The origin of the modern tropical West African marine Ostracod Fauna, with a description of the Ruggieriini n. tribe

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ABSTRACT – Many species and genera found today along the West African coast and shelf stretching from the Niger Delta northwards to Mauritania have their origins in a great faunal renewal that took place in the late Oligocene and early Miocene. The hemicytherids are absent from the Miocene, giving the faunas a very different appearance from contemporaneous North African, American, and Mediterranean faunas. Later recruitment to the West African faunas came from the Americas and the northern warm-water Atlantic during the Pliocene and Quaternary, including the hemicytherids. A new tribe of the Trachyleberididae, Ruggieriini, is described, with new genera Tetraruggieria, Afroruggieria, Nigeriruggieria, *and* Leoniruggieria.

RIASSUNTO – [Origine delle moderne faune ad Ostracodi marini dell'Africa occidentale tropicale, con descrizione della nuova tribù Ruggieriini] *– Numerosi generi e specie di Ostracodi che oggi si trovano lungo le coste e sulle piattaforme continentali dell'Africa occidentale, dal delta del Niger fino alla Mauritania, traggono origine da un grande rinnovamento faunistico che avvenne tra l'Oligocene superiore ed il Miocene inferiore. Gli hemicytheridi mancavano durante il Miocene, dando alle suddette faune un aspetto marcatamente diverso da quello delle faune contemporanee del Nord Africa, dell'America e del Mediterraneo. Soltanto più tardi, nel Pliocene-Quaternario, arrivarono in Africa occidentale forme provenienti dalle Americhe e dalle acque calde dell'Atlantico settentrionale, tra le quali gli hemicytheridi. Viene qui descritta la nuova tribù Ruggieriini, appartenente ai Trachyleberididae, alla quale sono ascritti i nuovi generi* Tetraruggieria, Afroruggieria, Nigeriruggieria *e* Leoniruggieria.

INTRODUCTION

The origins and distribution of modern West African ostracods are best understood by considering their geological history. Late Oligocene and Miocene faunas from the region can be used to differentiate genera of West African origin from immigrants. In this study only the infralittoral and shallow circalittoral environments of the equatorial realm of West Africa are considered. No attempt is made to analyse ecological niches within this belt, aspects of which have been studied in the works cited below. The ostracods were largely unaffected by the climatic fluctuations of the Pleistocene, so, apart from shoreline fluctuations associated with sea level change, the complications seen in higher latitude faunas is largely absent. The area considered is shown in Text-fig. 1.

These shelf faunas live in water with a fairly constant surface temperature of about 20-26°C. Recent ostracod faunas from the Congo River northwards to Mauritania have been documented in recent years by Babinot & Kouyoumonzakis (the Congo River of northern Angola, 1986), Omatsola (Nigeria; 1969, 1970a, b, 1971, 1972), Masoli (Ivory Coast, 1975), Keen (Sierra Leone, 1972), Witte (Gambia and Senegal, 1985, 1986a, 1993) Carbonnel (estuarine ostracods of Senegal and the Gambia, 1982, 1986b), Carbonel *et al.* (Senegal, 1983) and Rosenfeld & Bein (Mauritania, 1978). The distribution of the genera *Havanardia*, *Ruggieria*, and *Loculicytheretta* on the west

African shelf were described respectively by Keij (1973), Keen (1975) and Witte (1986b). Other pertinent papers are Reyment (1963, 1969), Reyment & Van Valen (1969), and Peypouquet (1977). It should be noted that most of this work has been carried out by workers with a palaeontological background, so that all of the studies are based on hard part morphology, with no studies of soft part anatomy. Older works by Brady (1880) and Scott (1894) include areas discussed in this paper, while southwards to Angola and Namibia, faunas have been described by Klie (1940), Hartmann (1974), and Dingle and co-workers (e.g. 1992, 1993). These studies now give us sufficient data to try to define the characteristics of the West African ostracod fauna. The common and abundant genera are obviously important, but genera of second rank, commonly present but not dominant, are equally important in defining a fauna.

Wood & Whatley (1994) have defined ostracod provinces for the region based on the latitudinal distribution of genera (Text-figs 2, 3). The reader is referred to this work for a discussion of the genera and relationship to water masses, and for the extensive list of generic distributions. Some of the genera concerned have no, or a very poor, fossil record, so are not dealt with here, as this present work is mainly concerned with those genera living today, and with a Neogene or older fossil record. Wood and Whatley recognised five provinces for the area lying between the equator and 20°N, which correspond with the northern half
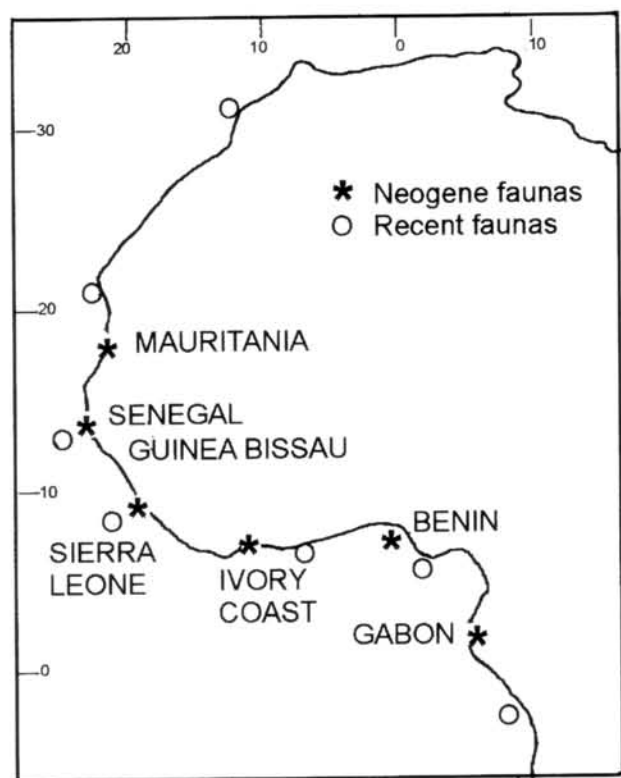
Text-fig. 1 - Map showing the positions of Neogene and important Recent ostracod studies.

of the Equatorial Realm. Our knowledge of Holocene ostracod faunas from this area is very patchy, with detailed systematic studies of living ostracods from only two areas, the Niger Delta in the south (publications of Omatsola and Reyment), and Senegal and the Gambia in the north (Witte, 1993). The major divide within these shallow marine climatic zones lies within the Mauritanian Province, which delimits the northern edge of the Equatorial Realm (Wood & Whatley, 1994). This more or less defines the spread of faunas considered in this study, i.e. the area from Gabon to southern Mauritania. The ostracod faunas from the Moroccan shelf (Llano, 1981a, b) have more in common with the Mediterranean and northern warm temperate Atlantic ostracods, lacking the characteristic genera of the warmer southern areas. However, the use of genera has its shortcomings, as many of those used by Wood and Whatley are present in other areas of the world. We do not have enough information yet to consider the distribution of species. This paucity of information may mean that the finer divisions indicated by Wood and Whatley are due more to localised facies distributions rather than provincial differences.

There have been a number of publications on West African Neogene faunas which give an understanding of the main features of the ostracods: Van den Bold (1966) on the Neogene of Gabon, Babinot (1981) on

the late Cretaceous to Pliocene of the Ivory Coast, Carbonnel (1986) on the Palaeocene-Miocene of Senegal and Guinea-Bissau, Carbonnel (1988a, b) on the late Cretaceous-Miocene of Mauritania, Keen (1975, 1994, 1995, 1996) on the late Miocene of Sierra Leone, and Carbonnel *et al.* (1996) on the late Oligocene of Benin.

OSTRACOD GENERA

One of the problems faced by ostracod workers is a working definition of the genus. This is especially difficult in areas such as West Africa, where ostracods have been studied only fairly recently, and by relatively few workers. This is in contrast to areas such as the Mediterranean where they have been studied by many researchers over a long period of time. There is a tendency in such situations to use well-known generic names, which can lead to misconceptions about geographical and stratigraphical distributions. For example, many of the West African ostracods have relatives in other parts of the world, especially in the Mediterranean, so the choice of using "Mediterranean" names, or creating new names, will have a great effect on the perceived relationships of the faunas. There is also the difficulty of distinguishing between true phylogenetic relationships and similarities based on homeomorphy. This can create a tendency to think of the Mediterranean as the original home of the ostracods, with migration to other areas. This study will suggest that many well-known Mediterranean genera in fact originated in the tropical and subtropical Atlantic and migrated into the Mediterranean.

