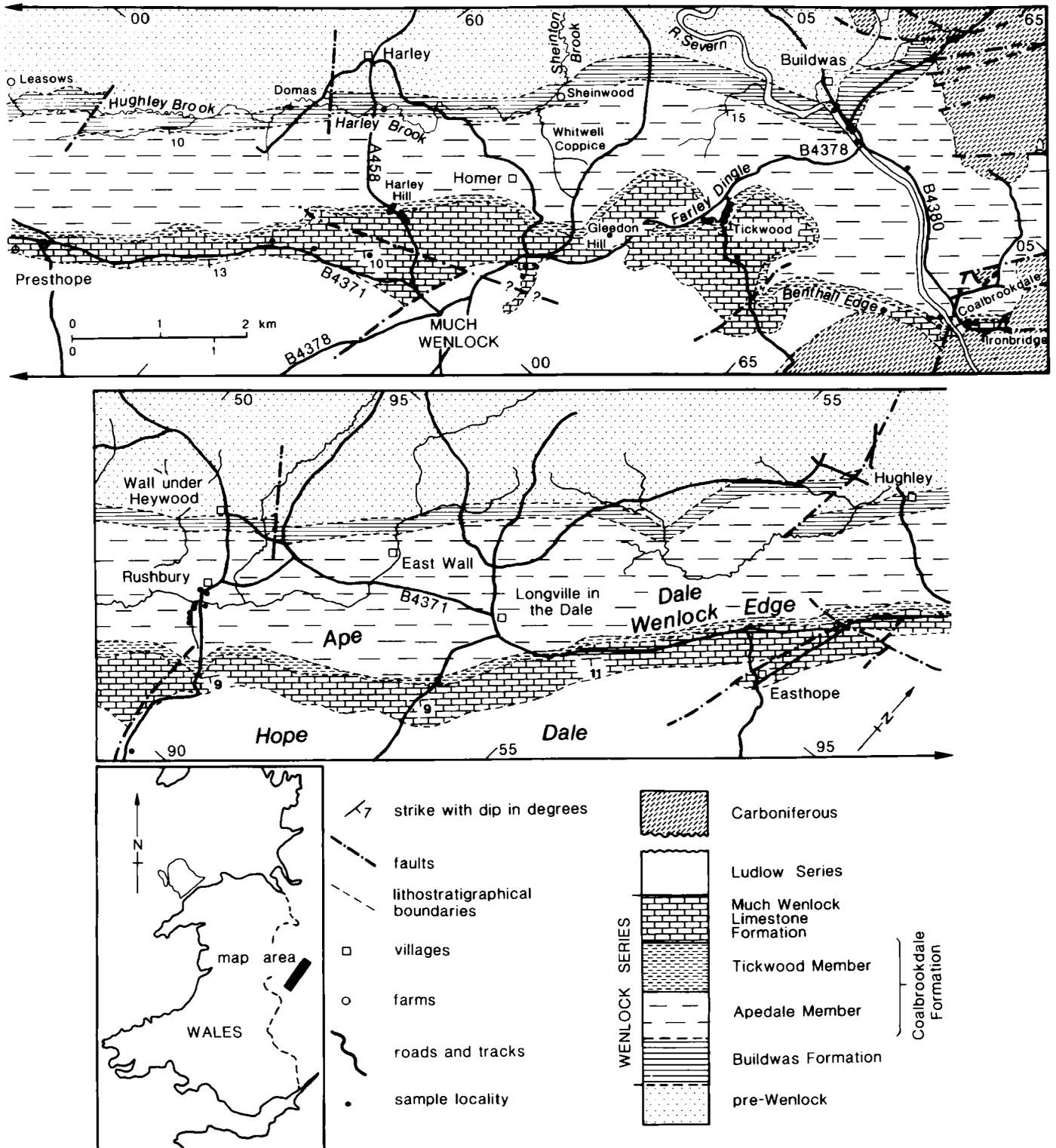
43. Benthall Edge, East: Small exposures along path just above and S of old railway track, S side of River Severn below E end of Benthall Edge, Shropshire. Farley Member of Coalbrookdale Formation; upper half of Homeric. Bassett *et al.* 1975; cf. Bassett, 1970, loc.9; Bassett, 1989. 43a, c. 100m W of Bower's Brook; SJ 6664 0352. 43b, c, 400m W of Bower's Brook; SJ 6635 0355.

44. Tickwood: E side of minor road from Lawley Cross to Wyke, and S of old railway bridge on W side of Tick Wood, c. 3km N of Much Wenlock, Shropshire. Farley Member of Coalbrookdale Formation; upper half of Homeric. References as loc. 34. Several closely spread localities, approximately same horizon. 44a, SJ 6382 0278. 44b, SJ 6380 0285. 44c, SJ 6379 0290. 44d, SJ 6381 0281.

47. Benthall Edge, West: Disused quarry on Benthall Edge, c. 500m NNW of Benthall Hall, Shropshire; SJ 6587 0315. Much Wenlock Limestone Formation; upper half of Homeric. Bassett *et al.*, 1975; Bassett, 1989.

48. Harley Hill Road: A458 road cutting, c. 1.2km NW of Much Wenlock, Shropshire. Shergold & Bassett, 1970, p.123, figs 7, 10; Bassett *et al.*, 1975, p.4; Bassett, 1989. 48a, N side of road, SJ 6095 0036; Farley Member (lower part) of Coalbrookdale Formation. 48b, S side of cutting, SJ 6099 0035; Farley Member (middle part) of Coalbrookdale Formation. 48c, N side of cutting, SJ 6103 0036; Farley Member (upper part) of Coalbrookdale Formation. 48d, N side of cutting, just below small bioherm, SJ 6107 0035; Much Wenlock Limestone Formation.

