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SOME ASPECTS OF THE PALAEOECOLOGY AND DISTRIBUTION OF NON-MARINE OSTRACODA FROM UPPER CRETACEOUS INTERTRAPPEAN DEPOSITS AND THE LAMETA FORMATION OF PENINSULAR INDIA

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ABSTRACT

Ninety-two valid or possibly valid ostracod species from the Maastrichtian intertrappeans and the Lameta Formation are listed in the text and are evaluated in terms of their probable ecology. Some of the 24 communities are analysed in detail. Twenty-two of the 24 localities are grouped into 8 areas (Gujarat, SE Rajasthan, Madhya Pradesh, Maharashtra I- Nagpur District, Maharashtra II- Chandrapur District, Andhra Pradesh, Karnataka, Maharashtra III- Bombay). The degree of communality in terms of numbers of species is expressed diagrammatically and is shown to be little influenced by geographical distance. The relationship between palaeoenvironment and distribution is discussed and explanations involving communality of palaeoenvironment are advanced. Relatively few species are very widespread. These seem to be taxa that are rather environmentally tolerant and, with a notable exception, with good dispersal potential. A surprisingly large number of the 92 species (41 or 44%) are confined to a single locality. Two major groups of communities from different areas are evaluated in more detail. In one case it is thought that water chemistry may have been the controlling factor in the observed difference in the populations of three localities, while in the other, a difference in environmental energy levels is invoked. It is hoped that, with the exposition of some of the virtues that Ostracoda enjoy in environmental reconstruction, future workers make greater use of them for this purpose.

Key words: Non marine ostracods, Upper Cretaceous Intertrappeens, Lameta Formation, Palaeoecology, Distribution

INTRODUCTION

The authors, based on their recent studies of the non-marine Ostracoda of the Upper Cretaceous intertrappean deposits, recognise some 92 valid and possibly valid species. A considerable greater number of names, other than those that appear here, have been used for these species in the past. However, this is not the place to reiterate synonyms but, if the reader is confused by the absence of certain well-known names for intertrappean ostracods, they are invited to consult the various papers by the authors that are cited in the reference list in which synonymies have been given in detail. However, not all of the 92 species have been present in the faunas we ourselves have studied, and most of these we include without change of name, as they were originally described or registered by other authors; such species are marked with an asterisk. We have only included records where they are accompanied by illustrations adequate to allow of identification. In one case, a generic name that is obviously wrong has been changed. The 92 species belong to 3 superfamilies, 15 families/subfamilies and 31 genera.

In the limited space available here, it is not possible to address in detail many of the issues that we raise. This we intend to do in a number of forthcoming papers, in which all aspects of the palaeoenvironment will be considered, using the Ostracoda in conjunction with other elements of the biota as evidence. The purpose of the present paper is to demonstrate that an evaluation of the palaeoecology of the Ostracoda can be an alternative or additional means by which fossil environments can be reconstructed.

In recent years there has been an increased interest in the Deccan volcanics, which were extruded in the Upper Cretaceous (late Maastrichtian), and earliest Palaeocene. Their significance in the debate concerning alleged mass extinctions at the Cretaceous-Tertiary boundary is considerable (Bajpai and Prasad, 2000). Ostracoda, together with Charophyta, palynomorphs, Mollusca and the microvertebrates including comminuted eggshells of dinosaurs, are some of the abundant fossils in the intertrappean deposits. The former have been the subject of considerable research.

PREVIOUS RESEARCH ON INDIAN UPPER CRETACEOUS NON-MARINE OSTRACODA

Sowerby (1840), Carter, (1852) and Jones (1860) first reported Ostracoda from the intertrappean beds. Following these pioneering studies, Bhatia and co-workers (Bhatia and Rana, 1985; Bhatia *et al.*,1990 a, b, 1996) described the ostracods from a number of localities and discussed their age and biogeographical affinities. Prasad (1986) recorded 5 species of Ostracoda from Asifabad in Andhra Pradesh, while Mathur and Verma (1988) described a fauna from the intertrappean beds of Rajasthan. Singh (1995) and Singh and Sahni (1996) discussed the age and faunal affinities of the Bombay intertrappeans, based on a variety of fossil groups with special attention being given to the Ostracoda. Udhoji and Mohabey (1996) considered the Ostracoda in their study of

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the age and palaeozoogeographical implications of the late Cretaceous Lameta Formation of Maharashtra. Sahni and Khosla (1994) and Khosla and Sahni (2000) reported the occurrence of Ostracoda in the Lameta Formation of Jabalpur Cantonment, in Madhya Pradesh. Bhandari and Colin (1999) described an important fauna from Anjar, Kachchh. Bajpai *et al.* (2004) described an interesting fauna with two new species from Phulsagar, Mandla District, Madhya Pradesh. Bajpai *et al.* (2005) provided a useful table illustrating the geographical distribution of 53 intertrappean ostracod species within Peninsular India. Khosla *et al.* (2005) in a study of the Lameta Formation of the Dongargaon area, in Chandrapur District, Maharashtra recorded 16 species, of which 5 are new.

The faunas from three localities in Kachchh (Kutch), in the state of Gujarat have been published in recent years: from Lakshmipur (Whatley and Bajpai, 2000a), Anjar (Whatley and Bajpai, 2000b), and Kora (Bajpai and Whatley, 2001). Another fauna, with several new taxa, has been described from two localities, Chandarki and Yanagundi in Gulbarga District, Karnataka State (Whatley *et al.*, 2002a). A further paper on the Ostracoda from Mohagaonkala in the Chhindwara District of Madhya Pradesh, is by Whatley *et al.* (2003a) and another on the Ostracoda from Mamoni, in the Kota District of Rajasthan by Whatley *et al.*, 2003b. Whatley *et al.* (2003c) have reviewed the ostracod genus *Paracypretta* Sars in these deposits. Furthermore, Whatley *et al.* (2002b) record new species and occurrences throughout the main intertrappean localities, while Whatley *et al* (2003d) detail the intertrappean species encountered in various collections in the Natural History Museum, London.

Many of the species we have encountered in these deposits had not been described previously, and many have been assigned to genera not hitherto recorded from these deposits. Other species are shown to have been previously incorrectly assigned to contemporary species described from Mongolia and China. Whatley and Bajpai (2000c) have shown

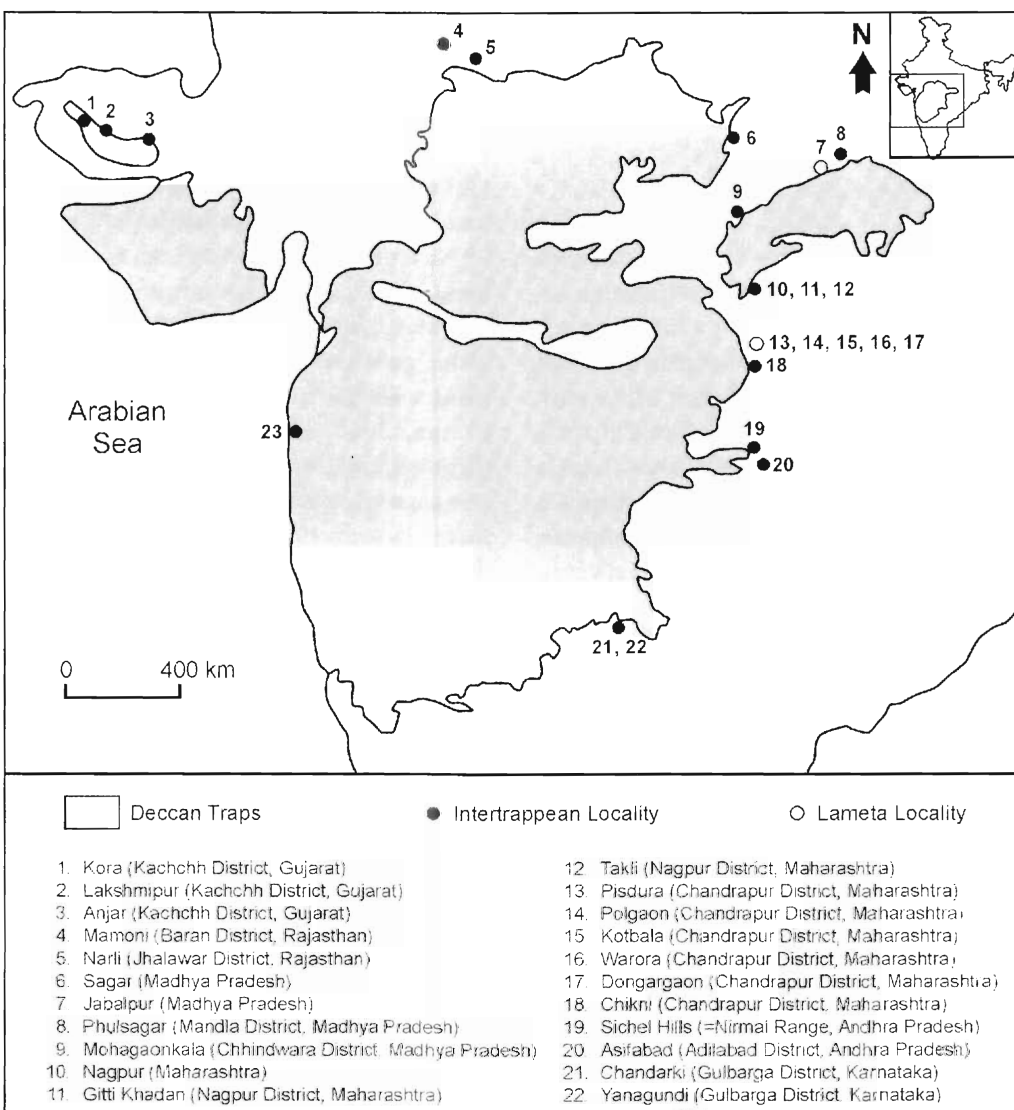

Fig. 1. Map showing freshwater ostracod-yielding localities in the Deccan volcanic province.

