

THE BIOGEOGRAPHY OF SOME CAINOZOIC OSTRACODA

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ABSTRACT. Following a brief review of some general considerations, the distributions in space and time of two exemplar sets of Cainozoic Ostracoda, one marine and the other dominantly freshwater but each containing about 150 species, are used to evaluate the alternatives of continental permanence or continental drift. Taxa are approached phenetically. Discontinuities and dispersal potentials provide appropriate scales of values. It is concluded that the evidence does not negate Drift Theory.

PALAEOBIOGEOGRAPHIC analyses inevitably deal with imperfect data involving problems of complexity and uncertainty. The imperfect data treated here correlate known living organisms and fossils and thus are fully empirical; and the presence world wide of considerable thicknesses of Cainozoic rocks, including many richly fossiliferous sequences, provides the operational security which palaeobiogeographers need to support, and to test further, ideas on the significance of particular distributions.

Ostracoda comprise over 35 000 described taxa (H. V. Howe, pers. comm.) the majority of which probably have been described from Cainozoic deposits. In recent years, there has been a tremendous boom in the description of new taxa (Table 1) so that now over 700 Cainozoic genera are known. This large number of genera, the majority of which are restricted to the Cainozoic, is indicative of the fact that a major adaptive radiation among Ostracoda has taken place since the Mid Cretaceous.

Ostracoda occur in virtually all kinds of aquatic environments. They are equally valuable palaeoecological indices in marine as well as freshwater assemblages

TABLE 1. Numbers of new species of ostracodes described (to the nearest higher 25), subspecies and *nomina nova* not included. Data from the *Zoological Record*, 1958-1968.

Approximate numbers new species described.

| <i>Year</i> | <i>Fossil</i> | <i>Living</i> |
|-------------|---------------|---------------|
| 1958 | 450 | 50 |
| 1959 | 300 | 125 |
| 1960 | 450 | 50 |
| 1961 | 150 | 50 |
| 1962 | 900 | 75 |
| 1963 | 400 | 125 |
| 1964 | 1000 | 150 |
| 1965 | 625 | 100 |
| 1966 | 475 | 175 |
| 1967 | 400 | 100 |
| 1968 | 650 | 25 |

(Oertli (ed.) 1971) and with this in mind I have chosen to use as exemplars taxa from two Cainozoic ostracode groups, one marine the other dominantly freshwater. These groups are the cytherettids and entocytherids, respectively.

GENERAL CONSIDERATIONS

Some general conclusions on marine and freshwater ostracode distributions during the Cainozoic have already been set out (McKenzie 1967, 1971*a*).

For the Tethys paper (McKenzie 1967), I reviewed the distributions of over 100 marine genera and concluded that the several patterns which these taxa exhibited all supported the main conclusion that the Tethyan corridor played a significant role in the dispersal of Cainozoic marine Ostracoda, especially during the Palaeogene. Recently, Benson and Sylvester-Bradley (1971) concentrating on deep-sea ostracodes concluded that even into Pliocene times, '... a relatively wide and deep gateway lay between Spain and Morocco'. This result complements a second conclusion of my Tethyan paper that in the Neogene disruption of the Tethyan corridor meant that the Mediterranean faunule was replenished mostly from the Atlantic since transfers from the Indo-Pacific were less likely after the Vindobonian.

On the other hand, Tethys provided an important latitudinal barrier to the dispersal of freshwater ostracodes. This barrier was absolute while Tethys stretched uninterrupted from the Gulf of Mexico to Australasia, via the Mediterranean and the site of the present Indo-Gangetic Plain, except for chance dispersals of either eggs or entire animals by such agencies as moist dust-laden winds or birds.

Important factors in such chance dispersions include the well-known high vagility of the desiccation-resistant eggs of cypridid ostracodes (van Morkhoven 1962); the brooding of early instars by some cytherids and darwinulids which apparently lack desiccation-resistant eggs (McKenzie and Hussainy 1968); and the capacity of some taxa to switch from a bisexual reproductive mode to a parthenogenetic one (cf. discussion in McKenzie 1971*a*). The latter factor, also observed in other arthropods, has been termed geographic parthenogenesis (e.g. Vandel 1940).

Another factor of importance which affects both marine and freshwater distributions is the influence of man upon environment. Thus, the digging of the Suez Canal led to the alteration of some marine distributions (Por 1971) and the cosmopolitan planting of rice is known to have affected the distributions of some freshwater species (Moroni 1967).

THE ALTERNATIVES

The biogeography of Cainozoic ostracodes in the context of this symposium could enable a decision to be reached in favour of one or other of the following alternatives:

1. The continents have maintained their present positions throughout the Cainozoic;
2. The continents have drifted during the Cainozoic over an Earth which in the same era has either (i) expanded very little if at all, or (ii) expanded considerably.

Alternative 2 implies that prior to the era under review some continents were relatively much closer together than they are today. Alternative 2 (ii) implies

further that the amount of change was greater than for 2 (i) by a suitable expansion factor.

The base maps which have been issued to contributors were computed as for alternative 2 (i) and include two major regions of uncertainty. These regions are Tethys and the periPacific.

THE SCALE OF VALUES

There is some difficulty in setting up a scale of values appropriate to the problem. A pertinent scale would be migration rate which is a function of time as well as distance. This scale is relatively unambiguous and objective and is manifestly capable of quantification. Unfortunately, the migration rates of ostracode taxa in general are not well known. There is no firm data on migration rate in entocytherids, for example, and the only specific data which I am aware of on migration rate in cytherettids is that which I have taken from Carbonnel's recent monograph on the Rhone Basin with respect to *Protocytheretta schoelleri* (Carbonnel 1969, p. 386). The rate for this species was about 1×10^{-4} km/yr.

A second scale of values, more fruitful with respect to the available data, is dispersal potential. Minimum values for this potential can be determined for several taxa in each of the two selected groups with a fair degree of certainty (Table 2).

TABLE 2. The dispersal potentials of some cytheretid and entocytherid taxa. Data from the literature or from collections. The entocytherid data probably indicate atypically large dispersal potentials, since in the literature most entocytherid species have very localized distributions.

| <i>Taxon</i> | <i>Range (in km)</i> | <i>Range (geographic)</i> | <i>Age</i> |
|--|--------------------------|---------------------------|------------|
| <i>Paracytheretta reticosa</i> Triebel | 2000 | Denmark-U.S.S.R. | Palaeocene |
| <i>Flexus plicata</i> (Münster) | 2500 | Britain-U.S.S.R. | U. Eocene |
| <i>Neocytheretta</i> sp. | 3500 | Torres Strait-Sahul Shelf | Recent |
| <i>Loculicytheretta pavonia</i> (Brady) | 3600 | Spain-Egypt | Recent |
| <i>Argenticytheretta miocenica</i> Rossi de Garcia | 2500 | Magellanes-Entre Rios | L. Miocene |
| <i>Bensonia knysnaensis</i> (Benson and Maddocks) | 1500 | Knysna-Namaqualand | Recent |
| <i>Entocythere claytonhoffi</i> Rioja | 1500 | Mexico | Recent |
| <i>Ankylocythere heterodonta</i> (Rioja) | 1000 | Mexico | Recent |
| <i>Uncinocythere equicurva</i> (Hoff) | 1000 | South-eastern U.S.A. | Recent |
| <i>Notocythere syssitos</i> Hart and Hart | 2000 | Tasmania-Queensland | Recent |
| <i>Lichnocythere tubrabucca</i> Hart and Hart | 650 | N.S.W.-Queensland | Recent |

Dispersal potential, like migration rate, is pertinent to biogeographic problems and also has the desirable properties of relative unambiguity and objectivity. And it can be quantified as a distance along geological time planes. Here the imperfect record becomes a significant factor. For example, the Palaeogene Ostracoda of the Indonesian region are not well known so that it is difficult to assess properly the dispersal potential of Palaeogene Indo-Pacific forms.