49. Lincoln Hill: Large, steeply dipping face at old workings on SW side of hill, c. 250m N of River Severn at Ironbridge, Shropshire. Horizon and references as loc. 47. 49a, top of face; SJ 6693 0381. 49b,



Text-fig. 3. Map showing geology of the type Wenlock area (redrawn from Bassett, 1989) and position of localities sampled (for details see text).

base of face,, directly below 49a. 49c, base of face, 10m SW of 49b.  
 50. Gleedon Hill: Top of section, NW side of Farley Quarry, E side of hill, 1.7km NNW of Much Wenlock, Shropshire; SJ 6298 0169. Horizon and references as loc.47.  
 51. Harley Hill Quarry: Small quarry on N side of A458 road, crest of hill, c. 1.2km NW of Much Wenlock, Shropshire; SJ 6110 0034. Horizon and references as loc.47.  
 52. Hayes Quarry: Quarry on N side of B4371 road, c. 2km SW of Much Wenlock, Shropshire; SO 6015 9915. Horizon and references as loc.47.  
 53. Coates Quarry: Quarry N side of B4371 road, c. 1.7km SW of Much Wenlock, Shropshire; SO 6045 9935. Horizon and references as loc.47.  
 54. Much Wenlock, Windmill: N of old windmill at Shadwell Rock Quarry, E side of B4378 road, c. 1km N of Much Wenlock, Shropshire; SJ 6247 0090. Horizon and references as loc.47.  
 55. Much Wenlock: Small quarry, c. 50m SW of old windmill at Shadwell Rock Quarry, E side of B4378 road, c. 1km N of Much Wenlock, Shropshire; SJ 6245 0078. Horizon and references as loc.47.  
 56. The Bank Quarry: Old quarry N side of path from the Bank to Blakeway Hollow, 1km SW of Much Wenlock, Shropshire; SO 6095 9973. Horizon and references as loc.47.  
 57. Audience Wood: Immediately N of minor road from Lawley Cross to Wyke and c. 200m due S of Tickwood Hall, 3.5km NW of Much Wenlock, Shropshire; SJ 6436 0246. Horizon and references as loc.47.  
 58. Presthope: Near road junction at Presthope, c. 4.5km SW of Much Wenlock, Shropshire; SO 5816 9741. Horizon and references as loc.47.  
 59. Millichope: Stream section c. 600m NW of Upper Millichope, Wenlock Edge, Shropshire; SO 5185 8987. Lower Elton Formation

(upper part); early Gorstian. Approximately loc.295 of Shergold & Shirley, 1968, fig. 1.

61. Shadwell Rock Quarry: Top of N face of quarry, just E of B4378 road, c. 1km N of Much Wenlock, Shropshire; SJ 6255 0090. Lower Elton Formation (lowermost part); early Gorstian. Shergold & Bassett, 1970, p.128; Bassett *et al.*, 1975; Bassett, 1989.

Additional localities:

*Buildwas*: N floor of River Severn at river bend some 440m SE of the church at Buildwas, Shropshire; SJ 6405 0455. Buildwas Formation (lower part); early Sheinwoodian. References as loc.34 above. This locality is close to (and at the same general horizon as) locality 35 'Buildwas' of Siveter (1980).

*Buildwas Abbey*: N bank of River Severn, c. 40m downstream from locality 37 'Buildwas Abbey' of Siveter (1980, see above); approximately SJ 6445 0447. Buildwas Formation (uppermost part); late early to early middle Sheinwoodian. References as loc.34 above.

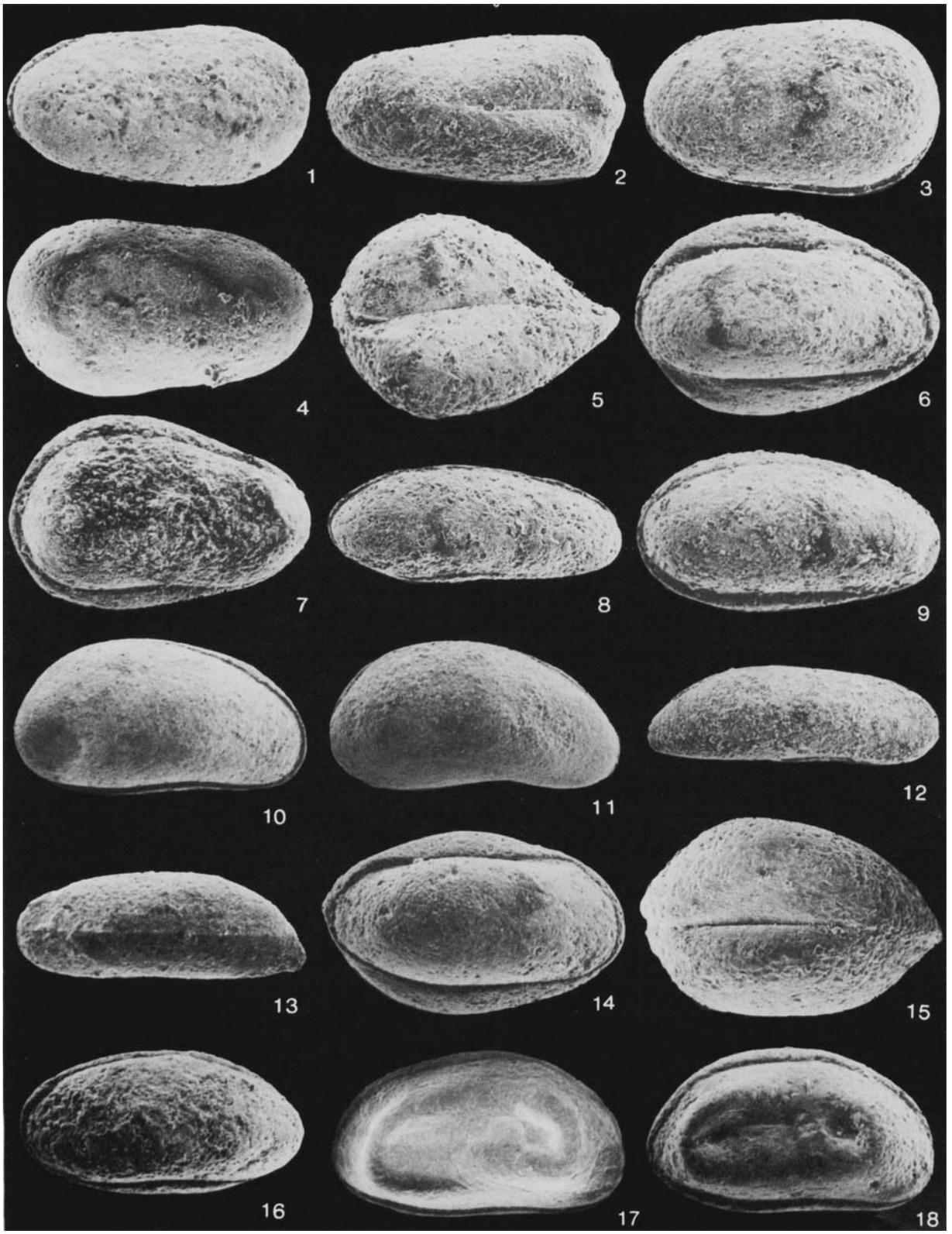
*Domas*: River bluff, E bank of Harley Brook, c. 100m S of its junction with Merrishaw Brook, near Domas, Ape Dale, Shropshire; approximately SJ 5925 0045. Buildwas Formation (lowermost part); early Sheinwoodian. References as loc.34 above. This locality is close to (and at a slightly older horizon than) locality 36 'Harley Brook' of Siveter, 1980.