that the Indian late Cretaceous intertrappean ostracods do not, as previously stated by many authors, indicate close Asian affinities. Rather, at the specific level they clearly constitute an endemic Indian fauna. In other respects, they exhibit as much affinity with African and European late Cretaceous ostracods as they do with other Asian faunas. Chinese and Mongolian faunas, while containing representatives of many of the genera that occur in India, are dominated by *Cypridea*, its allies and descendants. *Cypridea* and allies, however, are absent from most contemporary Indian faunas and where they occur, they are always very subordinate and usually very rare.

AGE OF THE FAUNAS

Most of the intertrappean ostracod faunas described by the various authors cited above, are of late Cretaceous (Maastrichtian) age, based on intergration of palaeontological, radiometric and magnetostratigraphic data on the Deccan basalts (Sahni and Bajpai, 1988).

Most modern studies on the age of the Deccan Traps, based on radiometric and magnetostratigraphic analyses, indicate that the volcanic activity was initiated during the Maastrichtian, at about 68 m. y. and ceased during the early Palaeocene at around 63 m. y., with the major pulse at 65 m. y. (Duncan and Pyle, 1988; Sahni and Bajpai, 1988; Venkatesan *et al.*,1996; Courtillot, 1990; Courtillot, *et al.*, 1886, 1988).

Many species are also shared with the Maastrichtian Lameta Formation, which is stratigraphically contiguous with the intertrappeans but is not constrained by lava flows. A feature of the Upper Cretaceous ostracod faunas of the intertrappeans, is that each new locality studied seems to contain a percentage of new species, which often subsequently prove to be to a certain degree endemic, while the remainder are more geographically widespread, perhaps more tolerant taxa. To what extent this is environmental/ ecological and to what extent truly zoogeographical is one issue this paper seeks to clarify. We can be reasonably certain that the differences in the faunas of even quite closely distant localities are not, however, due to their being of different ages, largely because of the wealth of radiometric and magnetostratigraphic data available.

THE OSTRACODA

The species are given in Table 1 below, in order of classification and alphabetically within that. The author (s) and date, together with localities in India at which they are recorded are also given. Some of the latter are in abbreviated form to which the following key applies: Anj=Anjar, Asif=Asifabad, Bomb=Bombay, Chand=Chandarki, Chik=Chikni, Dong=Dongargaon, Jab=Jabalpur, Lak=Lakshmipur, Mam=Mamoni, Mohag=Mohagaonkala, Nag=Nagpu, Phul=Phulsagar, Pis=Pisdura, Polg=Polgaon, Sag=Sagar, Yana=Yanagundi. The approximate position of the localities is given on the map (Fig. 1).

Table 1: List of species in order of classification.

Class **Ostracoda** Latreille, 1806
Order **Podocopida** Müller, 1894
Suborder **Podocopina** Müller, 1894
Superfamily **Cytheracea** Baird, 1850
Family **Limnocytheridae** Klie, 1938
Subfamily **Timiriaseviinae** Mandelstam, 1960
Genus ***Frambocythere*** Colin, 1980

1) *Frambocythere tumiensis lakshmiae* Whatley and Bajpai, 2000.	Lak, Mohag.
2) *Frambocythere tumiensis anjarensis* Bhandari and Colin, 1999.	Mam, Anj, Chand, Yana, Gitti Khadan, Dong

Genus ***Gomphocythere*** Sars, 1924

3) *Gomphocythere paucisulcatus* Whatley, Bajpai and Srinivasan, 2003.	Mohag, Bomb, Anj, Dong
4) *Gomphocythere dasyderma* Whatley, Bajpai and Srinivasan, 2002a.	Mam, Chand, Yana,
5) *Gomphocythere strangulata* (Jones), 1860.	Yana, Nag, Gitti Khadan, Lak, Asif, Mam, Polg, Pis
6) *Gompocythere akalypton* Whatley, Bajpai and Srinivasan, 2002.	Chand, Phul,
7) *Gomphocythere* sp. Whatley, Bajpai and Whittaker, 2002b.	Sag
8) *Gomphocythere gomphotatos* Whatley and Bajpai, 2000.	Lak
9) *Gomphocythere* sp. Whatley and Bajpai, 2000a.	Lak

Subfamily **Limnocytherinae** Klie, 1938
Genus ***Limnocythere*** Klie, 1938

10) *Limnocythere* sp. Whatley, Bajpai and Whittaker, 2003.	Chik
11) *Limnocythere* sp, Whatley, Bajpai and Whittaker, 2002b.	Anj, Mohag
12) *Limnocythere falsicarinata* Whatley and Bajpai, 2000a.	Lak, Anj, Dong
13) *Limnocythere bhatiai* Bajpai, Mohabey, Kapoor and Sharma, 2004.	Phul
14) *Limnocythere deccanensis* Khosla, Nagori and Mohabey, 2005.	Dong

Superfamily **Darwinulacea** Brady and Norman, 1889
Genus ***Darwinula*** Brady and Norman, 1885

15) *Darwinula torpedo* Whatley, Bajpai and Srinivasan, 2002.	Yana, Jab

Superfamily **Cypridacea** Baird, 1845
Family **Cyprididae** Baird, 1845
Subfamily **Bradycypridinae** Hartmann and Puri, 1974
Genus ***Paracypretta*** Sars, 1924

16) *Paracypretta subglobosa*	Mam, Sichel Hills

(Sowerby), 1840

17) *Paracypretta jonesi* Bhatia and Rana, 1984. — Gitti Khadan, Nag, Jab, Anj, Chand, Yana, Asif, Mam, Polg, Pis, Kora

18) *Paracypretta* sp. Whatley, Bajpai and Whittaker, 2002b.

19) *Paracypretta elizabethae* Whatley, Bajpai and Whittaker, 2002. — Kora, Anj, Chand

Genus ***Altanicypris*** Szczechura, 1978

20) *Altanicypris deccanensis* Whatley, Bajpai and Whittaker, 2002b. — Lak

21) *Altanicypris szczechurae* (Stankevitch) 1974 of Bhatia *et al.* 1996. — Asif, Takli

Subfamily **Cypridopsinae** Kaufmann, 1900

Genus ***Cypridopsis*** Brady, 1868

22) *Cypridopsis elachistos* Whatley, Bajpai and Srinivasan, 2003. — Mohag

23) *Cypridopsis hyperectyphos* Whatley and Bajpai, 2000b. — Mam, Lak, Kora, Yana, Dong,

24) *Cypridopsis palaicthonos* Bajpai and Whatley, 2001. — Lakhanpura, Kora, Central, India

25) ? *Cypridopsis whatleyi* Bajpai, Mohabey, Kapoor and Sharma, 2004. — Phul

26) *Cypridopsis wynnei* Whatley and Bajpai, 2000a. — Chik, Jab, Tak, Lak, Chand, Yana, Bomb, Warora Tehsil, Chunda, Asi

27) *Cypridopsis alphospilotos* Whatley and Bajpai, 2000a. — Sichel Hills

28) *Cypridopsis astralos* Whatley, Bajpai and Srinivasan, 2002. — Chand, Yana

29) *Cypridopsis legitima* Whatley, Bajpai and Whittaker, 2002b. — Lak, Jab

30) *Cypridopsis dongargaonensis* Khosla, Nagori and Mohabey, 2005. — Dong

31) *Cypridopsis sahni* Khosla, Nagori and Mohabey, 2005. — Dong

32) *Cypridopsis* sp. 1. Bajpai and Whatley, 2001. — Kora

33) *Cypridopsis* sp. 2. Bajpai and Whatley, 2001. — Kora, Jab

Genus ***Sarscypridopsis*** McKenzie, 1977

34) *Sarscypridopsis* sp. Bajpai and Whatley, 2001. — Kora

Genus ***Cetacella*** Martin, 1958

35) *Cetacella* sp. — Kora

Genus ***Zonocypris*** Müller, 1894

36) **Zonocypris gujaratennsis* Bhandari and Colin, 1999. — Anj

37) *Zonocypris labyrinthicus* Whatley, Bajpai and Srinivasan, 2003. — Mohag

38) *Zonocypris spirula* Whatley and Bajpai, 2000a. — Lak, Yana, Kora, Dong

Genus ***Potamocypris*** Kaufmann, 1960

39) *Potamocypris*? sp. Bhandari and Colin, 1999.