A simpler scale of values may be more effective. Therefore, I intend to use discontinuities in the distributions in time and space of specific phenons as well as their dispersal potentials in order to evaluate the alternatives.

CYTHERETTIDS

Cytherettids are shallow-water marine ostracodes which are commonly encountered in littoral and neritic faunas ranging in age from the Upper Cretaceous (Santonian) to the Recent. As considered here, the group may well be polyphyletic (cf. van Morkhoven (1963) on the position of *Loculicytheretta*, Ruggieri 1954 and Triebel and Malz (1969) on the scope of Cytherettinae) but polyphyly does not affect their utility as exemplars for Cainozoic marine Ostracoda. Three well-defined subgroups are recognized as belonging among cytherettids. These subgroups are: the cytherettines proper, argenticytherettines, and loculicytherettines. 21 genera have been assigned by various authors to the 3 subgroups. Of these genera, I shall exclude *Netrocytheridea* Howe and Laurencich 1958, included by Deroo (1966), and *Cytherettina* Mandelstam 1956, included in the Russian Treatise (Kashevarova *et al.* in Orlov (ed.) 1960), because these genera do not have an amphidont hinge as do other cytherettids; further, *Cytherettina* is an objective synonym of *Protocythere* Triebel 1938 which is accepted as belonging to a non-cytherettid group (Howe *et al.* in Moore (ed.) 1961). I shall also exclude *Buntonia* Howe 1935 and *Ambocythere* van den Bold 1957, included by Rossi de Garcia (1970), because these genera are usually associated with trachyleberidids. The remaining 17 generic names include several commonly accepted subjective synonyms (cf. Appendix) so that the final list consists of 12 genera. The generic characters which distinguish these are founded wholly upon carapace features several of which overlap. I therefore propose to ignore generic boundaries in the first instance and to approach the taxa phenetically.

A simple presence-absence table can be set up for the characters: inner margin; shell surface; loculi; eye tubercle. Since each character is coded for 2 states, there are 16 possible combinations (Table 3). As noted in the Table explanation, several of these combinations do not occur in the known cytherettid record.

The number of species involved in the phenons which do occur is considerable for cytherettines proper but relatively small for argenticytherettines and loculicytherettines (text-fig. 1). This pattern, however, of dominance numerically by one group

TABLE 3. The seven known combinations of cytherettid ostracodes for four specified characters each in two states. The characters are:

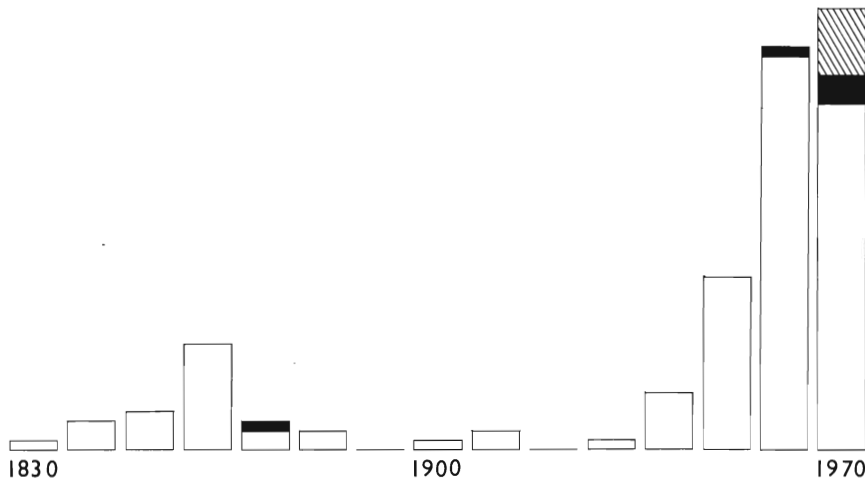
- A = presence (1) or absence (0) of an eye tubercle.
 B = presence (1) or absence (0) of posteroventral loculi in mature females.
 C = presence (1) or absence (0) of a regular inner margin in adults.
 D = presence (1) or absence (0) of an ornamented carapace. Ornamented includes pitted, punctate, reticulate, tuberculate, ribbed, or any combination of such ornament. Absence of ornament means smooth, e.g. as in *Cytheretta judaea* (Brady) 1868.

The combinations: 0100, 0110, 0010, 0101, 1111, 1100, 1110, 1010, and 1101 are not known in cytherettids as defined for this paper (cf. Appendix).

| Cytherettid Subgroups | Characters | | | |
|-----------------------|------------|---|---|--------|
| | A | B | C | D |
| Loculicytherettines | 0 | 1 | 1 | 1 |
| Argenticytherettines | 0 or 1 | 0 | 1 | 1 |
| Cytherettines | 0 or 1 | 0 | 0 | 0 or 1 |

among several which are thought to be related, is not unusual among Ostracoda or among animals generally (Nicol 1969) which reinforces the suitability of this particular set as an exemplar for marine species. A further point in favour is that cytheretids range in age from Upper Cretaceous to Recent, an ideal range in this context, with the type taxon, *Cytheretta* Müller 1894, making its first appearance in the basal Palaeocene (Oertli 1963).

