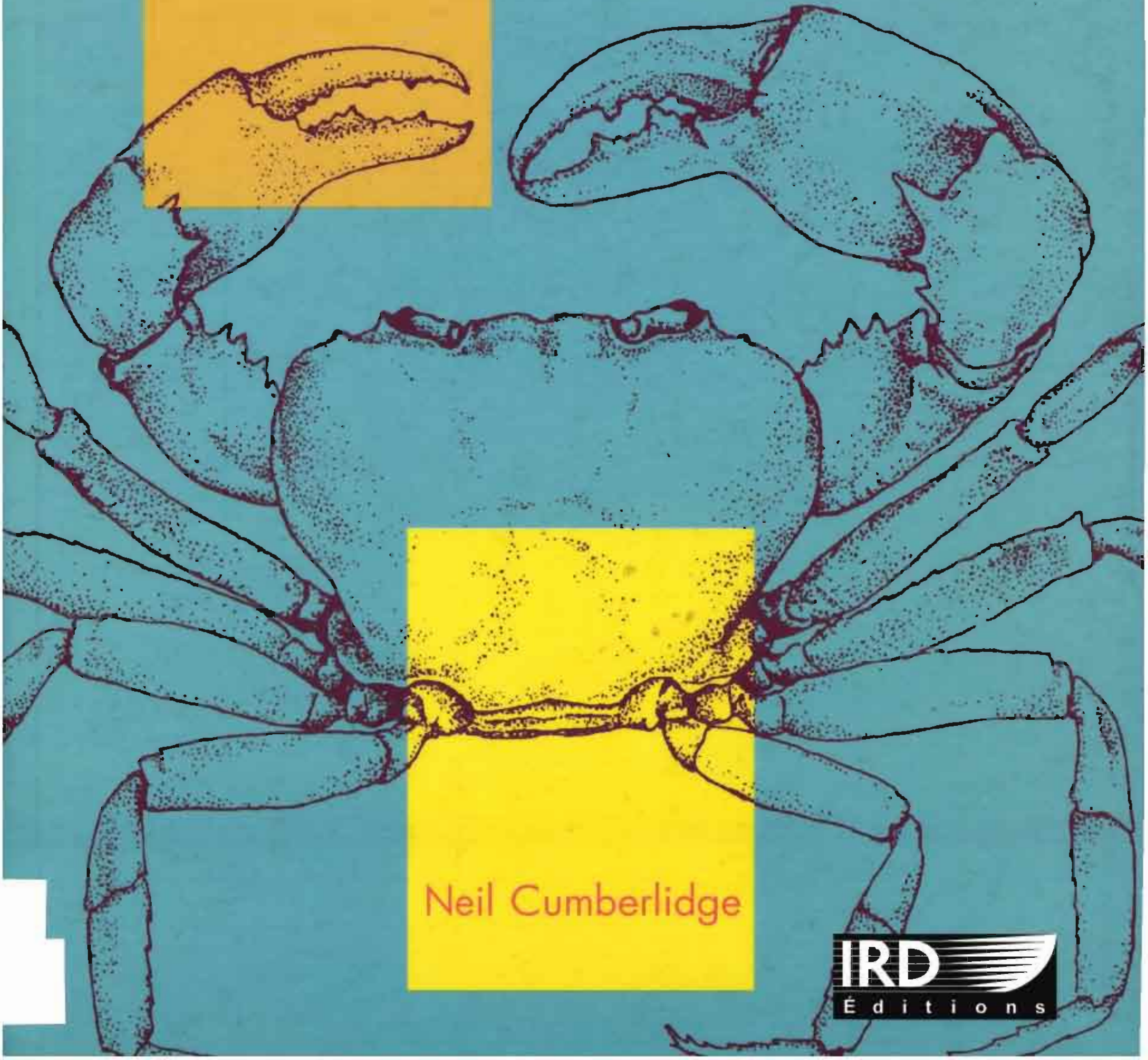
Faune et flore tropicales

The Freshwater Crabs of West Africa

Family Potamonautidae



Neil Cumberlidge

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The Freshwater Crabs of West Africa

Family Potamonautidae

For Louise

Neil CUMBERLIDGE

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Préface

Plus particulièrement spécialiste de crabes marins, j'ai grand plaisir à préfacer un ouvrage consacré aux crabes d'eau douce, qui sont intéressants à plus d'un titre. Les crabes d'eau douce (en anglais "true freshwater crabs") se sont complètement affranchis du berceau originel, la mer, et peuplent les régions tropicales et les zones chaudes-tempérées à tempérées des cinq continents. Ils n'ont pas de parents reconnaissables dans les océans. Ils passent toute leur existence en dehors du milieu marin. Ils habitent à l'intérieur des rivières et des cours d'eau, ou près des berges, dans les lacs, les étangs, les mares, parfois au cœur des montagnes jusqu'à 3 000 m d'altitude dans les torrents, ou ils s'aventurent à terre dans la forêt humide pour séjourner sous les feuilles ou parmi les racines, généralement dans une atmosphère humide, ou bien encore ils pénètrent au fond des grottes, devenant de vrais troglobies profondément modifiés. Mais certaines espèces peuvent non seulement survivre en dehors de l'eau mais aussi tolérer des conditions relativement sèches. Les crabes d'eau douce sont donc bien différents des diverses catégories de crabes marins qui ont pu coloniser les eaux saumâtres puis continentales, et même conquérir des habitats terrestres. Contrairement à nos crabes d'eau douce, ces représentants de familles marines qui, d'abord amphibies, se sont complètement adaptés à un nouvel environnement pour devenir crabes des rochers, crabes de sable, crabes violonistes, crabes des arbres, crabes de terre, montrent des liens de parenté avec d'autres familles vivant dans la mer. Et ils y retournent pour leur vie larvaire, parfois au prix de longues migrations.

En revanche, chez les vrais crabes d'eau douce, le développement est direct et se passe complètement en dehors de la mer. Après une longue période d'incubation, d'un très gros œuf sort un petit crabe directement éclos qui a déjà la forme des parents : c'est une miniature de l'adulte. Pendant un certain temps les jeunes vivent sous l'abdomen de la femelle, se promenant sur sa carapace ou alentour avec une protection parentale, comme on le voit chez des araignées ou des crapauds. Contrairement à ce qui se passe chez les crabes marins, il n'y a pas de stade planctonique, la zoé, et donc pas de dissémination puisque les phases nageuses ont été éliminées. C'est pourquoi un isolement géographique souvent très important caractérise les formes d'eau douce. La reconnaissance des espèces, souvent extrêmement difficile, doit faire appel à la morphologie des appendices sexuels mâles.

Le mémoire du Dr. Neil CUMBERLIDGE est une synthèse des connaissances sur les crabes d'eau douce de l'Ouest Africain et il couvre la faune de dix-huit pays de ce continent. Une seule famille, celle des Potamonautidae, est représentée, mais avec sept genres et 32 espèces, soit le tiers des espèces et sous-espèces de crabes dulçaquicoles actuellement recensées sur le continent africain. Cinq nouvelles espèces sont décrites et, au passage, est distinguée une nouvelle famille, dont les représentants habitent le lac Tanganyika. Le présent mémoire vient jalonner l'histoire des crabes d'eau douce africains, marquée par l'œuvre de Mary J. RATHBUN (1904-1906), en partie réalisée au Muséum national d'histoire naturelle, Paris, et de Richard Bott dont la monographie de 1955 traitait toute la faune brachyourienne de l'Afrique. Deux articles de Théodore MONOD, 1977 et 1980, avaient plus particulièrement concerné la faune sahélo-soudanaise. N. CUMBERLIDGE couronne ses recherches passées sur la faune africaine, ponctuées de nombreuses notes, par ce travail qui rassemble de très nombreuses données. Il s'est appuyé sur ses récoltes personnelles ainsi que sur le matériel déposé dans les grands musées, et notamment au Muséum national d'histoire naturelle, Paris. Pour chaque espèce, figurent une liste des synonymies et des références, une diagnose, des renseignements biogéographiques et écologiques. En outre, est dressée une histoire phylogénétique de la famille des Potamonautidae, où la question cruciale de la monophylie est discutée. Pour cela, nous est proposée la première analyse cladistique des crabes d'Afrique, qui se base sur 33 caractères morphologiques. Le clade Potamonautidae est en effet reconnu, avec deux branches principales qui sont interprétées comme deux sous-familles.

Une très intéressante étude morphométrique concernant les proportions du corps fait ressortir qu'une carapace plate est associée à une existence complètement aquatique, tandis qu'une carapace plus épaisse est mise en rapport avec une existence semi-terrestre ou terrestre.

Le mémoire du Dr. Neil CUMBERLIDGE sur les crabes d'eau douce de l'Ouest Africain fait suite à deux ouvrages consacrés à deux familles de crabes des eaux douces d'Amérique (tous deux par G. RODRIGUEZ, 1982 et 1992), pareillement publiés dans la série « Faune tropicale » de l'Orstom. L'Institut français de recherches pour le développement en coopération s'honore de publier des travaux d'ordre fondamental et, plus particulièrement, de systématique. Le savoir zoologique, avec la connaissance précise de la taxonomie des animaux, est à la base de toutes les autres sciences et peut seul permettre des recherches d'ordre biologique et appliqué.

Les crabes d'eau douce ont une grande importance économique. Ils forment une part non négligeable de l'alimentation dans certains pays. On sait qu'ils peuvent abriter le dernier stade larvaire (métacercaire) d'un ver trématode à l'origine de la paragonimose, ou distomatose pulmonaire, une maladie qui sévit gravement en Asie du Nord-Est et du Sud-Est, en Afrique et en Amérique latine. Le premier hôte est un mollusque (dont l'identité n'est pas connue en ce qui concerne l'Afrique), le crabe est le deuxième hôte, et le dernier un mammifère carnivore ou un primate. L'homme s'infeste en mangeant des crabes insuffisamment cuits : la métacercaire résiste à un quart d'heure d'ébullition. Le Bulletin de l'OMS de 1995 faisait état, pour le monde entier, de 30 millions de patients et, par ailleurs, estimait à 190 millions d'individus la population exposée du fait de l'ingestion de crabes. En Afrique, les pays les plus touchés actuellement seraient le Cameroun et le Nigeria. Seules deux espèces du tréma-tode *Paragonimus* sont connues en Afrique mais leur nombre est probablement plus élevé. Au moins sept espèces ouest-africaines de crabes d'eau douce ont été identifiées comme les hôtes intermédiaires de ce parasite pathogène : *Liberonautes latidactylus*, *L. paludicolis*, *L. chaperi*, *Sudanonautes africanus*, *S. aubryi*, *S. orthostylis*, *S. granulatus*, mais il est probable que d'autres espèces, récoltées dans les régions humides ou dans la savane de l'ouest africain et utilisées comme nourriture, sont dangereuses.

Comment reconnaître les espèces en question, comment en distinguer les formes les plus proches ? Dans quelles régions sont-elles présentes et dans quel habitat ? Quelles sont les autres formes potentiellement dangereuses ? Nous trouverons toutes ces informations dans le mémoire qui est publié ici. Diverses clefs dichotomiques pour permettre la reconnaissance à tous les niveaux, une excellente illustration, de nombreuses cartes de répartition, une bibliographie complète, ainsi qu'un index faciliteront l'utilisation de cet ouvrage.

Nous savons gré à l'auteur de nous offrir une œuvre de cette qualité, qui sera utile non seulement au taxonomiste, au biogéographe, à l'écologiste, mais aussi à tous ceux qui sont en charge de la gestion et de la protection de la diversité du vivant, à ceux qui étudient les problèmes de l'alimentation dans le monde, au médecin, au parasitologiste.

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Summary

The freshwater crabs of West Africa

The area of West Africa covered by this book includes eighteen countries: Mauritania, Senegal, The Gambia, Guinea Bissau, Guinea, Sierra Leone, Liberia, Côte d'Ivoire, Mali, Burkina Faso, Ghana, Togo, Benin, Niger, Nigeria, Chad, Cameroon and Equatorial Guinea (Bioko). Chad, Cameroon and part of Equatorial Guinea (Bioko) are usually treated as part of Central Africa rather than West Africa but these countries have been included because their freshwater crab faunas are principally West African in character (although endemic taxa and other species of Central African origin may also be represented in these countries). The West African faunal region is an informal subdivision of the Afrotropical (Ethiopian) zoogeographical region, and lies to the south of the European and Middle Eastern components of the Palaearctic zoogeographical region, where freshwater crabs of the genus *Potamon* (family Potamidae ORTMANN, 1896) are found. The West African freshwater crab fauna includes at least thirty two species in seven genera and one family. This fauna is arguably the most diverse in Africa and has a distinct character which differs greatly from that found elsewhere on the continent.

The present work brings together recent contributions to the taxonomy, distribution, and ecology of the entire West African freshwater crab fauna (BOTT, 1955, 1959, 1964, 1969a, 1970a; MONOD, 1977, 1980; CUMBERLIDGE, 1985a, 1987, 1991a, 1993a,b,c, 1994a,b, 1995a,b,c,d, 1996a,b, 1999; CUMBERLIDGE & CLARK, 1992; CUMBERLIDGE & SACHS, 1989a, 1991 and presents new information on phylogeny and biogeography. The past ten years or so have seen the establishment of two new genera (*Potamonemus* CUMBERLIDGE & CLARK, 1992 and *Louisea* CUMBERLIDGE, 1994) and the description of a number of new species from West Africa. The new species include *Globonautes leonensis* CUMBERLIDGE, 1987, *Sudanonautes kagoroensis* CUMBERLIDGE, 1991a, *Potamonemus mambilorum* CUMBERLIDGE & CLARK, 1992, *P. asylos* CUMBERLIDGE, 1993a, *P. sachsi* CUMBERLIDGE, 1993a and *Liberonautes nimba* CUMBERLIDGE, 1999. In addition, a number of other species which had formerly been recognised as subspecies (*Liberonautes paludicolis* CUMBERLIDGE & SACHS, 1989a, *L. nanoides* CUMBERLIDGE & SACHS, 1989a, *L. rubigimanus* CUMBERLIDGE & SACHS, 1989a, *L. chaperi* (A. MILNE-EDWARDS, 1887), *Sudanonautes orthostylis* (BOTT, 1955), *S. chavanesii* (A. MILNE-EDWARDS, 1886), *S. floweri* (DE MAN, 1901), *S. monodi* (BALSS, 1929), *Louisea balssi* (BOTT, 1959), and *L. edeaensis* (BOTT, 1969)) or as junior subjective synonyms (*Sudanonautes granulatus* (BALSS, 1929) and *S. faradjensis* (RATHBUN, 1921)) are recognised here as valid species. The present work adds a further four new species to the faunal list of the region: *Potamonautes reidi, Liberonautes grandbassa, L. lugbe* and *Sudanonautes nigeria.*

The systematics of the freshwater crabs of Africa has rarely been investigated within an evolutionary framework because the earlier classifications of RATHBUN (1904-1906) and BOTT (1955, 1970a,b) were formulated without indicating genealogical relationships. BOTT (1955, 1969a, 1970a,b) assigned West African species to the Potamonautidae BOTT, 1970a and the Gecarcinucidae RATHBUN, 1904 (Globonautinae BOTT, 1969b), while MONOD (1977, 1980) assigned West African species to the Potamidae and the Gecarcinucidae (Globonautinae). Both classifications imply that the West African freshwater crabs do not form a single monophyletic group.