Subfamily **Eucyprininae** Bronsthein, 1947

Genus ***Eucypris*** Vávra, 1891

40) *Eucypris pelasgicus* Whatley and Bajpai, 2000a. — Mohag, Lak, Kora, Phul, Tak, Dong

41) *Eucypris intervolcanus* Whatley and Bajpai, 2000a. — Mohag, Phul, Lak, Yana, Kora

42) *Eucypris catantion* Whatley, Bajpai and Whittaker, 2003. — Mam, Kora

43) ?*Eucypris verruculosa* Whatley, Bajpai and Srinivasan, 2002a. — Sichel Hills, Chand

44) *Eucypris phulsagarensis* Bajpai, Mohabey, Kapoor and Sharma, 2004. — Phul

45) **Eucypris* sp. cf. *Eucypris bajshinstavica* Khand and Stankevitch, 1975 of Khosla and Sahni, 2000. — Jab

46) *Eucypris* sp. cf. *Eucypris catantion* Whatley, Bajpai and Whittaker, 2003. [Ex *Darwinula* sp. 2 indet Khosla and Sahni, 2000]. — Jab

Subfamily **Herpetocypridinae** Kaufmann, 1900

Genus ***Mongolianella*** Mandelstam in Galeeva, 1955.

47) *Mongolianella cylindrica* (Sowerby) 1840. — Mam, Sichel Hills, Jab, Nutnoor, Lak, Anj, Kora, Mohag, Narli, Phul, Bomb

48) *Mongolianella subarcuata* Whatley, Bajpai and Whittaker, 2003. — Mam, Kora

49) *Mongolianella hislopi* (Jones), 1860. — Central India, Chand, Chikni, Polg, Asif, Gitti Khadan

50) **Mongolianella khamarinensis* Galeeva, 1956 of Khosla and Sahni, 2000. — Takli, Asif, Jab

51) *Mongolianella ashui* Khosla, Nagori and Mohabey, 2005. — Dong

52) *Mongolianella* sp. Whatley, Bajpai and Srinivasan, 2003. — Mohag, Anj

53) *Mongolianella* sp. A. Bajpai and Whatley, 2001. — Kora

54) **Mongolianella* sp. Khosla and Sahni, 2000. — Jab, Dong

55) **Mongolianella*? sp. 1 Bhandari and Colin, 1999. — Anj

Genus ***Moenocypris*** Triebel, 1959

56) ?*Moenocypris hunteri* (Jones) 1860. — Nag, Anj, Narli, Mam

57) **Moenocypris sastryi* Mathur and Verma, 1988. — Narli, Mam

Genus ***Valdoniella*** Babinot, 1980

58) **Valdoniella* ? sp. Bhandari and Colin, 1999. — Anj

Family **Candonidae** Kaufmann, 1900

Subfamily **Candoninae** Kaufmann, 1900

Genus ***Candona*** Baird, 1845

59) *Candona amosi* Whatley, Bajpai and Srinivasan, 2002. — Kora. Anj, Chand, Yana

60) *Candona mysorephaseolus* Whatley, Bajpai and Srinivasan, 2002. — Yana

61) **Candona altanulaensis* Szczechura and Blasyzk, 1970 of Bhatia *et al.*1996. — Asif, Takli

62) **Candona bagmodica* Stankevitch, 1977 of Bhatia *et al*, 1996. — Asif, Takli

63) **Candona henaensis* Jiang and Sun, of Bhatia *et al.*, 1996. — Asif, Takli

Genus ***Typhlocypris*** Vejdovsky, 1882

64) **Typhlocypris* sp. cf. *Typhlocypris arrecta* Chen and Ho, 1982 of Bhandari and Colin, 1999. — Anj

Genus ***Eucandona*** Daday, 1900

65) *Eucandona kakamorpha* Whatley, Bajpai and Srinivasan 2002. — Yana, Jab, Dong

Genus ***Paracandona*** Hartwig, 1899

66) *Paracandona* sp. Whatley, Bajpai and Srinivasan, 2002. — Chand

67) *Paracandona firmamentum* Whatley and Bajpai, 2000a. — Lak

68) *Paracandona* sp. 1. Bhandari and Colin, 1999. — Anj

69) *Paracandona jabalpurensis* Sahni and Khosla, 1994. — Jab

Family **Cyclocypridinae** Kaufmann, 1900

Genus ***Cyclocypris*** Brady and Norman, 1889

70) *Cyclocypris amphibolos* Whatley, Bajpai and Srinivasan, 2002a. — Mam, Yana, Kora, Dong

71) *Cyclocypris sahni* Bajpai and Whatley, 2000. — Kora, Jab, Polg, Pis

Genus ***Cypria*** Zenker, 1854

72) *Cypria cyrtonidion* Whatley and Bajpai, 2000a. — Mohag, Lak, Yana, Chand, Kora,Gitti Khadan, Mam, Narli, Dong

73) *Cypria intertrappeana* Bajpai and Whatley, 2000. — Kora

74) *Cypria* sp. Bajpai and Whatley, 2000. — Kora

Subfamily **Cypridinae** Baird, 1845

Genus ***Cypris*** O. F. Müller, 1776

75) *'*Cypris' semimarginata* Carter, 1852. — Bomb

76) *'*Cypris*' sp. Carter, 1852. — Bomb

Genus ***Pseudocypris*** Daday, 1910

77) *Pseudocypris ectopos* Whatley and Bajpai, 2000. — Lak

Genus ***Pseudoeucypris*** Schneider, 1957

78) **Pseudoeucypris* sp. Mathur and Verma, 1988. — Mam, Narli

Genus ***Mongolocypris*** Szczechura, 1978

79) **Mongolocypris* sp. cf. *Mongolocypris gigantea* Ye *et al.*, 1977 of Sahni and Khosla, 1994. — Jab

Family **Ilyocyprididae** Kaufmann, 1900

Subfamily **Cyprideinae** Martin, 1940

Genus ***Cypridea*** Bosquet, 1852

80) **Cypridea (Cypridea) cavernosa* Galeeva, 1955 of Bhatia *et al.*, 1996. — Asif, Takli

81) *Cypridea pavnaensis* Khosla, Nagori and Mohabey, 2005. — Dong

Genus ***Limnocypridea*** Lyubimova, 1956

82) *Limnocypridea ecphymatos* Bajpai and Whatley, 2000a. — Anj, Kora, Phul

Genus ***Talicypridea*** Khand, 1977

83) **Talicypridea biformata* Szczechura and Blaszyk, 1970 of Bhatia *et al.*, 1996. — Asif, Takli

84) *Talicypridea* sp. Bajpai and Whatley, 2000a. — Kora

Genus ***Trapezoidella*** Sohn, 1979

85)**Trapezoidella* sp. Udhoji and Mohabey, 1996. — Pis, Kotbala

Family **Notodromadidae** Kaufman, 1900

Subfamily **Notodromatinae** Kaufmann, 1900

Genus ***Centrocypris*** Vávra, 1895

86) *Centrocypris megalopus* Whatley and Bajpai, 2000a — Lak

Subfamily **Cyproidinae** Hartmann, 1963

Genus ***Cyprois*** Zenker, 1854

87) *Cyprois rostellum* Whatley and Bajpia, 2000a. — Lak, Kora

88) *Cyprois polygonum* Bajpai and Whatley, 2000. — Kora

89) **Cyprois* sp. Prasad, 1986. — Asif

90) *Cyprois* sp. Whatley and Bajpai, 2000a. — Lak

Family **Incertae sedis**

91) Genus indet sp. A. Bhatia *et al.*, 1996. — Takli

92) Genus indet sp. B. Bhatia *et al.*, 1996. — Takli

ECOLOGY

The non-marine species encountered in the Late Cretaceous of Peninsular India fall into a number of groups according to their mode of life. One simple, but effective and useful measure is associated with their ability as swimmers, and they range from those quite incapable of swimming to those that are very active and accomplished swimmers. The most capable swimmers are much less dependent on substrate, be it weed or sediment, than those that cannot swim or are poor swimmers. Although many good swimmers make use of aquatic vegetation, it is not necessarily essential to their mode of life, while some poor swimmers are very dependent on it. However, it is the experience of the senior author, that abundant vegetation is essential to the survival of most freshwater ostracods in that it affords a measure of protection from predators. Among the most virulent of their predators are larval fish and the minnow-sized adults of smaller species. In exhaustive collections of roadside ditches the length and breadth of Argentina in the early 1970's, if small fish were present, this was a guarantee that ostracods would be absent, unless the environment was weed-rich. In many cases in Argentina, one of the weed types present would be Charophyta, and these provided excellent shelter for ostracods. It is important to note that, in many instances where rich ostracod communities are recovered from the intertrappeans, these are associated with charophyte gyrogonia. Among many works that mention intertrappean and Lameta Formation Charophyta, it is significant with respect to the latter to note the considerable diversity of charophytes recorded by Mohabey (1996), who also uses their known shallow water distribution to deduce sublittoral lacustrine bathymetry when they are absent. Bhatia (1992) gives an important review of the fossil charophytes of India and Srinivasan *et al.* (1994) an excellent account of these plants in the intertrappean beds. The importance of aquatic plants to the survival of ostracods has been demonstrated by a number of authors (Benzie, 1989; Kiss, 2002, 2004; Patterson, 1993; Roca *et al.*, 1993; Uiblein *et al.*, 1996).

