Palaeoecology of a hypersaline Carboniferous ostracod fauna

Chris P. Dewey
Department of Geology and Geography, Mississippi State University,
Mississippi State, MS 39762, U.S.A.

ABSTRACT—A high abundance, low diversity ostracod fauna has been collected from the Lower Carboniferous Dimock and Phillips limestones in Nova Scotia, Canada. The ostracod fauna consists of Paraparchites sp. aff. P. kelletae Sohn and Beyrichiopsis lophota Copeland, as well as rare specimens of Acratia acuta (Jones & Kirkby), Bythocypris aequalis (Jones & Kirkby), and Chamishaella suborbiculata (Munster).

Growth parameters for the dominant ostracod, Paraparchites sp. aff. P. kelletae, show that a multi-generation, progenetic, parthenogenetic population developed. This reproductive strategy caused rapid population growth and thereby allowed the species to take advantage of the available environmental resources.

When considered together, the ostracod fauna and the sedimentology indicate that physiologically stressful hypersaline conditions prevailed. The combined data therefore provide evidence for hypersalinity tolerance and heterochronous development amongst Carboniferous ostracods.

INTRODUCTION

Lower Carboniferous deposits in the Maritime Basin of Nova Scotia, Canada, document a series of eustatically controlled, transgressive-regressive cycles (Giles, 1981). Tectonic activity resulted in the development of several interconnected sub-basins (Howie & Barss, 1975; Bradley, 1982). Consequently, the complex interaction of eustacy, tectonism and climate resulted in a range of palaeoenvironments that include alluvial fan, fluvial, brackish marginal-marine and hypersaline coastal sabkhas, as well as open and restricted marine settings. Most of these environments can be characterised by low temporal and spatial stability. According to Stearns (1976), Gould (1977) and McKinney (1986), unstable environments are often associated with heterochrony amongst living and fossil organisms. Stearns (1976) noted that parthenogenesis may occur in organisms that inhabit cyclic environments where the period of cyclicity is greater than the life cycle of the inhabitants. Stearns also suggested that several clutches may be produced per season in cyclic environments where the cyclic conditions are unpredictable. Using the term r-selection, Gould (1977) defined behavioural traits such as progenetic heterochrony and rapid population growth as being distinctive of unstable environments.

The Maritime Basin provides an ideal opportunity to study ecological tolerance and the effect of physiologically stressful conditions upon Carboniferous ostracod communities and populations.

Several ostracod assemblages have been described from the Lower Carboniferous of the Maritime Basin (Dewey, 1983, 1985, in press). Most of the assemblages are dominated by paraparchitacean ostracods, which are often considered to be indicative of nearshore environments (van Ameron et al., 1970; Becker et al., 1974; Bless, 1983). This paper examines the paraparchitacean-dominated ostracod fauna of a carbonate sabkha environment from the Windsor Group of the Minas-Shubenacadie Sub-Basin in Nova Scotia (Fig. 1).
STRATIGRAPHY AND DEPOSITIONAL ENVIRONMENTS

The Windsor Group is an internally and geographically complex stratigraphic unit because the development of formational terminology has tended to focus on the localised lithologies of each sub-basin. The Windsor Group is correlated with the Upper Mississippian of Midcontinental U.S.A. and the Visean of Europe, using foraminifera and palynomorphs (Mamet, 1970; Utting, 1980). For purposes of this study the formational terminology applied in the Shubenacadie Sub-Basin (sensu Giles, 1981) is used as a reference section (Fig. 2) because the sub-basin contains an almost uninterrupted succession through the Windsor Group in the general study area.

Fig. 2. Stratigraphic subdivisions of the Windsor Group.

The MacDonald Road Formation of the Shubenacadie Sub-Basin is considered to be laterally equivalent to the Miller Creek and Wentworth Station Formations which are the focus of this study in the Windsor type area. Both the Miller Creek and Wentworth Station consist of a repetitive series of anhydrites and gypsum, carbonates and fine grained siliciclastics. Megafaunal evidence indicates that the MacDonald Road and its lateral equivalents can be correlated with the Windsor B faunal subzone (Bell, 1929; Moore & Ryan, 1976).