The present work examines the phylogenetic history of the freshwater crabs of West Africa and the question of monophyly. The West African species are assigned to two main lines, the Potamonautidae and the Globonautinae (which is removed from the Gecarcinucidae). This classification is based on the results of a preliminary cladistic analysis of the West African freshwater crabs. The study uses thirty three morphological characters of the carapace, pereiopods, mandible, sternum, abdomen, and gonopods to derive the most parsimonious cladograms for the group. The analysis includes seven genera of West African freshwater crabs (*Potamonautes* MACLEAY, 1838, *Liberonautes* BOTT, 1955, *Sudanonautes* BOTT, 1955, *Potamonemus* CUMBERLIDGE & CLARK, 1993, *Louisea* CUMBERLIDGE, 1994a, *Globonautes* BOTT, 1959, and *Afrithelphusa* BOTT, 1969b) and employs data derived from thirty two ingroup taxa and five outgroup taxa (*Menippe* DE HAAN, 1833, *Goniopsis* DE HAAN, 1853, *Gecarcinucus* H. MILNE EDWARDS, 1844, *Potamon* SAVIGNY, 1816 and *Platythelphusa* A. MILNE-EDWARDS, 1887). The outgroup taxa comprise two marine crab genera, *Menippe* (Menippidae H. MILNE EDWARDS, 1834) and *Goniopsis* (Grapsidae MACLEAY, 1838, Grapsinae MACLEAY, 1838) and three freshwater crab genera, *Potamon* (Potamidae ORTMANN, 1896) from Europe, Middle East and parts of Asia, *Platythelphusa* (Platythelphusidae COLOSI, 1920) from

Lake Tanganyika in East Africa and *Gecarcinucus* (Gecarcinucidae RATHBUN, 1904) from Bombay, India. Data were entered into the data matrix using MacClade version 3.06, and character analyses were carried out using PAUP version 3.1 on a Macintosh. The analyses of thirty two characters yielded five most parsimonious trees all with 55 steps and a consistency index of 0.75, and a retention index of 0.79. The modifications to the existing classification proposed here are based on the results of this cladistic analysis. It should be stressed that the present classification was constructed using a regional fauna, rather than the fauna from the entire Afrotropical region. In this sense, then, the results are inevitably somewhat tentative and may ultimately be revised when data from other taxa from the rest of Africa and from other parts of the tropics are included. However, it is likely that future revisions will not alter substantially the relationships outlined here.

The modified classification proposed here differs in several respects from the classification used by other authors. All of the ingroup taxa were found to belong to two separate clades which are interpreted as the family Potamonautidae BOTT, 1970a and the subfamily Globonautinae BOTT, 1969a. The Globonautinae is supported by a number of robust synapomorphies, while the Potamonautidae is supported by fewer synapomorphies. BOTT (1955) established the Hydrothelphusinae BOTT, 1955 (for the genus *Hydrothelphusa* A. MILNE-EDWARDS, 1887) from Madagascar as a subfamily of the Potamonautidae. Since the genus *Hydrothelphusa* was not included as part of this study its taxonomic status awaits further evaluation. The Potamonautidae includes four West African genera (*Potamonautes*, *Liberonautes*, *Sudanonautes* and *Potamonemus*) while the Globonautinae BOTT, 1969a is expanded to include three genera (*Globonautes*, *Afrithelphusa* and *Louisea*). *Gecarcinucus* (representing the Gecarcinucidae) does not form part of the same clade as the Globonautinae or the Potamonautidae. The membership of the Globonautinae in the Gecarcinucidae is therefore uncertain. In addition, *Platythelphusa* from Lake Tanganyika is not included in the Potamonautidae clade. This taxon was previously classified by BOTT (1955) as a subgenus of *Potamonautes*; it is recognised here as belonging to a distinct genus (*Platythelphusa*) and is removed from the Potamonautidae. *Platythelphusa* is substantially different from the four genera of the Potamonautidae in the present study in a number of important characters of the carapace, frontal margin, mandibular palp, and gonopod 1. There is some support for the recognition of a new family, the Platythelphusidae COLOSI, 1920 for *Platythelphusa*.

Morphometric relationships of the dimensions and proportions of the carapace (such as carapace width, cw/fw; carapace length, cl/fw; carapace height, ch/fw, and frontal margin width, fw/cl) were investigated for all included species. Each was found to provide a useful index for making interspecific comparisons. Morphometric relationships of the dimensions and proportions of the carapace revealed trends in changes in the width, length and height of the carapace of species within a genus. It was found that these trends could be correlated with the habitat and lifestyle of each species. For example, a wide and flat carapace is associated with living a completely aquatic existence in lakes, large streams or in the major rivers (e.g., *Sudanonautes faradjensis* RATHBUN, 1921 and *Liberonautes chaperi* A. MILNE-EDWARDS, 1887), while a moderately high or very high carapace is associated with modifications of the branchial chambers for aerial respiration, and is typical of species with a semiterrestrial or terrestrial lifestyle (e.g., *Sudanonautes floweri* DE MAN, 1901, *S. monodi* BALSS, 1929, *Globonautes macropus* RATHBUN, 1898 and *Afrithelphusa monodosus* BOTT, 1959). Characters derived from carapace proportions were found to be useful secondary characters for the identification of species within a genus. No significant difference was found between the carapace proportions of male and female freshwater crabs examined in this study. In some species (e.g., *Potamonautes ecorssei* (MARCHAND, 1902), *Liberonautes chaperi* A. MILNE-EDWARDS, 1887, *Sudanonautes chavanesii* A. MILNE-EDWARDS, 1886 and *Globonautes macropus* RATHBUN, 1898, the carapace proportions were found to remain unaltered as an animal grows (no significant difference was found between carapace proportions between juvenile, subadult and adult animals) and the carapace proportions of specimens of any age were used. In other species (e.g., *Liberonautes paludicolis* CUMBERLIDGE & SACHS, 1989a, *Sudanonautes aubryi* H. MILNE EDWARDS, 1853 and *S. monodi* BALSS, 1929) the carapace proportions of adults were found to be significantly different from those of juvenile and subadult animals and in these cases only the carapace proportions of adults were used.

Trends in the change in the carapace proportions (such as from species with a moderately high carapace to species with a highly arched carapace) were found to be expressed separately in different genera, especially in those genera with large numbers of species (e.g., *Potamonautes*, *Liberonautes* and *Sudanonautes*). This was interpreted as parallel evolution within each genus associated with the radiation and subsequent adaptation to different habitats. For this reason characters derived from carapace proportions were considered to be homoplasious and were not used in the cladistic analysis.

The thirty two species of freshwater crabs found in the West African region represent about one-third of the species and subspecies presently known from the continent (Bott, 1955, 1959, 1960, 1964, 1968, 1969a, 1970a,b; Monod, 1977, 1980; Cumberlidge, 1985a, 1987, 1991a, 1993a,b,c, 1994a,b, 1995a,b,c,d, 1996a,b, 1999; Cumberlidge & Clark, 1992; Cumberlidge & Sachs, 1989a, 1991; Stewart, Coke & Cook, 1995; Stewart, 1997). Most of the species dealt with in the present study occur exclusively in West Africa (from Sénégal to Nigeria), while the range of several species of *Sudanonautes* extends into Central Africa. This latter area includes Cameroon, Chad, southern Sudan, the Central African Republic, Democratic Republic of Congo north of the river Zaire, Congo, Gabon, Equatorial Guinea (the island of Bioko). A number of other species of *Potamonautes* and *Erimetopus* Rathbun, 1894 that are not dealt with in the present work are also found in this part of Central Africa (Rathbun, 1904, 1905, 1906; Balss, 1936; Bott, 1955).

The taxonomic diversity of the West African region at the genus level (seven genera) is higher than that of the whole of the rest of continental Africa (four genera). Species diversity within the West African region clearly depends on vegetation cover, where the highest number of species occurs in rainforest ecosystems, and the fewest in savanna ecosystems. One species (*Potamonautes ecorssei* (Marchand, 1902) is even found in the desert zone in Mali, but only where the river Niger flows through Timbuktu. Eight of the thirty two species of West African freshwater crabs have a wide distribution over an extensive area, while less than half of all species (fourteen out of thirty two) have a restricted distribution. Three species (*Sudanonautes aubryi* A. Milne Edwards, *S. granulatus* Balss, 1929 and *Potamonemus sachsi* Cumberlidge, 1993a) have a disjunct distribution pattern, occurring in two geographically separated areas, but not in the interval between them.

The tropical rainforest zone in the West African region consists of two main parts, the Upper Guinea forest block (in Guinea, Sierra Leone, Liberia, Côte-d'Ivoire, Ghana and Togo), and the Lower Guinea forest (a much larger forest block in south east Nigeria, south Cameroon, Gabon, Congo, Central African Republic, and Democratic Republic of Congo). Each forest block supports a distinct freshwater crab fauna. These two forests are separated by a stretch of coastal savanna in Ghana, Togo and Benin known as the Dahomy Gap.

The freshwater crab fauna of the western part of the Upper Guinea forest (in Guinea, Sierra Leone, and Liberia) consists of thirteen species in three genera (*Liberonautes*, *Globonautes* and *Afrithelphusa*) which belong to either the Potamonautidae or the Globonautinae; eleven species and two genera (*Globonautes* and

Afrithelphusa) are endemic. This forest is dominated by species of *Liberonautes* but also includes representatives of the rare and threatened species of *Globonautes* and *Afrithelphusa*; *Potamonautes* and *Sudanonautes* are absent from this part of the forest. The freshwater crab fauna of the eastern part of the Upper Guinea forest (in Côte-d'Ivoire, Ghana and Togo) consists of six species in three genera (*Liberonautes*, *Potamonautes*, and *Sudanonautes*); only one species, *Potamonautes triangulus* Bott, 1959, is endemic. This part of the forest supports two species in each of these three genera, while *Globonautes* and *Afrithelphusa* are absent.

The Lower Guinea forest is the most species rich of the entire West African region and has representatives of *Sudanonautes*, *Potamonautes* and *Potamonemus* and the endemic genus *Louisea*. The freshwater crab fauna of the Lower Guinea forest is distinct from that of the Upper Guinea forest, and completely lacks representatives of *Liberonautes*, *Globonautes* and *Afrithelphusa*. The western part of the Lower Guinea forest in Nigeria is home to seven species in three genera (*Sudanonautes*, *Potamonautes* and *Potamonemus*) and includes two endemic species (*Sudanonautes nigeria* n. sp. and *Potamonautes reidi* n. sp.). The eastern part of the Lower Guinea forest in southern Cameroon consists of twelve species in four genera (*Sudanonautes*, *Potamonautes*, *Potamonemus* and *Louisea*) and includes five endemic species (*Sudanonautes orthostylis* Bott, 1955, *Potamonemus asylos* Cumberlidge, 1993a, *P. mambilorum* Cumberlidge & Clark, 1992, *Louisea edeaensis* Bott, 1969b and *L. balssi* Bott, 1959) and one endemic genus (*Louisea*).

Three relatively small areas of the African rainforest stand out as having an unusually high number of species and a higher than normal number of endemic species. These areas are in the Upper Guinea forest in West Africa, in the Lower Guinea forest in Nigeria and Cameroon, and in the forests of eastern Democratic Republic of Congo. The Pleistocene forest refuge hypothesis (see Hamilton, 1976 for a review) postulates that these species-rich areas of forest represent the oldest parts of the forest. It is suggested that throughout the Pleistocene epoch these areas of forest continued to receive sufficient rainfall while elsewhere in Africa the alternating moist and arid climatic periods associated with the northern ice ages and interglacials caused major shifts in the vegetation cover. The idea that there were small areas of stable, undisturbed areas of forest in Africa during the Pleistocene is supported by distributional data from independent studies of other groups (trees, mammals, butterflies, amphibia, and birds) which also identify (among others) these same three centres of species richness and endemism in the African forests (CARCASSON, 1964; HAMILTON, 1976; DIAMOND & HAMILTON, 1980; MAYR & O'HARA, 1986). The Earth is presently experiencing an interglacial period and mean global temperatures and rainfall are relatively high (in comparison with values during glacial periods). The last glacial period ended about 12,000 BP and since then the climate in West Africa has become wetter and warmer, and the forests have expanded so that the species-rich refuge areas are now part of a much larger expanse of younger-growth forest. The expansion of the African forests has allowed species of freshwater crabs from the refuge areas to disperse out of the refuges into the adjacent new growth forests. This may be responsible for the observed gradients of increasing species poverty with increasing distance from the refuge areas. This work deals only with events in the geologically recent past and does not address questions about the phylogeny and historical biogeography of the African freshwater crabs.

Aspects of the biology of the West African freshwater crabs, such as the respiratory system, reproductive system, growth patterns, development, and ecology are also discussed.

Résumé

Les crabes d'eau douce de l'Afrique occidentale

La région de l'Afrique de l'Ouest concernée par cette étude s'étend à dix-huit pays : Mauritanie, Sénégal, Gambie, Guinée-Bissau, Guinée, Sierra Leone, Liberia, Côte d'Ivoire, Mali, Burkina Faso, Ghana, Togo, Bénin, Niger, Nigeria, Tchad, Cameroun et Guinée Équatoriale (Bioko). Le Tchad, le Cameroun, et, en partie, la Guinée Équatoriale (Bioko) sont d'habitude considérés comme faisant partie de l'Afrique centrale plutôt que de l'Afrique occidentale mais ces pays ont été inclus car leur faune de crabes d'eau douce est plus proche par ses caractères de celle d'Afrique occidentale, malgré l'endémisme de certains taxons et la présence d'autres espèces originaires d'Afrique centrale. La région faunistique ouest-africaine est une subdivision informelle de la région zoogéographique afrotropicale (éthiopienne) ; elle s'étend au sud de l'Europe et du Moyen Orient, composantes de la région zoogéographique paléarctique, où sont rencontrés les crabes d'eau douce du genre *Potamon* (famille des Potamidae, ORTMANN, 1896). La faune ouest-africaine de crabes d'eau douce comprend au moins trente-deux espèces, réparties en sept genres et deux familles. Cette faune est sans aucun doute la plus diversifiée d'Afrique et présente un ensemble de caractères qui la sépare nettement de celles connues sur le reste du continent.

Dans le présent travail figurent, d'une part, les contributions les plus récentes à la connaissance de la taxonomie, de la répartition, de l'écologie de l'ensemble de la faune ouest-africaine de crabes d'eau douce (BOTT, 1955, 1959, 1964, 1969a, 1970a ; MONOD, 1977, 1980 ; CUMBERLIDGE, 1985a, 1987, 1991a, 1993a,b,c, 1994a,b, 1995a,b,c,d, 1996a,b, 1999 ; CUMBERLIDGE & CLARK, 1992 ; CUMBERLIDGE & SACHS, 1989a, 1991, et, d'autre part, de nouvelles informations sur leur phylogénie et leur biogéographie. Ces dix dernières années ont vu l'établissement de deux nouveaux genres (*Potamonemus* CUMBERLIDGE & CLARK, 1992 et *Louisea* CUMBERLIDGE, 1994) et de plusieurs espèces nouvelles d'Afrique de l'Ouest (*Globonautes leonensis* CUMBERLIDGE, 1987, *Sudanonautes kagoroensis* CUMBERLIDGE, 1991a, *Potamonemus mambilorum* CUMBERLIDGE & CLARK, 1992, *P. asylos* CUMBERLIDGE, 1993a, *P. sachsi* CUMBERLIDGE, 1993a, *Liberonautes nimba*, CUMBERLIDGE, 1999). De plus, un certain nombre d'autres espèces, qui étaient auparavant reconnues comme sous-espèces (*Liberonautes paludicolis* CUMBERLIDGE & SACHS, 1989a, *L. nanoides* CUMBERLIDGE & SACHS, 1989a, *L. rubigimanus* CUMBERLIDGE & SACHS, 1989a, *L. chaperi* (A. MILNE-EDWARDS, 1887), *Sudanonautes orthostylis* (BOTT, 1955), *S. chavanesii* (A. MILNE-EDWARDS, 1886), *S. floweri* (DE MAN, 1901), *S. monodi* (BALSS, 1929), *Louisea balssi* (BOTT, 1959) et *L. edeaensis* (BOTT, 1969b) ou comme synonymes juniors (*Sudanonautes granulatus* (BALSS, 1929) et *S. faradjensis* (RATHBUN, 1921) sont considérées ici comme des espèces valides. Enfin, quatre nouvelles espèces sont décrites qui viennent s'ajouter à l'inventaire faunistique de la région : *Potamonautes reidi, Liberonautes grandbassa, L. lugbe* et *Sudanonautes nigeria*.