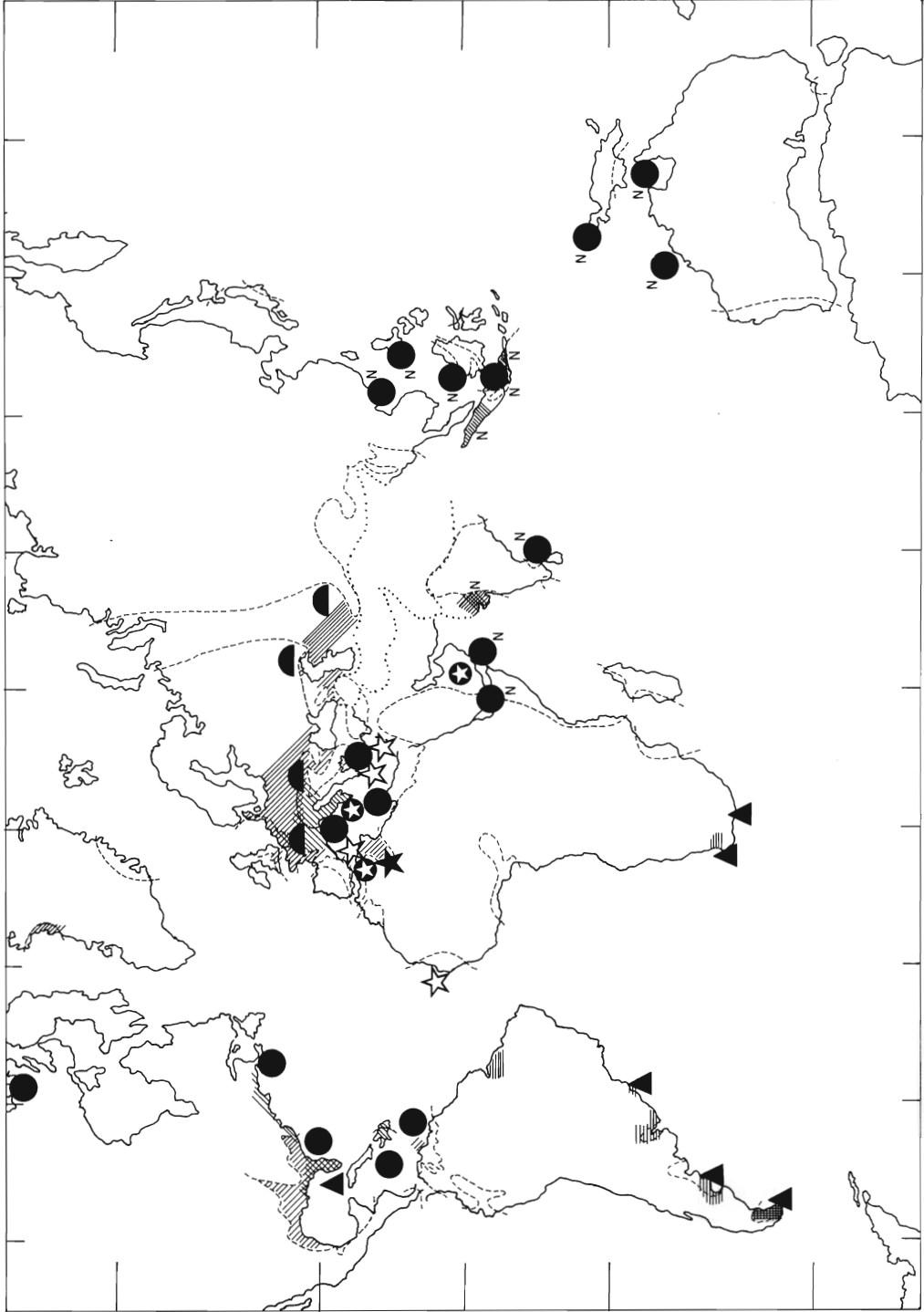
Loculicytherettines are ribbed and coarsely punctate forms with a regular inner margin which lack an eye tubercle and which are characterized above all by the presence in mature females of several posteroventral loculi. Usually, they are rare in ostracode assemblages. The type taxon was described by Brady (1866) but was not separated into a new genus until much later (Ruggieri 1954). Other taxa have



TEXT-FIG. 1. Descriptions of new species of cytheretids by decades, since 1830. Open block = cytherettines; Full block = loculicytherettines; Barred block = argenticytherettines.

been described and illustrated more recently (Apostolescu and Magné 1956, van Morkhoven 1963, Ruggieri 1963). Apart from the records in these papers, the group is known from Libya in both the Palaeogene and Neogene (J. Szczechura, pers. comm.). The loculicytherettines are completely absent in all records known to me, published or otherwise, from all areas beyond a zone extending from Gambia in the west to Saudi Arabia in the east. Fossils range from Algeria to Saudi Arabia, living loculicytherettines from Gambia to Port Said (text-fig. 2). Interestingly, there are no records from the Black and Azov Seas (Schornikov 1969).

Argenticytherettines are ribbed or reticulate or punctate forms without posteroventral loculi and characterized above all by a regular inner margin. *Argenticytheretta* Rossi de Garcia 1970, the type taxon, has a weak eye tubercle but the other genera, *Bensonina* Rossi de Garcia 1970 and *Grekoiffia* Rossi de Garcia 1970, lack this feature. They are common elements in some southern ostracode assemblages. The group was established only recently but already several taxa have been described (Rossi de Garcia 1966, 1969, 1970). Further, argenticytherettines are thought to include *Cytheretta knysnaensis* Benson and Maddocks 1964, a South African species, and



TEXT-FIG. 2. Upper Cretaceous and Cainozoic distributions of cytheretids on the Tertiary map. Dashed lines mark Eocene outcrops; Full semi-circles = Upper Cretaceous distributions of cytheretines; Sinistral hatching = Palaeogene distribution of cytheretines; Dextral hatching = Neogene distribution of cytheretines; Full circles = Recent distribution of cytheretines; N = *Neocytheretta* records; Vertical hatching = Palaeogene distribution of argenticytheretines; Horizontal hatching = Neogene distribution of argenticytheretines; Full triangles = Recent distribution of argenticytheretines; Open stars in full circles = Palaeogene distribution of locuicytheretines; Full star = Neogene distribution

two Caribbean forms (Rossi de Garcia 1970). Apart from the published records, the group is known from the Brazilian Miocene in well cores in Rio Grande do Sul Province and from outcrop in the Lower Miocene Pirabas Formation, near Capanema, in Para Province. Finally, they occur as low as the Oligo-Miocene in some wells in the Magellanes Basin, Chile. In South Africa, fossils related to the Benson and Maddocks species (cf. above) are known to occur in some Pleistocene assemblages from Namaqualand. The group is completely absent in all records known to me, published or otherwise, from all areas beyond a zone extending from the Gulf of Mexico in the north to Magellanes in the south and from Magellanes in the west to Knysna in the east. There are no records as yet from West Africa.

Cytherettines are smooth or ornamented forms without posterior loculi which typically lack an eye tubercle (exceptions include *Neocytheretta*) and which are characterized above all by an expanded and irregular sometimes deeply invaginated inner margin. They are common elements in numerous Northern Hemisphere ostracode assemblages and frequently typify Cainozoic European faunas (Ducasse 1969). As has been indicated (text-fig. 1), published records for cytherettines are much more numerous than for the other cytherettids treated herein, except that there are relatively few citations of some recently described taxa, specifically the genus *Neocytheretta*. Apart from the published records, Recent *Neocytheretta* species have been collected from a zone extending from the Philippines and Hong Kong in the east via Indonesia (including several Sahul Shelf species) and India to the Gulf of Aden and the Red Sea in the west. Fossils ascribed to *Paracytheretta* Triebel 1941 but with the characteristic eye tubercle of *Neocytheretta* are known from the Palaeogene of India (Lubimova *et al.* 1960) and the Neogene of Indonesia (Kingma 1948). The group is absent, in all Cainozoic records known to me, published or otherwise, from New Zealand (Eagar 1971), southern Australia, the southern Indian Ocean, South Africa, South America, and the eastern Pacific (Table 4).