The nature of the sedimentary substrate is fundamentally important to non swimmers, most of which are epifaunal, although some that are, at least partially infaunal, require particular sediments that are fine grained, soupy and colloidal, or alternatively are composed of poorly packed larger constituents.

The ecological and evolutionary relationships between the three superfamilies throughout the Mesozoic have been discussed by Whatley (1986, 1990, 1992).

The Cytheracea as a superfamily are non-swimmers. They lack the swimming setae on the anterior antennules and antennae and instead these appendages are adapted to perform other functions in this group. This is associated with the possession of 3 very strongly developed locomotary appendages (legs) on the thorax. The Cytheracea uniquely possess in the forehead a gland that produces threads similar to the "silk" of spiders. This has been shown to anchor the animal to the substrate in high-energy environments and to assist cytherid species to "climb" on aquatic plants (Whatley, 1976).

Most, if not all, cytheraceans are syngamic, although Henderson (1990, p.34) suggests that some species, such as *Limnocythere inopinata* (Baird) where males are rare, probably also reproduce parthenogentically. The Timiriaseviinae, typified here by *Frambocythere* and *Gomphocythere,* incubate the eggs and rear the early instars in the large brood patch of the female.

McKenzie (1971, p. 273) suggests that some species of *Limnocythere* may be endobenthonic, spending part of the day within the sediment and part on it, while *Gomphocythere* and *Frambocythere* are clearly epibenthonic walkers/crawlers. Although some species of *Limnocythere* have been recorded from temporary pools, most members of the family require permanent waters.

The Darwinulacea are also unable to swim, and incubate their eggs and retain early instars within a brood chamber. They seem to be entirely parthenogenetic at the present day and perhaps entirely syngamic in the late Palaeozoic and Triassic, but gradually through the Jurassic and early Cretaceous they lost their bisexuality and by the late Cretaceous, they may have all become parthenogenetic. *Darwinula* lives in permanent water bodies, mainly in ponds and lakes but it also occurs in streams.

The Cypridacea are much more of an ecological mixture, including as they do swimmers and non-swimmers. Many cyprids live in temporary pools and have evolved a desiccation and freeze resistant egg. Many of these species are parthenogenetic and the resting stages that are distributed by the wind, sometimes in the upper atmosphere, can develop and reproduce without the need for males; a very considerable dispersal advantage (Whatley, 1992). The cyprids are considered here in an approximate order from non-swimmers to excellent swimmers.

The Candonidae are unable to swim as the antennules and antennae lack natatory setae and are, instead, adapted for walking/crawling/burrowing which means of locomotion is aided by the terminal claws on the posterior furcae. Some species burrow in fine, soft sediment although other species (probably most) can be both epifaunal and infaunal. While common in leaf detritus, they are rare on living aquatic plants. The genus ranges from freshwater to mildly saline oligohaline waters. Most live in marshes, ponds or lakes and coastal lagoons but some can also tolerate slow flowing rivers and streams.

While modern species of *Ilyocypris* are good swimmers despite the fact that many of them spend considerable time walking/crawling on the sediment, most members of the extinct subfamily Cyprideinae were probably not able to swim far. Perhaps the exception to this are such species as *Limnocypridea ecphymatos,* although Russian species of the genus are much more angular and were more likely to be benthonic. In the case of *Cypridea* with its antero-ventral beak, this probably could swim poorly, but spent most time 'ploughing' through the surface sediment in its feeding mode. *Talicypridea* probably swam more efficiently and *Trapezoidella*, which we have included here rather in its own family (Sohn, 1979) from the original illustrations from the Lower Cretaceous of the United States, was probably similar [We do not believe that the species described by Udhoji and Mohabey, 1996 belongs to *Trapezoidella*; it certainly requires further study].

The Herpetocypridinae are all elongate and rather cylindrical in shape. The nominative genus *Herpetocypris* Brady and Norman is morphologically very similar to *Mongolianella* and is probably a good guide to the ecology of fossil taxa in the subfamily. In *Herpetocypris*, the swimming setae on the antennae are often short and although such species as the European and North African *H. reptans* Baird seem to swim quite well, they do so close to the bottom and often infest pond weed. (Whatley, 1983c). The genus occurs most commonly in lakes and ponds, although the senior author has collected *H. reptans* from quite fast flowing streams, but only those replete with weed. From their overall morphology, it is reasonable to assume that *Moenocypris* and *Valdoniella* had similar ecologies. Most modern species live in permanent water and it is reasonable to assume that this was the case in the Cretaceous.

The Eucypridinae are generally better swimmers than the Herpetocypridinae but, within *Eucypris,* this varies between species as can be seen by the variation in the length of the swimming setae on the antennae. Most *Eucypris* species live in temporary pools that dry out in the summer months, the species being represented then by desiccation resistant eggs that hatch with the rains. The adult ostracod and juvenile stages are, therefore, often only found in the winter or in the rainy season. This probably was also the case in the Deccan area during the Upper Cretaceous. While it is not possible from the overall morphology of a fossil species to distinguish those with a preference for temporary rather than permanent aquatic environments, presumably the environment of the intertrappeans was relatively humid to produce the vegetation that supported the large number of dinosaurs. Even so, many pools would have been temporary. Some idea of the ratio of temporary to permanent water species of *Eucypris* can be gained by a consideration of modern British species. Henderson (1990) records 11 species from the British Isles of which 10 occur in temporary ponds and ditches and only one species that seems only to occur in permanent waters.

The Cypridinae contain very good swimmers, such as *Cypris* Müller, but the taxa attributed to '*Cypris*' here, described by Carter (1852) from Bombay certainly belong to other genera. *Pseudocypris* is a swimmer but its large antero-ventral gape suggests that it spends much of its time bottom feeding. The only modern species described from India *P. patialaensis* Battish, 1977 was found in a narrow, shallow but weed-rich ditch near Rounni, on the Patiala-Nabha road in Punjab. *Pseudoeucypris* is also a good swimmer.

The Bradycypridinae are closely related to the Cypridopsinae but are less perfectly shaped and are probably only slightly if at all less well adapted as swimmers. Of the two representatives in this study, *Paracypretta* is well known as a good swimmer at the present day and has well developed natatory setae, while the extinct *Altanicypris* has the ovate carapace morphology associated with good swimmers.

The Cypridopsinae, with their generally spherical shape, are well designed to be good swimmers and modern species, such as the bi-hemispherically distributed species, *Cypridopsis vidua* (Müller) although usually occurring in weed rich ponds, swim actively in the open water. The genus in mainly found in permanent lakes and ponds; much more rarely in rivers and streams. *Sarscypridopsis* is also a good swimmer, although with its heavy ornament, *Zonocypris* is probably rather more sluggish.

The Cyclocypridinae are swimmers *par excellence.* They have an ideal carapace shape and very well developed natatory setae on the antennules. Modern *Cyclocypris* species are very active swimmers, and although some occur in temporary ponds, and others in only shallow permanent waters, many range from small ponds to large lakes. Recent species of *Cypria* are probably even better swimmers, and *C. opthalmica* (Jurine), an almost universally distributed Northern Hemisphere freshwater and oligohaline species is an excellent example of a genus requiring permanent water.

The Nodopthalminae are highly specialised ostracods with flattened ventral margins. They are active swimmers that progress ventral upwards close to the surface tension, to which they are able to cling at rest. They live in permanent and temporary waters and feed mainly on planktonic algae. *Centrocypris* is more elongate than *Notodromas* Lilljeborg, but seems to have a similar ecology. *Cyprois* has different appendages, is well adapted for swimming but lacks the flattened venter, the ability to 'hang' from the surface tension or to swim upside down. Most species live in temporary environments and are often only present in the winter or rainy season and this seems to be the same for *Centrocypris.*

Some of the 92 species reproduce sexually and are represented by male and female specimens, while others are parthenogenetic ard entirely female. Some species are known to utilise both means of reproduction, the choice being governed by geographical and/or ecological circumstances. In the present study, *Darwinula* appears to be parthenogenetic. Almost all Cytheracea are syngamic and the Timeriaseviinae of the Limnocytheridae exhibit considerable sexual dimorphism in the carapace, the brood pouches of the females being very pronounced in this study. *Limnocythere*, however, can be parthenogenetic (Henderson, 1990) and the apparent absence of males among any of the 5 species considered here, suggests that this form of reproduction was not uncommon.