La systématique des crabes d'eau douce d'Afrique a rarement été étudiée dans une approche évolutioniste car les précédentes classifications de RATHBUN (1904-1906) et de BOTT (1955, 1970a,b) ont été établies sans que les liens généalogiques aient été pris en compte. BOTT (1955, 1969a, 1970a,b) place les espèces ouest-africaines dans les familles des Potamonautidae BOTT, 1970a et des Gecarcinucidae RATHBUN, 1904 (Globonautinae BOTT, 1969b) alors que MONOD (1977, 1980) les place dans les Potamidae et les Gecarcinucidae (Globonautinae). Ces deux classifications impliquent que les crabes d'eau douce ouest-africains ne forment pas un groupe monophylétique.

En revanche, ce travail examine l'histoire phylogénétique des crabes d'eau douce de l'Afrique occidentale et pose la question de leur monophylie. Il assigne les espèces à deux phylums principaux, les Potamonautidae et les Globonautinae (qui sont retirés des Gecarcinucidae). Cette classification est fondée sur les résultats, encore préliminaires, d'une analyse cladistique des crabes d'eau douce ouest-africains. L'étude utilise trente-trois caractères morphologiques (de la carapace, des péréiopodes, de la mandibule, du sternum, de l'abdomen et des gonopodes) pour obtenir les cladogrammes les plus parcimonieux pour le groupe. L'analyse porte sur sept genres de crabes d'eau douce africains (*Potamonautes* MACLEAY, 1838, *Liberonautes* BOTT, 1955, *Sudanonautes* BOTT, 1955, *Potamonemus* CUMBERLIDGE & CLARK, 1993, *Louisea* CUMBERLIDGE, 1994a, *Globonautes* BOTT, 1959 et *Afrithelphusa* BOTT, 1969b), les données faisant appel à vingt-deux taxons "ingroup" et à cinq taxons "outgroup" (*Menippe* DE HAAN, 1833, *Goniopsis* DE HAAN, 1853, *Gecarcinucus* H. MILNE-EDWARDS, 1844, *Potamon* SAVIGNY, 1816 et

Platythelphusa A. MILNE-EDWARDS1887). Dans cet "outgroup", on trouve deux genres de crabes marins, *Menippe* (Menippidae H. MILNE-EDWARDS, 1834) et *Goniopsis* (Grapsidae MACLEAY, 1838, Grapsinae MACLEAY, 1838) et trois genres de crabes d'eau douce, *Potamon* (Potamidae ORTMANN, 1896) d'Europe, du Moyen Orient et de certaines régions d'Asie, *Platythelphusa* (Platythelphusidae COLOSI, 1920) du lac Tanganyika en Afrique de l'Est, et *Gecarcinucus* (Gecarcinucidae RATHBUN, 1904) de Bombay en Inde.

La matrice de données a été constituée selon la version MacClade 3.06 et l'analyse des caractères menée en utilisant la version PAUP 3.1 sur Macintosh. Les résultats se présentent sous la forme de cinq arbres les plus parcimonieux, tous avec 55 divisions, un indice de consistance de 0,75 et un indice de rétention de 0,79. Les modifications proposées par rapport aux précédentes classifications sont fondées sur les résultats de cette analyse cladistique. Il faut noter que cette nouvelle classification ne prend en considération qu'une faune régionale et non l'ensemble de la faune afrotropicale. En ce sens, bien entendu, les résultats ne représentent inévitablement qu'une première tentative ; ils pourront plus tard être corrigés quand seront analysées des données portant sur davantage de taxons d'Afrique ou d'autres régions tropicales. Cependant, il est probable que les futures révisions ne remettront pas fondamentalement en cause les liens entre espèces esquissés ici.

Cette nouvelle classification diffère en plusieurs points des précédentes. Tous les taxons ouest-africains se placent dans deux clades qui s'identifient respectivement à la famille des Potamonautidae BOTT, 1970a et à la sous-famille des Globonautinae BOTT, 1969a. La sous-famille des Globonautinae est étayée par de nombreuses et robustes synapomorphies, la famille des Potamonautidae par des synapomorphies moins nombreuses. BOTT (1955) a créé la sous-famille des Hydrothelphusinae dans la famille des Potamonautidae, pour le genre *Hydrothelphusa* A. MILNE-EDWARDS, 1887 de Madagascar. Le genre *Hydrothelphusa* n'est pas considéré dans cette étude ; sa position taxonomique sera évaluée ultérieurement. Les Potamonautidae comprennent quatre genres ouest-africains (*Potamonautes, Liberonautes, Sudanonautes* et *Potamonemus*), les trois autres genres (*Globonautes, Afrithelphusa* et *Louisea*) appartenant aux Globonautidae BOTT, 1969a. *Gecarcinucus* (représentant les Gecarcinucidae) ne fait pas partie des mêmes clades que les Globonautinae et les Potamonautidae. L'appartenance de la sous-famille des Globonautinae à la famille des Gecarcinucidae est donc incertaine. En outre, *Platythelphusa* du lac Tanganyika ne fait pas partie du clade Potamonautidae. Ce taxon avait d'abord été considéré par BOTT (1955) comme sous-genre de *Potamonautes* ; il est reconnu ici comme un genre distinct, nettement différent des quatre genres de Potamonautidae de cette étude par plusieurs caractères importants de la carapace, du bord frontal, du palpe mandibulaire et du gonopode 1. Ces arguments plaident pour l'élévation au rang de famille de la sous-famille des Platythelphusinae COLOSI, 1920.

Les relations morphométriques entre dimensions de la carapace : cw/fw, cl/fw, ch/fw, fw/cl (cw = largeur de la carapace, cl = longueur, ch = hauteur, fw = largeur du bord frontal) ont été établies pour chacune des espèces. Il s'est avéré que ces relations sont utiles dans les comparaisons interspécifiques ; elles mettent en évidence des tendances dans les changements de largeur, longueur et hauteur de carapace chez les espèces à l'intérieur d'un même genre, qui pourraient être en rapport avec l'habitat et avec le mode de vie de chaque espèce. Par exemple, une carapace large et plate est associée à une vie complètement aquatique dans les lacs et les grands cours d'eau (c'est le cas de *Sudanonautes faradjensis* (RATHBUN, 1921) et de *Liberonautes chaperi* (A. MILNE-EDWARDS, 1887) alors qu'une carapace modérément ou très haute, caractère lié à des modifications des chambres branchiales (adaptations à la respiration aérienne), est typique d'espèces semi-terrestres ou terrestres (par exemple *Sudanonautes floweri* (DE MAN, 1901), *S. monodi* (BALSS, 1929), *Globonautes macropus* (RATHBUN, 1898) et *Afrithelphusa monodosus* (BOTT, 1959). Les relations entre dimensions de la carapace constituent d'utiles caractères secondaires pour l'identification des espèces d'un même genre. Aucune différence significative n'apparaît entre proportions de la carapace des mâles et femelles des crabes d'eau douce examinés dans ce travail. Chez quelques espèces (comme *Potamonautes ecorssei* (MARCHAND, 1902), *Liberonautes chaperi* (A. MILNE-EDWARDS, 1887), *Sudanonautes chavanesii* (A. MILNE-EDWARDS, 1886) et *Globonautes macropus* (RATHBUN, 1898) les proportions de la carapace demeurent inchangées au cours de la croissance, que les individus soient juvéniles, subadultes ou adultes, ce qui permet de les utiliser quel que soit l'âge des spécimens. Chez d'autres espèces (par exemple *Liberonautes paludicolis* CUMBERLIDGE & SACHS, 1989a, *Sudanonautes aubryi* (H. MILNE-EDWARDS, 1853) et *S. monodi* (BALSS, 1929) les proportions de la carapace des adultes diffèrent significativement de celles des juvéniles et subadultes. Dans ce cas on a utilisé uniquement les adultes dans l'étude morphométrique.

Les tendances dans les changements de proportion de la carapace (tels qu'observés chez les espèces à carapace modérément haute jusqu'aux espèces à carapace fortement voûtée) s'expriment de façon particulière dans les différents genres, notamment dans ceux où l'on rencontre de nombreuses espèces (comme *Potamonautes, Liberonautes* et *Sudanonautes*). On l'a interprété comme une évolution parallèle à l'intérieur de chaque genre, associée au phénomène de radiation et à l'adaptation subséquente à différents habitats. Pour cette raison, les proportions de la carapace ont été considérées comme des caractères homoplasiques et n'ont pas été prises en compte dans les analyses cladistiques.

Les trente-deux espèces de crabes d'eau douce d'Afrique occidentale étudiées ici représentent environ un tiers des espèces et sous-espèces aujourd'hui connues sur ce continent (BOTT, 1955, 1959, 1960, 1964, 1968, 1969a, 1970a,b ; MONOD, 1977, 1980 ; CUMBERLIDGE, 1985a, 1987, 1991a, 1993a,b,c, 1994a,b, 1995a,b,c,d, 1996a,b, 1999 ; CUMBERLIDGE & CLARK, 1992 ; CUMBERLIDGE & SACHS, 1989a, 1991 ; STEWART, COKE & COOK, 1995 ; STEWART, 1997). La plupart vivent exclusivement en Afrique de l'Ouest (du Sénégal au Nigeria) alors que la répartition de plusieurs espèces de *Sudanonautes* s'étend jusqu'à l'Afrique centrale, qui comprend le Cameroun, le Tchad, le Sud-Soudan, la République Centre Africaine, le Zaïre au nord du fleuve Zaïre, le Congo, le Gabon, la Guinée Équatoriale (avec l'île de Bioko). Un certain nombre d'autres espèces appartenant aux genres *Potamonautes* et *Erimetopus* RATHBUN, 1894 et non considérées ici sont aussi rencontrées dans cette partie de l'Afrique centrale (RATHBUN, 1904, 1905, 1906 ; BOTT, 1955 ; BALSS, 1936).

La diversité taxonomique de l'Afrique occidentale au niveau du genre (sept genres) est plus élevée que celle du reste du continent africain dans son ensemble (quatre genres). La diversité spécifique en Afrique occidentale dépend du couvert végétal : le plus grand nombre d'espèces se rencontre dans les écosystèmes de forêts humides et le plus faible dans les écosystèmes de savane. Une espèce, *Potamonautes ecorssei* (MARCHAND, 1902), est même récoltée en zone désertique, au Mali, mais seulement dans le cours du fleuve Niger vers Tombouctou. Huit des trente-deux espèces de crabes d'eau douce ouest-africains ont une large répartition, couvrant une vaste zone alors que quatorze espèces, moins de la moitié, ont une aire de répartition limitée. Trois crabes (*Sudanonautes aubryi* (H. MILNE-EDWARDS, 1853), *S. granulatus* (BALSS, 1929) et *Potamonemus sachsi* CUMBERLIDGE, 1993a) montrent une répartition disjointe, en deux aires géographiques séparées.

La zone de forêt humide tropicale d'Afrique de l'Ouest comporte deux parties, le bloc forestier de haute Guinée d'une part (Guinée, Sierra Leone, Liberia, Côte d'Ivoire, Ghana et Togo), celui de basse Guinée d'autre part, beaucoup plus important (sud-est du Nigeria, Sud-Cameroun, Gabon, Congo, République

Centre Africaine, Zaïre). À chaque bloc forestier correspond une faune de crabes d'eau douce particulière. Ces deux forêts sont séparées par une étendue de savane côtière au Ghana, Togo et Bénin, connue sous le nom de "Dahomey gap".

Dans la partie occidentale de la forêt de haute Guinée (Guinée, Sierra Leone et Liberia), la faune comprend treize espèces réparties en trois genres (*Liberonautes, Globonautes* et *Afrithelphusa*) appartenant soit aux Potamonautidae, soit aux Globonautinae ; sept espèces et deux genres (*Globonautes* et *Afrithelphusa*) sont endémiques. Dans ce milieu, les espèces du genre *Liberonautes* dominent, alors que les représentants des espèces de *Globonautes* et *Afrithelphusa* sont rares et menacés de disparition ; *Potamonautes* et *Sudanonautes* sont absents de cette zone forestière. La faune de la partie orientale de la forêt de haute Guinée (Côte d'Ivoire, Ghana et Togo) est composée de six espèces qui prennent place dans trois genres (*Liberonautes, Potamonautes* et *Sudanonautes*) ; seule une espèce, *Potamonautes triangulus* Bott, 1959, est endémique. On dénombre deux espèces dans chacun des trois genres, alors que *Globonautes* et *Afrithelphusa* sont absents.

La forêt de basse Guinée est la plus riche en espèces de toute la région d'Afrique occidentale ; les genres *Sudanonautes, Potamonautes, Potamonemus* sont présents ainsi que le genre endémique *Louisea*. Cette faune se distingue donc de la précédente par l'absence des genres *Liberonautes, Globonautes* et *Afrithelphusa*. La partie occidentale de cette forêt, au Nigeria, abrite sept espèces (réparties en trois genres : *Sudanonautes, Potamonautes* et *Potamonemus*) parmi lesquelles deux espèces endémiques (*Sudanonautes nigeria* n. sp. et *Potamonautes reidi* n.sp.). La partie orientale, au Sud-Cameroun, est occupée par douze espèces et quatre genres (*Sudanonautes, Potamonautes, Potamonemus* et *Louisea*) ; quatre espèces (*Sudanonautes orthosyllis* (Bott, 1955), *Potamonemus asylos* Cumberlidge 1993a, *P. mambilorum* Cumberlidge & Clark, 1992, *Louisea edeaensis* (Bott, 1969b) et *L. balssi* (Bott, 1959) sont endémiques ainsi que le genre *Louisea*.