The type localities for both of these formations are in working quarries near the town of Windsor, at the western end of the Minas-Shubenacadie Sub-Basins (Fig. 3). The Wentworth Station Formation is a 50m thick predominantly evaporite-bearing cyclic unit that contains four limestone-siltstone-evaporite triplets (Fig. 4). Each of the limestones represents intertidal environments and the thick evaporites represent the supratidal environments of a coastal sabkha (Geldsetzer et al., 1980). The fine grained red-brown siliciclastics may be interpreted as distal sediments from alluvial fan deposits. According to Geldsetzer et al. (1980), the limestones represent short-lived transgressive events, whereas the evaporites represent regressive phases associated with sabkha progradation.

The limestones, which are the focus of this study, can be very fossiliferous but constitute less than 10% of the formational sediment. The Dimock and Phillips Limestones are thin dark grey-brown bioclastic wackestones which contain a high abundance, low diversity fauna of ostracods associated with the bryozoan Paleocrisidia and rare gastropods. The paucispecific biota and marked absence of corals and echinoderms in the limestones indicate that the transgressive waters were not of normal (35‰) marine salinity (Bosellini & Hardie, 1973; Boucot, 1981). Taken together, the sedimentological association with sabkha evaporites and the paucispecific fauna indicate that the transgressive limestones developed under hypersaline conditions.

OSTRACOD FAUNA

A high abundance, low diversity ostracod fauna was collected from bedding plane surfaces in the Phillips and Dimock Limestones. The ostracod fauna consists of only five species. More than 75% of the fauna in each limestone unit is composed of Paraparchites sp. aff. P. kellettae Sohn; an additional 20% of the fauna is composed of the fringed kloedenellacean Beyrichiopsis lophota Copeland, which is closely allied to the European form B. plicata (Jones & Kirkby). Acrutia acuta (Jones & Kirkby), Chamishaella suborbiculata (Munster), and Bythocypris aequalis (Jones & Kirkby)
are rare components of the fauna, but *B. aequalis* is absent from the Phillips Limestone. *A. acuta* and *C. suborbiculata* are common species in ostracod assemblages elsewhere in the Maritime Basin (Dewey, 1983, in press), however, their reduced occurrence in the Wentworth Station Formation may indicate that they were nearing their ecological limits. It is important to note the complete absence of the genus *Bairdia* or any related genera. *Bairdia* is considered to be a stenohaline form, indicative of normal marine salinities (Kornicker, 1961; Kaesler, 1982).

Ostracods that inhabit hypersaline environments can be demonstrated to be euryhaline (van Morkhoven, 1962; Sandburg, 1964; Gramman, 1971). This is illustrated by the euryhaline tendencies of the dominant elements of the Wentworth Station fauna. Firstly, the paraparochitaceans exhibit a range of salinity tolerance from brackish to hypersaline (Coryell & Rogatz, 1932; Copeland, 1957; Sohn, 1971; Robinson, 1978; Dewey, 1983, in press, herein). Secondly, previous descriptions of *Beyrichiopsis lophota* and the closely allied form *B. plicata* (Copeland, 1957; Robinson, 1978; ten Have, 1982) suggest that both species are diagnostic of brackish environments, and may be found in association with the freshwater genus *Carbonita*. The present occurrence of *B. lophota* in a hypersaline environment indicates a euryhaline tolerance.

The high individual abundances of a few species within this assemblage probably reflects a lack of competition with stenohaline species that cannot tolerate raised salinities, rather than a high nutrient supply (Levinton, 1970).

The low diversity and very high abundance, together with the generic character of the ostracod fauna, support the interpretation that the Dimock and Phillips limestones were not deposited under normal marine conditions. The combined lithological and palaeontological data clearly indicate a hypersaline setting.