*Harley*: S bank of Harley Brook 230m NE of the Feathers Inn, about 2.5km NW of Much Wenlock, Shropshire; SJ 6010 0116. Buildwas Formation (middle part); early Sheinwoodian. Bassett *et al.*, 1975, p.3; Bassett, 1989.

*Rushbury Road*: Two roadside exposures just S from St Peters Church, Rushbury, Ape Dale, Shropshire. Both in the Apedale Member, Coalbrookdale Formation (lower part); very late Sheinwoodian. Loc. a, E side of road bend, 108m at 203° from St Peters Church; SO 5132 9173; Bassett *et al.*, 1975, p.16, loc.26. Loc. b, W side of road entrance to house, 153m at 195° from St Peters Church; SO

#### Explanation of Plate 1.

Figs 1, 2. *Neckajatia subquadrata* (Jones, 1887). Fig. 1, carapace, left lateral view, ASU X-124, x 55. Loc.34, Shropshire; Apedale Member, Coalbrookdale Formation. Fig.2, carapace, dorsal view, ASU X-125, x 63; loc.40, Shropshire; Apedale Member, Coalbrookdale Formation.  
 Figs 3, 4. *Neckajatia symmetrica* (Jones, 1887). Fig. 3, carapace, left lateral view, ASU X-126, x 59. Fig. 4, carapace, right lateral view, ASU X-127, x 64. Both from north floor of River Severn, at river bend 440m SE of the church at Buildwas (= 'Buildwas' of 'Additional localities' list; see text), Shropshire; Buildwas Formation.  
 Figs 5, 6. *Daliella corbuloides* (Jones & Holl, 1869). Fig. 5, carapace, ventral view, ASU X-129, x 48. Fig. 6, carapace, right lateral view, ASU X-128, x 55. Both from approximately loc.48c, Shropshire; Farley Member, Coalbrookdale Formation.  
 Fig. 7. *Kuresaaria* sp. Carapace, right lateral view, ASU X-132, x 58. Loc.27f, West Midlands; Much Wenlock Limestone Formation.  
 Fig. 8. "*Cytherellina*" *elegans* (Jones, 1887). Carapace, right lateral view, ASU X=130, x 42. Loc.49, Shropshire; Much Wenlock Limestone Formation.  
 Fig. 9. "*Cytherellina*" sp. nov. Carapace, right lateral view, ASU X-131, x 48. Loc.18, Hereford & Worcester; Much Wenlock Limestone Formation.  
 Fig. 10. *Longiscella grandis* (Jones & Holl, 1869). Carapace, right lateral view, ASU X-133, x 24. Loc.34, Shropshire; Apedale Member, Coalbrookdale Formation.  
 Fig. 11. "*Longiscula*" *smithii* (Jones, 1887). Carapace, right lateral view, ASU X-134, x 30. Loc.27c, West Midlands; Much Wenlock Limestone Formation.  
 Figs 12, 13. "*Macrocypris*" *vineil* (Jones, 1887). Fig. 12, carapace, right lateral view, ASU X-135, x 26. Loc.43, Shropshire; Farley Member, Coalbrookdale Formation. Fig. 13, carapace, left lateral view, OS12272, x 30. Loc.39, Shropshire; Apedale Member, Coalbrookdale Formation.  
 Figs 14, 15. *Microcheilinella* cf. *M. confexa* Pranskevichius, 1971. Fig. 14, carapace, right lateral view, ASU X-137, x 60. Fig.15, carapace, dorsal view, ASU X-138, x 60. Both from loc.39, Shropshire; Apedale Member, Coalbrookdale Formation.  
 Fig. 16. *Microcheilinella ovalis* (Jones, 1887). Carapace, right lateral view, ASU X-136, x 48. Loc.50, Shropshire; Much Wenlock Limestone Formation.  
 Figs 17, 18. *Octonaria octoformis* Jones, 1887. Fig. 17, carapace, right lateral view, OS6648, x 36. Loc.43a. Shropshire; Farley Member, Coalbrookdale Formation. Fig. 18, carapace, right lateral view, ASU X-86, x 38. Loc. 48a, Shropshire; Farley Member, Coalbrookdale Formation.



51329168; Bassett *et al.*, 1975, p.16, loc.28. Loc. b lies stratigraphically slightly above loc. a.

*Lakehouse Brook, Rushbury*: S bank of Lakehouse Brook, c. 100m E of bridge on S side of Rushbury, Ape Dale, Shropshire; SO 5146 9167. Apedale Member, Coalbrookdale Formation (upper part); basal Homeric. At or very slightly above loc.30 of Bassett *et al.*, 1975, p.16. *Stoneyhill*: Roadside section 100m S of house at Stoney Hill, about 300m S of Woolhope, Hereford & Worcester; SO 6125 3535, Woolhope Formation; early Sheinwoodian. Squirrell & Tucker, 1960.

*Old Oaks Farm*: Loose blocks of Woolhope Limestone Formation from below outcrop at deserted Old Oaks Farm, May Hill Inlier, Gloucestershire; SO 687 223. Lawson, 1955.