ENTOCYTHERIDAE AND THEIR HOSTS

The commensals of the family Entocytheridae are characterized by a remarkable diversity of male copulatory processes upon which their generic taxonomy is often based (Hobbs and Hobbs 1970). The literature on entocytherids is specialized and the most helpful papers are probably the reviews by Hart (1962), and Hart and Hart

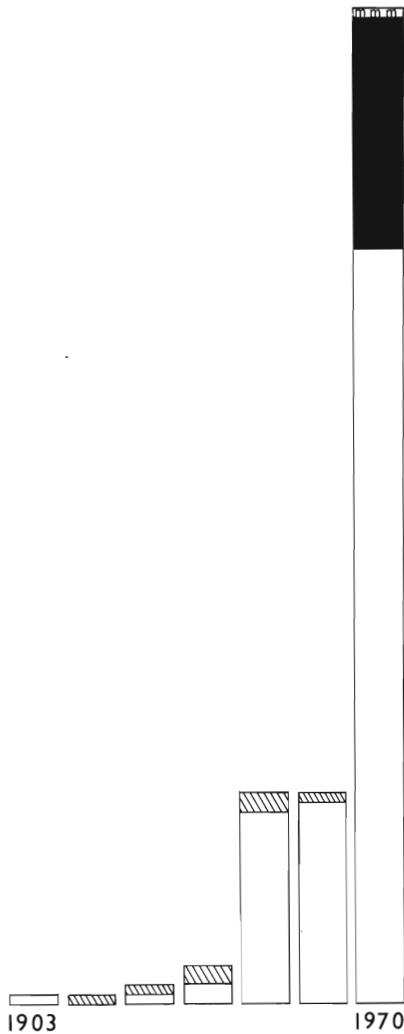
TABLE 4. Distributions in space and time of cytherettid subgroups. The time units are Cretaceous, Palaeogene, Neogene, Recent (from left to right). 0 = absence; 1 = presence; ?0 = ?absence. The geographical areas are 1 = Caribbean; 2 = southern Atlantic; 3 = northern Atlantic; 4 = Mediterranean; 5 = Indo-Pacific; 6 = southern Africa to Malagasy; 7 = southern Australasian (southern Australia and New Zealand). In the Cretaceous, Tethys was continuous from the Caribbean to Australasia and the northern Atlantic and Mediterranean areas were poorly defined.

| <i>Taxa</i> \ <i>Space</i> | 1 | 2 | 3 | 4 | 5 | 6 | 7 | <i>Time</i> |
|----------------------------|-------|------|------|------|------|-------|------|-------------|
| Loculicytherettines | 0000 | 0000 | 0000 | 0111 | 0000 | 0000 | 0000 | |
| Argenticytherettines | 00?01 | 0111 | 0000 | 0000 | 0000 | 00?01 | 0000 | |
| Cytherettines | 0111 | 0000 | 1111 | 1111 | 0111 | 0000 | 0000 | |

(1969), the Mexico and Cuba monograph (Hobbs 1971), the Australian monograph (Hart and Hart 1967), the record from India (Hart *et al.* 1967), and the latest revision of Sphaeromicolinae (Danielopol, in press). Over 160 species have been described (text-fig. 3). A simple phenetic key to the 4 known subfamilies is given in the recent Mexico and Cuba monograph (Hobbs 1971). Nearly 30 genera have been described for the group so far and text-fig. 3 indicates that it is not yet stabilized.

The distribution of Entocytheridae extends from continental America north of the Isthmus of Panama, through Cuba, to the Mediterranean, India, and Australasia. As far as I am aware, no fossils are known.

Commensals are dispersed passively. Their distributions depend upon the migratory behaviour of their hosts. The hosts for entocytherids are usually freshwater crayfishes, amphipods, and isopods (including phreatoicoids); and there is also a host record for the freshwater crab *Pseudothelphusa veracruzana* (Hobbs 1971). Since entocytherid fossils are unknown, the fossil records of their host taxa may provide some idea of the way in which these commensals achieved their present distribution.



TEXT-FIG. 3. Descriptions of new species of entocytherids by decades, since 1903. Open block = entocytherines; Full block = notocytherines; Barred block = sphaeromicolines; m = micro-syssittrines.

1. Pseudotelphusid crabs are not known as fossils but were previously classified with potamids which have a fossil record extending into the Neogene of Europe and India (Glaessner, in Moore (ed.) 1969). The present distribution of potamids is world wide (cf. Bishop 1967, pp. 119-120 for a very useful summary).
2. Gammaridean amphipods include the genus *Chelura* which is a host for some marine sphaeromicolinid entocytherids. Gammarideans range from Palaeogene to Recent with several fossil genera being reported from Caspian facies (Hessler, in Moore (ed.) 1969). Their present distribution is cosmopolitan but the records with entocytherid commensals are restricted to the Mediterranean region.
3. The ranges of fossils of sphaeromid and cirranid isopods extend over much of Tethys from Brazil and Mexico to Europe (Hessler 1969, van Straelen 1931). There are no Indian fossil records of which I am aware for these families. Their present distribution is cosmo-

politan but the records with commensal entocytherids are restricted to the Caribbean (Mexico to Cuba), the Mediterranean, and south-western India.

Phreatoicoid isopods range in age from Permian to Recent, with the fossils coming from Australia and Europe (Hessler 1969). Their present distribution extends from South Africa, to India and Australia. The significance of this distribution pattern has been commented upon by Barnard (1936) and McKenzie (1971*b*). Only the Australian forms are known to carry entocytherid commensals.

4. Freshwater crayfishes are by far the most common hosts for entocytherid ostracodes. Of these hosts, the North and Central American and the Cuban cambarine astacideans are the best studied. Genera which are known to act as hosts for Recent entocytherids range from the Palaeogene (Glaessner 1969). The other astacidean hosts are confined to Australasia (Hart and Hart 1967, Hobbs 1971). These Australasian forms belong to the family Parastacidae, the present distribution of which (Bishop 1967) ranges from South America, to Madagascar and Australasia. Parastacids are not known as fossils before the Quaternary (Glaessner 1969).

ANALYSIS

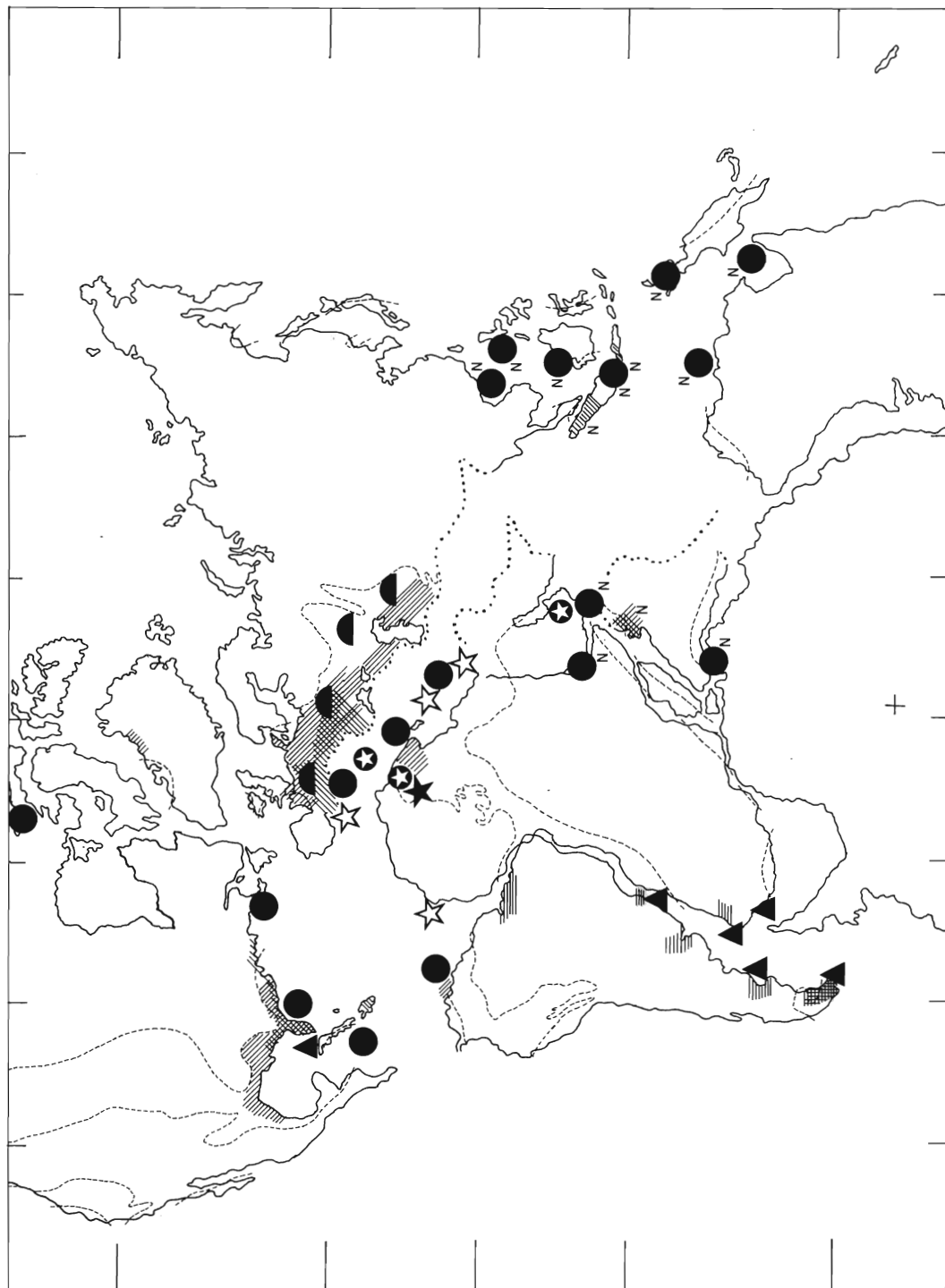
The cytherettid distributions are given in Table 4 and the Cainozoic results (fossil as well as living records) are plotted on the Tertiary map (text-fig. 2). Shallow marine biogeographic patterns are geologically transitory (Valentine 1971), so these Cainozoic distributions are only palimpsests of the Cretaceous ones. None the less, when they are superimposed upon the Cretaceous map (text-fig. 4) there is a partial biogeographic 'fit' which is analogous to the geomorphologic fit of the continental plates along coastlines (Meservey 1971) or isobaths (Smith and Hallam 1970). This 'fit' suggests that some cytherettids originally dispersed via the Tethyan corridor probably during the Late Cretaceous to Early Palaeogene.