**OSTRACOD POPULATIONS**

The very rich ostracod samples make it possible to examine the ways in which the fauna responded to the physiologically stressful conditions of a hypersaline environment.

Growth plots (Figs. 5,6) for *Beyrichiopsis lophota* and *Paraparchites* sp. aff. *P. kelletae* indicate that *in situ* multi-generation faunas developed during each transgressive phase. The scattergram for *Paraparchites* sp. aff. *P. kelletae* (Fig. 5) indicates that a full growth sequence is present. Heteromorphs are marked by a posterior broadening of female carapaces, which is visible as a distinct trend deviation in the length:width ratio. Even by allowing growth factors in excess of 1.26 (Przibram, 1931; Anderson, 1964), the sexual dimorphism visible in specimens larger than 1800 μm, cannot be attributed to adult sexual maturity. The heteromorphic character is therefore thought to be progenetic. Precocious sexual dimorphism has been noted in other ostracods (Guber, 1971; Whatley & Stephens, 1977; Rohr, 1979). The same growth chart shows that male technomorphs are very rare, which suggests that in these collections, *Paraparchites* sp. aff. *P. kelletae* is parthenogenetic. The occurrence of parthenogenesis in normally syngamic ostracods can be related to environmental stress and inter-instar competition (Bless & Pollard, 1975; van Harten, 1983). Despite the fact that collections were made on bedding plane surfaces it is unlikely that the collections represent a single contemporaneous population; however, the lack of instar.

---

**Fig. 4. Lithological profile of the Wentworth Station Formation.**

[Diagram showing the stratigraphy of the Wentworth Station Formation with labels for different strata such as Limestone, Dolomite, Shale/Siltstone, Gypsum/Anhydrite, and depths indicated.]
grouping might be attributed to continuous breeding cycles (Szczecuha, 1971; Keen, 1977). It is also possible to postulate that inter-instar competition would play a strong role in the development of a parthenogenetic fauna (van Harten, 1983). The size of the populations, together with parthenogenesis and progenesis, suggests that a rapidly developing ostracod fauna was attempting to take advantage of the available environmental conditions. In this sense therefore, Paraparchites sp. aff. P. kellettae was behaving as an opportunist (Levinton, 1970; Whatley, 1983) in the Wentworth Station Formation.

Comparison of scattergrams for B. lophota and P. sp. aff. P. kellettae shows that the former is a much smaller species. Comparison of Wentworth Station specimens with published sizes of both B. lophota and B. plicata (Copeland, 1957; Robinson, 1978; ten Have, 1982) indicates that B. lophota reached full size in the Wentworth Station Formation and shows no evidence of stunting. The heteromorphic character is expressed by a slight posterior broadening, but the scattergram (Fig. 6) indicates that mature heteromorphs are rare, which is similar to the plot figured by ten Have (1982). Since P. sp. aff. P. kellettae is larger than B. lophota, the paucity of heteromorphs in the latter cannot be explained by carapace transport. The ratio of heteromorphs to technomorphs therefore suggests that B. lophota was syngamic in the Wentworth Station collections.

CONCLUSIONS

In the Dimock and Phillips limestones of the Windsor Group in Nova Scotia, euryhaline ostracods developed abundant, low diversity communities in physiologically stressful conditions. Since raised salinities prevented the occurrence of normal marine stenohaline forms, the ecological niche space and nutrient supply was available for use by the eurytopic forms. Consequently, a physiologically harsh environment became highly favourable to the development of large populations of a few euryhaline species and allowed the successful development of transient, multi-generation faunas. Continuous breeding cycles, precocious sexual dimorphism and parthenogenesis ensured rapid population growth in Paraparchites sp. aff. P. kellettae, which was the most adaptable member of the community and allowed it to behave as an opportunist.