*Pack horse track, Rushbury*: Five localities along the old pack horse track and stream section to W of road just S of Rushbury, Ape Dale, Shropshire. Locs a-e, all Apedale Member, Coalbrookdale Formation (middle part). Loc. a, very early Homeric (very low *C. lundgreni* Biozone); locs b-e, all at stratigraphically successively higher levels in the lower one-half of the *C. lundgreni* Biozone. Loc. a, on NE bank of stream 35m SE from minor road at start of stream section; SO 5135 9148; slightly below loc.31 of Bassett *et al.*, 1975, p.16. Loc. b, on NE bank of stream 55m SE from minor road at start of stream section, SO 5136 9148; approx. loc.31 of Bassett *et al.*, 1975, p.16. Loc. c, on SW bank of stream 90m SE from minor road at start of stream section; SO 5140 9145. Loc. d, on SW bank of stream 105m SE of minor road at

start of stream section; SO 5142 9142. Loc. e, on SW bank of stream 140m SE of minor road at start of stream section; SO 5142 9140; approx. loc.34 of Bassett *et al.*, 1975, p.16.

## TAXONOMY

Most ostracod species treated in this study are undergoing revision and those revisions will be published elsewhere. The generic designations of some species are widely used and for those which we accept no special notation is made. The generic placements of some other species have been widely used but in our opinion need further study which will probably result in revision. In these cases the generic name has been placed in quotation marks. A few species are recognized as new and are left in open nomenclature in this paper, as are two species which are represented by only one specimen each. Furthermore, it should be noted that a few species described by Jones and Jones and Holl are known only from the type collections in the British Museum (Natural History). We have been unable to verify these species in our collections and therefore these species are not considered in this paper. Table 1 summarises the generic level taxonomy used in this paper and gives the original combination and author(s) for all previously described species which are listed in Figure 4 and illustrated on Plates 1 and 2.

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### Explanation of Plate 2

Fig. 1. *Primitvothlipsurella obtusa* Petersen & Lundin, 1989. Carapace, right lateral view, ASU X 120, x 60. Loc.37, Shropshire; Buildwas Formation.

Figs 2, 3. *Primitvothlipsurella v-scripta* (Jones & Holl, 1869). Fig. 2, left valve, ASU X-110, x 45. Fig. 3, carapace, right lateral view, OS 6646, x 45. Both from loc.18, Hereford & Worcester; Much Wenlock Limestone Formation.

Fig. 4. *Scaldianella simplex* (Krause, 1891). Carapace, left lateral view, ASU X-140, x 68. Loc.27f, West Midlands; Much Wenlock Limestone Formation.

Fig. 5. *Alanella* sp. Carapace, right lateral view of abraded specimen, ASU X-141, x 35. Loc.39, Shropshire; Apedale Member, Coalbrookdale Formation.

Fig. 6. *Rectella* sp. nov. Carapace, right lateral view, ASU X-1139, x 52. Loc.39, Shropshire; Apedale Member, Coalbrookdale Formation.

Fig. 7. *Steusloffina* sp. Carapace, right lateral view of damaged specimen, ASU X-144, x 28. Loc.34, Shropshire; Apedale Member, Coalbrookdale Formation.

Fig. 8. *Silenis mawii* (Jones, 1887). Carapace, right lateral view, ASU X-142, z 44. Loc.18, Hereford & Worcester; Much Wenlock Limestone Formation.

Fig. 9. *Silenis longus* Abushik, 1971. Carapace, right lateral view, ASU X-143, x 30. Loc. 49, Shropshire; Much Wenlock Formation.

Fig. 10. *Tubulibairdia* sp. nov. Carapace, right lateral view, ASU X-145, x 63. Loc.37, Shropshire; Buildwas Formation.

Fig. 11. "*Bairdiocypris*" *phaseolus* (Jones, 1887). Carapace, right lateral view, ASU X-147, x 53. Loc.34, Shropshire, Apedale Member, Coalbrookdale Formation.

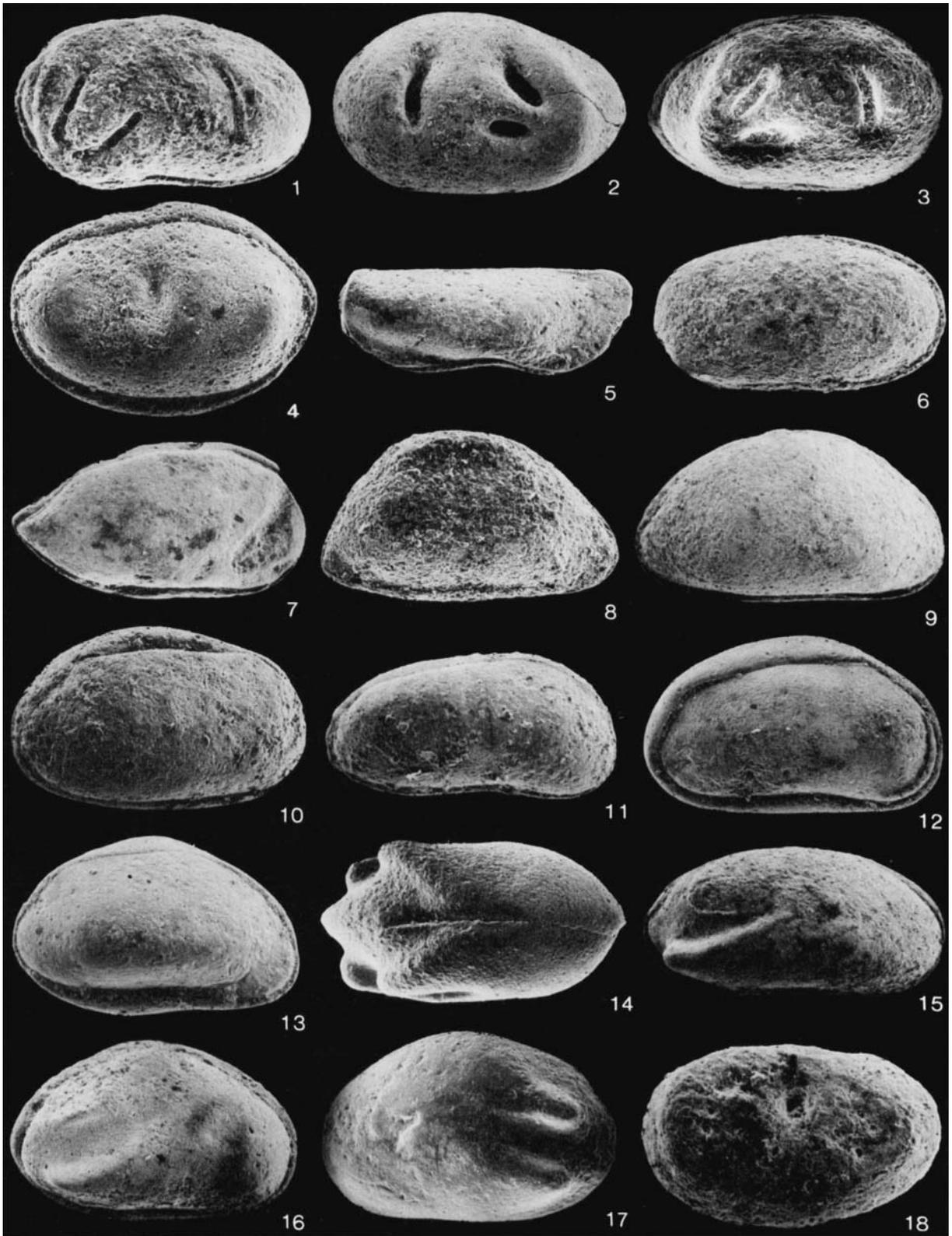
Fig. 12. "*Bairdiocypris*" *crassula* (Jones, 1887). Carapace, right lateral view, ASU X-146, x 49. Loc.27f, West Midlands; Much Wenlock Limestone Formation.