The use of a name of a taxon makes a statement, implying facts about its distribution and possibly its evolution. Most ostracod workers accept the present consensus on species definition, but the genus is more difficult. We have been reluctant to make use of the rank of subgenus, and if it is used it will almost certainly be subsequently elevated to the rank of genus. The genus has become the workhorse of biogeography and diversity studies, so what are the criteria for defining them? The following points should be considered: the genus, and subgenus, should be monophyletic, with all species within the genus having a common ancestor. The genus, or subgenus, should have morphological characters that are unique to it, and separate it from its sister groups, although in the case of ostracods we often deal in terms of unique character groupings. Many ostracod workers are palaeontologists, dealing with species lineages and stratigraphical distribution, which inevitably feeds into taxonomic concepts. Most workers would agree that there should be no major stratigraphical discontinuities in the range of a genus. As an example from the West African ostracods, Keij (1973) has argued for the separation of living *Havanardia* Pokorny, 1968, from somewhat similar forms found only in the Triassic. Geographically separated distributions are more diffi-
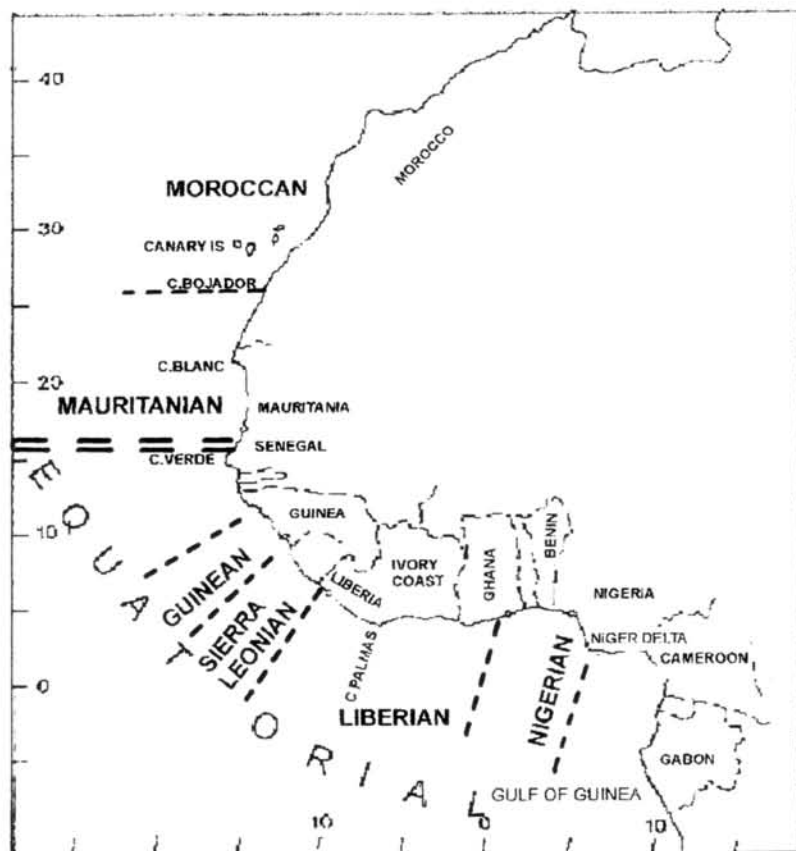
Text-fig. 2 - West African ostracod provinces, adapted from Wood & Whatley (1994).

cult to deal with, and this is especially common with circumtropical genera. Intuitively, disjunct distributions suggest isolation from each other and therefore taxonomic differentiation, the greater the distance the greater the likelihood that we are dealing with different genera. However there is always the possibility of new information leading to the 'closing of the gaps', leading to a major revision of ideas. Finally, there is consensus. Described genera need to be accepted by peer groups for any legitimacy. Ideas of what constitutes a genus change through time, although at any one time there may be broad agreement.
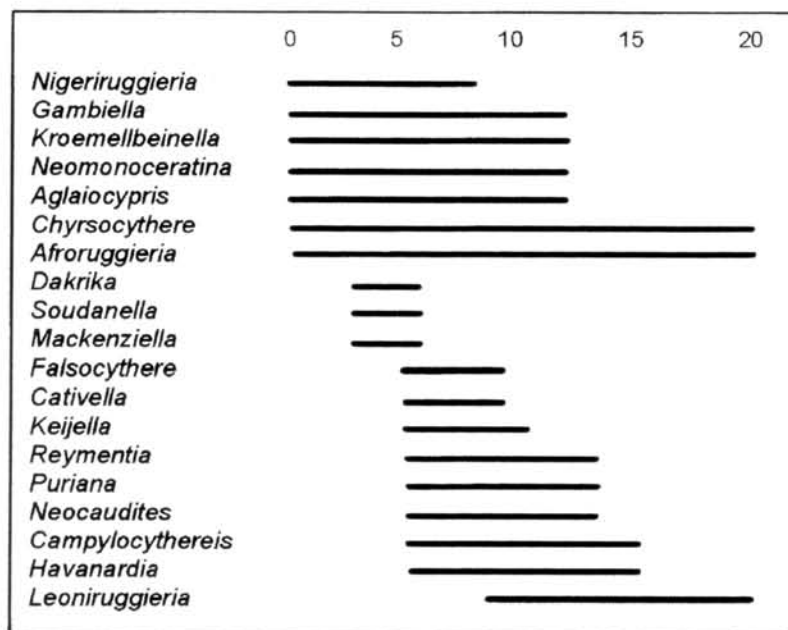
WEST AFRICAN MARINE OSTRACOD GENERA

In this section comments are made on the geographical distribution, stratigraphical record, and biogeographical significance of some important taxa.

CYTHERELLIDS AND BAIRDIIDS

The first group to be considered is the cytherellids, which has not been described in any detail from west Africa. However, species of *Cytherella* Jones, 1849 are common, occurring from brackish coastal lagoons (Omatsola, 1970) through coastal environments to the shelf edge and into deeper water. The shelf of Sierra

Leone has yielded at least four species, one of which may be referable to *Cytherelloidea* Alexander, 1929, a genus that seems to be mostly absent from tropical west Africa, although it is present off southern Africa (Hartmann, 1974; Dingle 1993). Smooth and punctate species are also present in the late Oligocene and Miocene but are so far undescribed. Cytherellids have been present in the region since the Cretaceous, but it is impossible with the current state of knowledge to know whether any indigenous lineages are present, or how important immigration has been. This is also true of the Bairdiidae, which has formed an important part of the fauna since the Cretaceous, and is well represented, but undescribed, in late Oligocene and Miocene sediments. Most material seems to be referable to *Bairdoppilata* Coryell, Sample & Fields, 1935. Keen (1972) showed that on the shelf of Sierra Leone, bairdiids reach their greatest concentration on sands and shelly sands towards the edge of the continental shelf in water between 50 and 100 m deep, where they can form up to 30% of the ostracod fauna. *Paranesidea multiforma* Witte, 1993 was described from beach sediments of Senegal and Gambia, and has also been observed by the present author from similar environments in Sierra Leone. Witte (1993) also described a new species of *Triebelina*, *T. intermedia* Witte, 1993, again from beach sediments of Senegal and Gambia.

Text-fig. 3 - Latitudinal range of selected West African ostracod genera; figures refer to degrees north of the equator.

This species shows some resemblance to *Havanardia*, the subject of a detailed study by Keij (1974), who described three new species from Nigeria, Ghana, and Sierra Leone, occurring from the beach to water depths of 80 m. *Havanardia* had been regarded as a Caribbean genus, so its widespread occurrence off of West Africa suggests links between the two regions. No fossils of the genus are known from West Africa, but Keij (1976) described Pliocene specimens from Jamaica; Jellinek (1989) extended the range of the genus to East Africa and Madagascar, and further specimens have been recorded from India and the Miocene of Midway Atoll (see Malz & Lord, 1986). The genus appears to have a circumtropical distribution, with an unknown origin.

