On the affinities of three fossil ocypodid crabs and their relevance to the time and place of origin of the genus *Macrophthalmus* (Crustacea: Brachyura)

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All the species of *Macrophthalmus* described from fossil material belong to the still extant subgenus *Venitus*. *M. vindobonensis* and *M. aquensis*, the two earliest known species of the genus, are closely related to the extant *M. latreillei*, while *M. guamensis* is conspecific with *M. leptophthalmus*.

Doubt is cast on Remy's (1952) theory of the late Tertiary migration of *Macrophthalmus* from the Mediterranean, its suggested place of origin, to the Indo-West Pacific, its present distributional range. Instead it is proposed that *Macrophthalmus* arose in the Indo-West Pacific during the late Eocene-Oligocene, and extended its range into the Mediterranean during the early-middle Miocene. The Mediterranean species became isolated during the late Miocene by a land bridge, and probably became extinct following the elevation of their brackish habitat during the late Miocene-Pliocene.

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Introduction

The ocypodid genus *Macrophthalmus* Latreille at present exhibits a widespread Indo-West Pacific distribution and contains some 70 species described from neontological material (of these, however, probably only about 35 species are valid—Barnes, 1967). Some of these species, e.g. *M. setosus* H. Milne Edwards, *M. latifrons* Haswell and *M. japonicus* (de Haan), are also known from fossil or subfossil specimens (Etheridge & McCulloch, 1916; Kaneko, 1951).

The palaeontological history of this genus extends back to the middle Miocene (Glaessner, 1924) and about ten species have been described from fossil or subfossil material. A few of these species, e.g. *M. latreillei* (Desmarest), are still extant.

This paper is concerned with the three earliest known species of *Macrophthalmus*, *M. aquensis* A. Milne Edwards & Brocchi, *M. vindobonensis* Glaessner and *M. guamensis* Kesling. Three aspects of the biology of these species are discussed: (a) their affinities with other species of *Macrophthalmus*, (b) Remy's (1952) theory that *Macrophthalmus*

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arose during the Miocene in what is now the Mediterranean Sea and later migrated into the Indo-West Pacific region, and (c) the position of these species in relation to the early evolution of *Macrophthalmus*.

The affinities of the species under discussion

The most striking feature of all the *Macrophthalmus* species described from fossil remains is their close morphological similarity to *M. latreillei*, itself first described as a fossil and often recorded since in that condition, e.g. by Etheridge & McCulloch, 1916 (as *M. depressus*), Kesling, 1958, Kaneko, 1958, Barnes, 1966a, etc. Three of these species, *M. desmaresti* Lucas, *M. granulosus* de Man, and *M. emarginatus* (Desmarest), have actually been synonymized with *M. latreillei* by various authors.

The three species under discussion in this paper are no exceptions, all three clearly belong to the subgenus *Venitus* Barnes, of which *M. latreillei* is the type species.

Macrophthalmus guamensis

In 1958 Kesling described a new species of *Macrophthalmus*, *M. guamensis*, from specimens that had been dredged from Apra Harbour, Guam. The age of the specimens could not be determined with any degree of accuracy, Kesling stating (p. 215) that they were "at least as young as the Eocene and may be as young as Recent". Although "the exact age of the crabs will remain in doubt" (p. 217), Kesling suggested that the most plausible age for them was Pleistocene. This assessment was, however, based in part on the evidence of Remy's (1952) theory, Kesling ruling out a pre-Pliocene age because "this genus originated in the Mediterranean region in middle Miocene, it probably could not have migrated to Guam before at least the Pliocene" (p. 216) (see later discussion).

Judging from the species with which Kesling compared the new species, and from his list (p. 219) of species referable to *Macrophthalmus*, Kesling was unaware of the great similarity shown by a little-known Recent crab, *Euplax leptophthalmus*, to *Macrophthalmus*. This latter species was described by H. Milne Edwards (1852) from specimens allegedly, but doubtfully, collected in Chile, South America, and was placed by that author in a new genus, *Euplax* Milne Edwards. The species is at present known from only two specimens, those deposited in the Muséum National d'Histoire Naturelle, Paris, by Milne Edwards. Barnes (1966b) showed that *E. leptophthalmus* fell well within the generic limits of *Macrophthalmus*, and it was assigned by that author (Barnes, 1967) to the subgenus *Venitus*.