Fig. 13. "*Bairdiocypris*" *phillipsiana* (Jones & Holl, 1869). Carapace, right lateral view, ASU X-148, x 34. Loc.43, Shropshire; Farley Member, Coalbrookdale Formation. Figs 14, 15. *Thlipsura martinsoni* Petersen & Lundin, 1974. Fig. 14, carapace, dorsal view, OS 6644, x 35. Loc.34, Shropshire; Apedale Member, Coalbrookdale Formation. Fig. 15, carapace, right lateral view, ASU X-13, x 34. Loc.37, Shropshire; Buildwas Formation.

Figs 16, 17. *Thlipsura corpulenta* Jones & Holl, 1869. Fig. 16, carapace, right lateral view, ASU X-149, x 44. Fig. 17, carapace, left lateral view, OS 6642, x 45. Both from loc.49, Shropshire; Much Wenlock Limestone Formation.

Fig. 18. *Columatia variolata* (Jones & Holl, 1865). Right valve lateral view, ASU X-107, x 65. Loc.49, Shropshire; Much Wenlock Limestone Formation.

Repositories: ASU - Arizona State University, Department of Geology, Tempe, Arizona.  
OS = British Museum (Natural History), London.



This Paper	Original Combination
" <i>Bairdiocypris</i> " <i>crassula</i>	<i>Macrocypris crassula</i> Jones, 1887
" <i>Bairdiocypris</i> " <i>phaseolus</i>	<i>Bythocypris phaseolus</i> Jones, 1887
" <i>Bairdiocypris</i> " <i>phillipsianus</i>	<i>Bairdia phillipsiana</i> Jones & Holl, 1869
<i>Columatia variolata</i>	<i>Primitia variolata</i> Jones & Holl, 1865
" <i>Cytherellina</i> " <i>elegans</i>	<i>Macrocypris elegans</i> Jones, 1887
<i>Daleiella corbuloides</i>	<i>Cythere corbuloides</i> Jones & Holl, 1869
<i>Longiscella grandis</i>	<i>Cytherellina siliqua</i> var. <i>grandis</i> Jones & Holl, 1869
" <i>Longiscula</i> " <i>smithii</i>	<i>Pontocypris smithii</i> Jones, 1887
" <i>Macrocypris</i> " <i>vinei</i>	<i>Macrocypris vinei</i> Jones, 1887
<i>Microcheilinella</i> cf. <i>M. convexa</i>	<i>Microcheilinella convexa</i> Pranskevichius, 1971
<i>Microcheilinella ovalis</i>	<i>Bythocypris concinna</i> var. <i>ovalis</i> Jones, 1887
<i>Neckajatia subquadrata</i>	<i>Cythere?</i> <i>subquadrata</i> Jones, 1887
<i>Neckajatia symmetrica</i>	<i>Bythocypris symmetrica</i> Jones, 1887
<i>Octonaria octoformis</i>	<i>Octonaria octoformis</i> Jones, 1887
<i>Primitivothlipsurella obtusa</i>	<i>Primitivothlipsurella obtusa</i> Petersen & Lundin, 1989
<i>Primitivothlipsurella v-scripta</i>	<i>Thlipsura v-scripta</i> Jones & Holl, 1869
<i>Scaldianella simplex</i>	<i>Thlipsura simplex</i> Krause, 1891
<i>Silenis longus</i>	<i>Silenis longus</i> Abushik, 1971
<i>Silenis mawii</i>	<i>Pontocypris mawii</i> Jones, 1887
<i>Thlipsura corpulenta</i>	<i>Thlipsura corpulenta</i> Jones & Holl, 1869
<i>Thlipsura martinsoni</i>	<i>Thlipsura martinsoni</i> Petersen & Lundin, 1974

Table 1. Alphabetical list of previously described species shown on Figure 4 and in Plates 1 and 2 and the original taxonomic combination.

## COMMENTS ABOUT THE STRATIGRAPHIC DISTRIBUTION CHART

It is significant to indicate how the stratigraphic distributions, as portrayed in Figure 4, were established, in order to convey as well as possible the level of accuracy implied by the chart. The chart represents, in effect, the occurrence of nonpalaeocope species through the type Wenlock succession in Shropshire. Where samples have been taken from outside Shropshire (e.g. the English West Midlands), the local ranges of the species obtained are normally embraced by their respective ranges in Shropshire and therefore do not normally necessitate extensions to the ranges on the chart. The upper range terminations shown in Figure 4 for *Silenis longus*, *S. mawii* and "*Bairdiocypris*" *crassula* are based on samples from the Malvern Hills, and the upper range termination shown for *Kuresaaria* sp. is based on samples from the Dudley/Walsall area (Figs 1, 2). These range terminations are therefore based on correlations to the type Wenlock area as shown in Figure 2. The stratigraphic position of each sample from the type Wenlock area was established from plots of the sample localities on the Shropshire field maps of Dr M.G. Bassett. The precision with which sample localities are plotted and the precision with which the boundaries of some graptolite biozones are established (Bassett *et al.*, 1975) results in variable levels of accuracy in plotting the stratigraphic distribution of the ostracods. The stratigraphic position of some samples is known very precisely; that is, within a third or less of a graptolite biozone. For other samples, the level of accuracy is only within a graptolite biozone. In Figure 4 ranges are plotted according to the

following.