Trois aires forestières africaines, d'étendue relativement limitée, se caractérisent par un nombre d'espèces inhabituellement élevé, ce qui vaut également pour le nombre d'espèces endémiques. Elles vivent dans la forêt de haute Guinée en Afrique de l'Ouest, dans la forêt de basse Guinée au Nigeria et au Cameroun et dans les forêts de l'est Zaïre. Selon l'hypothèse de l'existence de zones-refuges au pléistocène (voir Hamilton, 1976 pour les références), ces aires forestières à richesse spécifique élevée constituent les parties les plus anciennes de la forêt. Il est suggéré qu'au cours du pléistocène ces aires forestières ont continué à recevoir des précipitations en quantité suffisante alors que, partout ailleurs en Afrique, l'alternance de climats humides et arides associés aux âges glaciaires et interglaciaires a causé des dommages majeurs au couvert végétal. L'idée que de petites aires de forêts stables et non perturbées ont subsisté en Afrique au cours du pléistocène s'appuie sur des données de répartition tirées de travaux indépendants de celui-ci et portant sur d'autres taxons (arbres, mammifères, papillons, amphibiens et oiseaux) qui identifient, parmi d'autres, les mêmes centres de richesse spécifique et d'endémisme dans les forêts africaines (CARCASSON, 1964 ; HAMILTON, 1976 ; DIAMOND & HAMILTON, 1980 ; MAYR & O'HARA, 1986). Notre planète est aujourd'hui entrée dans une période interglaciaire et la moyenne générale des températures et des précipitations est relativement élevée (comparée aux valeurs des périodes glaciaires). La dernière période glaciaire s'est achevée aux environs de 12 000 ans BP et depuis, en Afrique occidentale, le climat est devenu plus humide, plus chaud, et les forêts se sont étendues, si bien que les aires-refuges riches en espèces font maintenant partie d'un ensemble beaucoup plus vaste de forêts plus jeunes. Cette expansion des forêts africaines a permis aux espèces de crabes d'eau douce de se disperser à partir des aires-refuges vers les jeunes forêts adjacentes. Ceci peut rendre compte de la plus grande pauvreté faunistique observée au fur et à mesure que l'on s'écarte des aires-refuges. Ce travail s'intéresse seulement aux événements du quaternaire récent et n'aborde pas la phylogénie et l'histoire biogéographique des crabes d'eau douce d'Afrique.

Des aspects de la biologie des crabes d'eau douce d'Afrique occidentale, tels que le système respiratoire, la reproduction, la croissance, le développement et l'écologie sont également discutés.

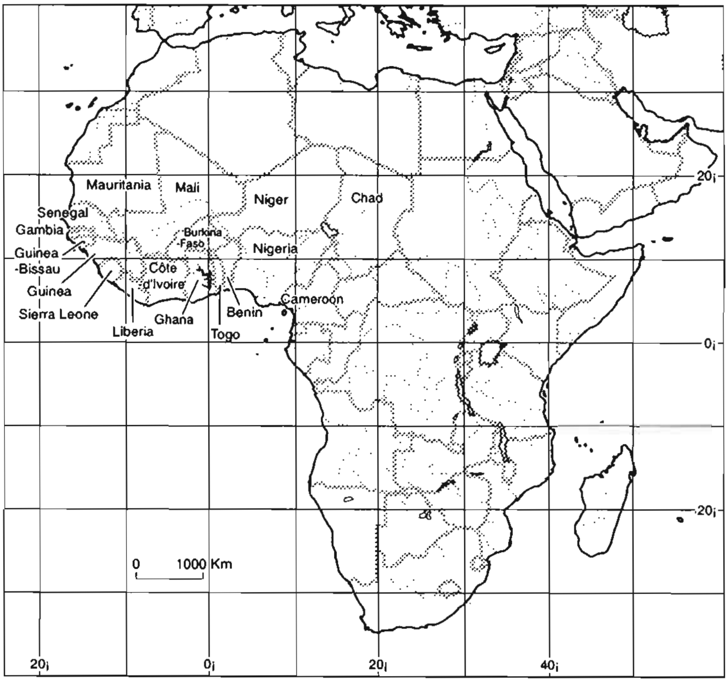

FIG. 1. The countries of West Africa plus Cameroon and Chad.

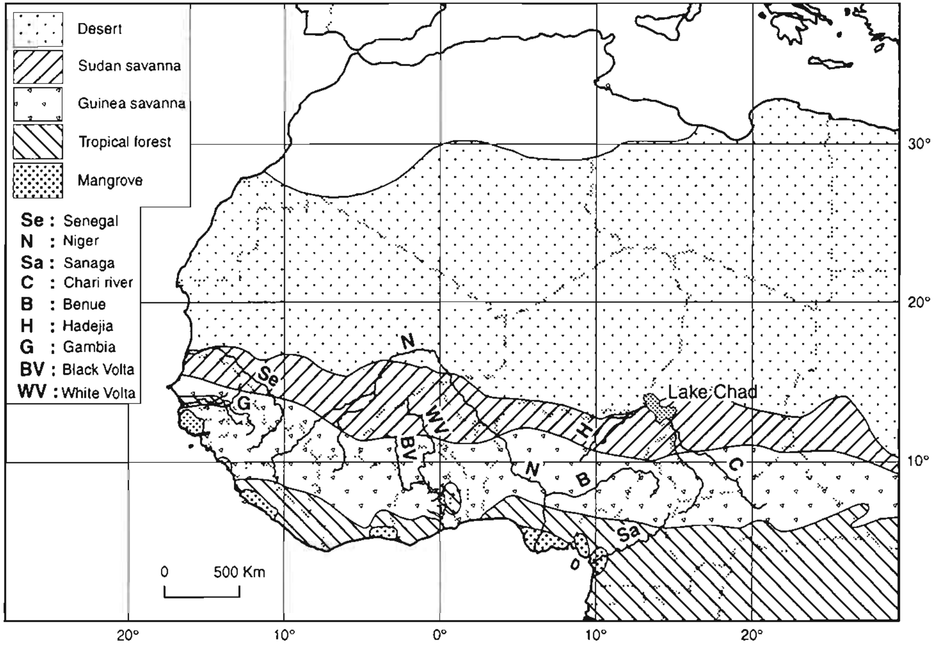

FIG. 2. The vegetation zones of West Africa. Solid black lines, rivers; filled black areas, lakes; dashed line, country boundary; thin line, boundary between ecosystems.

Introduction

The area of West Africa covered by this book includes eighteen countries (fig. 1, 2): Mauritania, Senegal, the Gambia, Guinea Bissau, Guinea, Sierra Leone, Liberia, Côte d'Ivoire, Mali, Burkina Faso, Ghana, Togo, Benin, Niger, Nigeria, Chad, Cameroon, and Equatorial Guinea (Bioko). Chad, Cameroon, and part of Equatorial Guinea (Bioko) are usually treated as part of Central Africa rather than West Africa but these countries have been included because their freshwater crab faunas are principally West African in character (although endemic taxa and other species of Central African origin may also be represented in these countries). The West African faunal region is an informal subdivision of the Afrotropical (Ethiopian) zoogeographical region, and lies to the south of the European and Middle Eastern components of the Palaearctic zoogeographical region, where freshwater crabs of the genus *Potamon* (family Potamidae) are found. The West African freshwater crab fauna includes at least thirty two species in seven genera and two families. This fauna is arguably the most diverse in Africa and has a distinct character which differs greatly from that found elsewhere on the continent.

Freshwater crabs are of great economic importance moreover, because these animals form a significant part of the diet of large numbers of people in this part of the continent. Freshwater crabs in West Africa are also of medical interest because they serve as second intermediate hosts to *Paragonimus africanus* and *P. uterobilateralis*, the parasites that cause lung fluke disease in humans (VOELKER, SACHS, VOLKMER & BRABAND, 1975; VOELKER & SACHS, 1977; NOZAIS, DOUCET, DUNAN & ASSALE N'DRI, 1980; SACHS & VOELKER, 1982; UDONSI, 1987; SACHS & CUMBERLIDGE, 1990, 1991; OLLIVIER, BOUSSINESQ, ALBARET, CUMBERLIDGE, CHIPPAUX, FARHATI & BAYSSADE-DUFOUR, 1995).

Despite these considerations, the study of African freshwater crabs has been somewhat neglected over the years. Consequently, these animals are not known nearly as well as their South American and Asian counterparts. For example, the South American freshwater crabs have been studied in recent years by a number of authors (BOTT, 1969a; PRETZMANN, 1968, 1972; RODRIGUEZ, 1982, 1992; MAGALHÃES & TÜRKAY, 1996a,b,c), as have the Asian freshwater crabs (BOTT, 1970b; NG, 1988, 1990, 1991, 1995; NG & WORWOR, 1990; NG & NAIYANETR, 1993;

NG & DUDGEON, 1991; DAI, ZHOU, & PENG, 1995; DAI, 1997; DAI & TÜRKAY, 1997; TÜRKAY & DAI, 1997). The African fauna has been monographed only twice in the 20th century, by RATHBUN (1904, 1905, 1906) and by BOTT (1955). Although MONOD's (1977, 1980) works on West Africa have contributed greatly to our knowledge of the taxonomy of these animals, his identification keys are now out of date. There is at present no single publication summarising the advances that have been made in the last few years concerning the taxonomy of the freshwater crabs of this important region of Africa.

Since 1955 the most comprehensive works on the taxonomy of the freshwater crabs of Africa were those by BOTT (1955, 1959, 1964, 1969b, 1970a,b). These publications include a 350-page monograph (BOTT, 1955) which laid the foundations for the modern taxonomy and classification of the freshwater crabs of all of Africa. BOTT's (1955) monograph summarised the state of knowledge in the field at that time, and is still used by many as the standard taxonomic reference work on African freshwater crabs. However, BOTT's (1955, 1959, 1964, 1969b, 1970a,b) conclusions were not based on a phylogenetic treatment of the group; furthermore, while these publications are vast in scope, they contain many inconsistencies. MONOD's (1977, 1980) accounts of the freshwater crabs of West Africa focused mainly on the Sahelo-Soudanienne region, and represent the most recent summaries of BOTT's taxonomic views of the freshwater crab fauna of this region.

A number of works dealing with the taxonomy of the West African freshwater crab fauna (CUMBERLIDGE, 1985a, 1987, 1991a, 1993a,b,c, 1994a,b, 1995a,b,c,d, 1996a,b, 1999; CUMBERLIDGE & CLARK, 1992; CUMBERLIDGE & SACHS, 1989a, 1991; have led to the refinement of BOTT's and MONOD's taxonomy of the group. The present work brings together these recent contributions to the taxonomy, distribution, and ecology of the entire West African freshwater crab fauna and introduces new information on phylogeny and biogeography.

History of freshwater crab studies in West Africa

The first record of the existence of freshwater crabs in Africa was the description of the river crab *Thelphusa berardi* AUDOUIN, 1825 from the Nile in Egypt. A second species from Egypt

(*T. niloticus* H. MILNE EDWARDS, 1837) was described twelve years later, together with *T. perlatus* H. MILNE EDWARDS, 1837 from South Africa. The first species to be described that is included in the present work was *T. aubryi* H. MILNE EDWARDS, 1853 which was reported from Gabon in Central Africa. During the latter part of the 19th century (from 1869 to 1887) A. MILNE EDWARDS described four more species of freshwater crabs included here from localities in West Africa (Côte-d'Ivoire) and Central Africa (Gabon). For most of the 19th century all freshwater crabs from Africa were assigned to one family, the Thelphusidae H. MILNE EDWARDS, 1837, and all species were placed in a single genus, *Thelphusa* H. MILNE EDWARDS, 1837. Towards the end of that century, the family name was revised to the Potamonidae ORTMANN, 1896 which was adopted by the majority of subsequent authors. In a later opinion, the Potamonidae was emended to the Potamidae because of a grammatical error (Opinion 712, *Bull. Zool. Nomenclature*, 21, 1964). The habit of referring to all freshwater crabs as potamonids (and later as potamids) dates back to this time.

A number of authors (ORTMANN, 1897; RATHBUN, 1904, 1905, 1906; ALCOCK, 1910a; BOUVIER, 1917a,b, 1921; COLOSI, 1920; BALSS, 1957) assumed that the freshwater crabs formed a monophyletic group and placed all of the world's freshwater crabs in a single family. However, each of these authors has proposed a different classification system for the group.

ORTMANN (1897) divided the family Potamonidae into four subfamilies: (1) Potamoninae ORTMANN, 1896 (for *Parathelphusa* H. MILNE EDWARDS, 1853, *Erimetopus* RATHBUN, 1894 and *Potamon* SAVIGNY, 1816); (2) Deckeniinae ORTMANN, 1897 (for *Deckenia* HILGENDORF, 1869); (3) Potamocarcininae ORTMANN, 1897 (for *Epilobocera* STIMPSON, 1860, *Hypolobocera* ORTMANN, 1897, *Kingsleya* ORTMANN, 1897 and *Potamocarcinus* H. MILNE EDWARDS, 1853); and (4) Trichodactylinae H. MILNE EDWARDS, 1853 (for *Trichodactylus* LATREILLE, 1828, *Orthostoma* ORTMANN, 1897 and *Dilocarcinus* H. MILNE EDWARDS, 1853). ORTMANN, 1897 included the African species in the Potamoninae and the Deckeniinae.

Perhaps the most significant contribution at this time was made by RATHBUN (1904, 1905, 1906) who published a comprehensive analysis of the taxonomy of the freshwater crabs of Africa in three major volumes that dealt with the freshwater crabs of the world. The Old World freshwater crabs (including the majority of the African species), and the Pseudothelphusidae ORTMANN, 1893 from South America were dealt with in the 1904 and 1905 volumes of RATHBUN's monograph. The Trichodactylinae from South America, the Deckeniinae from East Africa, and the

Gecarcinucinae from Asia are included in RATHBUN'S 1906 volume. In these three works RATHBUN developed a classification system for all of the known species of freshwater crabs of the world, and produced identification keys to the subfamilies, genera, subgenera, and species. The separation of the higher categories in RATHBUN'S classification relied on characters of the third maxilliped, eyestalk, antenna, carapace, and cheliped (and did not use characters derived from the gonopods or mandible).

RATHBUN (1904, 1905, 1906) assigned all of the world's freshwater crabs to a single family (the Potamonidae) and separated the major groups of crabs into five subfamilies: (1) the Potamoninae (for *Potamon*, *Hydrothelphusa* A. MILNE EDWARDS, 1872, *Platythelphusa* A. MILNE EDWARDS, 1887, *Limnothelphusa* CUNNINGTON, 1902 and *Erimetopus*); (2) the Pseudothelphusinae ORTMANN, 1893 (for *Pseudothelphusa*, *Potamocarcinus*, *Epilobocera* and *RATHBUNia* NOBILI, 1896); (3) the Trichodactylinae (for *Trichodactylus*); (4) the Gecarcinucinae RATHBUN, 1904 (for *Gecarcinucus* H. MILNE EDWARDS, 1844); and (5) the Deckeniinae (for *Deckenia*). Three of these subfamilies (Potamoninae, Gecarcinucinae and Deckeniinae) are found only in the Old World while the other two (Trichodactylinae and Pseudothelphusinae) occur exclusively in the New World.

RATHBUN'S (1904, 1905, 1906) taxonomic conclusions were, for the most part, adopted by the majority of subsequent of authors. ALCOCK (1910a) provisionally accepted the broad conclusions of RATHBUN'S classification: that the freshwater crabs of the world comprised a single family (the Potamonidae) and that this family was divided into five subfamilies. However, ALCOCK (1910a) expressed a number of reservations about RATHBUN'S (1904, 1905, 1906) conclusions at the subfamily level and favoured a system in which the Potamonidae had only two subfamilies (the Potamoninae and the Parathelphusinae). Nevertheless, ALCOCK (1910a) limited his formal taxonomic actions to the recharacterisation of some of RATHBUN'S subfamilies. According to ALCOCK (1910a) the Potamoninae comprised six genera: *Potamon*, *Hydrothelphusa*, *Platythelphusa*, *Erimetopus*, *Acanthothelphusa* and *Parapotamon*. ALCOCK (1910a) also raised the number of genera in the Gecarcinucinae from one (*Gecarcinucus*) to four (*Gecarcinucus*, *Cylindrothelphusa* ALCOCK, 1909, *Perithelphusa* and *Parathelphusa*).