The nature of the environment was such that the development of ostracod populations was controlled more by physical factors than by biological ones.

Manuscript received November 1986
Revised manuscript accepted March 1987
REFERENCES
Ameron, H. W. J. van, Bless, M. J. M. & Winkler-Prins, C. F., 1970. Some palaeontological and stratigraphic aspects of the upper Carboniferous Sama Formation (Asturias, Spain). Meded. Rijks geol. Dienst, Leiden Nieuwe Serie, 21, 9–79.

Anderson, F. W. 1964. The law of ostracod growth. Palaeontol., London 7, 85–104.

Bell, W. A. 1929. Horton-Windsor district, Nova Scotia. Mem. geol. Surv. Brch Canada, Ottawa, 155, 268 pp.

Becker, G., Bless, M. J. M., Streel, M. & Thorez, J. 1974. Palynology and ostracode distribution in the upper Devonian and basal Dinantian of Belgium and their dependence of sedimentary facies. Meded. Rijks geol. Dienst, Leiden, Nieuwe Serie, 25, No. 2, 99 pp.

Bless, M. J. M. 1983. Late Devonian and Carboniferous ostracode assemblages and their relationship to the depositional environment. Geologie, Berlin, 92, 31–53.

Bless, M. J. M. & Pollard, J. E. 1975. Quantitative analysis of dimorphism in Carbonita humilis (Jones and Kirkby) Bull. Am. Paleon. Inst., Ithaca, 65, 109–127.

Bosellini, G. & Hardie, L. A., 1973. Depositional theme of a marginal marine evaporite. Sedimentology, 20, 5–27.

Boucot, A. J. 1981. Principles of benthic marine paleoecology. Academic Press, New York. 463 pp.

Bradley, D. C. 1982. Subsidence in late Palaeozoic basins in the northern Appalachians. Tectonics, 1, 107–123.

Copeland, M. J. 1957. The Arthropod fauna of the Maritime Provinces. Mem. geol. Surv. Brch Canada, Ottawa, 286, 110 pp.

Coryell, H. N. & Rogers, H., 1932. A study of the ostracode fauna of the Arroyo Formation, Clearfork Group of the Permian in Tom Green County, Texas. Amer. Midl. Nat. Rep., Ser., 13, 378–395.

Dewey, C. P. 1983. Ostracode paleoecology of the lower Carboniferous of western Newfoundland. 8th Int. Symposium on Ostracoda, Houston, 104–115.

Dewey, C. P. 1985. Lower Carboniferous ostracode assemblages from Nova Scotia. 9th Int. Symposium on Ostracoda, Shizuoka, abstracts with program, 50–51.

Dewey, C. P. In press. Lower Carboniferous ostracode assemblages from Nova Scotia. 9th Int. Symposium on Ostracoda, Shizuoka, 487–495.

Geldsetzer, H., Giles, P., Moore, R. & Palmer, W., 1980. Trip 22: Stratigraphy, sedimentology, and mineralization of the Carboniferous Windsor Group, Nova Scotia. Halifax, '80 GAC/MAC field trip guidebook, 42 pp.

Giles, P. 1981. Major transgressive-regressive cycles in middle to late Visean rocks of Nova Scotia, Nova Scotia Dept. of Mines and Energy, Paper 81-2, 27 pp.

Gould, S. J. 1977. Ontogeny and phylogeny. Harvard Univ. Press, Cambridge, Mass., 501 pp.

Gramman, F. 1971. Brackish or Hyperhaline? Notes of paleoecology based on Ostracoda. Bull. Cent. Rech. Pau., 5, suppl., 93–99.

Guber, A. L. 1971. Problems of sexual dimorphism, population structure and taxonomy of the Ordovician genus Tetradella (Ostracoda). J. Paleont., Chicago, 45, 6–22.

Harten, M. van. 1983. Resource competition as a possible cause of sex ratio in benthic ostracodes. In Maddocks, R. F. (Ed.), 8th Int. Symposium on Ostracoda, Houston, 568–580.