1) If a sample representing the lowest occurrence of a species is known to come from some part of a graptolite biozone, but it is not known exactly which part, the range in Figure 4 has been drawn to the base of that graptolite biozone.

2) If a sample representing the highest occurrence of a species is known to come from some part of a graptolite biozone, but it is not known exactly which part, the range in Figure 4 has been drawn to the top of that graptolite zone.

3) All range lines through the *Cyrtograptus rigidus* and *C. linnarssoni* biozones are dashed because we have no samples which definitely come from either of those biozones. Accordingly, the ranges of *Longiscella grandis*, *Tubulibairdia* sp. nov., *Thlipsura martinsoni* and *Primitivothlipsurella obtusa* could conceivably extend as high as the top of the *C. linnarssoni* Biozone but almost certainly not higher.

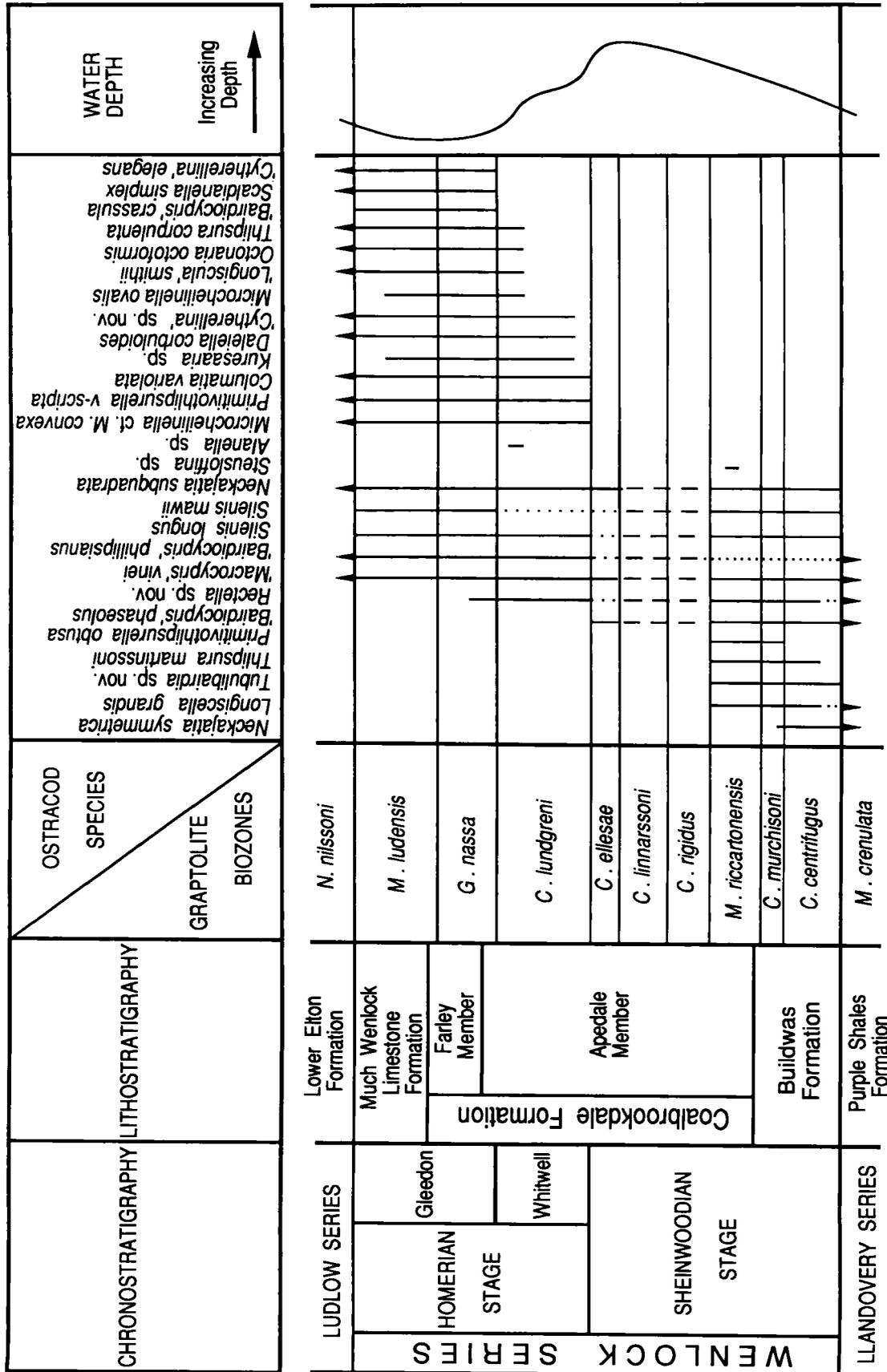
4) Ranges shown as dotted lines indicate the presumed existence of the species through the indicated time interval because of their known or reported occurrence above and below the interval indicated by dots.

5) Arrows at the bottom and/or top of a range indicate that the species is known to range into Llandovery and/or Ludlow strata in the type Wenlock area.

## LIMITATIONS OF THE DATA

The significance of the data in any chart which purports to show the chronostratigraphic ranges of species of any group of organisms is limited by several factors such as, 1) validity of the chronostratigraphic framework used, 2) the nature of exposures sampled, 3) the sampling density, 4) the number of specimens identified, and 5) the confidence with which the taxa can be defined. Of these we choose to comment here only on 3, 4 and 5 because the chronostratigraphic framework has been discussed by Bassett *et al.* (1975) and the nature of the exposures has been mentioned above (see MATERIALS AND METHODS).