BOUVIER (1917a,b, 1921) proposed a different classification for the freshwater crabs. He divided the Potamonidae into two groups according to whether the terminal segment of the mandibular palp was simple (these he called the Eupotamonea) or bilobed (these he called the Parapotamonea). BOUVIER (1917a,b, 1921) recognised four subfamilies of freshwater crabs, the Potamoninae, Trichodactylinae, the Gecarcinucinae and the Pseudothelphusinae. Interestingly, BOUVIER (1917a,b, 1921) assigned both the Old World Potamoninae and the New World Trichodactylinae to the Eupotamonea and the Old World Gecarcinucinae and the New World Pseudothelphusinae to the Parapotamonea. The Potamoninae of BOUVIER included two genera *Potamon* and *Hydrothelphusa*, while the Gecarcinucinae included only *Gecarcinucus* and *Parathelphusa*.

COLOSI (1920) reviewed previous classifications of the freshwater crabs and proposed a new version of his own which recognised the distinctness of *Platythelphusa* from Lake Tanganyika. COLOSI (1920) divided the Potamonidae into two main groups (which he called the Protopotamonida and the Eupotamonida) according to the insertion, position and form of the antenna. The Protopotamonida were recognised by an antenna that arises posteriorly to the orbit and which has a long, straight second article that is not distorted by the front of the carapace. The Protopotamonida comprised a single subfamily, the Platythelphusinae COLOSI, 1920 which he erected to accommodate the genus *Platythelphusa*. The Eupotamonida were recognised by an antenna that arises close to the internal angle of the orbit and which has a short second article that is distorted by the front of the carapace. COLOSI (1920) divided the Eupotamonida into the New World Trichodactylina (for the Trichodactylinae which lack spines on the dactyli of the walking legs and whose third maxilliped merus is slim) and the Old and New World Echinodactylina (for the Potamoninae, Pseudothelphusinae and Gecarcinucinae which all possess stiff spines on the dactyli of the walking legs, and a broad third maxilliped merus). The Old World Potamoninae were subdivided by COLOSI (1920) into three tribes, the Potamonini (for *Potamon*), the Propotamonini (for *Erimetopus*) and the Deckenini (for *Deckenia*). The Old World Gecarcinucinae were divided by COLOSI (1920) into two tribes, the Hydrothelphusini (for *Hydrothelphusa*) and the Parathelphusini (for *Gecarcinucus* and *Parathelphusa*).

In summary, the classifications of ORTMANN (1897), RATHBUN (1904, 1905, 1906) and ALCOCK (1910a) separated Old World and New World freshwater crab taxa into different subfamilies while those of BOUVIER (1917a,b, 1921) and COLOSI (1920) included both Old World and New World crabs in the same higher taxon.

In the late 19th Century and the early part of the 20th century a number of other workers added to our knowledge of the freshwater crab fauna of the region of Africa under study here. In 1898, M. J. RATHBUN described *Potamon (Geothelphusa) macropus* RATHBUN, 1898 from Liberia, and DE MAN (1901) described *Potamon (Potamonautes) floweri* from southern Sudan. Next, MARCHAND (1902) described *Potamon* (*Potamonautes*) *ecorssei* from the river Niger in Niger, and DE MAN (1903) described *Potamon* (*Potamonautes*) *latidactylum* from Ghana. These early authors relied almost entirely on characters of the carapace, legs, abdomen, third maxilliped, and cheliped for identification, and did not consider characters of the mandible and gonopods to be important.

Most of the African species of freshwater crabs were assigned by RATHBUN (1904, 1905, 1906) to the Potamoninae (table I). That author distinguished the Potamoninae from the other subfamilies by characters of the frontal margin (greater than 1/6 of the carapace width), the merus of the third maxilliped (broader than long), the length of the eyestalk (long or short), the form of the basal segment of the antenna (wider than long), and the degree of development of the postfrontal crest (complete or incomplete). RATHBUN's (1904) genera were distinguished by characters of the carapace (the outline, the epibranchial tooth, the orbital margin, the sidewall, and the front), the third maxilliped (the longitudinal sulcus on the ischium), the pereiopods (spines on the dactylus), and the abdomen (the degree of separation of the segments). RATHBUN (1904, 1905, 1906) recognised eight subgenera in the genus *Potamon* and included species from all parts of the Old World (see tables I, II). Four subgenera of the genus *Potamon*: *Potamonautes*, *Potamon*, *Parathelphusa*, and *Geothelphusa*, included African representatives. RATHBUN's (1904, 1905, 1906). Subgenera were distinguished by differences in the postfrontal crest, the exorbital angle, the epibranchial tooth, the anterolateral margin, and the merus of the cheliped.

Potamon (*Potamonautes*) included a total of fifty nine species, of which thirty seven were African, the rest Asian. This subgenus was recognised by a distinct postfrontal crest, a distinct exorbital angle and epibranchial tooth, and smooth anterolateral margins of the carapace. *Potamon* (*Parathelphusa*) included a total of thirty six species, of which six were African, one Madagascan and the rest Asian. This subgenus was identified by similar characters to those of *Potamon* (*Potamonautes*), except that the anterolateral margin of the carapace of *Potamon* (*Parathelphusa*) was clearly toothed. *Potamon* (*Geothelphusa*) included a total of thirty nine species, of which five were African and the rest Asian. This subgenus was recognised by an incomplete postfrontal crest, by a blunt and low exorbital angle, by the absence of the epibranchial teeth, and by completely smooth anterolateral margins. Finally, *Potamon* (*Potamon*) included a total of seventy five species, of which two were African, five Madagascan, and the rest Asian. This subgenus was identified by an incomplete and interrupted postfrontal crest where the epigastric and postorbital crests do not touch, by a single epibranchial tooth, and by the lack of teeth on the anterolateral margins. RATHBUN's (1904-1905) assignments to genera and subgenera took no account of the geographic origin of the material, and grouped together species from anywhere in the world as long as they possessed a particular carapace character (table I). This methodology alone provides good reason to doubt that RATHBUN's (1904, 1905, 1906) genera and subgenera are robust natural taxonomic groups.

Of the thirty seven species of African freshwater crabs that were referred by RATHBUN to *Potamon* (*Potamonautes*) only four are from West Africa. These are included in the present work under two genera: *Sudanonautes* BOTT, 1955 (*S. africanus* (A. MILNE EDWARDS, 1869), *S. aubryi* (H. MILNE EDWARDS, 1853), and *S. floweri* (DE MAN, 1901)), and *Liberonautes* BOTT, 1955 (*L. latidactylus* (DE MAN, 1903)). Of the six species referred by RATHBUN to *Potamon* (*Parathelphusa*) only two, *P. (P.) chavanesii* (now *Sudanonautes chavanesii* (A. MILNE EDWARDS, 1886)) and *P. (P.) chaperi* (now *Liberonautes chaperi* (A. MILNE EDWARDS, 1887)) are from West Africa. Of the five species referred by RATHBUN to *Potamon* (*Geothelphusa*) only *P. (G.) macropus* (now *Globonautes macropus* (RATHBUN, 1898)) is from West Africa. Finally, of the two species referred by RATHBUN to *Potamon* (*Potamon*) only *P. (P.) nigrensis* (now *Potamonautes ecorssei* MARCHAND, 1902) is from West Africa.

Freshwater crabs collected by American and European expeditions to Africa in the early part of the 20th Century proved to include three new taxa: *Potamon* (*Potamonautes*) *faradjensis* RATHBUN, 1921 (now *S. faradjensis*) from Democratic Republic of Congo, *Potamon* (*Potamonautes*) *decazei granulata* BALSS, 1929 (now *S. granulatus*), and *P. (P.) a. monodi* BALSS, 1929 (now *S. monodi*) from Cameroon. Later, BALSS (1936) produced an important study of the freshwater crab fauna of the Democratic Republic of Congo river basin, which included several species dealt with in the present work, but none that were new species. In that work BALSS (1936) provided some of the first detailed drawings of the gonopods (male pleopods) of African freshwater crabs. A few years later CHACE (1942) published a list summarising all of the described taxa of African freshwater crabs up to that date. CHACE (1942, 1953) also recognised the importance of providing detailed drawings of the gonopods in his studies of East African freshwater crabs. The next contribution to the field was made by CAPART (1954) who made careful studies of the carapace and gonopod 1 of all of the type specimens of freshwater crabs from Africa held in the MNHN, Paris. CAPART's illustrations continue to be useful today, for they describe carapace and gonopod 1 characters in detail, and most of them depict type specimens. Neither CHACE nor CAPART adopted RATHBUN's (1904, 1905, 1906) classification for the freshwater crabs. In the absence of consensus, CHACE (1942) simply assigned all species of African freshwater crabs to *Potamon*, while CAPART (1954) assigned all species of African freshwater crabs to *Potamonautes* (table II).

In 1955 Richard BOTT published a major monograph on the freshwater crabs of Africa, which included the first new classification of the group for fifty years. BOTT (1955) redescribed most of the continent's fauna, basing his classification on characters of the gonopods as well as on characters derived from somatic morphology, and revived interest in characters of the mandible. BOTT's (1955) conclusions differed greatly from those of ORTMANN, 1897, RATHBUN (1904, 1905, 1906), ALCOCK (1910a), BOUVIER (1917a,b, 1921) and COLOSI (1920) and laid the foundations of the modern taxonomy of the group. BOTT examined a great deal of new material from Central Africa (held in the MRAC, Tervuren), as well as a lot of other material from the collections of the SMF, Frankfurt, the ZMB, Berlin, and other museums.

BOTT's (1955) classification (table III) assigned the freshwater crabs of the world to three families: the Potamonidae, the Pseudothelphusidae and the Deckeniidae. The Potamonidae included the Trichodactylinae, a New World freshwater crab group, as well as three Old World freshwater crab groups. Both the Deckeniidae (which included *Deckenia*) and the Pseudothelphusidae (which included *Pseudothelphusa* and a number of other genera) were formerly subfamilies that BOTT elevated to the family level. The Deckeniidae were distinguished by characters of the respiratory openings and the frontal region, while the Pseudothelphusidae were recognised by characters of gonopod 1, the third maxilliped, the mandibular palp, the inner orbital angle, the abdomen, and the front. The Potamonidae were distinguished by characters of gonopod 1, the third maxilliped, the mandibular palp, the inner orbital angle, the abdomen, the position of the exhalent openings, the basal segment of the antenna, and the front.

BOTT's (1955) Potamonidae included four subfamilies: the Potamoninae (for *Potamiscus*, *Potamon*, *Potamonautes*, *Sudanonautes* and *Liberonautes*) the Gecarcinucinae (for *Gecarcinucus*), the Hydrothelphusinae H. MILNE EDWARDS, 1877 (for *Hydrothelphusa*), and the Trichodactylinae (for *Trichodactylus*). The four subfamilies were distinguished by characters of the mandibular palp, the third maxilliped, gonopod 1, and the abdomen. BOTT (1955) assigned all of the freshwater crabs from Africa to the

Potamoninae, and included African species in four out of the five genera: *Potamon*, *Potamonautes*, *Sudanonautes* and *Liberonautes*. Of these, only *Potamonautes*, *Sudanonautes* and *Liberonautes* have West African representatives. *Potamon* is found in north Africa (Tunisia, Algeria and Morocco), southeast Europe, the Middle East and Asia, and *Potamiscus* ALCOCK, 1909 (which was misspelt *Potamoniscus* in BOTT, 1955, 1970a) is from the Himalayas.

The large African genus *Potamonautes* was radically revised by BOTT (1955) who included thirty eight species and fourteen subspecies in the genus and established fifteen new subgenera (table III). The four species of *Potamonautes* from West Africa included in the present work were assigned by BOTT (1955) to two different subgenera: *Platypotamonautes* BOTT, 1955 and *Isopotamonautes* BOTT, 1955. BOTT (1955) also established two genera: *Sudanonautes* (with two subgenera, three species and four subspecies), and *Liberonautes* (a monotypic genus). Furthermore, BOTT (1955) placed a number of described taxa from West Africa in synonymy. The only new taxon from West Africa in that work was *Sudanonautes (S.) decazei orthostylis* BOTT, 1955 from Cameroon. BOTT further developed and revised his taxonomic conclusions in his subsequent works (BOTT, 1959, 1960, 1964, 1969b, 1970a, 1970b) giving his final opinion on the taxonomy and classification of the continental African freshwater crabs in BOTT (1970b) (table IV).

BOTT (1955) was one of the first authors to formally recognise that the freshwater crab fauna of the African continent was distinct from that of Europe, Asia, Australia, and South America. BOTT (1955) grouped all of the African species into four exclusively African genera (*Potamonautes*, *Sudanonautes*, *Liberonautes*, and *Deckenia*). None of these genera included species from outside of the continent (except for *Deckenia alluaudi* A. MILNE EDWARDS, 1887 from the Seychelles, which was recently removed from *Deckenia* and assigned to the new genus *Seychellum* NG, STEVCIC & PRETZMANN, 1995). In later works, BOTT (1969b,c, 1970b) implied close phylogenetic links between certain species of freshwater crabs found in West Africa, South Africa, Madagascar and India by including African species in two different subfamilies (the Globonautinae BOTT, 1969b and the Gecarcinucinae) of the Gecarcinucidae RATHBUN, 1904.

Comprehensive revisonary works of the kind carried out by BOTT (1955) in which the two gonopods and the mandibular palp provide many of the important taxonomic characters require the direct examination of all types. This is necessary because the early date of the original descriptions of the majority of the African taxa means that the literature lacks any reference to gonopod and mandible structure. Unfortunately, BOTT did not examine the types of many of the taxa from West Africa. Consequently, quite a few of BOTT's (1955) descriptions of species, and many of his synonymizations of taxa were made without any direct knowledge of the structure of the gonopods of the relevant type material. Some of BOTT's (1955) descriptions and redescriptions of species therefore consist of an account of the type or types drawn from the literature, supplemented by other data, illustrations, and photographs based on museum specimens other than the types. As a direct consequence of this methodology BOTT's (1955) work includes a large number of errors of identification, nomenclature, and synonymy. Many of these errors can be directly attributed to the failure of that author to routinely examine all of the necessary type material.

BALSS (1957) did not accept BOTT's (1955) taxonomic conclusions and proposed his own classification for the freshwater crabs of the world (table II). Like many workers before him, BALSS (1957) assigned all of the freshwater crabs of the world to a single family (the Potamonidae), but that author recognised only four subfamilies: the Potamoninae, the Gecarcinucinae, the Pseudothelphusinae, and the Trichodactylinae. BALSS (1957) included the African freshwater crabs in the Potamoninae, with a number of genera (*Deckenia*, *Erimetopus*, *Hydrothelphusa*, *Platythelphusa* and *Potamon*) and subgenera of *Potamon* (*Potamonautes*, *Geothelphusa* and *Potamon*). Most of the West African species were placed in the genus *Potamon* and were assigned to one of the latter three subgenera, with the majority of species in either *Potamon* (*Potamonautes*) or *Potamon* (*Geothelphusa*).