BUNTONIINAE APOSTOLESCU, 1961

The subfamily Buntoniinae has been an important component of ostracod faunas in West Africa since the beginning of the Palaeogene. Carbonnel (1986) refers to this early Palaeocene event as the 'Explosion of the Buntoniinae', regarding West Africa as its cradle of origin. During this early period in their evolution, the buntoniids were especially abundant in shallow marine environments, forming a major part of the Trans-Saharan fauna. They also formed a major part of the early Tertiary faunas of South America (Bertels, 1976; van den Bold, 1977). Van den Bold discussed their evolution and migration, concluding that they originated in western Africa and spread to northern South America in the late Cretaceous, from where they migrated northwards to central America during the early Palaeocene reaching north America

by the Eocene; they only reached southern South America in the Miocene. *Basslerites* Howe, 1937, which first appeared during the Eocene in West Africa, took the same path, but later, in the Miocene (van den Bold, 1977). Today, *Buntonia* is more common in deeper offshore waters. Carbonnel described the huge amount of variation present in shape and ornament during this early phase, a character that was lost during the Eocene and Neogene. It is difficult to state the exact number of species present in the Palaeocene and Eocene, but there must be in excess of fifty; Carbonnel (1986a) lists 34 species of *Buntonia* from the Palaeogene of west Africa. Further difficulties are presented in determining the exact generic status of many of the species described, with the probability of several new genera in the waiting. It is noticeable that it was from this region that Apostolescu (1961) decided to create the new subfamily, with the description of 28 species from the late Eocene and early Tertiary of West Africa. The Buntoniinae were distinguished from the Trachyleberidinae on the basis of carapace outline, with a pyriform to subtriangular outline quite different from the quadrate outline of the Trachyleberidinae, as is the ovoid to subovoid dorsal outline; the central muscle scars are not in a pit as in the Trachyleberidinae, and there is no external subcentral tubercle. The genera commonly found in west Africa are *Buntonia* Howe, 1935, *Isobuntonia* Apostolescu, 1961, *Protobuntonia* Grekoff, 1953, *Soudanella* Apostolescu, 1961, and *Togoina* Apostolescu, 1961. *Benisymmetricythere* Carbonnel, de Klatz, Horvath, Lang & Oyede, 1996 is so far only recorded from the late Oligocene of Benin (Carbonnel *et al.*, 1996). Only *Buntonia* and *Soudanella* have survived until the present in the west

African faunas and can therefore be regarded as relicts of a much richer past diversity. *Buntonia* is not common in Neogene faunas. Van den Bold (1966) also described *Quasibuntonia* Ruggieri, 1958 from late Miocene deep-water sediments of Gabon. The commonest living species from the Niger Delta area was described as a species of *Buntonia*, *B. olokundudui* Reyment & Van Valen, 1969. This species demonstrates the taxonomic problems, as it almost certainly is not a *Buntonia* as normally understood; Babinot (1981), who found it as a fossil in the Pliocene of offshore Ivory Coast, suggested it might belong to *Ruggieria*; it also has some resemblance to *Keijella*. Interestingly, Dingle (1993) observed that while *Buntonia* is virtually absent in Cretaceous and Palaeogene rocks of southern Africa, it was relatively diverse and moderately abundant during the Quaternary (and Recent). *Isobuntonia* Apostolescu, 1961 and *Soudanella* Apostolescu, 1961 are more typical of the west African late Cretaceous and early Palaeogene, and are known from North Africa. *Soudanella* and *Togoina* were present in the Palaeogene and Neogene of Argentina (Bertels, 1976), the presence of these ostracods on the two sides of the Atlantic originating from the time when the Atlantic Ocean was much narrower than today. *Soudanella* and *Isobuntonia* are representative of the indigenous fauna. *Soudanella*, as already mentioned, is still present as an important component of modern faunas, but *Isobuntonia* is not known from strata younger than the Oligocene.

RUGGIERIA-LIKE OSTRACODS

Ruggieria Keij, 1957 is one of the most characteristic genera of the West African shelf, typically occurring at water depths of 20-70 m. Nine living species have been recorded from the region, together with seven species from the late Oligocene-Miocene (Van den Bold, 1966; Omatsola, 1972; Keen, 1975, 1996; Babinot, 1981; Carbonnel, 1986, 1988, 1996). The oldest species has been recorded from the Eocene of Senegal-Bissau (Carbonnel, 1986a, 1988). A new tribe, Ruggieriini is established for this group of species in the systematic section of this paper, where a full discussion can be found.

DAKRIKA AND OTHERS

The taxon which includes *Carinovalva* Sissingh, 1973 and *Dakrika* Omatsola, 1972 has had a mixed history in the Mediterranean region where three generic names have been available: *Lixouria* Uliczny, 1969, *Incongruellina* Ruggieri, 1958, and *Carinovalva*. Uliczny designated *Cythereis unicostulata* Kuiper, 1918 as type species of *Lixouria*, which was subsequently illustrated by Sissingh (1973) and Malz (1981). They show this species to be a member of the genus *Cytheretta*; Malz clearly states that *Lixouria* is a junior synonym of *Cytheretta*, while Sissingh states that it is

related to the Cytherettinae. *Incongruellina* differs from *Carinovalva* in having prominent anterior, ventral, and posterior vestibules, distinct asymmetry of the carapace, posterior marginal spines only on the right valve, and a well developed accommodation groove in the left valve. The taxon being considered here is therefore that of Sissingh, namely *Carinovalva*. However, at the same time as Sissingh was preparing his work, Omatsola (1972) described a new genus, *Dakrika*, from the Holocene of the Niger Delta, which may be the same taxon as *Carinovalva*. Carbonnel (1986) regarded *Dakrika* and *Carinovalva* to be synonymous with the genus *Dahomeya* Apostolescu, 1961, a West African genus from the Palaeocene and Eocene. These three genera are indeed very similar, all have a larger left valve but appear fairly symmetrical in dorsal view, all have anterior and posterior marginal spines on both valves, an eye tubercle, similar hinge with no accommodation groove, and similar simple marginal pore canals. There are differences however; *Dahomeya* has a more curved dorsal margin than the straight margins of *Dakrika* and *Carinovalva*, has a prominent vestibule, unlike the other two, and has a single ovoid frontal muscle scar where the other two have a "u"-shaped frontal muscle scar. *Dakrika* species have coarse pitting on the surface, whereas *Carinovalva* tend to be smooth, or have fine pitting (Pl. 1, figs 21, 23). The ventral swelling and associated ridge ends in a posterior spine in most species of *Carinovalva*, and in the type species of *Dakrika*; *Dahomeya* species have a very weakly defined ventral ridge. It is not clear whether this feature is important in defining species or in defining genera. Babinot (1981) placed four Neogene species into *Dakrika*, including forms lacking a pronounced ventral ridge. Keen (1996) described the new species *Carinovalva fourahensis* which has a "centro-ventral swelling and a suggestion of a weak ventral ridge, especially in the right valve. There is no postero-ventral spine developed in association with the ventral swelling" (page 309). As with previous authors, the generic assignment of this species presented difficulties; *Dahomeya* was rejected on account of its vestibule and frontal muscle scar; the choice between *Carinovalva* and *Dakrika* was made on the basis of the lack of the strong postero-ventral spine of *Dakrika*. So whether these two genera are synonymous depends upon the importance of the ventral ridge. The type species of *Carinovalva*, *Incongruellina* (*Lixouria*) *keiji* Sissingh, 1972 has a distinct ventrolateral keel, which may have a posteriorly or laterally directed spine; in the type species this ventral swelling is almost alar-like, as it also is in the species *C. aquila* (Ruggieri, 1972). The four other species placed into his new genus (without illustration) by Sissingh all have a strong swelling and posterior spine. However, *Carinovalva carinata* (Moyes, 1965), regarded as a junior synonym of *Carinovalva testudo* (Namias, 1900) by Sissingh, has a ventral ridge rather than a swelling, and some members of this species group lack the posterior

spine. Sissingh also listed the median hinge element of *Carinovalva* as smooth or crenulated; *C. fourahensis* has a median element that is strongly crenulated at the posterior, becoming almost smooth towards the anterior. In conclusion, it does appear that there is a group of ostracods with much in common, and where the ventral ridge and swelling encompasses a range of morphologies. There is a difference in size. *Carinovalva* species are mostly within the range of 740-950 μm, *Dakrika* 600-650 μm. It is not clear how important this size difference is; it seems to have been present for some 30 million years, suggesting two quite different gene pools. At the moment it seems sensible to retain the two genera: *Dakrika* ranges from the late Oligocene through to the Recent in West Africa, while *Carinovalva* is found in the Oligocene to early Pleistocene of the Mediterranean area, and Miocene-Pliocene in the eastern Atlantic of France and Iberia. Both reached their peak of diversity during the Miocene. It is worth noting that Malz (1981), when presented with a similar problem decided to create a new genus, *Yajimaina*, for a group of Pliocene-Recent species with a similar morphology to *Carinovalva* from Taiwan and Japan, postulating geographical separation of the two genera during migration along the shorelines of Tethys during the Miocene. This idea could be extended to earlier migration from West Africa northwards to the Tethys. The only living species, *D. robusta* Omatsola, 1972, is recorded from fine grained sediments at depths of between 30 and 80 m, water temperature 21°C, from the Niger Delta of Nigeria.