Given the above ecological information, and the generic composition of the various communities that are subjected to analysis here (detailed in the next section), it is immediately evident that these communities are made up of taxa with different ecologies. In consequence, it is difficult to assign a particular palaeoenvironment to any of the localities; difficult but not impossible, because certain taxa provide clearer clues than others. For example, those localities with *Candona* are likely to have had soft substrates to allow this taxon to adopt its normal infaunal mode of life. Similarly, those communities containing Herpetocypridinae are likely to represent environments of permanent water and in most cases ponds or lakes rather than streams or rivers. Given the very widespread distribution of *Mongolianella cylindrica*, for example, it would suggest that such permanent environments were widespread in the intertrappeans. *Cypridopsis* would in general also be a guide to permanent waters as would the Cytheracea as a superfamily.

The argument for temporary pools is supported above all by *Eucypris*, a common and, with 7 species, a diverse genus in the intertrappeans. However, in many cases it occurs with taxa more typical of permanent waters. In these cases, it is probable that *Eucypris* and other taxa such as *Cyprois*, *Centrocypris* that prefer temporary waters, lived around the margins of ponds and lakes in areas that dried out in the dry season, while *Mongolianella, Cypridopsis* and other taxa requiring more permanent waters would retreat to the deeper parts of the water body. The fact that the valves and carapaces of these species of different ecologies occur together is due to *post-mortem* transportation.

An attempt is made below to reconstruct the palaeoenvironment of a number of localities.

DIVERSITY

With 92 species, belonging to 3 superfamilies, 17 families and subfamilies and 30 genera, the ostracod diversity is high for a non-marine environment. However, given the diversity/ area relationship, one should not forget the huge area over which the sampling localities are distributed. It is also important to note that no locality has yielded the complete total of 92 species, nor anywhere near that number. If fact, the locality that yielded the highest simple species diversity, Kora, with 21 species has just less than 25% of the total. However, in the context of modern non-marine ostracod faunas, 22 species represent a high diversity community.

The mean number of species per locality, taking into account all 24 of them is 3.7, but if only the 19 localities with 4 or more species are calculated, then the mean is 4.7. Perhaps a better assessment of the simple specific diversity is as follows: number of localities with 20 or more species = 1; number of localities with 15-19 species = 4; number of localities with 10-14 species = 5, number of localities with 5-9 species = 8, number of samples with 1-4 species = 6.

We analysed 24 different localities, and these are listed below, together with the authors responsible for recording the various faunas and the number of species:

1) Kora, Western Kachchh (Kutch), Gujarat. Bajpai and Whatley, 2001. 21 spp.

i) *Eucypris catantion*	ii) *Paracypretta elizabethae*
iii) *Paracypretta* sp.	iv) *Cypridopsis palaicthonos*
v) *Cypridopsis* sp. 1	vi) *Cypridopsis* sp. 2
vii) *Sarscypridopsis* sp.	viii) *Cetacella* sp.
ix) *Cypria cyrtonidion*	x) *Cypria intertrappeana*
xi) *Cypria* sp.	xii) *Candona amosi*
xiii) *Eucypris pelasgicos*	xiv) *Eucypris intervolcanos*
xv) *Mongolianella cylindrica*	xvi) *Limnocypridea ecphymatos*
xvii) *Talicypridea* sp.	xviii) *Cyprois rostellum*
xix) *Cyprois polygonum*	xx) *Zonocypris spirula*
xxi) *Cyclocypris amphibolos*	

2) Lakshmipur, Kachchh (Kutch) District, Gujarat. Whatley and Bajpai, 2000. 17 spp.

i) *Limnocythere falsicarinata*	ii) *Frambocythere tumiensis lakshmiae*
iii) *Gomphocythere gomphomatos*	iv) *Pseudocypris ectopos*
v) *Gomphocythere* sp.	vi) *Centrocypris megalopus*
vii) *Zonocypris spirula*	viii) *Cypridopsis wynnei*
ix) *Cypridopsis hyperectyphos*	x) *Cypridopsis legitima*
xi) *Paracandona firmamentum*	xii) *Eucypris intervolcanos*
xiii) *Mongolianella*	xiv) *Cypria cylindrica cyrtonidion*
xv) *Cyprois rostellum*	xvi) *Cyprois* sp.
xvii) *Altanicypris deccanensis*	

3) Anjar, Kachchh (Kutch) District, Gujarat. Bhandari and Colin, 1999 and Whatley and Bajpai, 2000. 13 spp.

i) *Limnocythere falsicarinata*	ii) *Frambocythere tumiensis anjarensis*
iii) *Gomphocythere strangulata*	iv) *Candona amosi*
v) *Paracandona* sp. 1	vi) *Typhlocypris* sp. cf. *T. arrecta*
vii) *Valdoniella* sp.	viii) *Mongolianella*? sp. 1
ix) *Potamocypris* ? sp.	x) *Zonocypris gujaratensis*
xi) *Paracypretta jonesi*	xii) *Limnocypridea ecphymatos*
xiii) *Mongolianella khamariniensis*	

4) Mamoni, Kota District, SE Rajasthan. Whatley, Bajpai and Whittaker, 2003, plus Bhatia *et al.* 1990a, and Mathur and Verma, 1988. 13 spp.

i) *Frambocythere tumiensis anjarensis*	ii) *Gomphocythere dasyderma*
iii) *Paracypretta subglobosa*	iv) *Cypridopsis hyperectyphos*
v) *Mongolianella cylindrica*	vi) *Mongolianella subarcuata*
vii) *Eucypris catantion*	viii) *Cyclocypris amphibolos*

ix) *Gomphocythere strangulata* x) *Altanicypris szczechurae*
xi) *Cyprois cyrtonidion* xii) *Moenocypris sastryi*
xiii) *Pseudoeucypris* sp.

5) Narli, Jhalawar District, SE Rajasthan. Mathur and Verma, 1988. 5 spp.
i) *Cyprois cyrtonidion* ii) *Moenocypris sastryi*
iii) *Moenocypris hunteri* iv) *Mongolianella cylindrica*
v) *Paracypretta subglobosa*

6) Sagar, Madhya Pradesh. Whatley, Bajpai and Whittaker, 2003. 1 sp.
i) *Gomphocythere* sp.

7) Lameta Formation, Jabalpur Cantonment, Madhya Pradesh. Sahni and Khosla, 1994 and Khosla and Sahni, 2000. 16 spp.
i) *Paracypretta jonesi* ii) *Eucypris* sp. cf. *E. bajshinstavica*
iii) *Mongolianella cylindrica* iv) *Mongolianella khamarienensis*
v) *Mongolianella* sp. vi) *Mongolocypris* sp. cf. *M. gigantea*
vii) *Cypridopsis wynnei* viii) *Cypridopsis* sp. 2
ix) *Candona amosi* x) *Eucandona kakamorpha*
xi) *Paracandona jabalpurensis* xii) *Cyclocypris sahnii*
xiii) *Cypridea (Pseudocypridea)* sp. xiv) *Eucypris* sp. cf. *E. catantion*
xv) *Cypridopsis legitima* xvi) *Darwinula torpedo*

8) Phulsagar, Mandla District, Madhyra Pradesh. Bajpai, Mohabey, Kapoor, and Sharma, 2004. 8 spp.
i) *Gomphocythere akalypton* ii) *Limnocythere bhatiai*
iii) ?*Cypridopsis whatleyi* iv) *Limnocypridea ecphymatos*
v) *Eucypris pelasgicus* vi) *Eucypris intertrappeana*
vii) ?*Eucypris phulsagarensis* viii) *Mongolianella cylindrica*

9) Mohagaonkala, Chhindwara District, Madhya Pradesh. Whatley, Bajpai and Srinivasan, 2003. 9 spp.
i) *Frambocythere tumiensis lakshmiae* ii)*Gomphocythere paucisulcatus*
iii) *Paracypretta jonesi* iv) *Cypridopsis elachistos*
v) *Zonocypris labyrinthicos* vi) *Eucypris pelasgicos*
vii) *Eucupris intervolcanos* viii) *Mongolianella* sp.
ix) *Cypria cyrtonidion*

10) "Nagpur", Maharashtra. NHM Collections. Whatley, Bajpai and Whittaker, 2003. 1sp.
i) *Moenocypris hunteri*