A comparison between *M. leptophthalmus* (see photographs of holotype male in Barnes, 1966b, Plate 24, Figs 3–4—the photographs being two of a set kindly supplied, on request, by Dr D. Guinot of the Paris Museum) and *M. guamensis* (see photographs of holotype and paratypes in Kesling, 1958, Plate 3, Figs 9–10, Plate 8, Fig. 3, Plate 10, Figs 10–13, Plate 11, Figs 4–8, and Plate 12, Fig. 18) discloses no means by which the two species may be distinguished. Indeed one cannot help but be surprised by the almost exact similarity, considering that the time interval separating the specimens was probably long. The only difference between *M. leptophthalmus* and *M. guamensis* appears to be the slightly larger tooth on the index of the latter species, this difference, however, is minimal compared with the variations seen in the size and shape of this tooth in other species, e.g. *M. crassipes*

Milne Edwards, *M. crinitus* Rathbun, *M. telescopicus* (Owen), etc. (Barnes, 1967). Thus there can be little doubt that the two species are conspecific, and *M. guamensis* must be reduced to a synonym of *M. leptophthalmus* (H. Milne Edwards, 1852).

Macrophthalmus aquensis and *Macrophthalmus vindobonensis*

M. aquensis occurs with specimens of *Ostrea crassissima* in Vindobonian deposits of clay (Milne Edwards & Brocchi, 1879) or chalk (Remy, 1952) in the region of Aix-en-Provence (Mont Perrin). Several specimens have been discovered, Remy (1952), for example, examining 35 specimens (all females) of which six were possibly exuviae, but only the carapace, the abdomen (both male and female) and the pereiopods of this species are known. The chelae are badly preserved (Milne Edwards & Brocchi, 1879) or absent (Remy, 1952).

Milne Edwards & Brocchi (1879) compared this species with *M. depressus* Rüppell and *M. pacificus* Dana, but Remy (1952) realized the resemblance between it and *M. latreillei* and *M. vindobonensis*. He stated (p. 28): "Par la conformation générale de la carapace et par l'importance des dents situées sur le bord latéral, *M. aquensis* ressemble à *M. latreillei*", but he considered that ". . . la taille . . . paraît plus petite pour *M. aquensis*" (p. 28). Certainly the dimensions given for *M. aquensis* by Remy (17·2 mm carapace breadth and 13·2 mm carapace length) are small compared with those of fully adult *M. latreillei*, but they are within the size range of that species, and further they fit almost exactly (to within one-sixth of a standard error) the regression line equation given by Barnes (In press) for *M. latreillei* (carapace length = 0·65 carapace breadth + 2·13 mm). Thus the size difference between the two species would not seem necessarily valid.

A comparison between the descriptions of *M. aquensis* of Milne Edwards & Brocchi (1879: 15–16) and Remy (1952: 27–28) and the still extant *M. latreillei* discloses the great similarity shown by the two species, indeed any differences between them seem trivial, but it must be emphasized that our knowledge of *M. aquensis* is still limited. Thus the exact status of the latter must remain in doubt, although in all the characters preserved it is clearly very closely allied to, if not actually synonymous with *M. latreillei*.