The series of taxonomic notes by BOTT (1959, 1964, 1969b, 1970a,b) added a number of new species to the freshwater crab fauna of West Africa. Notably, BOTT (1969b) established the Globonautinae as a new subfamily of the Potamonidae, for *Globonautes* (type species *Potamon* (*Geothelphusa*) *macropus* RATHBUN, 1898 from Liberia). BOTT (1959) also assigned two other new taxa (*Globonautes monodosus* BOTT, 1959 from Guinea and *G. balssi* BOTT, 1959 from Cameroon) to the Globonautinae, and described *Potamonautes* (*Platypotamonautes*) *triangulus* BOTT, 1959 from Ghana. BOTT (1969b) described *Globonautes macropus edeaensis* BOTT, 1969b from Cameroon and *Afrithelphusa gerhildae* BOTT, 1969b from Guinea, and revived *Afrithelphusa afzelii* (COLOSI, 1924); BOTT (1970a) described *Potamonautes* (*Isopotamonautes*) *senegalensis* BOTT, 1970a from Senegal.

The two works published by BOTT in 1970 (BOTT, 1970a,b) had a great impact on the modern taxonomy of the freshwater crabs. BOTT (1970a) established a major new classification for all freshwater crabs which included three new superfamilies and eleven families (table IV). The three superfamilies were the Pseudothelphusoidea ORTMANN, 1893, the Parathelphusoidea COLOSI, 1920, and the Potamoidea ORTMANN, 1896. BOTT (1970a) recognised higher taxonomic levels by placing major emphasis on characters of the mandible, first gonopod, frontal margin, and the postfrontal crest. The Pseudothelphusoidea included three neotropical families: the Trichodactylidae H. MILNE EDWARDS, 1853, the Pseudothelphusidae ORTMANN, 1893, and the Potamocarcinidae ORTMANN, 1897. The Potamoidea included five families: two African (the Potamonautidae BOTT, 1970a and the Deckeniidae), and three Eurasian (the Potamidae, the Sinopotamidae BOTT 1970b, and the Isolapotamidae BOTT, 1970b). The Parathelphusoidea included three families: the Gecarcinucidae, the Sundathelphusidae BOTT, 1969b, and the Parathelphusidae Alcock, 1910a.

BOTT (1970b) recognised the Potamoidea by three characters: a mandibular palp with a simple, undivided terminal segment, a front lacking a median frontal triangle, and a gonopod 1 with three segments plus a long terminal article. BOTT (1970a) included the Potamonautidae in the Potamoidea, and distinguished this family by two characters: a two-segmented mandibular palp, and a sharply defined postfrontal crest (in most cases). BOTT (1970a) recognised the Parathelphusoidea by two characters: a mandibular palp with a divided, clearly bilobed terminal segment, and a gonopod 1 with three segments plus a long terminal article. BOTT (1970a) recognised the Gecarcinucidae by one additional character: the lack of a median frontal triangle. According to BOTT (1970a) the Gecarcinucidae and the Potamonautidae both have a two-segmented mandibular palp, both lack a median forehead triangle, and both have a gonopod 1 with three segments plus a long terminal article. This means that (according to BOTT, 1970a) the difference between these families rests on the form of the terminal segment of the mandibular palp: it is simple and undivided in the Potamonautidae and divided and bilobed in the Gecarcinucidae.

BOTT (1970b) included the majority of the African freshwater crabs in the Potamoidea, and assigned only a few African species to the Parathelphusoidea. The Potamoidea were distinguished from the Parathelphusoidea by differences in the form of the terminal segment of the mandibular palp: it is a simple (single) posterior lobe in the Potamoidea and it is bilobed (with an additional large anterior lobe) in the Parathelphusoidea. The Potamonautidae and the Deckeniidae are distinguished from the other families by the number of segments of the mandibular palp: the palp has two segments in the Potamonautidae and Deckeniidae, and three segments in the other three families of the Potamoidea.

The Sundathelphusidae and the Parathelphusidae (as conceived by BOTT, 1970b) are entirely Asian families, while the Gecarcinucidae is mainly an Asian family, although a few species of African freshwater crabs were assigned to this family (BOTT, 1969b, 1970b). BOTT (1969b, 1970b) established the Gecarcinucidae largely on the basis of the bilobed mandibular palp (along with other characters) and designated *Gecarcinucus jacquemonti* H. MILNE EDWARDS, 1844 from India as the type species. This family was established with three subfamilies: (1) the Globonautinae (for *Globonautes*), (2) the Gecarcinucinae (for *Afrithelphusa* BOTT, 1969b, *Barytelphusa* ALCOCK, 1909, *Inglethelphusa* BOTT, 1970b, *Cylindrotelphusa* ALCOCK, 1909 and *Gecarcinucus* H. MILNE EDWARDS, 1844), and (3) the Liothelphusinae (for *Sartoriana* BOTT, 1969b, *Travancoriana* BOTT, 1969b, *Lepidothelphusa* COLOSI, 1920, *Phricotelphusa* ALCOCK, 1909, *Thelphusula* BOTT, 1969b, *Liotelphusa* ALCOCK, 1909, *Adeleana* BOTT, 1969b and *Gubernatoriana* BOTT, 1970b). The Globonautinae was conceived of as an exclusively African subfamily, while the Gecarcinucinae was a mainly Asian subfamily, except for *Afrithelphusa* from West Africa and *Gecarcinautes* BOTT, 1960 from South Africa and Madagascar (BOTT, 1965).

The taxonomic structure of the West African freshwater crabs today

ORTMANN (1897), RATHBUN (1904, 1905, 1906), ALCOCK (1910a,b), BOUVIER (1917a,b), COLOSI (1920) and BALSS (1957) considered all of the world's freshwater crabs to be a monophyletic group and assigned them to a single family (the Potamonidae). This view contrasts radically with the works of BOTT (1955, 1959, 1960, 1965, 1970a,b), who conceived of the world's freshwater crabs as a polyphyletic or paraphyletic group and assigned them first (BOTT, 1955, 1959, 1960, 1965) to three families and later (BOTT, 1970a,b) to three superfamilies and eleven families. When comparing evolutionary views of the phylogenetic history of the group and the two classifications that derive from these views, the schemes are similar but the taxa grades are different. For example, the Potamoninae of RATHBUN (1904, 1905, 1906) includes approximately the same taxa as the Potamidae (formerly the Potamonidae, Opinion No. 712) and the Potamonautidae of

BOTT (1970a), while the subfamilies Deckeniinae, Gecarcinucinae, Trichodactylinae and Pseudothelphusinae of RATHBUN (1904, 1905, 1906) include approximately the same taxa as the families Deckeniidae, Gecarcinucidae, Trichodactylidae and Pseudothelphusidae of BOTT (1970a). RATHBUN's genus *Potamon* actually includes representatives of Asian genera (*Potamon*) and African genera (*Potamonautes*, *Sudanonautes*, and *Liberonautes*). On the other hand, some of RATHBUN's (1904, 1905, 1906) other taxa (*Hydrothelphusa*, *Platythelphusa* and *Erimetopus*) are judged here to be valid genera.

The Gecarcinucidae

When BOTT (1969b, 1970b) established this family (by elevating the subfamily Gecarcinucinae) he assigned to it two genera from West Africa, and justified their inclusion on the basis of a shared character: a mandibular palp with a bilobed terminal segment. The Gecarcinucinae was originally established by RATHBUN (1904), and although this contribution actually appears in RATHBUN (1906) it has conventionally been cited by subsequent authors as RATHBUN (1904). The Gecarcinucinae was considered by RATHBUN to be a subfamily of the Potamonidae, with *Gecarcinucus jacquemonti* H. MILNE EDWARDS, 1844, from India as type species. RATHBUN (1904) established this subfamily for a single species, which was distinguished by characters of the front (very narrow), carapace (highly arched), and of the endopod of the first maxilliped (exposed, rather than covered by the third maxilliped). However, none of these characters, taken alone, is unique to this taxon. ALCOCK (1910a) was the first to describe the bilobed terminal segment of the mandibular palp of the Gecarcinucinae. That author was impressed by the similarity between the mandibular palp (and other characters) of *Gecarcinucus* and of *Parathelphusa*. However, ALCOCK (1910a) did not propose any formal changes to RATHBUN's (1904, 1905, 1906) classification (although he noted that he was inclined to include *Gecarcinucus* in the Parathelphusidae). In 1960 BOTT (1960) erected the genus *Gecarcinautes* for *G. brincki* BOTT, 1960 from South Africa which he assigned to the Gecarcinucinae RATHBUN, 1904. However, this species has since been transferred to *Potamonautes* as *P. brincki* in the family Potamonautidae (CUMBERLIDGE, 1996b; STEWART, 1997).

Madagascan freshwater crabs

BOTT (1960) originally included three taxa from Madagascar in *Gecarcinautes*: *Thelphusa goudoti* H. MILNE EDWARDS, 1853, *T. madagascariensis* A. MILNE EDWARDS, 1872 and *Potamon* (*P.*) *bombetokensis* RATHBUN, 1904. A few years later BOTT (1965) revised the freshwater crabs of Madagascar. BOTT (1965) classified the Madagascan freshwater crabs in a single family (then called the Potamonidae) and assigned species to one of three subfamilies: the Potamoninae (for *Madagapotamon* BOTT, 1965), the Gecarcinucinae (for *Gecarcinautes*), and the Hydrothelphusinae (for *Hydrothelphusa*). The three taxa originally included in *Gecarcinautes* by BOTT (1960) were assigned by BOTT (1965) as follows: *T. goudoti* remained in *Gecarcinautes* as *G. goudoti*, *T. madagascariensis* was transferred to *Hydrothelphusa* as a subspecies of *H. agilis*, and *P. (P.) bombetokensis* was transferred to *Hydrothelphusa* as a junior synonym of *H. humbloti*. The Potamoninae included *Madagapotamon humberti* BOTT, 1965, *M. gollhardi* BOTT, 1965, and *M. ankaraharae* (NOBILI, 1905), the Gecarcinucinae included *Gecarcinautes a. antilongensis* (RATHBUN, 1905), *G. a. vondrozi* BOTT, 1965 and *G. goudoti* (H. MILNE EDWARDS, 1853), and the Hydrothelphusinae included *Hydrothelphusa a. agilis* (A. MILNE EDWARDS, 1872), *H. a. madagascariense* (A. MILNE EDWARDS, 1872), and *H. humbloti* (RATHBUN, 1904). Recently, NG & TAKEDA (1994) made a number of changes to the work of BOTT (1965) in a study that described *Skelosophusa*, a new genus of freshwater crab from Madagascar with three species: *S. gollardi* (BOTT, 1965), *S. prolixa* NG & TAKEDA, 1994 and *S. eumeces* NG & TAKEDA, 1994.

BOTT's (1970b) revision of the freshwater crabs of the world raised the number of families of freshwater crabs to eleven. Unfortunately, the Madagascan freshwater crabs were not discussed by BOTT (1970b) and there are, therefore, a number of taxonomic questions still outstanding. For example, BANARESCU (1991) assigned the Hydrothelphusinae (represented by *Hydrothelphusa*, which he considered to be a monotypic genus) to the Gecarcinucidae (Gecarcinucoidea). That author also agreed with the placement of *Gecarcinautes* in the Gecarcinucinae (Gecarcinucidae), but he was uncertain of the familial placement of *Madagapotamon*. On the other hand, NG & TAKEDA (1994) assigned specimens from Madagascar to two subfamilies each belonging to a different family: the Hydrothelphusinae (for *Hydrothelphusa* and *Skelosophusa*) and the Gecarcinucinae (for *Gecarcinautes*). NG & TAKEDA (1994) included *Hydrothelphusa*, together with *Madagapotamon* and *Skelosophusa* NG & TAKEDA , 1994 in the Potamonautidae (Potamoidea) and *Gecarcinautes* in the Gecarcinucidae (Gecarcinucoidea). Although NG & TAKEDA (1994) assigned *Madagapotamon* BOTT, 1965 (which they judged to be a monotypic genus) to the Potamonautidae, they did not comment on its subfamily assignment.

NG & TAKEDA (1994) included three species in *Skelosophusa*: *S. gollardi* (BOTT, 1965), *S. prolixa* NG & TAKEDA, 1994 and *S. eumeces* NG & TAKEDA, 1994 and also made a number of changes to the work of BOTT (1965). NG & TAKEDA (1994) considered *Potamon pittarelli* NOBILI, 1905 (which had been overlooked by BOTT in his 1965 work) to be a fourth species of *Gecarcinautes*.

There is still disagreement over the proper family assignment of the Hydrothelphusinae. According to BANARESCU (1991) this subfamily belongs in the Gecarcinucidae, while NG & TAKEDA (1994) place this subfamily in the Potamonautidae. Prior to NG & TAKEDA's (1994) contribution, the Potamonautidae included no subfamilies. This debate only serves to underline the uncertainty surrounding the family and subfamily status of the Hydrothelphusids and of *Madagapotamon*. Furthermore, the assignment of the Hydrothelphusinae to the Potamonautidae by NG & TAKEDA (1994) without properly addressing the relationships of the hydrothelphusids to the other members of this family, raises significant questions regarding the subfamily status of the large number of non-Madagascan members of this principally-African family. The answers to these questions are of some relevance to the present work.

NG, STEVCIC & PRETZMANN (1995) described the mandibular palp of the Hydrothelphusines as "2-segmented, with a simple terminal segment which is not bilobed." However, the terminal segment of the mandibular palp of *Hydrothelphusa agilis* is neither bilobed, nor simple: rather the palp has a large posterior lobe and a smaller anterior lobe (about 1/4 to 1/2 the size of the posterior lobe). A similarly configured mandibular palp is also seen in *H. madagascariensis* which was illustrated by CALMAN (1913). This evidence does not support the assertion by NG *et al.* (1995) that the mandibular palp of the hydrothelphusines has a simple terminal segment (i.e., it is not bilobed). Nevertheless, it is apparent that NG *et al.* (1995) recognise that the terminal segment of the mandibular palp of the hydrothelphusines is not simple, and that it does, in fact, have an additional anterior process or lobe. For example, NG *et al.* (1995) suggested that the hydrothelphusines represent an intermediate form between freshwater crabs with a mandibular palp with a simple terminal segment (no anterior lobe on the terminal segment) and those with a bilobed terminal segment (a large anterior lobe on the terminal segment).

The mandibular palp of *Seychellum alluaudi* A. Milne Edwards & Bouvier, 1893 has been examined in the present work: the anterior lobe of the terminal segment of the mandibular palp of *Seychellum* Ng, Stevcic & Pretzmann, 1995 was found to be somewhat larger than that of *Hydrothelphusa agilis*, but not dramatically so. However, Ng *et al.* (1995) used the single character of the mandibular palp to justify the assignment of *Seychellum* (with a bilobed palp) and *Hydrothelphusa* (with either a simple palp or a small anterior process, according to those authors) to two separate superfamilies (Gecarcinucoidea and Potamoidea respectively).

Conclusions

Summaries of most of Bott's final taxonomic conclusions concerning West Africa are available in Monod (1977, 1980). However, the latter author differed from Bott by placing the West African freshwater crabs in the Potamidae and the Gecarinucidae (rather than in the Potamonautidae and the Gecarcinucidae) due to a concern regarding the proliferation of freshwater crab families. Subsequent workers (Bowman & Abele, 1982; Cumberlidge, 1986a-1996; Ng, 1988; Banarescu, 1991; Ng & Takeda, 1994; Stewart, Coke & Cook, 1995; Stewart, 1997) have retained the Potamonautidae as a family, although others (Guinot, Jamieson & Tudge, 1997) have cast doubts upon a clear distinction between the Potamidae and the Potamonautidae.

Monod's works are restricted to the freshwater crabs of the savanna and Sahel in West and Central Africa and provide identification keys for the fauna of this region. Bott's (1970a,b) classification of the freshwater crabs of the world was provisionally adopted by Ng (1988) who expressed doubts about the validity of some of Bott's taxonomic conclusions concerning Asian freshwater crabs. Ng (1988), following an earlier comment by Holthuis (1974), pointed out that Bott's (1970b) superfamily Parathelphusoidea should properly be called the Gecarcinucoidea Rathbun, 1904 according to priority.