Returning to text-fig. 2, discontinuities between the ranges of locucytherettines, argenticytherettines, and the cytherettine *Neocytheretta* are apparent but the ranges of the other cytherettines, which extend over all from the Gulf of Mexico to central Asia, link these separated taxa. These other cytherettines include the ancestral Cretaceous forms, e.g. *Paracytheretta* (Santonian to Eocene), whereas the locucytherettines and *Neocytheretta* range only from the Eocene and the argenticytherettines possibly from the Oligocene.

Text-fig. 4 shows that Cretaceous outcrops fail to match the distribution pattern of Argenticytherettinae except in southern South America, that the Locucytherettinae distribution is consistent with outcrop; that the *Neocytheretta* pattern becomes more disrupted when India is fitted back against Madagascar-Africa and Antarctica; that the distribution pattern of other cytherettines 'fits' with the computed continental redistribution which requires an increase in contiguity between North America and Europe during the Cretaceous.

The large dispersal potentials of some cytherettids (Table 2) indicate that, given favourable environmental conditions, they can disperse far relatively fast.

Where discontinuities occur, therefore, either effective contemporary land or



TEXT-FIG. 4. Upper Cretaceous and Cainozoic distributions of cytheritids on the Cretaceous map. Legend as for text-fig. 2. Dashed lines mark Upper Cretaceous outcrops.

oceanic barriers to dispersal must have operated or else the 'barriers' are temporal, as in text-figs. 4 and 5 where some taxa postdate the reconstruction used. In this latter case, some patterns may appear to be disrupted (e.g. *Neocytheretta*) and others fail to match the stratigraphy (e.g. *Argenticytherettinae*). When the system is considered dynamically, however, and the time framework is adjusted such mismatches disappear.

The distributions of some entocytherid host taxa are given in Table 5. The table indicates that although suitable host groups (phreatoicoids and parastacids) occur in South America and South Africa, no entocytherids are recorded from these areas.

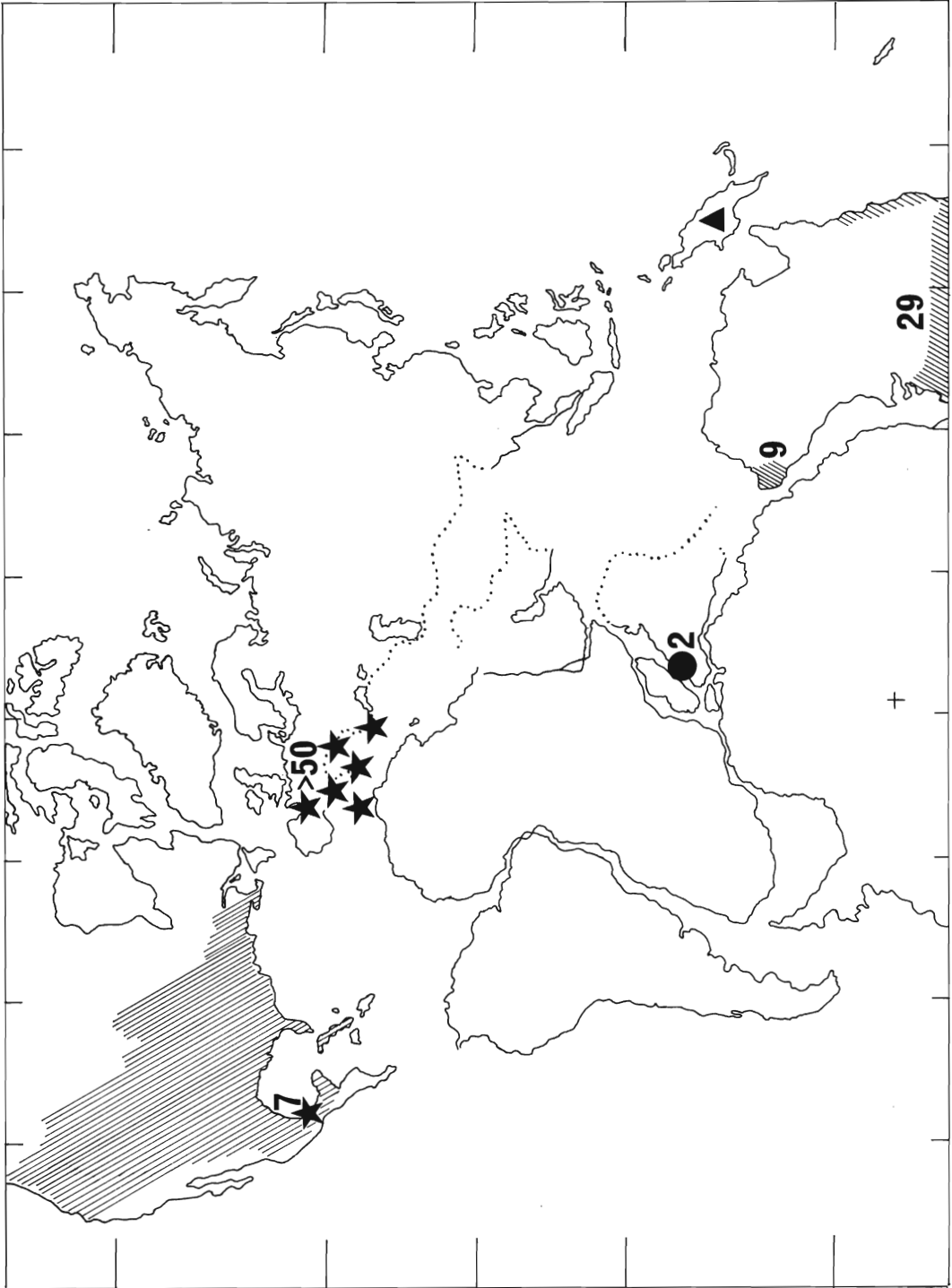
TABLE 5. The distributions in space and time of some taxa which are known to act as hosts for Recent entocytherids. The time units are Mesozoic, Palaeogene, Neogene, Recent (from left to right). 0 = absence; 1 = presence. The geographical regions are 1 = Neartic; 2 = Neotropic; 3 = Palaearctic; 4 = Ethiopian; 5 = Oriental; 6 = Australasian. For notes on the other host taxa—gammarideans, cirrolanids, and sphaeromids—see text.