CHRYSOCYTHERE RUGGIERI, 1962

Chrysocythere is a very typical West African genus, and is common today on the west African shelf. According to Dingle (1993), it is found widely in Eocene to Recent sediments from west and southern Africa. It appeared in the mid Miocene of the Mediterranean, and especially typifies the late Miocene. At least six species are found living on the shelf of southern and west Africa today; the most widely distributed living species is *C. faviostriata* (Brady, 1870), which occurs from Nigeria to Senegal, and is one of the most abundant ostracods in shelf faunas. Omatsola (1972) studied its distribution on the Niger Delta, and distinguished two subspecies. These were absent from fine grained substrates. Witte (1993) suggested these two subspecies might be polymorphs rather than subspecies; Tolder-Farmer (unpublished thesis, 1985) studied the morphological variation of this species in the coastal mangrove areas of Senegal. This species is also recorded from the late Miocene of Gabon (Van den Bold, 1966), the early Miocene and Pliocene of the Ivory Coast (Babinot, 1986) and the late Miocene of Senegal (Carbonnel, 1986). *C. boldi* Omatsola 1972 is very similar to *C. faviostriata*. Both of these species differ considerably from the type species of *Chryso-*

cythere, *C. cataphracta* Ruggieri, 1962; in lateral outline they are more tapered towards the posterior, with a more curved dorsal margin; the ornamentation is different, with much weaker longitudinal ridges and correspondingly stronger reticulation between the ridges; and they are noticeably smaller than typical *Chrysocythere*, females being 520-700 μm compared with 720-900 μm. It is most likely that these species belong to an undescribed genus. However, species similar to *C. cataphracta* do occur in West Africa (*C. cataphracta* Carbonnel, 1996, *non* Ruggieri, 1962, late Oligocene and Miocene; *C. oulofi* Carbonnel, 1986, mid Miocene; *C. buncensis* Keen, 1995, late Miocene). The living species *C. ornata* has been studied by Bertholon & Carbonel (1991, 1996) from the shelf of Gabon southwards to the mouth of the Congo River; they recognised nine distinct morphotypes based on the development of the longitudinal ridges and the intercostals reticulation, which they believed to be related to ontogenetic development and the environment.

In conclusion, it seems that *Chrysocythere* appeared in the Eocene of west and southern Africa, underwent an evolutionary radiation in the late Oligocene and Miocene, spreading to the Mediterranean area in the mid Miocene. It appears to be at its greatest diversity today along the western coasts of Africa.

OTHER TRACHYLEBERIDS

Keijella Ruggieri, 1967, is recorded in West Africa from the Oligocene (Carbonnel *et al.*, 1996), Miocene (Babinot, 1981; Carbonnel, 1986; Keen, 1996), and Holocene (Witte, 1993). However there are sufficient differences in the hinge and ornamentation to create doubt about the generic assignment of the species.

According to Witte (1993), species of *Neocaudites* Puri, 1960 are characteristic minor elements of late Miocene to Recent faunas of the East Coast of America and the Caribbean. It is also found living today on the west African coast, where two endemic species are known from Nigeria (Omatsola, 1972), a third indigenous species is found along the coast of Senegal and the Gambia, and a fourth species, the eastern American coastal *N. atlantica* Cronin, 1979, has been recorded by Witte from West Africa. Witte (1993) therefore regarded the genus as an Atlantic taxon. The earliest definite species from West Africa is from the late Miocene of Sierra Leone (Keen, 1996).

Falsocythere Ruggieri, 1972 is often confused with *Neocaudites*, as any casual look at synonymy lists will reveal. The main difference appears to be the greater number of radial pore canals in *Neocaudites*. The genus has a circumtropical distribution today from the Caribbean, Atlantic, Mediterranean, Indian and Pacific Oceans. Fossil occurrences in the Miocene suggest a Tethyan origin. It was already present in the Caribbean, West Africa, the Mediterranean, and Pacific Ocean. There is also confusion over the type species, *Occultoythereis maccagnoi* Ciampo, 1971; Witte

(1993) believes this to be a junior synonym of *F. terryi* (Holden, 1967). Witte records this species from the Congo through to Senegal in West Africa, and in the Mediterranean, Red Sea, and Indo-west Pacific. The oldest definite species known from West Africa was figured by Keen (1996) from the late Miocene of Sierra Leone, but a possible earlier species has been figured by Carbonnel *et al.*, 1996, from the late Oligocene of Benin as *Costa* aff. sp. 3 Salahi, 1966. This resembles Miocene specimens referred to *F. maccagnoi*, although this may be superficial because it is described as having a wide anterior vestibule. *Neocytherideis*? aff. *nigeriensis* Omatsola, 1972 appears to have the characteristics of the genus. Thus, this genus may have originated in the late Palaeogene of western Tethys and West Africa, and spread to the eastern USA and the Caribbean. Mid Miocene examples are known from Libya and Egypt, described as *Falsocythere maccagnoi*.

Puriana Coryell & Fields, 1953 is found today along the west African shelf from Nigeria to Guinea Bissau. Omatsola recorded six species from the western Niger Delta, where it is one of the most abundant ostracods, but appears to be restricted to sandy substrates at about 20 m depth; it is found as a major component of the fauna on a similar substrate on the shelf of Sierra Leone at depths of generally less than 30 m. It is found fossil as the species *Puriana mandinguie* Carbonnel 1986 in the Serravallian/Tortonian of Senegal, the Tortonian of Sierra Leone (Keen, 1996), and *Puriana interrasilis* Van den Bold, 1966 from the post Miocene (Pliocene?) of Gabon. This latter species may still be living in the Niger Delta (Omatsola, 1972). *Puriana* is therefore one of the important components of Miocene to Recent ostracods from tropical West Africa. It is also well know from the Caribbean, Central America, the Gulf coast, and the eastern seaboard of the USA as far north as the Carolinas, and is recorded from the Miocene to Recent.

KROEMMELBEINELLA MOSTAFAWI, 1984 AND THE CYTHERIDEINAE SARS, 1925

Kroemmelbeinella was described by Mostafawi (1984) from the late Pliocene of the island of Kos, Greece, and subsequently from other Pliocene and Recent localities around the Mediterranean. It is present in the Tortonian of the Guadalquivir Basin of southern Spain, which opens into the Atlantic, as well as the late Miocene of Sierra Leone and Senegal, and the Pliocene of Gabon (Keen, 1996). The oldest species referable to the genus appears to be *Eocytheropteron vandenboldi* Carbonnel, 1996, from the late Oligocene of Benin, although this is a very small species (length of 260 μm). Therefore, its area of origination could well be the eastern Atlantic rather than the Mediterranean. It is certainly a more important component of the Miocene-Recent faunas of West Africa than it is of comparable faunas in the Mediterranean. Witte (1986, 1993), who considers it to be a subgenus of

Perissocytheridea Stephenson, 1932, has described several species from the Recent of West Africa, and given a detailed account of the taxon. *Kroemmelbeinella* is a common component of very shallow nearshore and intertidal environments. One of its distinguishing features is having a larger right valve, with a reversed merodont hinge, i.e. the terminal teeth are in the left valve, although Witte (1993) has described one species where this is not the case. Sexual dimorphism is pronounced, with much longer males. Lateral outline is characterised by a pointed caudal process. The shape of this ostracod distinguishes it from *Perissocytheridea*, and I follow Mostafawi in regarding it as a full genus. This has the merit of bringing out more clearly biogeographical relationships.