The classification of the freshwater crabs of the world provided by Bott (1970a,b) proposed eleven families, and these were listed in the classification of the Brachyura by Bowman & Abele (1982), but without the three superfamily divisions. The African freshwater crabs were assigned by Bott (1970a,b) to four families, the Potamonautidae and Deckeniidae (both endemic to Africa) and the Gecarcinucidae and Potamidae (both additional-ly found elsewhere). Three of these four families are recognised here with the addition of the Platythelphusidae, a family endemic to Africa (present work). The Asian and Australasian freshwater crabs were assigned by BOTT (1970a,b) to six families, the Parathelphusidae, Gecarcinucidae, Sundathelphusidae, Potamidae, Isolapotamidae and the Sinopotamidae. However, NG (1988) considered the Isolapotamidae and the Sinopotamidae to be junior synonyms of the Potamidae, and a number of authors (NG, 1988, 1990, 1991, 1995; NG & WORWOR, 1990) considered the Sundathelphusidae to be a junior subjective synonym of the Parathelphusidae. The neotropical freshwater crabs were assigned by BOTT (1970a,b) to three families, the Pseudothelphusidae, the Potamocarcinidae and the Trichodactylidae. However, subsequent authors (RODRIGUEZ, 1982, 1992) judged only two neotropical families to be valid, and considered the Potamocarcinidae to be a junior subjective synonym of the Pseudothelphusidae. Depending on which taxonomic authorities are followed, the world's freshwater crabs can be assigned to either 12 families or 8 families.

The results presented here for the freshwater crabs of West Africa, taken together with the taxonomic conclusions of RODRIGUEZ (1982, 1992) for the neotropical fauna and of Ng (1988) for the Asian fauna, raise doubts concerning the validity of some of BOTT's (1970b) eleven families. It is likely that some of BOTT's families and superfamilies are not natural taxa, and that further detailed studies are sure to revise BOTT's (1970b) taxonomic conclusions.

Moreover, much of BOTT's taxonomic work concerning West Africa (and indeed, the rest of the continent and Madagascar) has proved to be of limited use to subsequent workers, especially when it comes to the identification of specimens. In particular BOTT's (1955, 1965, 1970a,b) descriptions, identification keys, and classifications are unreliable, and nearly all are in need of revision.

The present work is the result of a great deal of revisionary work on the West African species (CUMBERLIDGE, 1985a, 1987, 1991a, 1993a,b,c, 1994a,b, 1995a,b,c,d, 1996a,b, 1999; CUMBERLIDGE & CLARK, 1992; CUMBERLIDGE & SACHS, 1989a, 1991; based on new discoveries and on the redescription of each species following direct examination of original type material. Emphasis is placed on characters of the gonopods, mandibles, and selected somatic characters; morphometric relationships of the carapace dimensions and proportions are introduced here as an additional taxonomic character. The early results of this renewed effort have been the establishment of two new genera (*Potamonemus* CUMBERLIDGE & CLARK, 1992 and *Louisea* CUMBERLIDGE, 1994a) and the description of a number of new species. The new species include *Globonautes leonensis* CUMBERLIDGE, 1987, *Sudanonautes kagoroensis* CUMBERLIDGE, 1991a, *Potamonemus mambilorum* CUMBERLIDGE & CLARK, 1992, *P. asylos* CUMBERLIDGE, 1993a, *P. sachsi* CUMBERLIDGE, 1993a, and *Liberonautes nimba* CUMBERLIDGE,1999, *Liberonautes grandbassa, L. lugbe, Potamonautes reidi* and *Sudanonautes nigeria*. In addition, a number of other species which had formerly been recognised as subspecies (*Liberonautes paludicolis* CUMBERLIDGE & SACHS, 1989a, *L. nanoides* CUMBERLIDGE & SACHS, 1989a, *L. rubigimanus* CUMBERLIDGE & SACHS, 1989a, *L. chaperi, Sudanonautes orthostylis, S. chavanesii, S. floweri, S. monodi, Louisea balssi* and *L. edeaensis*) or as junior subjective synonyms (*Sudanonautes granulatus* and *S. faradjensis*) are now recognised to be valid species (table V). This work represents an attempt to bring together these recent contributions in a single volume, and to reinterpret some of the phylogenetic relationships within the group as a whole.

List of species

This list indicates the classification employed in the present study, which is based on the results of the cladistic analysis presented later in this work. This classification is provisional, since it is based on data from only one part of the Afrotropical region. In particular, this study includes only four species of *Potamonautes*, which is a small fraction of the known species. The works of BOTT (1955, 1959, 1970a) indicate that there are at least fifty six species of *Potamonautes*, and revisionary work on this genus currently in progress by the author indicates that the number of valid species in this large genus can be confidently expected to increase substantially.

Family Potamonautidae BOTT, 1970a

Genus *Potamonautes* MACLEAY, 1835

1. *Potamonautes ecorssei* (MARCHAND, 1902)
2. *Potamonautes triangulus* BOTT, 1959
3. *Potamonautes senegalensis* BOTT, 1969b
4. *Potamonautes reidi* n. sp.

Genus *Liberonautes* BOTT 1955

5. *Liberonautes chaperi* (A. MILNE EDWARDS, 1887)
6. *Liberonautes latidactylus* (DE MAN, 1903)

7. *Liberonautes paludicolis* CUMBERLIDGE & SACHS, 1989a
8. *Liberonautes nanoides* CUMBERLIDGE & SACHS, 1989a
9. *Liberonautes rubigimanus* CUMBERLIDGE & SACHS, 1989a
10. *Liberonautes nimba* CUMBERLIDGE, 1999
11. *Liberonautes lugbe* n. sp.
12. *Liberonautes grandbassa* n. sp.

Genus *Sudanonautes* BOTT, 1955

13. *Sudanonautes aubryi* (H. MILNE EDWARDS, 1853)
14. *Sudanonautes africanus* (A. MILNE-EDWARDS, 1869)
15. *Sudanonautes chavanesii* (A. MILNE-EDWARDS, 1886)
16. *Sudanonautes floweri* (DE MAN, 1901)
17. *Sudanonautes faradjensis* (RATHBUN, 1921)
18. *Sudanonautes granulatus* (BALSS, 1929)
19. *Sudanonautes monodi* (BALSS, 1929)
20. *Sudanonautes orthostylis* (BOTT, 1955)
21. *Sudanonautes kagoroensis* CUMBERLIDGE, 1991a
22. *Sudanonautes nigeria* n. sp.

Genus *Potamonemus* CUMBERLIDGE & CLARK, 1992

23. *Potamonemus mambilorum* CUMBERLIDGE & CLARK, 1992
24. *Potamonemus sachsi* CUMBERLIDGE, 1993
25. *Potamonemus asylos* CUMBERLIDGE, 1993

Family Uncertain

Subfamily Globonautinae BOTT, 1969b

Genus *Globonautes* BOTT, 1959

26. *Globonautes macropus* (RATHBUN, 1898)

Genus *Afrithelphusa* BOTT, 1969b

27. *Afrithelphusa afzelii* (COLOSI, 1924)
28. *Afrithelphusa monodosus* (BOTT, 1959)
29. *Afrithelphusa gerhildae* BOTT, 1969b
30. *Afrithelphusa leonensis* (CUMBERLIDGE, 1987)

Genus *Louisea* CUMBERLIDGE, 1994a

31. *Louisea balssi* (BOTT, 1959)
32. *Louisea edeaensis* (BOTT, 1969b)

Material examined

The material used in the present study comes from a number of different sources. The main sources were the collections of African freshwater crabs in the major museums in Europe and in the USA. In most cases, the material in these museums has been complied over a time period of more than a hundred and fifty years. These museum collections typically include type material, together with large series of specimens of freshwater crabs from all parts of Africa. Most of these specimens have been identified by museum taxonomists using the identification keys of either RATHBUN (1904, 1905, 1906) or BOTT (1955). However, it is clear that neither of these major works is entirely adequate for identifying African species (especially those from West Africa), and so the majority of freshwater crab specimens in these institutions are at present incorrectly determined. These museum collections also include specimens of freshwater crabs from West Africa which have defied identification in the past and which have remained undetermined until recently (CUMBERLIDGE, 1985a-1997). Another source of material for this study were freshwater crabs collected by the author during a number of extended stays in different African countries, together with other specimens which were donated by colleagues. All of the latter specimens are now held in the author's collection at NMU.

Collecting localities

The notes accompanying most museum specimens are limited and usually only provide the date, locality and collector, and include little other biological information. The ecological accounts in the present work are based on the author's (or colleagues) field notes and are limited to the relatively few localities that have been experienced first hand. Most specimens of *Sudanonautes monodi, S. floweri* and *S. aubryi* collected by the author in the savanna zones of northern Nigeria and Togo were dug by hand from their burrows. In the case of *Sudanonautes monodi* and *S. aubryi* ecological notes were compiled from observations of natural populations in the field and from captive populations in laboratories of the Department of Biological Sciences, Bayero University, Kano, Nigeria. Specimens of *Sudanonautes africanus, S. floweri, S. kagoroensis, Potamonautes reidi* and *Potamonemus sachsi* collected by the author in the rainforests of Nigeria and Cameroon were caught by hand in streams. Specimens of all species of *Liberonautes* collected by the author and Professor Dr. R. SACHS and his teams of workers in the Liberian rainforests were mostly caught in baited basket traps set overnight in streams and rivers. Specimens of *Globonautes macropus* collected by the author in the rainforest zone of Liberia were taken from holes in trees. For these, both field notes and laboratory observations are available (see species descriptions).

The exact location of the collecting sites of specimens is indispensable for the accurate description of the range of a species. This task is complicated by the brevity of some of the labels accompanying the specimens and by the large scale changes in the names of cities, towns, villages, and geographical features that occurred in the 1960s following the end of the colonial era in West Africa. For these reasons I have appended a gazetteer (Appendix 1) of all of the localities mentioned in the text.

Repositories and abbreviations

AMNH	American Museum of Natural History, New York, NY, USA.
FMNH	Field Museum of Natural History, Chicago, IL, USA.
IFAN	Institut fondamental d'Afrique Noire, Dakar, Sénégal.
IUCN	International Union for the Conservation of Nature, Gland, Switzerland.
MCZ	Museum of Comparative Zoology, Harvard, MA, USA.
MNHN	Muséum national d'histoire naturelle, Paris, France.
MRAC	Muséum royal de l'Afrique Centrale, Tervuren, Belgium.
NHML	The Natural History Museum, London, U.K..
SMNH	Swedish Museum of Natural History (Naturhistoriska Riksmuseet) Stockholm, Sweden.
MHNG	Muséum d'histoire naturelle, Geneva, Switzerland.
NHMW	Naturhistorisches Museum, Wien, Austria.
NMU	Northern Michigan University, Marquette, MI, USA.
NNM	Nationaal Naturhistorisch Museum, Leiden, The Netherlands.
SMF	Senckenberg Museum, Frankfurt, Germany.
UZM	Universitetes Zoologiske Museum, Copenhagen, Denmark.
USNM	The United States National Museum of National History, Smithsonian Institution, Washington DC, USA.
ZIM	Zoological Institute and Museum, Hamburg, Germany.
ZMB	Museum für Naturkunde der Humboldt-Universität, Berlin, Germany.
ZSM	Zoologisches Staatssammlung, München, Germany.

cw	the distance across the carapace at the widest point.
cl	carapace length measured along the median line, from the anterior to the posterior margin.
ch	carapace height, the maximum height of the cephalothorax.

fw	front width, the width of the front measured along the anterior margin.
sw	sternum width, the width of the sternum measured across the widest point.
s	thoracic sternite.
e	episternite.
s4/s5, s4/s5, s5/s6, s6/s7, s7/s8	sternal sutures between adjacent sternites.
s4/e4, s5/e5, s6/e6, s7/e7	episternal sutures between adjacent sternites and episternites.
a1-a7	abdominal segments 1-7.
P1-P5	pereiopods 1-5.
coll.	collected by.
m	male.
f	female.
r	correlation coefficient.

The abbreviated date format is day.month.year.

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TABLE 1

The number of species and subspecies of freshwater crabs found in Africa, Madagascar and Asia, according to RATHBUN (1904-1906).
The West African taxa are shown in bold-face type.

	Number of species or subspecies				
	Total	All Africa	West Africa	Madagascar	Asia
Family Potamonidae					
Subfamily Potamoninae					
Potamon (Potamonautes)	59	37	**5**	0	22
Potamon (Parathelphusa)	36	6	**2**	1	29
Potamon (Geothelphusa)	39	5	**1**	0	34
Potamon (Potamon)	75	2	**1**	5	68
Potamon (Perithelphusa)	4	0	**0**	0	4
Hydrothelphusa	1	0	**0**	1	0
Platythelphusa	1	1	**0**	0	0
Limnothelphusa	1	1	**0**	0	0
Erimetopus	1	1	**0**	0	0
Subfamily Deckeninae					
Deckenia	2	2	**0**	0	0

TABLE II

Some past taxonomies of West African freshwater crabs

Author & classification	Taxon in present work
RATHBUN (1904-1905)	**Present Work**
POTAMONIDAE	POTAMONAUTIDAE
POTAMONINAE	
Potamon (Potamon) nigrensis	*Potamonautes ecorssei*
Potamon (Parathelphusa) chavanesii	*Sudanonautes chavanesii*
Potamon (Parathelphusa) chaperi	*Liberonautes chaperi*
Potamon (Potamonautes) ecorssei	*Potamonautes ecorssei*
Potamon (Potamonautes) latidactylus	*Liberonautes latidactylus*
Potamon (Potamonautes) africanus	*Sudanonautes africanus*
Potamon (Potamonautes) aubryi	*Sudanonautes aubryi*
Potamon (Potamonautes) floweri	*Sudanonautes floweri*
Potamon (Potamonautes) decazei	*Sudanonautes aubryi*
Potamon (Potamonautes) pobeguini	*Sudanonautes aubryi*
Potamon (Potamonautes) pelii	*Sudanonautes aubryi*
POTAMONIDAE	GECARCINUCIDAE
	GLOBONAUTINAE
Potamon (Geothelphusa) macropus	*Globonautes macropus*
BALSS (1929)	**Present Work**
POTAMONIDAE	POTAMONAUTIDAE
POTAMONINAE	
Potamon (Parathelphusa) chavanesii	*Sudanonautes chavanesii*
Potamon (Potamonautes) africanus	*Sudanonautes africanus*
Potamon (Potamonautes) faradjensis	*Sudanonautes faradjensis*
Potamon (Potamonautes) decazei	*Sudanonautes aubryi*
Potamon (Potamonautes) decazei granulata	*Sudanonautes granulatus*
Potamon (Potamonautes) pobeguini	*Sudanonautes aubryi*
Potamon (Potamonautes) aubryi	*Sudanonautes aubryi*
Potamon (Potamonautes) aubryi monodi	*Sudanonautes monodi*
Potamon (Potamonautes) anchetiae	*Sudanonautes granulatus*
	Potamonemus sachsi
CAPART 1954	**Present Work**
POTAMONIDAE	POTAMONAUTIDAE
Potamonautes chavanesii	*Sudanonautes chavanesii*
Potamonautes africanus	*Sudanonautes africanus*
Potamonautes aubryi	*Sudanonautes aubryi*
Potamonautes decazei	*Sudanonautes aubryi*
Potamonautes pobeguini	*Sudanonautes aubryi*
Potamonautes floweri	*Sudanonautes floweri*
Potamonautes monodi	*Sudanonautes monodi*
Potamonautes chaperi	*Liberonautes chaperi*
Potamonautes nigrensis	*Potamonautes ecorssei*

TABLE III

An abbreviated version of the classification of West African freshwater crabs in BOTT (1955).