| Taxa | Space | | | | | | Time |
|---------------|-------|------|------|------|------|------|------|
| | 1 | 2 | 3 | 4 | 5 | 6 | |
| Phreatoicoids | 0000 | 0000 | 1000 | 0001 | 0001 | 1001 | |
| Astacids | 0011 | 0000 | 1111 | 0000 | 0001 | 0000 | |
| Parastacids | 0000 | 0001 | 0000 | 0001 | 0001 | 0001 | |
| Potamids | 0000 | 0001 | 0011 | 0001 | 0011 | 0001 | |

There are several possible explanations. For instance, the blank records may be due to a lack of sampling. Alternatively, entocytherids may have occurred formerly but were later displaced by other symbionts, such as the temnocephalids which associate with South American parastacids. Thirdly, the ancestors of modern parastacids and phreatoicoids may have dispersed on southern continents before the entocytherid ancestors adapted to a commensal habit; and, subsequently, only the Australasian hosts were favoured.

The remaining host taxa are marine gammaridean amphipods and freshwater cirrolanid and sphaeromid isopods. The distribution of these groups is cosmopolitan today but the fossils are known mostly from Europe and the Americas and the records with entocytherids likewise mainly have Tethyan affinities. All these records with entocytherids are from marginal environments such as estuaries (Hart *et al.* 1967), bays (Hart 1962, p. 140), and caves or subterranean streams or other localities near the Mediterranean and European Atlantic coasts (Hart 1962, Danielopol 1971) with the exception of a cavernicole Mexican species (Hart 1962, p. 139). The entocytherid symbionts are either sphaeromicolines (Hart 1962, Danielopol, in press) or microsystitines (Hart *et al.* 1967).

Considering the Recent entocytherid distributions only, when these are transferred to the Cretaceous map (text-fig. 5) they plot on either side of Tethys—in northern America, the Mediterranean, and Atlantic coasts of Europe and Africa, south-western India, and Australasia. In a recent comment, Danielopol (1971, p. 190) concludes, ' . . . This distribution suggests that the ancestor group of the recent Entocytheridae [my transposition from Entocytherinae] inhabited the Tethys Ocean.' I would add that the distributions of host taxa also suggest a dispersion originally via Tethys for the group, probably during the Palaeogene. Since then, as



TEXT-FIG. 5. Cainozoic distributions of entocytherids on the Cretaceous map. Sinistral hachuring = Entocytherinae, for which there are many hundreds of records and over 100 species. Dextral hachuring = Notoocytherinae; the figures indicate the number of records (to 1967); there are 6 south-west Australian species and 18 eastern Australian and Tasmanian species. Full circle = Microsystirinae; two records (to 1967) of a single species. Full stars = Sphaeromicrolinae; 7 records in the marginal Caribbean (to 1971) of a single species; over 50 records from southern Europe and Africa referring to 6 species. Full triangle = Record from New Guinea. In addition, entocytherids are known from New Zealand and Hawaii. The New Guinea and New Zealand records are of Notoocytherinae. The Hawaii record is of *Antyocythere sinuosa* which was imported into Hawaii on the crayfish *Cambarus clarki* either from Louisiana or California.

with the cytherettids, increasing land and oceanic barriers have led to the development of the present distribution patterns.

Since restricted distributions are characteristic in the records of most entocytherids their known dispersal potentials are usually small. Nevertheless, some taxa have dispersal potentials comparable to those of cytherettids (Table 2).

EVALUATION

It is clear that the null hypothesis, that the observed distributions in the two exemplar sets are random, is difficult to sustain. Of the seven subgroups, five are clearly restricted in their regional distribution. Of the remaining two, cytherettines are ancestral among cytherettids and evidently dispersed via Tethys, while sphaeromicolines, which I believe are the ancestral group in entocytherids, also are associated closely with Tethyan environments. Non-random distributions, however, do not necessarily imply that the continents have drifted during the Cainozoic. This remains to be evaluated.

Discontinuities and dispersal potentials are opposite sides of the same distributional coin. Discontinuity data reflects breaks in distribution patterns whereas dispersal potential data usually emphasize the ranges of taxa between distribution breaks. Both aspects are influenced by environmental factors, such as sea temperatures and currents in the marine realm and aquatic microclimates, salinity, etc., on the land.

Assuming biological continuity in the exemplars, their responses to the environmental factors which have governed their dispersion have not changed much during the Cainozoic. Thus, *Neocytheretta*, which is a tropical to subtropical taxon today, probably dispersed along warm corridors throughout its history; forms with long-distance larvae always have increased their ranges by riding longshore or oceanic currents during the pelagic stages of their life cycles; entocytherid species with highly mobile hosts always disperse further than those whose host species have a limited vagility in similar terrains. Variations in the environmental factors themselves are and would have been rapidly accommodated to as long as they were within the tolerances of the animals affected by them.

The alternatives to be evaluated offer a choice between the *status quo* (continental and oceanic permanence) and Drift Theory in terms of the evident non-random distributions of organisms in the exemplar sets. Since environmental factors govern dispersion each factor may be considered as a partially correlated state in the total environmental complex. Whatever environmental factor (state) is brought to bear upon the distributions it should be accorded a higher value, on theoretical grounds, for the Drift alternative because, as the time sequence is reversed and the continents migrate back to the Mid-Cretaceous configurations required by Drift Theory (text-figs. 4 and 5), the distances between separated taxa become progressively less until dispersal potentials operate to effect distributional continuity across former barriers. There is no parallel distance change in the *status quo* alternative.

It is axiomatic that, given environmental continuity, animals disperse more readily over short distances than over long ones. On theoretical grounds, therefore, the decreasing distance (= increasing contiguity) criterion weights the values for all relevant environmental factors and tips the scale in favour of the Drift alternative.

Employing Drift Theory, biogeographic continuity/discontinuity correlates simply and well with continental continuity/discontinuity in space and time.

Thus, the Atlantic and the northern Indo-Pacific evidently were sufficiently effective barriers by the Eocene to halt the spread beyond the northern African region of loculicytherettines whereas earlier (during the Late Cretaceous and Early Palaeogene) they were unable to prevent cytherettines dispersing—from Europe to northern America and from central Asia to India (text-figs. 3–5). On the other hand, the hypothesis of continental and oceanic permanence not only ignores the massive body of physical evidence in favour of Drift but seeks more complex biogeographic explanations or else calls upon sweepstakes dispersal to explain how the many land and oceanic barriers have been successfully overcome in order to account for the observed distributions of cytheretid and entocytherid ostracodes over vast distances.