The Cytherideinae Sars, 1925, have a poor fossil record in West Africa. Today, two species of *Cyprideis* Jones, 1857 live in coastal areas from Nigeria through Sierra Leone to Senegal (Omatsola, 1970a; Keen, 1972; Witte, 1993). *Miocyprideis leybarensis* Carbonnel, 1986 has been described from coastal estuaries of Senegal (Carbonnel, 1982, 1986; Witte, 1993). Keen (1996) mentions rare *Cytheridea* Bosquet, 1852 in Tortonian sediments but otherwise this genus is absent from west Africa. Carbonnel (1986) described *Annomocytheridea tropicalis* sp. nov. from the Serravallian/Tortonian of Senegal, and Keen (1996) figured *Annomocytheridea* cf. *tropicalis* from the Tortonian of Sierra Leone; this genus had only been recorded from North America prior to this. Carbonnel published a paper (1989a) on the brackish water ostracods from the Early Eocene of Senegal, in which he described a new species of the mainly European genus *Neocyprideis*, *N. priani* n. sp., together with a discussion of *Ouachitaia guiersensis* Carbonnel, 1989. This latter genus was only known from the Palaeocene-Eocene of the Caribbean and North America, while *Neocyprideis* is known from the Cretaceous-Miocene. Carbonnel argued that these two genera, only present in the early Eocene lignites of Senegal, migrated to the region via ocean currents in the case of *Ouachitaia*, and migratory birds in the case of *Neocyprideis*. While not directly applicable to the modern fauna, this suggests different ways in which migration could have occurred. Unfortunately, the history of brackish water ostracods is very fragmentary for West Africa.

NEOMONOCERATINA KINGMA, 1948

Neomonoceratina has had a circumtropical distribution since Miocene times. It occurs in the Miocene of west Africa: *N. bignonaeensis* Carbonnel, 1986 from the Serravallian/Tortonian of Senegal, *Neomonoceratina* sp. Keen from the Tortonian of Sierra Leone, and *N. mediterranea* (Ruggieri, 1953) from the latest Miocene and Pliocene of Gabon (van den Bold, 1966). Today, there are two species, *N. ikorodunsis* Omatsola, 1970 and *N. iddoensis* Omatsola, 1970 which are found from Nigeria to Senegal. This genus is abundant is

shallow coastal waters in West Africa today. It was especially common in late Miocene sediments from North Africa.

HEMICYTHERIDS

The Hemicytherinae, Puri 1953 are common in shallow marine waters along the coast of West Africa, but are rarely dominant. Omatsola (1972) and Witte (1993) described species belonging to the genera *Mutilus* Neviani, 1928 and *Aurila* Pokorny, 1955 from the Niger Delta, Gabon, and Ivory Coast (Omatsola, 1972) and Senegal and Gambia (Witte, 1993); *Aurila* is common on sand and shelly sand substrates of the shelf of Sierra Leone (Keen, 1972), where it can form up to 20% of the ostracod fauna. The subfamily is totally absent from Miocene faunas from West Africa, in startling contrast to contemporaneous faunas from the Mediterranean, adjacent Atlantic basins, and other areas. The oldest species from West Africa were recorded by Van den Bold, 1966, from the post-Miocene of Gabon: *Aurila punctata* (von Munster, 1930) which is known from the Pliocene of Europe, and *Mutilus* aff. *convolutus* (Brady, 1868), a Recent species from Mauritius. It appears that these genera migrated to West Africa from the Mediterranean area or the northern eastern Atlantic during the early Pliocene.
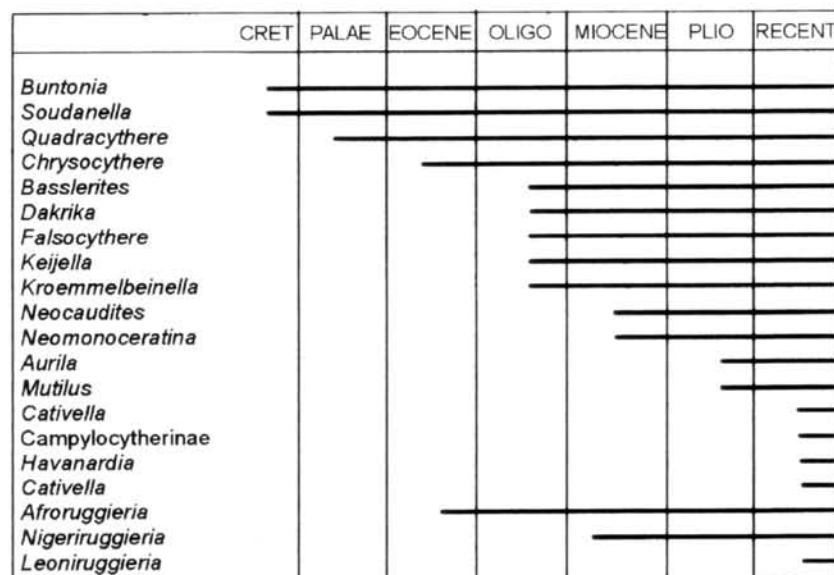
OTHER OSTRACODS

Various genera and species of the Paracyprididae have been described from the Tertiary and Recent of West Africa, but once again it is impossible to attach any biogeographical significance to them with the present state of knowledge. Loxoconchids and cytherurids are present in faunas throughout the Tertiary, but are difficult to use in biogeographic studies. *Gambiel-*

la Witte, 1985 is present throughout the West African region, and Witte also recorded it from the tropical Pacific Ocean, indicating a circumtropical distribution within the littoral realm; in 1993, Witte also reported the genus from the Recent of Bermuda.

LIVING GENERA WITH NO FOSSIL RECORD IN WEST AFRICA

Finally, there are some genera that are common today, but have no fossil record in West Africa. *Campylocythereis* Omatsola, 1971 has three described species from the western Niger Delta (Omatsola, 1971), and is also known from Angola (Hartmann, 1974), Sierra Leone ('*Leguminocythereis*' of Keen, 1972) and Gambia (Witte, 1993). *Mackenziella* Omatsola, 1972 is recorded by Omatsola from Nigeria, Ghana, and Sierra Leone, and *Reymentia* Omatsola, 1972 is recorded by the same author from Nigeria and the Ivory Coast, and it is present on the coast of Gambia (Witte, 1993). Omatsola placed all three genera within the Campylocytherinae Puri, 1953. This subfamily has strong connections with the Gulf Coast and eastern seaboard of the U.S.A., where it is known from the Miocene onwards, suggesting a possible migration to west Africa during the Pliocene with subsequent independent evolution. *Loculicytheretta* Ruggieri, 1954 is a minor, but interesting, part of the West African fauna. Three living species are known from West Africa, and a further one, *L. pavonia* (Brady) from the Mediterranean. No fossil occurrences are reported from West Africa, but *L. pavonia* is known from the Pliocene-Recent of the Mediterranean Basin. However, the oldest species of the *L. pavonia* group are known from the Atlantic basins of southern France, Spain, and Morocco. Keen (1998) argued the case for an Atlantic, and perhaps even a west African, origin for the modern species of this genus, rather than a Mediterranean one as be-

	CRET	PALAE	EOCENE	OLIGO	MIOCENE	PLIO	RECENT
Buntonia							
Soudanella							
Quadracythere							
Chrysocythere							
Basslerites							
Dakrika							
Falsocythere							
Keijella							
Kroemmelbeinella							
Neocaudites							
Neomonoceratina							
Aurila							
Mutilus							
Cativella							
Campylocytherinae							
Havanardia							
Cativella							
Afroruggieria							
Nigeriruggieria							
Leoniruggieria							

Text-fig. 4 - Stratigraphical ranges of selected living ostracod genera of West Africa.

lieved by, for example, Witte (1986). The genus is unknown in the Americas. *Cativella* Coryell & Fields, 1937 was regarded as a thermophilic genus by Wood & Whatley (1994), and is only found as far north as Sierra Leone; this is a typical Caribbean-Gulf Coast genus, although it should be noted that Van den Bold (1977) doubted the identification of this genus in west Africa, believing species assigned to it are more similar to *Chrysocythere*. The leptocytherids are also present, described by Witte (1993) from Senegal and The Gambia; these are perhaps migrants from the north. *Xestoleberis* Sars, 1866 is present in coastal environments throughout the region, but like the other taxa discussed here, has no fossil record in West Africa.

THE ORIGINS OF THE FAUNA

The origins of the modern West African ostracod faunas can be traced back to the late Cretaceous. At that time a great seaway briefly extended across the Sahara from Nigeria to Libya, connecting to the western Tethys Ocean, while to the north and west lay the young central Atlantic with its American and Caribbean borderlands much closer to west Africa than they are today. The shallow marine ostracods of North and West Africa at that time had a great deal in common at the species level because they were able to migrate through the intermittent Trans-Saharan Seaway. This connection closed during the early Eocene, and after this the ostracods evolved in their own separate ways, with just the occasional species in common during the mid and late Eocene (Keen *et al.*, 1994). Presumably, these ostracods migrated along the coasts of North and West Africa, which was then the only possible route. The relationship with South America was more at the generic level.