Have, R. ten. 1982. Studies on Irish Lower Carboniferous ostracodes. Unpub. Ph.D. thesis, Univ. Dublin, 262 pp., refs., 61 pls.

Howie, R. D. & Barss, M. S. 1975. Upper Palaeozoic rocks of the Atlantic Provinces, Gulf of St. Lawrence and adjacent continental shelf. Geol. Surv. Can. Paper 74–30, 3, 35–51.

Kaesler, R. L. 1982. Ostracoda as environmental indicators in late Pennsylvanian subsurface shales. 3rd North Amer. Pal. Conv. Proc., 1, 275–280.

Keen, M. C. 1977. Ostracod assemblages and the deposition- al environments of the Headon, Osborne, and Bembridge Beds (upper Eocene) of the Hampshire Basin. Palaeontology, London 20, 405–445.

Kornicker, L. S. 1961. Ecology and taxonomy of Recent Bairdiinae (Ostracoda). Micropaleontology, New York, 7, 55–70.

Levinton, J. S. 1970. The palaeoecological significance of opportunistic species. Lethaia, 3, 69–78.

Mamet, B. L. 1970. Carbonate microfacies of the Windsor Group (Carboniferous), Nova Scotia and New Brunswick. Geol. Surv. Can. Paper 70–71, 121 pp.

McKinney, M. L. 1986. Ecological causation of heterochrony: A test and implications for evolutionary theory. Paleobiol., 12, 282–289.

Moore, R. G. & Ryan, R. J. 1976. Guide to the invertebrate fauna of the Windsor Group in Atlantic Canada. Nova Scotia Dept. of Mines and Energy, Paper 76–5, 57 pp.

Morkhoven, F. P. C. van. 1962. Post-Palaeozoic Ostracoda. Their morphology, taxonomy and economic use. Elsevier, New York, 204 pp.

Przibram, M. 1931. Connecting laws of animal morphology. Four lectures held at the University of London. Univ. London Press, 62 pp.

Robinson, E. 1978. The Carboniferous. In Bate, R. H. & Robinson, E. (Eds). A Stratigraphical Index of British Ostracoda Geol. Jour. Spec. Issue No. 8, 121–166, Seel House Press, Liverpool.

Rohr, W. M. 1979. Nachweise von praadulten Sexualdimorphismus bei den Podocopa (Ostracoda) und Grossen-Variabilitat brackicher Ostracoden. Neues Jb. Geol. Paläont. Abh., Stuttgart, 158, 346–380.

Sandburg, P. A. 1964. The ostracod genus Cyprideis in the Americas. Stockh. Contr. Geol., 12, 1–178.

Soehn, J. G. 1971. New late Mississippian ostracode genera and species from northern Alaska. United States Geol. Surv. Prof. Pap., 711–A, 24 pp.

Stearns, S. C. 1976. Life history tactics: A review of the ideas. Quart. Rev. Biol., 51, 3–47.

Szczechura, J. 1971. Seasonal changes in reared fresh-water species, Cyprinotus (Heterocyprius) incongruens, and their importance in the interpretation of variability in fossil ostracodes. Bull. Cent. Rech. Pau., 5, suppl., 191–206.

Utting, J. 1980. Palynology of the Windsor Group (Mississippian) in a borehole at Stewiacke, Shubenacadie Basin, Nova Scotia. Can. Journ. Earth Sci., 17(B), 1031–1045.

Whatley, R. 1983. The application of Ostracoda to paleoenvironmental analysis. In Maddocks, R. F. (Ed.), 8th Int. Symposium on Ostracoda, Houston, 51–73.

Whatley, R. C. & Stepens, J. M. 1977. Precocious sexual dimorphism in fossil and Recent Ostracoda. In Loffler, H. & Danielopol, D., Proc. 6th Int. Symposium on Ostracods, Saalfelden, 69–91.