CONCLUSIONS

The distributions of two exemplar sets of mainly Cainozoic Ostracoda have been considered in relation to the alternatives of continental permanence or continental drift. The sets are Cytherettidae, a family of shallow marine free-living taxa; and Entocytheridae, a family of symbionts which are dominantly freshwater in their affinities. Entocytherids have no known fossil record, so the scanty data on the known fossil records of their host taxa were used. Cytherettids, especially cytherettine cytherettids, are common Tertiary fossils.

There are four recognized subgroups in entocytherids and three in cytherettids. Of the cytherettid subgroups, two range from the Mid Palaeogene and one, the cytherettines, ranges at least from the Upper Cretaceous. The scanty data on entocytherid host taxa as fossils is consistent with the idea that sphaeromicolines range at least from the Palaeogene but the other entocytherid subgroups may be more recent. It is suggested that cytherettines are the ancestral cytherettids and that sphaeromicolines are ancestral entocytherids, and further, that both dispersed originally via Tethys.

When the distributions of the various subgroups are plotted, discontinuities are revealed. When dispersal potentials are considered, several taxa in both sets are shown to range widely in specified time planes. Because, given environmental continuity, animals disperse over short distances more readily than over long ones (especially when barriers need to be overcome), the alternative which specifies increasing contiguity between continents as time is reversed, i.e. Drift Theory, is favoured over the alternative which specifies no change in the present continental positions.

The Cainozoic data, recognized as palimpsests of earlier distribution patterns, may be transferred to the Cretaceous map provided for this symposium. When this is done for cytherettids, discontinuities with much of the Cretaceous stratigraphy are apparent for the subgroup Argenticytherettinae which ranges from the Palaeogene, but, excepting *Neocytheretta* (Eocene–Recent), stratigraphic continuity is maintained in the subgroup Cytherettinae which ranges from the Upper Cretaceous. There is no significant result from this test for Loculicytherettinae (Palaeogene–Recent). When the same test is applied to entocytherids, marked discontinuities

persist between entocytherines, microsystirines, and notocytherines, but sphaeromicoline contiguity seems to be improved although it is noted that the Caribbean marginal records are few.

The improvement in continuity for a subgroup ranging from the Cretaceous is consistent with the greater contiguity which Drift Theory specifies for this time. Further, the failure to disperse more widely of a subgroup ranging from the Eocene is likewise consistent with the increasing separation since the Cretaceous which the Theory demands; and the relatively rapid movement of India northwards which the Theory postulates following the Cretaceous break-up of Gondwanaland is necessary to give a smooth distribution pattern to an Indo-Pacific taxon ranging from the Eocene.

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APPENDIX

The genera assigned to cytherettids, accepted in this paper, are as follows:

| | |
|--------------------------|---|
| <i>Cytheretta</i> | Müller 1894, type species <i>rubra</i> Müller 1894. |
| <i>Pseudocytheretta</i> | Cushman 1906, type species <i>edwardsi</i> Cushman 1906. |
| <i>Cylindrus</i> | Neviani 1928, type species <i>jurinei</i> Münster 1830. |
| <i>Flexus</i> | Neviani 1928, type species <i>plicata</i> Münster 1830. |
| <i>Prionocytheretta</i> | Mehes 1941, type species <i>prima</i> Mehes 1941. |
| <i>Paracytheretta</i> | Triebel 1941, type species <i>reticosa</i> Triebel 1941. |
| <i>Loculicytheretta</i> | Ruggieri 1954, type species <i>pavonia</i> Brady 1866. |
| <i>Eucytheretta</i> | Puri 1958, type species <i>plicata</i> Münster 1830. |
| <i>Protocytheretta</i> | Puri 1958, type species <i>daniana</i> Brady 1869. |
| <i>Heptaloculites</i> | Ruggieri 1963, type species <i>gortanii</i> Ruggieri 1963. |
| <i>Neocytheretta</i> | van Morkhoven 1963, type species <i>snelli</i> Kingma 1948. |
| <i>Semicytheretta</i> | Deroo 1966, type species <i>furcifera</i> Bosquet 1847. |
| <i>Acuticytheretta</i> | Deroo 1966, type species <i>infundibuliformis</i> van Veen 1935. |
| <i>Golcocythere</i> | Grundel 1968, type species <i>costanodulosa</i> Grundel 1968. |
| <i>Argenticytheretta</i> | Rossi de Garcia 1970, type species <i>miocenica</i> Rossi de Garcia 1970. |
| <i>Bensonia</i> | Rossi de Garcia 1970, type species <i>argentinensis</i> Rossi de Garcia 1966. |
| <i>Grekoiffia</i> | Rossi de Garcia 1970, type species <i>australis</i> Rossi de Garcia 1970. |

Of these genera, *Pseudocytheretta*, *Cylindrus*, and *Prionocytheretta* are commonly accepted subjective synonyms of *Cytheretta*; *Eucytheretta* is an objective synonym of *Flexus*; *Golcocythere* is a subjective synonym of *Paracytheretta*. Recently, a new genus *Palaeocytheretta* has been recorded as a *nomen nudum* from the marine Aptian-Albian of the 'Mediterranean realm' of the U.S.S.R. (Andreev and Mandelstam, in Oertli (ed.) 1971).

REFERENCES

- ANDREEV, YU. N. and MANDELSTAM, M. I. 1971. Biogeographical associations of Cretaceous ostracods in the U.S.S.R. In OERTLI, H. J. (ed.), *Paléocologie des Ostracodes Colloque Pau (1970)*, Bull. Cent. Rech. Pau, 5 suppl., 615-629. Pau.
- APOSTOLESCU, V. and MAGNÉ, J. 1956. Quelques espèces nouvelles d'ostracodes du Lutétin supérieur d'Algérie. *Cah. géol. Thoiry*, 34, 337-344.
- BARNARD, K. H. 1936. Geographical zoology. *S. Afr. geogr. J.* 20, 3-12.