11) Gitti Khadan, Nagpur District, Maharashtra. Bhatia and Rana, 1984. 6 spp.
i) *Paracypretta jonesi* ii) *Frambocythere tumiensis anjarensis*
iii) *Gomphocythere dasyderma* iv) *Mongolianella hislopi*
v) *Mongolianella cylindrica* vi) *Cypria cyrtonidion*

12) Takli, Nagpur District, Maharashtra. Bhatia, Prasad and Rana, 1996. 13 spp.
i) *Frambocythere tumiensis anjarensis* ii) *Gomphocythere strangulata*
iii) *Altanicypris szczechurae* iv) *Cypridea (Cypridea) cavernosa*
v) *Candona altanulaensis* vi) *Candona bagmodica*
vii) *Candona henaensis* viii) *Limnocypridea ecphymatos*
ix) *Paracypretta* sp. x) *Talicypridea biformata*
xi) *Cypridopsis wynnei* xii) *Mongolianella cylindrica*
xiii) *Moenocypris hunteri*

13) Lameta Formation of the Nand and Dongargaon-Pisdura-Polgaon-Kotbala areas, Maharashtra, Chandrapur District. Udhoji and Mohabey, 1996. 5 spp.
i) *Paracypretta jonesi* ii) *Gomphocythere strangulata*
iii) *Cypria cyrtonidion* iv) *Mongolianella hislopi*
v) *Trapezoidella* sp.

14) Lameta Formation of the Dongargaon Area, Chandrapur District, Maharashtra. Khosla, Nagori and Mohabey, 2005. 17 spp.
i) **Limnocythere deccanensis* ii) *Limnocythere falsicarinata*
iii) *Frambocythere tumiensis anjarensis* iv) *Gomphocythere paucisulcatus*
v) *Gomphocythere strangulata* vi) *Paracypretta jonesi*
vii) *Zonocypris spirula* viii) *Cypridopsis dongargaoensis*
ix) *Cypridopsis hyperectyphos* x) *Cypridopsis sahni*
xi) *Mongolianella ashui* xii) *Mongolocypris* sp.
xiii) *Eucypris pelasgicos* xiv) *Eucandona kakamorpha*
xv) *Cyclocypris amphibolos* xvi) *Cypria cyrtonidion*
xvii) *Cypridea pavnaensis*

15) Chikni, Chandrapur District, Maharashtra. Malcolmson collection, NHM, London. Sowerby in Malcolmson, 1840, Whatley *et al.*, 2002, 2003a, b.5 spp.
i) *Paracypretta subglobosa* ii) *Limnocythere* sp.
iii) *Cypridopsis wynnei* iv) *Mongolianella hislopi*
v) *Gomphocythere strangulata*

16) Warora Tehsil, Chandrapur District, Maharashtra. Sladen Expedition, NHM, London. Whatley *et al.*, 2003. 2 spp.
i) *Cypridopsis wynnei* ii) *Mongolianella hislopi*

17) Nutnoor (or Hutnoor), Sichel Hills, Andhra Pradesh. Sowerby in Malcolmson, 1840. spp.
i) *Paracypretta subglobosa* ii) *Mongolianella cylindrica*
iii) *Mongolianella hislopi* iv) *Moenocypris hunteri*
v) *Gomphocythere strangulata*

18) Sichel Hills, (Nirmal Range) Andhra Pradesh. Malcolmson collection, NHM, London. Sowerby in Malcolmson, 1840, Whatley *et al.*, 2002, 2003a, b. 4 spp.
i) *Paracypretta subglobosa* ii) *Cypridopsis alphospilotos*
iii) ?*Eucypris verruculosa* iv) *Mongolianella cylindrica*

19) Asifabad, Andhra Pradesh. Bhatia, Prasad and Rana, 1996, plus Prasad, 1986. 12 spp.

i) *Frambocythere tumiensis anjarensis*	ii) *Gomphocythere strangulata*
iii) *Cypridea (Cypridea) cavernosa*	iv) *Limnocypridea ecphymatos*
v) *Mongolianella cylindrica*	vi) Genus indet A.
vii) Genus indet B.	viii) *Moenocypris hunteri*
ix) *Talicypridea biformata*	x) *Paracypretta jonesi*
xi) *Mongolianella hislopi*	xii) ?*Cyprois* sp.

20) Chandarki, Gulbarga District, Karnataka. Whatley, Bajpai and Srinivasan, 2002. 10 spp.

i) *Frambocythere tumiensis anjarensis*	ii) *Gomphocythere akalypton*
iii) *Gomphocythere dasyderma*	iv) *Paracypretta jonesi*
v) *Cypridopsis wynnei*	vi) *Cypridopsis astralos*
vii) *Mongolianella cylindrica*	viii) *Eucypris verruculosa*
ix) *Paracandona* sp.	x) *Cypria cyrtonidion*

21) Yanagundi, Gulbarga District, Karnataka. Whatley, Bajpai and Srinivasan, 2002. 16 spp.

i) *Darwinula torpedo*	ii) *Frambocythere tumiensis anjarensis*
iii) *Gomphocythere strangulata*	iv) *Gomphocythere dasyderma*
v) *Paracypretta jonesi*	vi) *Zonocypris spirula*
vii) *Cypridopsis wynnei*	viii) *Cypridopsis hyperectyphos*
ix) *Mongolianella cylindrica*	x) *Eucypris intervolcanos*
xi) *Candona amosi*	xii) *Candona mysorephaseolus*
xiii *Eucandona kakamorpha*	xiv) *Cyclocypris amphibolos*
xv) *Cypria cyrtonidion*	xvi) *Cypridopsis astralos*

22) Bombay intertrappeans, Maharashtra (iii). Carter, 1852, plus Singh, 1995 and Singh and Sahni, 1966 and Whatley, Bajpai and Whittaker, 2003. 9 spp.

i) '*Cypris*' *semimarginata*	ii) '*Cypris*' sp.
iii) *Mongolianella cylindrica*	iv) *Gomphocythere paucisulcata*
v) *Cyprois rostellum*	vi) *Paracandona firmamentum*
vii) *Cypria* cf. *intertrappeana*	viii) *Cypridopsis palaichthonos*
ix) *Cypridopsis wynnei*	

23) "Central India", Sankey Collection, NHM, London. Whatley, Bajpai and Whittaker, 2003. 2 spp.

i) *Mongolianella hislopi*	ii) *Cypridopsis palaicthonos*

24) Lakhanpura, Rewa. NHM Sladen Expedition. Whatley, Bajpai and Whittaker, 2003. 1 sp.

i) *Cypridopsis palaichthonos*

In addition to the above are some faunas that have been described in such a way that we have not been able to use them in our formal analysis. For example, the otherwise very informative paper by Mohabey (1996) on the Lameta Formation of the Nand-Dongargoan Inland basin, Maharashtra, contains important environmental information but lacks illustrations so that the identifications cannot be confirmed and anyway, several taxa are identified only to generic level.

DISTRIBUTION

Many of the above listed communities are from very closely adjacent localities and an attempt is made here to rationalise them, by grouping them into 8 geographical regions. These are as follows:

1) Gujarat: Comprising Kora, Anjar and Lakshmipur (Kutch district).
2) SE Rajasthan: Comprising localities so entitled, together with Mamoni (Kota District) and and Narli (Jhalawar District).
3) Madhya Pradesh: Sagar, Jabalpur, Phulsagar (Mandla District), Mohagaonkala (Chhindwara District).
4) Maharashtra I: Gitti Khadan, Takli (Nagpur District).
5) Maharashtra II: Pisdura, Polgaon, Kotbala, Warora Tehsil, Dongargaon, Chikni (Chandrapur District).
6) Andhra Pradesh: Sichel Hills [Nirmal Range], Nutnoor (Hutnoor), Asifabad (Adilabad District).
7) Karnataka: Chandarki, Yanagundi (Gulbarga District).
8) Maharashtra III: Bombay.

Most of the 92 species/subspecies are confined to the intertrappeans and/or the Lameta Formation. Some species occur in a large number of localities, while others are much more restricted, some being confined to a single locality, still others are widely distributed although not occurring in many localities. A breakdown of the number of samples in which species occur is very revealing as the following data show: Number of species occurring in 1 locality: 41 (46%); 2 localities: 19 (21%); 3 localities: 9 (10%); 4 localities: 6 (6.7%); 5 localities: 4 (4.5%); 6 localities: 3 (3.4%); 7 localities: 1 (1%); 8 localities: NIL; 9 localities: 9 (1.1%); 10 localities: NIL; 11 localities: 2 (2.2); 12 localities: 1 (1.1%); 13 localities: 1 (1.1%).

The mean number of localities at which the species occur is 2.66.