Sampling density through the Wenlock strata analyzed in this study is variable. Substantially more samples are from Homeric strata than from Sheinwoodian strata. This fact, coupled with the fact that Homeric samples normally yield more nonpalaeocopes per unit volume of rock, means that approximately 75-80% of the 16,000-17,000 specimens identified came from the upper half of the Wenlock. Even so, this means that more than 3,000 nonpalaeocopes have been identified from 36 samples of Sheinwoodian strata. We conclude that, although sampling density is less for the Sheinwoodian strata than for the Homeric strata, additional sampling is unlikely to significantly change the ranges shown in Figure 4, except that the ranges of *Longiscella grandis*, *Primitivothlipsurella obtusa*, *Thlipsura martinsoni* and *Tubulibairdia* sp. nov. could be extended upwards by as much as two graptolite biozones.



Text-fig. 4. Range diagram of nonpalaeocope ostracods in the Wenlock Series of the Welsh Borderland and the English West Midlands; based mainly on data from the type Wenlock area; see text (COMMENTS ABOUT THE STRATIGRAPHIC DISTRIBUTION CHART) for explanation of arrows, and dotted and dashed lines.

Mabillard (1981) and Mabillard & Aldridge (1985) reported the occurrence of "*Bairdiocypris*" *phillipsianus* in the Llandovery (Purple Shales) and lower Wenlock (lower Buildwas Fm.) at Leasows and Domas in the Welsh Borderland. One of us (RFL) has confirmed these occurrences. Because our Sheinwoodian samples have not yielded this species, we conclude that "*B*" *phillipsianus* is very rare or absent from Sheinwoodian strata of the area above the basal 2.25 metres of the Buildwas Fm.

Palaeozoic nonpalaeocope ostracods generally have not received appropriate attention in biostratigraphy because many of them are smooth, rather nondescript forms which require quantitative methods of shape analysis for adequate species definitions. The Wenlock nonpalaeocope faunas studied here are no exceptions to this rule. Accordingly, we indicate those species which under present knowledge are the most useful biostratigraphically because of their relatively restricted chronostratigraphic ranges and their morphological attributes which permit nonspecialists to identify them with confidence. In the Sheinwoodian part of the Wenlock, *Longiscella grandis*, *Primitivothlipsurella obtusa* and *Thlipsura martinssoni* are common to abundant species which are easily recognized. In addition, "*Bairdiocypris*" *phaseolus* and *Neckajatia symmetrica* are common Sheinwoodian faunal elements but distinction of these species from "*B.*" *crassula* and *N. subquadrata*, respectively, depends on analysis of large collections of each species. Specimens of intermediate morphology are not uncommon. *Silenis longus*, *Silenis mawii*, "*Macrocypris*" *vinei* and *Rectella* sp. nov. are distinctive and common but all range into or through the Homeric part of the sequence.

The Homeric is readily distinguished from the Sheinwoodian on the basis of nonpalaeocope faunas because such distinctive species as *Octonaria octoformis*, *Thlipsura corpulenta*, *Primitivothlipsurella v-scripta*, *Scaldianella simplex*, *Daleiella corbuloides* and *Columatia variolata* are common to abundant elements of the fauna. *Kuresaaria* sp. is restricted to the Homeric Stage but it is not a common element of the fauna. "*Bairdiocypris*" *phillipsianus* is exceedingly common in the Homeric but its occurrence (Mabillard, 1981; Mabillard & Aldridge, 1985) in the Llandovery and early Sheinwoodian denies its potential value as an indicator of Homeric age. Species of *Microcheilinella*, "*Longiscula*," and "*Cytherellina*" are less useful for biostratigraphy because they are less well defined and are morphologically more variable than the others listed above.

#### NONPALAEOCOPE ZONATION

Figure 4 shows two assemblage zones which clearly distinguish Homeric from Sheinwoodian strata. The Sheinwoodian assemblage is characterized by the first twelve species listed on Figure 4. Of these *Neckajatia symmetrica*, *N. subquadrata*, *Primitivothlipsurella obtusa*, *Thlipsura martinssoni*, *Silenis*

*longus* and the new species of *Rectella* and *Tubulibairdia* are the most common species. Five of the twelve species are restricted to the Sheinwoodian part of the Wenlock and two of those have been reported from Llandovery strata in the type Wenlock area.

The Homeric assemblage is characterized by the last thirteen species listed on Figure 4 in association with the several Sheinwoodian species which range into the Homeric. The occurrence of *Rectella* sp. nov. with other Homeric species suggests an early Homeric age. Ten of the thirteen species which are restricted to the Homeric part of the Wenlock Series range into the Ludlow. Figure 4 also shows that seven of these thirteen species do not range lower than the upper part of the *Cyrtograptus lundgreni* Biozone.

Lineage zones are defined by the ancestor-descendant relationships of *Thlipsura martinssoni* (see Petersen & Lundin, 1974) and *T. corpulenta* (see Lundin & Petersen, 1975) and *Primitivothlipsurella obtusa* (see Petersen & Lundin 1989) and *P. v-scripta* (see Lundin & Petersen, 1989). These four species are clearly defined and easily recognized. The ancestor in each lineage has never been found to occur with the descendant and, as shown in Figure 4, the descendant is known only from rocks which are distinctly younger than those of the ancestor. A similar relationship between "*Bairdiocypris*" *phaseolus* and "*B.*" *crassula* is probable but less well established. Furthermore, it is likely that *Columatia variolata* is a descendant of the *Neckajatia symmetrica*-*N. subquadrata* lineage (Lundin, 1988).

Because ostracod zonation of the type Wenlock Series should include data on beyrichiacean ostracods as well as that for other groups which have not yet been evaluated, we propose no formal biozonation here. However, it is possible to summarize the data on nonpalaeocope ostracods as follows. Two assemblage zones clearly distinguish the Sheinwoodian and Homeric stages. The Homeric assemblage can be further subdivided into early and late Homeric subzones based on the occurrence of *Rectella* sp. nov. with any of the species which do not range into the Sheinwoodian. Thirteen Homeric species range into the Ludlow, at least six Wenlock species range into the Llandovery and five species range throughout the type Wenlock Series. Finally, ancestor-descendant relationships have been defined in several nonpalaeocope lineages, segments of which essentially coincide with the assemblage zones referred to above.