Witte (1993) recognised six groups of ostracod species from the modern faunas of West Africa: endemic species, species in common with the warm temperate north east Atlantic, species of American origin, relict Tethyan species which have close relatives in the Indo-Pacific region, cosmopolitan circumtropical species, and finally a group of species which appear to have been dispersed through the agency of human shipping. Van den Bold (1977) discussed the origin and migration of genera during the late Cretaceous to the Recent between North America, Central America, the Caribbean, South America, Antarctica, West Africa, and the Mediterranean. He showed migration from West Africa of *Buntonia*, *Soudanella*, *Protobuntonia*, and *Basslerites* to South America, and *Ruggieria* and *Chrysocythere* to the Mediterranean; immigrants to West Africa were *Mutilus* from the Mediterranean, with migration of *Ruggieria* and *Chyrsocythere* back to West Africa during the Miocene, and *Togoina* from South America during the Palaeocene. The present-day fauna is therefore the result of a complex of immigration and migration of taxa. The evolution of indigenous elements can be traced back to the early Palaeogene.

There was a major renewal of the fauna during the late Oligocene, with many of the genera present today first appearing in the geological record of West Africa. This Palaeogene-Neogene fauna has a decidedly modern appearance and contains species that are so similar to modern ones that it is highly likely that they are ancestral to the living species.

The discussion here centres on relationships at a higher taxonomic rank than the species, because few West African species are known from outside the region. Endemic species are therefore interpreted as those with ancestry within West Africa. Text-fig. 4 shows the stratigraphical range of selected genera within western Africa. Endemic species are those of the genera *Buntonia* and *Soudanella*, which have a long history stretching back to the Late Cretaceous, but which are no longer dominant elements of the fauna. *Chrysocythere* and the ruggieriines have been present since the Eocene and still have their major centre of diversity off the coasts of western Africa; the latter especially became abundant during the Neogene renewal. *Dakrika* and *Kroemelbeinella* evolved during the Oligocene to become an important part of the Neogene renewal. Other endemic species are probably to be found amongst the cytherellids, bairdiids, paracyprids, loxoconchids, and cytherurids, all of which have a long geological record in the region. Taxa with an American connection are the Campylocytherinae Puri, 1960, which have no fossil record in West Africa, but have endemic genera, suggesting time for evolution of these new taxa, possibly during the Pliocene or Pleistocene. *Cativella* is another American genus without a West African fossil record, but once again, with no species in common with the Americas. *Puriana* Coryell & Fields, 1953 has a great deal of diversity today in West Africa, and often forms a significant part of the shallow marine fauna; it has been present in the region since the mid Miocene, so it is as typical of West Africa as of the Americas, and is therefore best regarded as an Atlantic genus. *Neocaudites* has been present in West Africa since the late Miocene, and is part of an Atlantic taxon rather than American. Circumtropical genera, living in all major tropical provinces around the world, possibly with a Tethyan connection, include *Falsocythere* and *Neomonoceratina*, both present in the region since the Miocene, and *Gambiella* and *Havanardia* which have no fossil record in West Africa. *Loculicytheretta* is probably of eastern warm Atlantic origin. Genera that may have been considered to have a Mediterranean or Tethyan origin, such as *Ruggieria*, *Chrysocythere*, *Dakrika*, *Kroemelbeinella*, and *Loculicytheretta* are better thought of as having an African Atlantic origin. *Chrysocythere*, the ruggieriines, and the *Dakrika-Carinovalva* group seem to have dispersed eastwards along Tethys to reach East Africa and the Indian Ocean region during the late Oligocene and early Miocene. *Aurila* and *Mutilus* migrated into West Africa during the early Pliocene from the Mediterranean or northern Atlantic. Finally, *Cyprideis* mi-
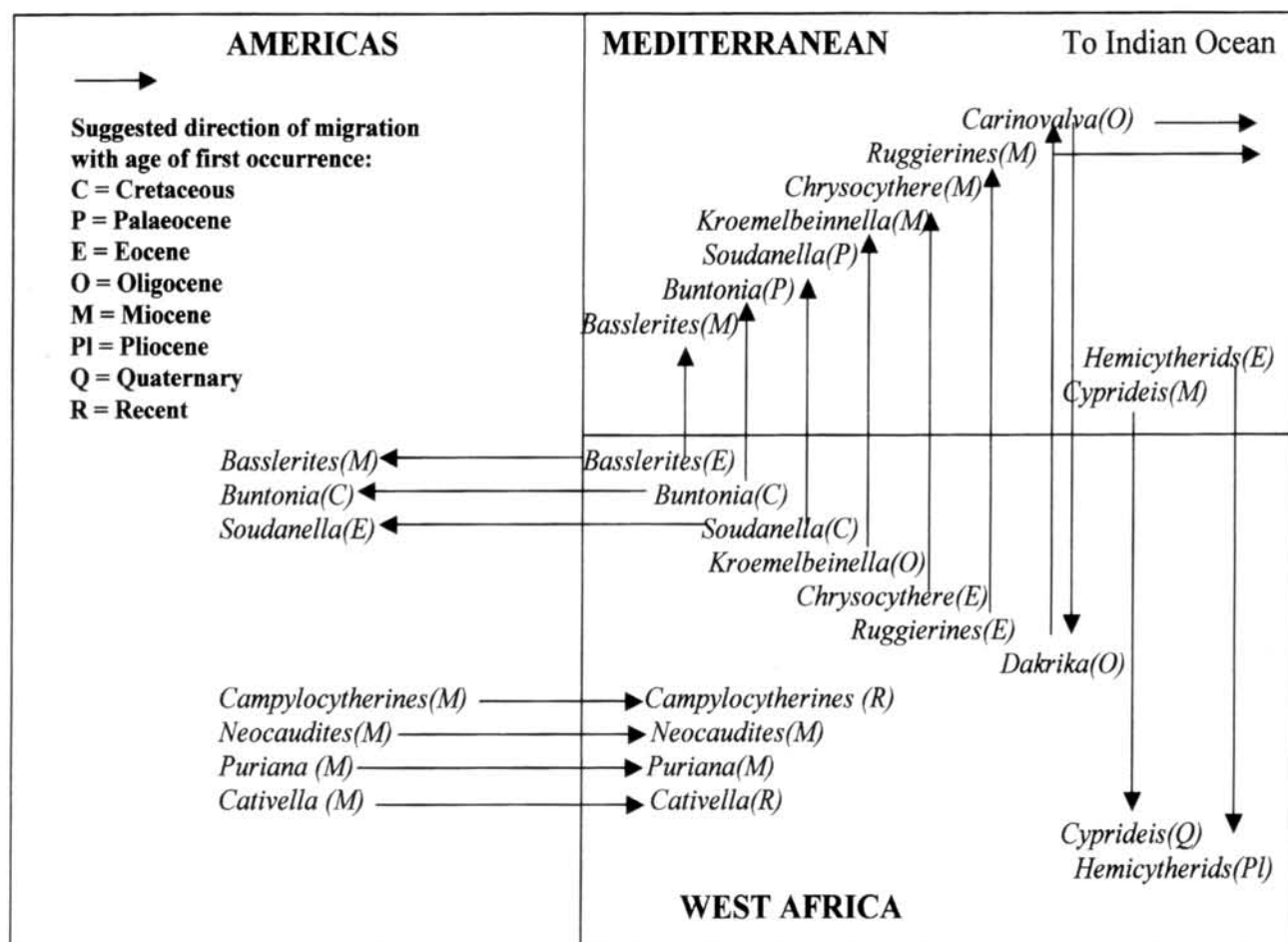
Text-fig. 5 - Immigration and emigration of selected West African ostracod genera between West Africa, the Americas, and the Mediterranean region. Letters in brackets refer to time of first appearance of the genus in the particular region. C, Cretaceous; P, Palaeocene; E, Eocene; O, Oligocene; M, Miocene: Pl, Pliocene; Q, Quaternary.

grated from Europe or North Africa during the late Pliocene or Pleistocene.

Witte (1993) listed three species which he believed owed their presence in West Africa to the agency of human transport from the Indo-Pacific. These are *Kotoracythere inconspicua* (Brady, 1880), *Tanella gracilis* Kingma, 1948, and *Keijia demissa* (Brady, 1868).

Text-fig. 5 summarises migration of genera into and out of West Africa.

SYSTEMATICS

RUGGIERIINI n. tribe

Species referable to this new tribe are common components of the West African fauna, and as discussed previously, fall into three distinct groups of species. It is proposed here to elevate these groups to the rank of genus, and together with the Mediterranean species are placed into a new tribe, the Ruggieriini. When these groups were first described (Keen, 1975), it was

hoped that soft parts from the living species would soon be described; nearly thirty years on this hope has not materialised, so these new genera are based entirely on carapace morphology.