The 5 most commonly occurring species and the number of localities they occur in, are *Paracypretta jonesi* (13), *Mongolianella cylindrica* (12), *Cypridopsis wynnei* (11), *Cypria cyrtonidion* (11), *Gomphocythere strangulata* (9), and these species occur respectively in 6, 5, 7, 6 and 5 of the 8 areas listed above. These five species are evidently to some degree environmentally tolerant and it is interesting in that the first 4 are cyprids that, with the possible exception of *Mongolianella cylindrica*, possess desiccation resistant eggs that, together with parthenogenetic reproduction is a great dispersal advantage (Whatley, 1986, 1988, 1992). *Gomphocythere strangulata,* a cytherid, enjoyed neither of these advantages, yet was also widely distributed. Perhaps the most extraordinary statistic, however, is the very large number (41) and percentage (46%) of species that are confined to a single locality, with a further 28 species (31%) being confined to 2 or 3 localities. While a possible explanation for this phenomenon is that it represents inadequate study, this seems unlikely given the number of high quality studies that have been made in which large numbers of specimens have been recovered. In many instances, species that are often abundant enough to be described as new, seem to be genuinely confined to their type locality and are not encountered even in abundant ostracod faunas analysed from adjacent or subjacent localities. These species, and the localities to which they are confined are: *Gomphocythere gomphomatos* (Lak), *Limnocythere bhatiai* (Phul), *L. deccanensis* (Dong, *Altanicypris deccanensis* (Lak), *Cypridopsis elachistos* (Mohag), *C. alphospilotos* (Sichel Hills), *C. dongargaonensis* (Dong), *C. sahni* (Dong), ?*C. whatleyi* (Phul), *Zonocypris gugaratensis* (Anj), *Z. labyrinthicus* (Mohag), *Eucypris phulsagarensis* (Phul), *Mongolianella ashui* (Dong), *Paracandona firmamentum* (Lak), *P. jabalpurensis* (Jab), *Cypria intertrappeana* (Kora), *Pseudocypris ectopos* (Lak), *Centrocypris megalopus* (Lak), *Cyprois polygonum* (Kora).

The plethora of species confined to single localities is probably a measure of the enhanced rate of evolutionary activity taking place in the non-marine intertrappeans. The entire volcanic interval seems to have lasted for a relatively short geological interval close to the Cretaceous/Tertiary boundary. During this interval, land surfaces within the Deccan Volcanic Province, and their faunas and floras seem to have been wiped out by lava flows and ash falls on a periodic basis, followed by intervals when the flows were gradually recolonised by plant and then animal communities. This very instability may have been one of the major contributory factors in the rapid evolutionary activity that took place here over this relatively short interval in pools that were often geographically isolated.

Fig. 2 is a tie-line diagram designed to illustrate, in terms of number of species, the degree of communality between all the 8 areas into which the sample localities have been grouped. What the diagram clearly shows is that there is relatively little relationship between levels of communality and geographical distance. For example, the highest communality of 14 species is between the three localities in Kutch and those grouped together in the Chandrapur District of Mahharashtra, notwithstanding the fact that they are separated by some 1,300 km, the next highest communality of 13 species is between Rajasthan and Gulbarga District, Karnataka, a distance of about 1200 km. The third highest number of common species (11) is between Kutch and Karnataka almost 1200 km. No other link is higher than 9 (Rajasthan to Andhra Pradesh, 850 km), and there is one of 8 (Kota to Chandrapur, about 800 km) and two of 7 (Kutch to the Nagpur District, 1200 km; Chandrapur to Gulbarga, about 500 km).

High levels of communality, of course, can only occur between areas with large numbers of species, but this fails to explain the very low levels of communality between relatively adjacent areas both with large number of species. For example, only 4 species are common between the 2 localities in Rajasthan (20 spp.) and the 4 localities in Madhya Pradesh (29 spp.) that are separated by only some 250 km, and many other examples can be seen in Fig. 2.

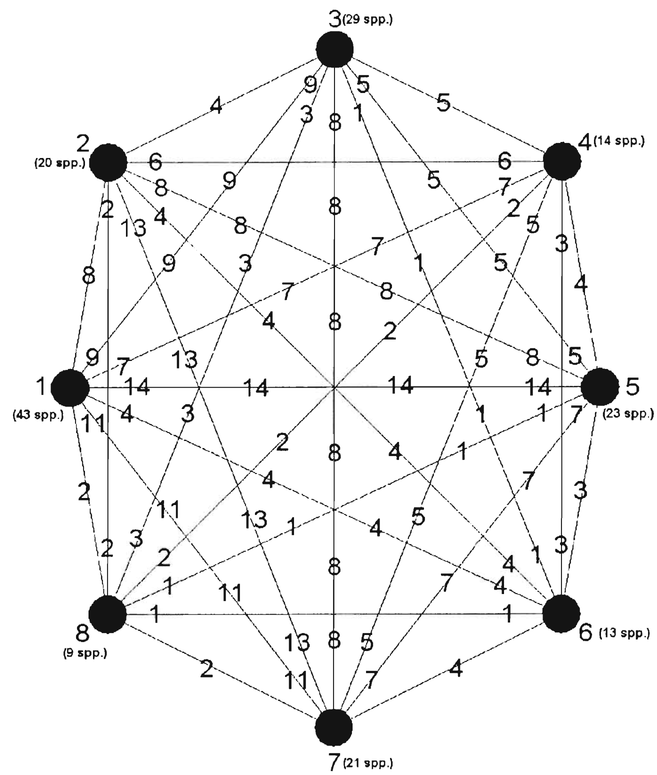

Fig. 2. Tie-line diagram showing the number of common ostracod species between the various continental infra-and intertrappean localities of peninsular India. Key to localities is as follows :
1. Gujarat (Lakshmipur, Kora, Anjar); 2. SE Rajasthan; 3. Madhya Pradesh; 4. Maharashtra I (Nagpur); 5. Maharashtra II (Chandrapur); 6. Andhra Pradesh; 7. Karnataka; 8. Maharashtra III (Bombay).

TWO CASE STUDIES

Many of these anomalies may be due to the fact that in compiling the data for this study, we have grouped faunas from localities together without consideration of the age of the deposits, or whether they are intertrappean or belong to the Lameta Formation. However, although space considerations preclude exhaustive analysis here, environmental/ecological differences must play a major part and an attempt is made to account for the observed differences between the fauna of the three relatively adjacent localities in Kutch (Anjar, Lakshmipur, Kora) and the even closer two localities in Karnataka (Chandarki and Yanagundi).

KUTCH

A total of 43 species occur at the three Kutch localities. Kora is the locality with the most diverse community of 21 species. Of these, 8 (35%) are confined to this locality, 1 (4.3%) only occurs elsewhere in Kutch at Lakshmipur, 7 occur at either Lakshmipur or Anjar and elsewhere, 2 occur at both Anjar and Lakshmipur and elsewhere, and 4 (17.4%) have their only other occurrence (s) at localities outside Gujarat.

Lakshmipur has 17 species. Of these 6 (35.3%) are confined to this locality, 1 (5.9%) only occurs elsewhere in Kutch at Kora, 5 (29.4) occur at either Anjar or Kora and elsewhere, 1 occurs at both Anjar and Kora and elsewhere, and 3 (17.6%) only occur at localities beyond Kutch.

Anjar has the lowest diversity of the three localities with just 13 species. Of these, 6 (46.2%) are endemic to this locality, no species occur exclusively here and also elsewhere in Kutch, 3 species (23.1%) occur at one other locality in Kutch and elsewhere, while 3 species occur only elsewhere beyond Kutch.

The above data are interesting in that they reveal a minimum percentage endemicity of 31.8% and a maximum of 46.2 %. There is surprisingly high endemicity in that the localities are only tens of kilometres apart. However, although the endemicity of each locality is notable, so too is that of Kutch as a whole, in that if the species that are endemic to each site are added to those endemic to Kutch as a whole [8 + 6 + 6 = 20 + the 2 species that occur only in a number of the three localities in Kutch = 22]. As a percentage of the total Kutch fauna of 43 species, this represents an endemicity of 51.2%, an extraordinarily high figure, although the large minority of 49% of species occur also outside Kutch.

Notwithstanding this high endemicity, probably in part a function of the large number of species to occur in Kutch, of all the 8 areas, it shows the highest number of species shared with other areas. For example, as Fig. 2 shows, it has 14 ((32.5%) species common with Chandrapur District, 11 (25.6%) species common with Karnataka, 9 species (21%) with Madhya Pradesh and 8 species (18.6%) with SE Rajasthan. Given the principles outlined above, a good case can be made for the areas with the highest levels of communality being those endowed with the most similar palaeoenvironments. This and its converse are tested below with respect to the three localities.