Much of what has been said in connection with *M. aquensis* also applies to *M. vindobonensis*. This species, described by Glaessner in 1924, occurs with molluscs of the genera *Cardium*, *Natica*, *Buccinum*, *Solen*, etc., in Helvetian deposits of fine or sandy clay at Teiritzberg (80 specimens), Unterolberndorf (many specimens), Wetzelsdorf (five specimens), and St Florian (one specimen), in Niederösterreich and Steiermark (Austria) (Glaessner, 1924, 1928). *M. vindobonensis* although clearly showing affinities with *M. latreillei*, departs more in structural plan from that species than does *M. aquensis*, and Glaessner (1924) has listed a number of differences between the two species. Most important of these differences is probably the greater relative carapace breadth shown by *M. vindobonensis* (over the size range 10–15 mm carapace length the length/breadth ratio of *M. latreillei* being in the region of 1 : 1·3, whereas in the Miocene species the ratio is in the region of 1 : 1·5). Differences in the carapace granulation, the shape of the anterolateral teeth, and the overall size can also be noted (Glaessner, 1924). Stress, however, cannot be placed on these latter characters in view of the fact that Glaessner's specimens appear to be juveniles, judging from his schematic figuring of the male chelae of one of the larger specimens in his Fig. 2(a) (Glaessner, 1924: 113), and juvenile *M. latreillei* of the same

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size as the specimens of *M. vindobonensis* discovered possess anterolateral teeth of approximately the same shape as those seen in the latter species. The degree and extent of carapace granulation in *M. latreillei* is also subject to great geographical variation. Despite the differences in carapace proportions between *M. latreillei* and *M. vindobonensis*, the latter species appears to be more closely related to the former species than to any other known *Macrophthalmus*.

Remy's theory of the migration of *Macrophthalmus*

M. aquensis and *M. vindobonensis*, the two earliest known *Macrophthalmus* species, are both known only from deposits found on the northern shores of the Mediterranean, *M. aquensis* from the upper Vindobonian of Aix-en-Provence, and *M. vindobonensis* from the Helvetian of the Vienna basin. The later, remaining, species (both fossil and extant) are confined to the Indo-West Pacific region, with the exception of *M. impressus* (Desmarest) recorded as a subfossil from the region of Rome by Desmarest (1817: 1822), a record which, as stated by Remy (1952), "is sufficiently doubtful for it to be neglected".

To explain this apparent change in distribution from the western Mediterranean basin during the Miocene, to the Indo-West Pacific region during the Pleistocene and Holocene, Remy (1952) proposed the following theory: *Macrophthalmus* originated in the Mediterranean, but at the end of the Tertiary the genus migrated (via larvae?) from the Mediterranean to the Indo-West Pacific in order to maintain stable environmental conditions in the face of a changing Mediterranean region. This theory was supported by Kesling (1958), but without further comment.

Several arguments can be raised against Remy's two main points that (*a*) *Macrophthalmus* arose in the Mediterranean because it is only in that region that fossils of pre-Pliocene age have been discovered, and (*b*) that *Macrophthalmus* migrated out of the Mediterranean at the end of the Tertiary.

The lack of Miocene fossil material from the Indo-West Pacific is not altogether surprising considering the relatively minute amount of palaeontological research that has taken place over much of that area, and the absence in many areas of adequate stratigraphical correlations (see, for example, Kesling, 1958). This negative evidence does not yet place the origin of the genus, with any degree of certainty, in the only region where specimens have so far been found.

Leaving aside the feasibility of a migration of littoral crabs from the western Mediterranean basin to the Indo-West Pacific (which itself is open to debate), the timing of such a migration is of interest. The Mediterranean basin has been confluent with the Indo-West Pacific region for much of the Tertiary. During the Eocene the Tethys Sea probably extended from what is now the Atlantic to what is now the Pacific, this condition lasting throughout the Oligocene and lower Miocene (Moreau, 1952). In the later Miocene, however, the Mediterranean basin became separated from the Indo-West Pacific by a land bridge which was elevated across the Arabian peninsula, this land bridge probably fluctuating considerably, both in position and extent, during that period (Krenkel, 1925; Macfadyen, 1933). From the later Miocene to the present day the land bridge, although fluctuating, has probably separated these two water masses, with, in addition, a Sicilo-Tunisian bridge further dividing the old Tethys Sea during the late Pliocene (Moreau, 1952).