Diagnosis – A member of the Trachyleberidinae with an ovate to triangular carapace in lateral view, left valve with a prominent hinge-ear, arched dorsal margin, anterior and posterior marginal spines; ornamentation with a ventral ridge ending in a prominent postero-ventral spine, remainder of carapace with ornament of ridges and reticulation.

Description – The tribe is characterised by an ovate carapace in lateral view, tending towards triangular with greatest height near the anterior and with an upturned posterior end; the prominent eye tubercle is associated with an anterior hinge ear in the left valve; the two valves are markedly different in lateral outline, the smaller right valve having a straighter dorsal margin and is more triangular in shape. Both valves

have well developed anterior and posterior marginal spines, the anterior spine tending to be smaller and more numerous. Sexual dimorphism is prominent with more elongate males. A ventral ridge is always present, ending in a postero-ventral spine. The anterior marginal rib varies in its strength, sometimes being virtually absent, and being a useful specific character. Internally, the hinge is holamphidont; the right valve has a prominent conical anterior tooth, a postjacent socket with a raised ventral rim joining onto the anterior tooth, a straight crenulated grove, and an ovate smooth posterior tooth. There is a prominent eye socket. The left valve has complimentary elements, and the anterior socket has a raised ventral rim. The marginal area is broad, has no vestibules, and moderately numerous simple wavy radial pore canals. The central muscle scars have a 'u'-shaped frontal scar and four adductors scars, the second from dorsal being more elongate than the others. A fulcral point is present above and to the anterior of the dorsal-most adductor scar (Pl. 1, figs 18, 24). Normal pore canals are simple. Genera are based on the ornamentation of the carapace.

Remarks – The genus was originally described by Keij (1957) from the Burdigalian of the Aquitaine Basin, south west France, and is common in Miocene and Pliocene deposits of the Mediterranean area, although no species have been described in living faunas from the Mediterranean.

The type species of *Ruggieria*, *R. micheliniana* (Bosquet, 1852) from the Burdigalian of the Aquitaine Basin, France, is characterised by an ornamentation of longitudinal ridges with coarse puncta between them, and with a large smooth area at the anterior; species with this type of ornamentation appear to be restricted to the early and mid Miocene and are known throughout the Mediterranean area from the Atlantic basins of France and Portugal to Turkey in the east. A second type of ornamentation is that seen in *R. tetraptera* (Seguenza, 1880), which consists primarily of a ventral ridge and a median ridge of varying strength, sometimes with small tubercles present. This group seems to be restricted to the late Miocene to Pleistocene, and is present throughout the Mediterranean from southern Spain to northern Iraq. A third type is represented by *R. angustata* (Seguenza, 1880), which has several short longitudinal ridges present in the median and posterior parts of the valve, and is the closest in ornament to the west African species, especially *R. boldi* Keen, 1975. This species is present in the late Miocene and is usually believed to be related to *R. tetraptera*.

The West African species fall into three groups (Keen 1975). The first of these is typified by *R. triangulata* Omatsola, 1972; this group is more elongate and triangular in lateral outline, lacking the markedly convex ventral margin of the Mediterranean groups. The main difference is in the ornamentation, with well

developed and fairly numerous longitudinal ridges. This group has been recorded from the late Oligocene of the Ivory Coast and the Neogene of the area between Gabon and Mauritania; one record has been made from the mid-late Eocene of Senegal (Carbonnel, 1982). One member of this group, *R. lekkii* Omatsola, 1972, which is found from Congo in the south to Senegal in the north, has been the subject of intense morphological study by Bertholon & Carbonel (1992, 1996) and Bertholon (1995) who believe they can recognise heterochrony, with adult morphological variation related to environment. They distinguished nine morphs based on ornamentation related to substrate, which obviously poses a problem for the recognition of fossil species. The second group, typified by *R. martinsoni* Omatsola, 1972, possesses three prominent longitudinal ridges and a more swollen central area of the valves in lateral view. This group is recorded as fossil from the Miocene of the Ivory Coast (Babinot, 1981) and Sierra Leone (Keen, 1975), and as a living ostracod from the Congo River to Sierra Leone. The third group has a single ventral ridge with the remainder of the surface faintly reticulate. In outline it is similar to genera such as *Bosquetina*, although the hinge is quite different. Only two species are referred to this group, *R. cytheropteroides* (Brady, 1880) which is recorded by Dingle (1992) from off south west Africa between 19 and 35 degrees of latitude (Namibia and South Africa) and *R. leonensisis* Keen, 1975, known from offshore Sierra Leone and Mauritania (Keen, 1975; Rosenfeld & Bein, 1978). Two similar species have been described from the northern Indian Ocean (Dingle, 1992). This group seems to inhabit deeper water than the other living species of *Ruggieria*, being found between 60 and 290 m (Keen, 1975; Dingle, 1992).

Ruggieriines have also been described from the early Miocene of East Africa and India. *Ruggieria microreticulata* (Khosla & Nagori, 1989) seems to be representative of a group of species from India with ornamentation suggestive of *Ruggieria micheliniana*, differing by having a stronger reticulation covering the whole carapace. *R. dorukae* Bassiouni, 1979 is more similar to these Indian species, and may even be intermediate between them and *R. micheliniana*. Ahmad *et al.* (1991) described *Ruggieria furcilla* sp. nov. from Lindi, Tanzania, placing it within the *R. triangualata* group described by Keen (1975). It certainly has a similar ornamentation to this group, but differs in lateral outline with its pronounced postero-ventral swelling. The closest West African species is *Ruggieria* aff. *triangulata* Omatsola, 1972, illustrated by Carbonnel *et al.* (1996) from the late Oligocene of Benin. For the moment these species are not assigned to any of the new genera.

The stratigraphical and geographical distributions discussed above, indicate that the main centre of evolution and dispersal of *Ruggieria*-like ostracods has been tropical West Africa. This region has yielded the old-

est members of the taxon, and throughout the Neogene and still today there have been more species in West Africa, and they have formed a more important part of the infralittoral faunas than elsewhere. The oldest "Mediterranean" members are found in the eastern Atlantic basins of France and Portugal, suggesting that an Atlantic origin is as likely as a Mediterranean origin. However, the presence of the new tribe in areas around the Indian Ocean suggests dispersal along the shores of Tethys during the latest Oligocene or early Miocene.

RUGGIERIA Keij 1957

Type species – *Cythere micheliniana* Bosquet, 1957.

Diagnosis – ornamentation of longitudinal ridges with coarse puncta between them, and with a large smooth area at the anterior.

Remarks – Species placed within this genus are *R. micheliniana* and *R. dorukae* Bassiouni, 1979.

Range – Early-Mid Miocene; Atlantic coasts of southern France and Spain, Mediterranean, Turkey, (?) India.

TETRARUGGIERIA n. gen.

Type species – *Cythere tetraptera* Seguenza, 1880.

Etymology – Referring to its characteristic oblong shape.

Diagnosis - Rectangular outline, ornament of ventral ridge and a median ridge of varying strength, sometimes with small tubercles present.

Remarks – Species placed within this genus are *R. tetraptera* and its subspecies and *R. bicarinata* Bonaduce, Ruggieri, Russo & Bismuth, 1992 and *R. monastirensis* Bonaduce, Ruggieri, Russo & Bismuth, 1992.

Range – Mid (?), late Miocene-Pleistocene; Southern Spain, Mediterranean, northern Iraq.

AFRORUGGIERIA n. gen.

Type species – *Ruggieria triangulata* Omatsola, 1972.

Etymology – After Africa, its area of distribution.

Diagnosis – Elongate and triangular in lateral outline, lacking the markedly convex ventral margin of the Mediterranean groups, with well developed and fairly numerous longitudinal ridges.

Remarks – Species placed within this genus are *R. triangulata*, *R. beninensis* Omatsola, 1972, *R. lekkii* Omatsola, 1972, *R. nigeriana* Omatsola, and *R. boldi* Keen, 1975.

Range – Mid Eocene-Recent; West Africa, Gabon to Mauritania.

EXPLANATION OF PLATE 1

Catalogue numbers: A and GLAHM refers to collections of the Hunterian Museum, University of Glasgow; Io, Natural History Museum, London.