- BENSON, R. H. and SYLVESTER-BRADLEY, P. C. 1971. Deep-sea ostracodes and the transformation of ocean to sea in the Tethys. In OERTLI, H. J. (ed.), *Paléoécologie des Ostracodes Colloque Pau (1970)*, *Bull. Cent. Rech. Pau*, 5 suppl., 63–91. Pau.
- BISHOP, J. A. 1967. The zoogeography of the Australian freshwater decapod Crustacea. In WEATHERLEY, A. H. (ed.), *Australian Inland Waters and their Fauna: Eleven Studies*, 107–122. Canberra.
- BRADY, G. S. 1866. On new or imperfectly known species of marine Ostracoda. *Trans. zool. Soc. Lond.* 5, 359–393.
- CARBONNEL, G. 1969. Les Ostracodes du Miocène Rhodanien. *Docums Lab. Géol. Sci. Lyon*, 32, 1–469.
- DANIELOPOL, D. L. 1971. Quelques remarques sur le peuplement ostracodologique des eaux douces souterraines d'Europe. In OERTLI, H. J. (ed.), *Paléoécologie des Ostracodes Colloque Pau (1970)*, *Bull. Cent. Rech. Pau*, 5 suppl., 179–190. Pau.
- (in press). Definition de la tribu Hartiellini nov. et remarques sur la poecilogenie de *Hartiella dudichi* (Ostracoda, Entocytheridae, Sphaeromicolinae). *Trav. Inst. Spéol. Emile Racovitza*, 10.
- DEROO, G. 1966. Cytheracea (Ostracodes) du Maastrichtien de Maastricht (Pays-Bas) et des régions voisines; résultats stratigraphiques et paléontologiques de leur étude. *Meded. géol. Sticht.*, Ser. C, 2, 1–197, 1–42.
- DUCASSE, O. 1969. Biozonation de l'Éocène nord-aquitain. *Bull. Soc. géol. Fr.* 11, 491–501.
- EAGAR, S. H. 1971. A check list of the Ostracoda of New Zealand. *J. roy. Soc. N.Z.* 1, 53–64.
- GLAESSNER, M. F. 1969. *Treatise on invertebrate paleontology* (ed. MOORE, R. C.), Part R, *Arthropoda* 4(2), R399–R651. Lawrence.
- HART, C. W., JR. 1962. A revision of the ostracods of the family Entocytheridae. *Proc. Acad. nat. Sci. Philad.* 114, 121–147.
- and HART, D. G. 1967. The entocytherid ostracods of Australia. *Ibid.* 119, 1–51.
- — 1969. Evolutionary trends in the ostracod family Entocytheridae, with notes on the distributional patterns in the Southern Appalachians. In HOLT, P. C. (ed.), *The Distributional History of the Biota of the Southern Appalachians, Part I: Invertebrates*, 179–190. Blacksburg.
- NAIR, N. B., and HART, D. G. 1967. A new ostracod (Ostracoda: Entocytheridae) commensal on a wood-boring marine isopod from India. *Notul. Nat.* 409, 11 pp.
- HESSLER, R. R. 1969. *Treatise on invertebrate paleontology* (ed. MOORE, R. C.), Part R, *Arthropoda* 4(1), R360–R393. Lawrence.
- HOBBS, H. H., JR. 1971. The entocytherid ostracods of Mexico and Cuba. *Smithson. Contr. Zool.* 81, 55 pp.
- and HOBBS, H. H., III 1970. New entocytherid ostracods with a key to genera of the subfamily Entocytherinae. *Ibid.* 47, 19 pp.
- HOWE, H. V. et al. 1961. *Treatise of invertebrate paleontology* (ed. MOORE, R. C.), Part Q, *Arthropoda* 3, Q322–Q330. Lawrence.
- KASHEVAROVA, N. P., MANDELSTAM, M. I., and SCHNEIDER, G. F. 1960. *Basic palaeontology* (ed. ORLOV, YU. A.), *Trilobita and Crustacea*, 8, 365–421. Moscow. (In Russian.)
- KINGMA, J. TH. 1948. *Contributions to the knowledge of the young Caenozoic Ostracods from the Malayan Region*, 106 pp. Utrecht.
- LUBIMOVA, P. S., GUHA, D. K., and MOHAN, M. 1960. On Ostracoda of Jurassic and Tertiary deposits from Kutch and Rajasthan (Jaisalmer), India. *Bull. geol. min. metall. Soc. India*, 22, 1–61.
- MCKENZIE, K. G. 1967. The distribution of Caenozoic marine Ostracoda from the Gulf of Mexico to Australasia. In ADAMS, C. G. and AGER, D. V. (eds.), *Aspects of Tethyan biogeography, Syst. Assoc. Publ.* 7, 219–238.
- 1971a. Palaeozoogeography of freshwater Ostracoda. In OERTLI, H. J. (ed.), *Paléoécologie des Ostracodes Colloque Pau (1970)*, *Bull. Cent. Rech. Pau*, 5 suppl., 207–237. Pau.
- 1971b. Remarks. In STODDART, D. R. and YONGE, SIR M. (eds.), *Regional variation in Indian Ocean coral reefs, Symp. zool. Soc. Lond.* 28, 543–547. London.
- and HUSSAINY, S. U. 1968. Relevance of a freshwater cytherid (Crustacea, Ostracoda) to the continental drift hypothesis. *Nature, London.* 220, 806–808.
- MESERVEY, R. 1971. The coastline fit of Africa and South America. *Palaeogeogr. Palaeoclimat. Palaeoecol.* 9, 233–243.
- MORKHOVEN, F. P. C. M. VAN 1962. *Post-palaeozoic Ostracoda*, 1, 204 pp. Amsterdam.
- 1963. *Post-palaeozoic Ostracoda*, 2, 478 pp. Amsterdam.
- MORONI, A. 1967. Ostracodi delle risaie italiane: sistematica, ecologia, distribuzione geografica. *Studium Parmense*, 79 pp. (preprint).

- NICOL, D. 1969. The number of living species of molluscs. *Syst. Zool.* **18**, 251-254.
- OERTLI, H. J. 1963. *Faunes d'Ostracodes du Mésozoïque de France*, 57 pp., 90 pls. Leiden.
- (ed.) 1971. *Paléocologie des Ostracodes Colloque Pau (1970)*, *Bull. Cent. Rech. Pau*, **5** suppl., 953 pp. Pau.
- POR, F. D. 1971. One hundred years of Suez Canal—a century of Lessepsian migration: retrospect and viewpoints. *Syst. Zool.* **20**, 138-159.
- ROSSI DE GARCIA, E. 1966. Contribucion al conocimiento de los Ostracodos de la Argentina 1. Formacion Entre Rios, de Victoria Provincia de Entre Rios. *Revta Asoc. geol. Argent.* **21**, 194-208.
- 1969. Algunos Ostracodos del Enterriense de Parana (Provincia de Entre Rios, Republica Argentina). *Ibid.* **24**, 276-280.
- 1970. Amendment a la sub-famille Cytherettinae Triebel 1952 Famille Cytherettidae (Triebel) Howe 1961. In SAID, R. et al. (eds.), *Proceedings of the Third African Micropaleontological Colloquium*, 217-223. Cairo.
- RUGGIERI, G. 1954. Iconografia degli Ostracodi marini del Pliocene e del Pleistocene italiani. Parte 2^a. *Atti Soc. ital. Sci. nat.* **93**, 561-575.
- 1963. *Heptaloculites gortanii* n. gen., n. sp., ostracode con loculi dell'Eocene della Sicilia. *G. Geol.* **31**, 1-5.
- SCHORNIKOV, E. I. 1969. Subclass Ostracoda. In KISELEVA, M. I. et al. (eds.), *Keys to the fauna of the Black and Azov Seas*, **2**, *Free-living invertebrates, Crustacea*, 163-260. Kiev. (In Russian.)
- SMITH, A. G. and HALLAM, A. 1970. The fit of the southern continents. *Nature, Lond.* **225**, 139-144.
- STRAELEN, V. VAN 1931. Crustacea Eumalacostraca. In QUENSTEDT, W. (ed.), *Fossilium Catalogus 1: Animalia Pars 48*, 98 pp. Berlin.
- TRIEBEL, E. and MALZ, H. 1969. Die Ostracoden der deutschen Kreide, 4: *Paracytheretta calkeri* und ähnliche Arten aus dem Santon. *Senckenberg. leth.* **50**, 433-445.
- VALENTINE, J. W. 1971. Plate tectonics and shallow marine diversity and endemism, an actualistic model. *Syst. Zool.* **20**, 253-264.
- VANDEL, A. 1940. La parthénogénèse géographique. IV. Polyploidie et distribution géographique. *Bull. Biol. Fr.-Belg.* **74**, 94-100.

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