Only 2 species (*Mongolianella cylindrica* and *Candona amosi*) are common to all three localities in Kutch, although they both also occur outside the area. These are taxa one would normally associate with permanent water, and the presence of *Candona* suggests that the substrate was soft and muddy. A further 6 species (*Cypria cyrtonidion, Eucypris pelasgicos, E. intervolcanos, Cypridopsis hyperectyphos, Cyprois rostellum* and *Zonocypris spirula*) occur at both Kora and Lakshmipur, all but *C. rostellum* also occurring in other areas; while only *Paracypretta elizabethae* occurs at both Kora, Anjar and elsewhere. *Limnocythere falsicarinata* is the only species to occur at both Lakshmipur and Anjar as well as elsewhere. *Cypria, Limnocythere, Cypridopsis, Zonocypris* and probably *Paracypretta* are all to a degree indicative of permanent waters, while *Cyprois,* and *Eucypris* are indices of temporary waters.

Taking account of all the taxa occurring at each locality, it would seem that those indicative of permanent water dominate, although a significant component of forms usually associated with temporary waters also occur. The only means of definitively resolving this apparent enigma would be to resample the localities, taking into account the vertical intervals between samples, their relative and absolute ages, the nature of the lithology and any obvious hiatuses, and a consideration of other available palaeontological evidence. However, it seems likely that each locality comprised a core of permanent water in a basin that flooded out onto surrounding land during the monsoon and dried out around the periphery during the dry season. The system seems to have been principally lacustrine, although during the dry season, small ponds would have become isolated and eventually desiccated. In years with a poor or failed monsoon, the system would experience harsher conditions of drought, but the evidence suggests that the major bodies of water did not dry out. Possibly the three localities represented lacustrine environments within a river system that united them, but the fact that so few species are shared in common perhaps militates against this. One of the major factors that serve to differentiate water bodies is their chemistry, and this can result in adjacent ponds sometimes having very different faunas (Curry, 1999; De Deckker, 1983, 1988; De Deckker and Forester, 1988; Forester, 1986; Smith, 1993). We suggest that this is probably the reason why the three localities in Kutch have so few species in common.

A recent study by Sanyal *et al.* (2005) uses stable isotope analysis to reconstruct the environment of deposition at Lakshmipur. The senior author is concenned since this work expands the technique so far back in time beyond the Pleistocene, the normal limit for such studies (Lister, 1988; Schwalb *et al.*, 1999). The authors state that they are studying the original shell material of the two ostracod species they examined. Given the time interval, however, they may be analysing material that had been replaced in diagenesis, albeit in a delicate replication of the original and retaining many of the carapace characteristics of the original animal. Oxygen isotope studies using fossils with such massive calcite as the guards of belemnites have been used back to the Mesozoic with some confidence, but fragile ostracod carapaces are a different matter. A further possible problem is that while the ostracods were collected from a khaki shale, their shell material, prior to analysis, was added to crushed limestone from a different bed. The conclusion drawn was that deposition was under "highly evaporitic conditions". The limestone may have been deposited under more arid conditions than the shale, which seems likely given the muddy nature of the latter. The senior author's concerns are twofold. Firstly, "highly evaporitic" implies deposition from more saline residues than those that would deposit limestone, such as gypsum or halite etc. and there seems to be no evidence of the presence of evaporitic minerals. Secondly, from the fossil ostracods it is obvious that these communities lived in bodies of water, rich in weeds but which to some extent dried out around the margins during the dry season. That the area must have been well vegetated is attested to by the herbivorous dinosaur population and the ostracods provide evidence in the presence of 43 species occurring in a fairly small area, many of them endemic to Kutch, of a thriving fauna living in a well-established aquatic regime. This is not to say that desiccation did not take place here during the dry season, it certainly did and there is evidence from elsewhere in the intertrappeans that lakes dried up causing mass mortality to vertebrates unable to drink elsewhere. This seems to have been the case at Naskal in Andhra Pradesh (Prasad and Khajuria, 1996, p. 358).

Today, Kutch is an area of extreme desiccation, with little or no standing water and small prospect of collecting modern non-marine ostracods. There are, of course, many studies of ostracods from areas where conditions were highly evaporitic, such as Whatley and Cusminsky (1999). In this latter study, in the circumstances of highest desiccation, fossil ostracods are associated with evaporitic minerals and are of low diversity.

KARNATAKA

The two localities studied in this state are both in the Gulbarga District. They are Chandarki and Yanagundi, and are separated by some 5 to 6 km. They are both stream sections and their lithostratigraphy is given in Whatley *et al.* (2002a, p. 164) who also record 19 species from the two localities. Subsequently, Whatley *et al.* (2002b), added a further 3 species.

In the present study, the faunas of the two localities have been separated, as shown in the communities 20 and 21 above. Ten species occur at Chandarki, 2 of which (*Paracandona* sp. and *Eucypris verruculosa*) are unique to that locality and 1 (*Cypridopsis astralos*) only occurs elsewhere at Yanagundi. Six species also occur at Yanagundi and elsewhere in the study, although two species, while occurring elsewhere in the study, do not occur at Yanagundi.

More than twice as many species (22) occur at Yanagundi. Of these, only *Candona mysorephaseolus* is confined to this locality, while *Cypridopsis astralos* only occurs elsewhere at Chandarki. Six species occur at Chandarki and elsewhere, although the majority category of species (8) are those that occur elsewhere but not at Chandarki.

Given that the localities are very adjacent geographically, there are considerable differences in their faunas and the simple species diversity of Yanagundi is more than double that of Chandarki. These differences may be due to lithology, although, as shown in Whatley *et al.* (2002a, p. 176, Fig. 2), the ostracod bearing horizons at each locality are from rather similar strata and there does not appear to be any obvious major diagenetic phenomenon to account for the differences.

A possible answer would seem to be palaeoecological. *Mongolianella cylindrica* was used in Kutch to suggest permanent water, and this occurs at both localities, although the other index species for this type of water body, *Candona amosi* occurs only at Yanagundi. However, this may reflect another factor because, although the lithologies appear similar, almost certainly the bottom conditions at Yanagundi were of soft mud to allow the three candonids (*Candona mysorephaseolus, Candona amosi,* and *Eucandona kakamorpha*) to burrow within it. The only candonid represented at Chandarki is a single specimen of *Paracandona*. *Gomphocythere* is represented by two species at each locality and with *Frambocythere,* this is a further indication of permanent water as is the abundance of *Cypridopsis* and *Cypria* at both localities, although species of both these genera can survive desiccation. Additional evidence is provided by fossils of a freshwater ray and other fishes, freshwater molluscs and charophytes (see Whatley *et al.*, 2002a).

The presence of *Eucypris* at both localities is, however, a good guide to temporary waters and it is likely, as in Kutch, that the peripheral part of the water body was subject to desiccation during the dry season, although the other index taxon used previously, *Cyprois*, does not occur in Karnataka. The best conclusion that can be arrived at without further specialist sampling to allow of proper statistical analysis, is that the two localities differed in the nature of the substrate. This, however, may have been the consequence of differences in energy levels. It is suggested that Chandarki was subjected to higher energy levels than Yanagundi, as evidenced by the finer substrate at the latter, this being suggested by the greater number and diversity of candonids. Further evidence for this is the presence of *Darwinula torpedo*, only at the latter locality; the genus being usually associated with low energy environments. It is also possible that the very abundant occurrence of *Gomphocythere akalypton* at Chandarki could be because of its preference for higher energy conditions than those obtaining at Yanagundi.

ENVOI

Our aim in this work has been to outline those particular aspects of the ecology of non-marine Ostracoda that could be of palaeoenvironmental significance. This has, of necessity, been outlined in very broad, general terms because of the nature of the data, but we hope we have demonstrated the potential for the use of Ostracoda so as to encourage future workers to utilise them. Future studies, however, if they are to produce more reliable data, must be designed in such a way that the initial samples are taken so as to embrace all possible lithologies in any section. The vertical distance between samples should be carefully measured, the lithology described, the sampled weighed, any sedimentary structures or minerals noted and other palaeontological evidence taken into account on a bed by bed basis.

In processing the samples, the technique used should be as non destructive, chemically and physically, as possible so as to ensure the preservation of the smallest instar stages. The residue should be carefully passed over a nest of dry sieves and coarse, medium and fine fractions then exhaustively examined for microfossils and all ostracods, of all sizes should be picked out, identified to species level and counted.

The importance of assessing both adults and juveniles is that, by this means a population age structure profile of all species can be attained. This is critically important in differentiating autochthonous from allochthonous components in a population, a fundamental procedure in accurately reconstructing palaeoenvironments. These are essentially simple, if somewhat time consuming, procedures and simple guides to their operation are given in a number of papers by the senior author (Whatley, 1983 a, b, 1988a; Ware and Whatley, 1983). Other aspects of the ecology and evolution of Mesozoic and particularly Cretaceous Ostracoda would be of particular relevance to workers in this field and are to be found in Whatley (1986, 1988b, 1990, 1992). For any aspirant, or indeed experienced worker in non-marine ostracods of any age, notwithstanding the fact that it is concerned with Recent European faunas, we strongly recommend an excellent book by Meisch (2000), which is so very informative on so many aspects of the group.

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