Fig. 1	- *Ruggieria* aff. *dorukae* Bassiouni, 1979. Male RV, Lower Miocene, Sirt Basin, Libya; A12641, length 670 μm (x 72).
Figs 2-4, 19	- *Afroruggieria* n. gen. *triangulata* (Omatsola, 1972). 2) female LV of complete carapace, Serie de N'Tchengue, Gabon, Io 4822, L = 770 μm, (x 60); 3) male LV of complete carapace; 4) male RV, Recent, Sierra Leone, Io 4821, L = 770 μm, (x 60); 19) dorsal view, Serie de N'Tchengue, Gabon, Io 4823, L = 830 μm, (x 60).
Figs 5, 9, 11, 12	- *Afroruggieria boldi* (Keen, 1975). Bullom Formation, SLBH 9, nr. Freetown, Sierra Leone. 5) female RV int. view, L = 690 μm (x 60); 9) male RV, Io 4828, L = 690 μm (x 54); 11) female RV, Io 4826, L = 690 μm (x 52); 12) female carapace, ventral view, Io 4840, L = 700 μm.
Figs 6, 7, 13, 16	- *Tetraruggieria* n. gen. aff. *tetraptera* (Seguenza, 1880). Marne Azzure, Carmona, Spain. 6) male RV, L = 714 μm (x 70); 7) female LV, L = 720 μm (x 68); 13) male LV, L = 670 μm (x 70); 16) female RV int. view, L = 830 μm (x 60).
Figs 8, 10, 18	- *Leoniruggieria* n. gen. *leonensis* (Keen 1975). Recent, Sierra Leone. 8) female LV, Io 4817, L = 890 μm (x 55); 10) Female RV int. view, Io 4818, L = 860 μm (x 55); 18) same specimen as fig. 10, central muscle scars (x 300).
Figs 14, 15	- *Nigeriruggieria* n. gen. *martinsoni* (Omatsola, 1972). Recent, Sierra Leone. 14) RV, Io 4834, L = 750 μm (x 60); 15) LV, Io 4833, L = 630 μm (x 65).
Figs 17, 24	- *Nigeriruggieria bullomensis* (Keen, 1975). Bullom Formation, SLBH 9, nr. Freetown, Sierra Leone. 17) male RV, Io 4842, L = 600 μm (x 60); 24) female LV, Io 4844, central muscle scars (x 350).
Fig. 20	- *Chrysocythere cataphracta* Ruggieri, 1962. Female RV, Lower Miocene, Sirt Basin, Libya; A12573, length 716 μm, (x 60).
Fig. 21	- *Carinovalva carinata* (Moyes, 1965). Female LV, L = 580 μm (x 85), Marne Azzure, Tortonian, Carmona, Spain.
Fig. 22	- *Chrysocythere buncensis* Keen, 1994. Male RV, GLAHM 101151, L = 890 μm (x 56), Bullom Formation, SLBH 9, nr. Freetown, Sierra Leone.
Fig. 23	- *Dakrika fourahensis* (Keen, 1996). Female LV, GLAHM 101179, L = 510 μm (x 83), Bullom Formation, SLBH 9, nr. Freetown, Sierra Leone.
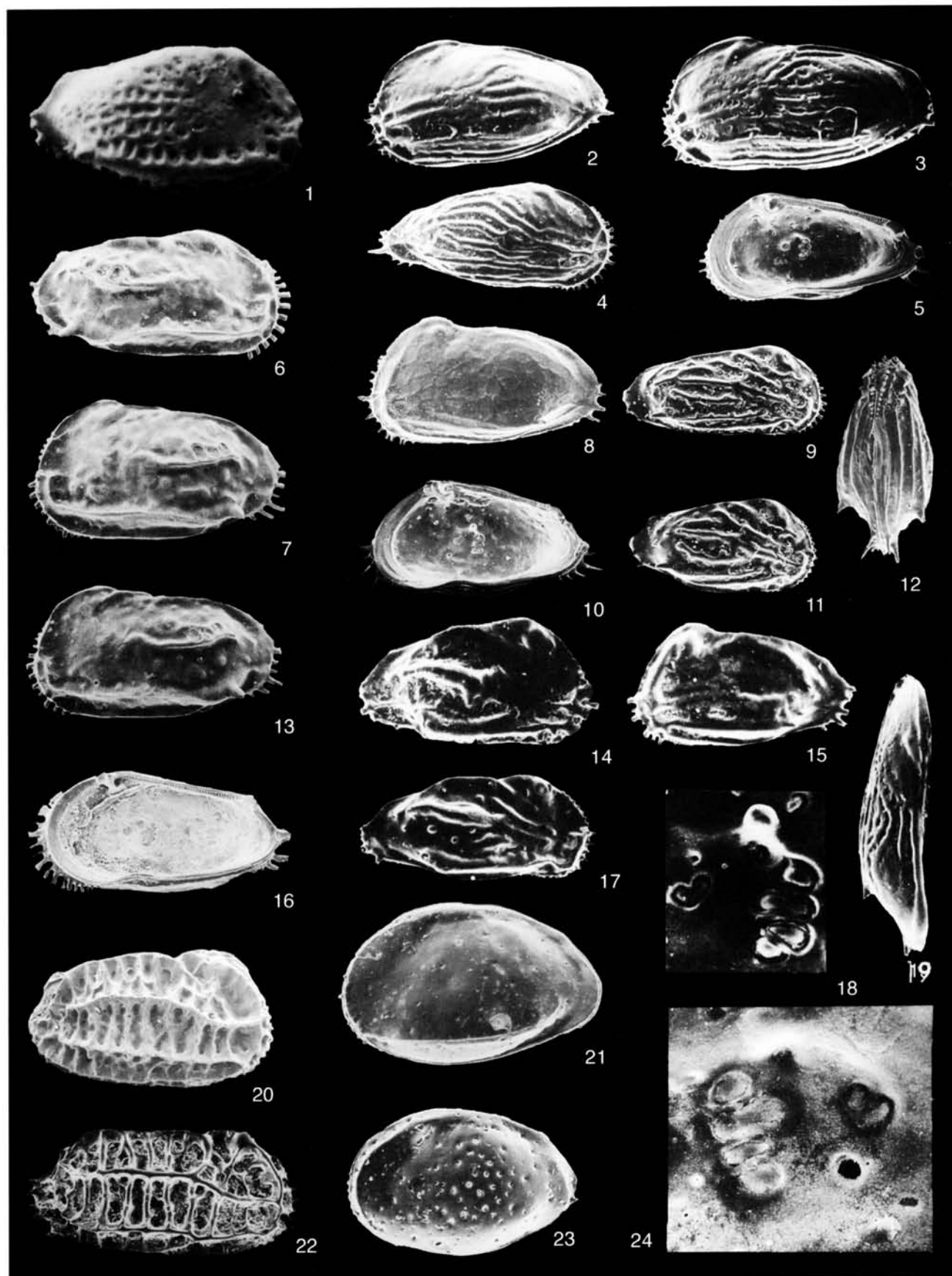
	Lateral outline of left valve	Swollen central area	Longitudinal ridges	tubercles	reticulation
Ruggieria	Rectangular to ovate	no	Several with coarse puncta between	none	none
Tetraruggieria	Rectangular	no	Ventral and median	May be present	none
Afroruggieria	Elogate-triangular, strongly convex ventral margin	no	Several	none	Yes in some specimens
Nigeriruggieria	Triangular	yes	Three prominent	none	none
Leoniruggieria	Prominent hinge ear in left valve	yes	Ventral ridge only	none	Faint

Tab. 1 - Comparison of selected characters among *Ruggieria* and the new genera *Tetraruggieria*, *Afroruggieria*, *Nigeriruggieria*, and *Leoniruggieria*.

NIGERIRUGGIERIA n. gen.

Type species – *Ruggieria martinsonni* Omatsola, 1972.

Etymology – After Nigeria.

Diagnosis – Triangular in lateral outline with three prominent longitudinal ridges and a more swollen central area of the valves in lateral view.

Remarks – Species placed within this genus are *R. martinsonni*, *R. tricostata* Omatsola, 1972, and *R. boldi* Keen, 1975.

Range – Early Miocene-Recent; West Africa, Congo to Sierra Leone.

LEONIRUGGIERIA n. gen.

Type Species – *Ruggieria leonensis* Keen, 1975.

Etymology – After Sierra Leone.

Diagnosis – Left valve with prominent hinge-ear and curved dorsal margin, ornamentation consists of a single ventral ridge with the remainder of the surface faintly reticulate.

Remarks – Species placed within this genus are *R. leonensis* and *Cythere cytheropteroides* (Brady, 1880).

Range – Quaternary-Recent; Africa from South Africa to Mauritania; northern Indian Ocean.

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