The whole of the Mediterranean basin shore-line would not, of course, have provided suitable habitats for this genus, and it is necessary to examine the changing conditions in the Mediterranean during the Tertiary.

Macrophthalmus is today a littoral, essentially subtropical and tropical, frequently brackish or estuarine, genus, and the habits of its species were probably not any different in the Miocene (Remy, 1952; Kesling, 1958). Indeed, Hedgpeth (1957) has stated that euryhalinity may well be a physiological characteristic not of species but of whole phyletic lines.

In the Eocene, the Vienna basin, Italy, and part of Southern France were submerged under the Tethys Sea, but only in a localized area of southern France would there seem to have been suitable conditions for *Macrophthalmus*, much of the remaining area having had a coarse sand or marl bottom. In the Oligocene southern France was elevated, and it was not until the middle Miocene that southern France, the Vienna basin, and the connecting perialpine depression became predominantly estuarine or brackish. (It is from this northern Mediterranean brackish facies that the earliest European *Macrophthalmus* have been recovered.) At the end of the Miocene, however, much land re-emerged, and the Vienna basin became an isolated brackish area. This continued into the Pliocene (von Bubnoff, 1926–36; Gignoux, 1943; Wills, 1951). During the early Tertiary the Mediterranean basin was probably warmer than at present, and enjoyed a tropical or subtropical climate (Wills, 1951; Moreau, 1952).

Thus it can be said that the Mediterranean probably provided optimum conditions for *Macrophthalmus* only during the middle and late Miocene, and it was during the latter period that these optimum regions became isolated by land from both the remainder of the Mediterranean and the Indo-West Pacific. It would seem very unlikely that this genus both arose in those areas and migrated out in the middle-late Miocene.

It seems, however, quite possible that the genus arose in an area other than the western Mediterranean (South East Asia?, see Barnes, 1968), during the Oligocene or early Miocene (discussed later), and spread through much of the Tethys Sea, entering the Mediterranean basin in the early middle Miocene before the separation of that region from the Indo-West Pacific by the Arabian land bridge. The species that had entered the Mediterranean would then have been isolated in that region in the late Miocene. These isolated species occurring in the northern brackish Mediterranean (*M. vindobonensis* and *M. aquensis*) would have become extinct as a result of the re-emergence of much of their habitat during the late Miocene and Pliocene, and possibly as a result of the cooling climate of the northern Mediterranean during the later Tertiary. The species occurring to the east of the Arabian land bridge survived to the present day, or were ancestral to extant species, with, no doubt, fluctuations in distribution including varying degrees of repenetration into the extreme eastern Mediterranean basin during periods of fluctuation of the land bridge.

The early evolution of *Macrophthalmus*

As has been stated earlier, the oldest known material of *Macrophthalmus* can be referred to the subgenus *Venitus*. Barnes (1967), in his review of the evolution of the extant species of this genus, hypothesized that the ancestral form of *Macrophthalmus* was of a structure approximating closely to that found in the extant subgenus *Mopsocarcinus* Barnes, and

that *Venitus* could be regarded as a somewhat specialized offshoot from that stock. (The reasons for placing *Venitus* as a specialized side branch of *Macrophthalmus* evolution are given in that paper.) If the opinions of Barnes (1967) are correct, then *Macrophthalmus* must be appreciably older than the age of the earliest specimens (middle Miocene) so far discovered. Indeed it has earlier been suggested that the genus entered the Mediterranean not later than the early middle Miocene, and that before entering the Mediterranean the genus had arisen in the Indo-West Pacific and spread through much of that region, suggesting an origin not later than early Miocene.

The Brachyura arose in the Triassic (Woods, 1946; Glaessner, 1957), and in the Jurassic the Dromiacea were dominant, the Brachygnatha showing only minor divergences. The Brachygnatha, however, radiated out markedly and became dominant during the Cretaceous (Glaessner, 1957; Woods, 1965).

Thus the origins of *Macrophthalmus* must be sought between the Cretaceous and the early Miocene, and the author would suggest a late Eocene-Oligocene origin for this genus.

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