It is noteworthy that several of the British nonpalaeocope species listed on Figure 4 offer potential for international correlation with coeval forms in the Gotland, East Baltic and Podolian sequences. Development of these correlations depends on further taxonomic studies, and biostratigraphic studies of the Gotland nonpalaeocopes presently being done by one of us (RFL).

## OBSERVATIONS AND CONCLUSIONS.

Analysis of the diversity, abundance and distribution of nonpalaeocene ostracods in the type Wenlock Series and its Welsh Borderland-West Midlands correlatives demonstrates the following:

1. Diversity (number of species) declines from moderate levels (twelve species) in the early Sheinwoodian to low levels (three species) in the late Sheinwoodian. Diversity returns to early Sheinwoodian levels (eleven species) in the early Homeric and increases to high levels (sixteen species) in the late Homeric.
2. Although no quantitative data are available, abundance of specimens follows a similar pattern. The late Sheinwoodian and very early Homeric samples yield the fewest specimens whereas the early Sheinwoodian and late Homeric samples are more prolific. In general, nonpalaeocene ostracodes are most abundant in the late Homeric strata.
3. The Sheinwoodian and Homeric faunas are distinctly different. As indicated above (see NONPALAEOCOPE ZONATION), of the twenty-five species (excluding *Steusloffina* sp. and *Alanella* sp. which are represented by only one specimen each) considered here, only six occur in Sheinwoodian and Homeric strata, six are restricted to the Sheinwoodian and thirteen are restricted to the Homeric. Of the latter thirteen species, six enter the section in the very early Homeric (lower part of the *C. lundgreni* Biozone) and seven enter the section in the middle part of the Homeric (upper part of the *C. lundgreni* to lower part of the *G. nassa* biozones).

These observations on diversity and distribution of nonpalaeocene ostracods are similar to those of various authors who have presented data for other groups of organisms. Siveter's (1978, 1988, 1989) data for palaeocene ostracods (primarily beyrichiaceans) is virtually identical to that for the nonpalaeocenes. Aldridge et al. (1979) and Aldridge, Dorning & Siveter (1981) have reviewed data on the distribution of chitinozoa, acritarchs, miospores, ostracods and conodonts. Bassett (1989a, b) has presented a summary of the data for brachiopods. Siveter, Owens & Thomas (1989) have summarized distributional data for selected species of various fossil groups including trilobites, graptolites, corals, bivalves, brachiopods and gastropods. Although all groups have not responded in the same way in detail, the general pattern of relatively rich and diverse faunas in the early Sheinwoodian followed by poor and restricted faunas in the late Sheinwoodian and a return to rich and very diverse faunas in the Homeric (especially the late Homeric) is clear.

Many authors (e.g. Calef & Hancock, 1974; Hurst, 1975a, b; Bassett, 1976; Aldridge, Dorning & Siveter, 1981; Siveter, Owens & Thomas, 1989) have related faunal changes in the type Wenlock series to changes in water depth. The primary faunal change which occurs around the Sheinwoodian-Homeric boundary is particularly interesting because it occurs, in the type Wenlock Series, within a rock sequence of remarkably

uniform lithology, i.e., the middle part of the Coalbrookdale Formation. Bassett et al. (1975) characterized the sediments of this interval as "monotonous." Water depth change, along with changes in other environmental parameters which are related to bathymetry, over the offshore portion of a platform which was already receiving primarily fine-grained clastics, as indicated by the lower part of the Coalbrookdale Formation, represents a reasonable framework within which to interpret the nonpalaeocene data. Accordingly, we conclude that the changes in diversity, abundance and composition of the nonpalaeocene ostracod faunas of the type Wenlock Series indicate the following.

1. Generally stable and relatively shallow water levels during the early Sheinwoodian (*C. centrifugus* through *M. riccartonensis* biozones). This interval is represented by the Buildwas Formation and lower part of the Coalbrookdale Formation. No important change in the nonpalaeocene fauna occurs within this interval.
2. Abrupt or gradual increase in water depth during the late Sheinwoodian (*C. rigidus* through *C. ellesae* biozones). The abruptness with which water depth increased cannot be judged from our data because the *C. rigidus* and *C. linnarssoni* biozones are not represented in our collections. The low abundance and low diversity of nonpalaeocenes in the *C. ellesae* Biozone suggests that water depths (and related parameters) were approaching the limits of Silurian benthic nonpalaeocene tolerance. We conclude that Wenlock water depths reached their maximum during this interval, which is represented by the upper part of the lower one-half of the Coalbrookdale Formation. We further conclude that these water depths were in excess of those represented by the lower Elton beds because the lower Elton nonpalaeocene fauna is significantly more diverse than that of the latest Sheinwoodian.
3. Relatively abrupt decrease in water depth during the early Homeric (early *C. lundgreni* Biozone). This conclusion is based upon the introduction or reintroduction of nine species which have not been found in the *C. ellesae* Biozone.
4. Another relatively abrupt decrease in water depth in the middle Homeric (late *C. lundgreni* to earliest *Gothograptus nassa* biozones). This represents the upper part of the Apedale Member of the Coalbrookdale Formation and this conclusion is based on the introduction of seven species which do not occur below the upper part of the *C. lundgreni* Biozone and the reintroduction of one species (*Silenis mawii*) which occurs also in the early Sheinwoodian.
5. The major differences between the Sheinwoodian (primarily early Sheinwoodian) nonpalaeocene fauna and that of the Homeric are a reflection of the occurrence, loss of and recurrence of relatively shallow water environments in the shelf area of the eastern margin of the Welsh Basin during Wenlock time. Evolution of early Sheinwoodian lineages resulted in the replacement of some Sheinwoodian ancestors by Homeric de

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with the Homerian recurrence of shallow water. Several species which range throughout the Wenlock, or at least occur in both Sheinwoodian and Homerian strata, do not occur in the latest Sheinwoodian but recur in the Homerian. Finally some Sheinwoodian species became extinct prior to the recurrence of shallow water environments in the Homerian.

6. Any shift toward deeper water conditions across the Wenlock-Ludlow boundary was gradual. Of the sixteen nonpalaeocope species known from latest Homerian strata, thirteen are known to occur in lower Ludlow (lower Elton) strata.

These conclusions lead us to modify the Wenlock portion of the sea level curve of Siveter, Owens & Thomas (1989) as shown in Fig. 4.

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