- **I. Family Potamonidae**
  - Subfamily Potamoninae
    - *Potamonautes*
      - *(Erimetopus)*
        - *P. (E.) brazzae brazzae*
        - *P. (E.) brazzae frontospinosus*
      - *(Platythelphusa)*
        - *P. (P.) armata armata*
        - *P. (P.) armata conculata*
      - *(Platypotamonautes)*
        - *P. (P.) ecorssei*
        - *P. (P.) triangulus*
      - *(Isopotamonautes)*
      - *(Potamonautes s. st.)*
      - *(Obesopotamonautes)*
      - *(Gerdalopotamonautes)*
      - *(Orthopotamonautes)*
      - *(Lobopotamonautes)*
      - *(Arcopotamonautes)*
      - *(Acanthothelphusa)*
      - *(Rotundopotamonautes)*
      - *(Tripotamonautes)*
      - *(Lirrangopotamonautes)*
    - *Sudanonautes*
      - *(Sudanonautes)*
        - *S. (S.) africanus africanus*
        - *S. (S.) africanus chavanesii*
        - *S. (S.) africanus chaperi*
        - *S. (S.) decazei decazei*
        - *S. (S.) decazei orthostylis*
      - *(Convexonautes)*
        - *S. (C.) aubryi aubryi*
        - *S. (C.) aubryi floweri*
        - *S. (C.) aubryi monodi*
    - *Liberonautes*
      - *L. latidactylus*
    - *Potamon*
    - *Potamiscus*
  - Subfamily Trichodactylinae
  - Subfamily Hydrothelphusinae
    - *Hydrothelphusa*
  - Subfamily Gecarcinucinae
    - *Gecarcinucus*
- **2. Family Deckeniidae**
  - *Deckenia*
- **3. Family Pseudothelphusidae**

TABLE IV
Classification of African freshwater crabs in BOTT (1970a,b).
The African genera are shown in bold-face.

I.	Superfamily	PARATHELPHUSOIDEA (= GECARCINUCOIDEA)		
1.	Family	GECARCINUCIDAE		
	Subfamily		GECARCINUCINAE	
				Gecarcinucus
				Gecarcinautes
				Afrithelphusa
				Barythelphusa
				Inglethelphusa
				Cylindrothelphusa
	Subfamily		GLOBONAUTINAE	
				Globonautes
	Subfamily		LIOTHELPHUSINAE	
2.	Family	SUNDATHELPHUSIDAE		
3.	Family	PARATHELPHUSIDAE		
	Subfamily		SPIRALOTHELPHUSINAE	
	Subfamily		CEYLONOTHELPHUSINAE	
	Subfamily		SOMMANIATHELPHUSINAE	
	Subfamily		PARATHELPHUSINAE	
II.	Superfamily	POTAMOIDEA		
4.	Family	POTAMONAUTIDAE		
				Potamonautes
				Sudanonautes
				Liberonautes
5.	Family	DECKENIIDAE		
				Deckenia
6.	Family	POTAMIDAE		
			POTAMINAE	
				Madagapotamon
			POTAMISCINAE	
7.	Family	SINOPOTAMIDAE		
8.	Family	ISOLAPOTAMIDAE		
III.	Superfamily	PSEUDOTHELPHUSOIDEA		
9.	Family	PSEUDOTHELPHUSIDAE		
10.	Family	POTAMOCARCINIDAE		
IV.	Other families (not assigned to a superfamily)			
11.	Family	TRICHODACTYLIDAE		

TABLE V

Comparison of present classification of West African freshwater crabs with that of BOTT (1955-1970a,b)

Taxon in present work	Taxon in BOTT (1955-1970a,b)
POTAMONAUTIDAE	POTAMONIDAE
POTAMONAUTINAE	POTAMONINAE
Potamonautes ecorssei	*Potamonautes (Platypotamonautes) ecorssei*
Potamonautes triangulus	*Potamonautes (Platypotamonautes) triangulus*
Potamonautes senegalensis	*Potamonautes (Isopotamonautes) senegalensis*
Liberonautes chaperi	*Sudanonautes (Sudanonautes) africanus chaperi*
Liberonautes latidactylus	*Liberonautes latidactylus*
Sudanonautes aubryi	*Sudanonautes (Convexonautes) aubryi aubryi*
	Sudanonautes (Sudanonautes) pelii pelii
	Sudanonautes (Sudanonautes) decazei decazei
	Potamonautes pobeguini
Sudanonautes africanus	*Sudanonautes (Sudanonautes) africanus africanus*
Sudanonautes chavanesii	*Sudanonautes (Sudanonautes) africanus chavanesii*
Sudanonautes floweri	*Sudanonautes (Convexonautes) aubryi floweri*
Sudanonautes faradjensis	*Sudanonautes (Sudanonautes) africanus chaperi*
Sudanonautes monodi	*Sudanonautes (Convexonautes) aubryi monodi*
Sudanonautes granulatus	*Sudanonautes (Sudanonautes) decazei granulata*
Sudanonautes orthostylis	*Sudanonautes (Sudanonautes) decazei orthostylis*
	GECARCINUCIDAE
GLOBONAUTINAE	GLOBONAUTINAE
Globonautes macropus	*Globonautes macropus macropus*
Afrithelphusa monodosus	*Globonautes monodosus*
Louisea edeaensis	*Globonautes macropus edeaensis*
Louisea balssi	*Globonautes macropus balssi*
	GECARCINUCIDAE
GLOBONAUTINAE	GECARCINUCINAE
Afrithelphusa gerhildae	*Afrithelphusa gerhildae*
Afrithelphusa afzelii	*Afrithelphusa afzelii*

West African taxa described since 1970

Potamonautes reidi
Liberonautes paludicolis
Liberonautes nanoides
Liberonautes rubigimanus
Liberonautes nimba
Liberonautes lugbe
Liberonautes grandbassa
Sudanonautes kagoroensis
Sudanonautes nigeria
Potamonemus mambilorum
Potamonemus sachsi
Potamonemus asylos
Afrithelphusa leonensis

Cladistic Analysis of the West African Freshwater Crabs

Freshwater Crab Morphology and Explanation of Terminology

Body Plan (fig. 3-13, table VI)

The body of African freshwater crabs (like all brachyurans) consists of twenty segments plus the telson divided into two main regions, the cephalothorax (fourteen segments) and the abdomen (six segments plus the telson). The cephalothorax is subdivided into the head (with six segments and six pairs of appendages) and the thorax (with eight segments and eight pairs of appendages). The ventral part of the cephalothorax (the plastron, or thoracic sternum) consists of a series of eight fused segments (the thoracic sternites). The abdomen of both male and female African freshwater crabs consists of six true segments plus the telson. The first abdominal segment (a1) is proximal and lies next to the posterior margin of the carapace, while the rounded telson (a7) forms the distal end of the abdomen. The abdomen is normally held flexed against the sternum and in both sexes covers the sterno-abdominal cavity. The abdomen is highly modified for reproduction in both sexes and has lost the locomotory and respiratory functions seen in other decapods. The abdomen shows sexual dimorphism in sexually mature animals: that of adult males is much smaller than the sternum, while that of adult females is as big as the sternum. The anus of male and female freshwater crabs opens on abdominal segment 6; the telson is capable of limited movement, relaxing slightly to allow defecation while the rest of the abdomen remains secure.

The different pairs of appendages of the cephalothorax and abdomen are each specialised for a variety of functions including feeding, locomotion, reproduction and sensing the environment. The appendages of freshwater crabs show one of two basic structural plans: they are either biramous (with an endopod and an exopod) or uniramous (with only an endopod). A typical biramous appendage (such as a female abdominal pleopod) consists of a peduncle or stem (the coxa and the basis) with two branches: an inner endopod and an outer exopod. The endopod is usually the larger of the two and typically consists of five segments (the ischium, merus, carpus, propodus and dactylus), while the exopod is usually shorter and has fewer segments. A typical uniramous appendage (such as the male gonopod) consists of a peduncle (the coxa and the basis) plus the endopod. Male freshwater crabs have abdominal appendages only on the first two abdominal segments (a1 and a2), while female freshwater crabs only have appendages on four abdominal segments (a2-a5). Abdominal segment a6 and the telson of freshwater crabs always lack appendages in both sexes.

Fig. 14 (*see* "Data analysis" below) summarizes the relationships of the West African genera, while fig. 15-53 (*see* "Systematic Study" below) illustrate the important taxonomic characters of the group.

Cephalothorax

Carapace (fig. 3A-B)

The carapace of West African freshwater crabs has a transversely oval outline and it is typically about 1.5 times broader than long. In West African freshwater crabs the anterior margin of the frontal region of the carapace (the front) is usually deflexed so that part of it covers the antennulular fossae. The dorsal part of the carapace is joined to the underlying thoracic structures, but the sidewalls of the carapace (the branchiostegites) are free and their lower edges are not fused to the body walls. The lateral borders of the dorsal carapace are sharply defined and there is a clear separation between the dorsal surface of the carapace and the sidewalls. The sidewalls enclose the two branchial (gill) chambers in which the gills (or other respiratory organs) lie. Respiratory water normally enters each gill chamber ventrally under the lower edges of the carapace sidewalls and leaves anteriorly via the two conspicuous efferent openings at the corners of the buccal cavity (CUMBERLIDGE, 1986).

The texture of the dorsal surface of the carapace may be either rough (with fields of granules or carinae in some species (fig. 20B, D, F, G, H) or almost completely smooth in other species (fig. 20C)). The carapace of African freshwater crabs is typically cut by a pattern of grooves (sulci), representing sites of internal muscle attachment and of underlying organs (fig. 3A). For example, the middle part of the dorsal carapace from anterior to posterior is divided by surface grooves into frontal, gastric, cardiac and intestinal regions. The frontal region lies between the orbits, the gastric region occupies the middle of the carapace behind the front and the gastric grooves coincide with the boundaries of the stomach. The cardiac region lies immediately behind the gastric region and the cardiac grooves indicate the position of the heart. The intestinal region lies behind the cardiac region and the intestinal sulcus overlies the intestines. The hepatic regions occupy the antero-lateral corners of the carapace lateral to the orbits and the branchial regions lie posterior to the hepatic regions. The area of the carapace behind the upper margin of each orbit is the orbital region. Two cervical grooves divide the gastric region from the branchial regions of the dorsal carapace and either terminate at the postorbital crest or at the epibranchial tooth (from where they continue down over the sidewalls forming the vertical grooves). In most African freshwater crabs there is a postfrontal crest running horizontally across the dorsal anterior carapace between the epibranchial teeth, in a line behind the frontal region and the orbital regions. The postfrontal crest (fig. 3A-B) is composed of two epigastric crests (on the anterior margins of the meso-gastric regions) fused at their lateral ends to two postorbital crests (posterior to the orbits) which in most species extend to the anterolateral margins. There is typically a short mid groove in the middle of the postfrontal crest formed from the junction of the two epigastric lobes or crests, which may or may not be forked at its posterior end.

Carapace border (fig. 3A)

The anterior border of the carapace consists of the frontal margin and the two orbital margins, while the posterior carapace is delimited by the posterior border. Between these borders lie the curved lateral borders of the carapace that separate the dorsal surface from the sidewall. These borders are subdivided into anterolateral and posterolateral margins. The anterolateral margins are directed inward anteriorly, while the posterolateral margins are directed inward posteriorly. In African freshwater crabs the frontal margin may be slightly indented or straight, it may be wide or quite narrow, and it may project straight out or be deflexed so that it partly covers the antennulular fossae. The superior margin of the orbit extends from the lateral edges of the front to the exorbital angle, which marks the beginning of the anterolateral margin. The orbits of freshwater crabs house the eyestalks and consist of two long transverse cavities in the anterior carapace on either side of the front. The upper orbital margin is formed from a continuation of the frontal margin while the lower orbital margin is part of the carapace sidewall. These two orbital margins meet laterally at the exorbital angle which in some species is shaped like a pointed tooth and in others is continuous with the anterolateral margin. The upper and lower orbital margins do not meet medially so that this part of the orbit is not completely closed, forming a gap (the orbital hiatus). The orbital hiatus of African freshwater crabs is occupied superiorly by the basal joint of the antenna and inferiorly by a small orbital (occlusal) tooth.

Exorbital angle (fig. 3A)

In *Menippe*, *Goniopsis*, *Platythelphusa* and *Potamon* the exorbital angle is large and pointed (the plesiomorphic state). In *Gecarcinucus* the exorbital angle is low and is continuous with the anterolateral margin (the apomorphic state). The exorbital angle in the African freshwater crabs varies: it is either a large triangular structure, or it is small and not detectable.

Epibranchial tooth (fig. 3A)

Nearly all genera of West African freshwater crabs have an epibranchial tooth on the anterolateral margin at the point where the postfrontal crest meets. An epibranchial tooth can also be identified in other groups of freshwater crabs (*Potamon*, fig. 12F, *Platythelphusa*, fig. 8A and *Gecarcinucus*, fig. 8B) and in the grapsid *Goniopsis* (fig. 8E)) while in *Menippe* (fig. 8F) this tooth corresponds to the large tooth immediately behind the tooth-like exorbital angle (the plesiomorphic state). In African freshwater crabs the absence of an epibranchial tooth probably represents the extreme apomorphic condition whereby the tooth is so reduced in size it is difficult to locate. The presence or absence of an epibranchial tooth and the size and shape of this tooth was used by RATHBUN (1904-1906) to assign crabs to genus or subgenus (taxa that are approximately equivalent to family level taxa in BOTT's (1970b) classification). However, the size of the epibranchial tooth within genera of West African freshwater crabs varies according to species. The size of the epibranchial tooth (relative to the exorbital angle and the other teeth on the anterolateral margin) and the shape of the epibranchial tooth (whether it is pointed or blunt, or reduced to a notch) can be used to distinguish between species of West African freshwater crabs.

Intermediate tooth (fig. 3A)

The outgroup taxa and most genera of West African freshwater crabs lack a tooth on the anterolateral margin between the epibranchial tooth and the exorbital angle. In some genera

(*Sudanonautes* (fig. 30, 31), *Liberonautes* (fig. 20) and *Louisea* (fig. 46F-G, pl. 3-4) there is an intermediate tooth between the exorbital angle and epibranchial tooth (the apomorphic state).

Anterolateral margin (fig. 3A)

The ornamentation on the anterolateral margin behind the epibranchial tooth and the beginning of the posterolateral margin varies from a series of sharp teeth (*Menippe* (fig. 8F) and *Platythelphusa* (fig. 8A)) (the plesiomorphic state), to granular (*Potamon*, fig. 12F), to completely smooth (*Goniopsis* (fig. 8E)). There is a trend within genera of West African freshwater crabs towards the loss of the anterolateral margin teeth (the apomorphic state). Large teeth on the anterolateral margins are found in some, but not all, species of *Sudanonautes* (fig. 30E), *Liberonautes* (fig. 20F) and *Potamonautes* (fig. 15D). Those species of African freshwater crabs that have large teeth on the anterolateral margins of the carapace are found almost exclusively living in the major rivers (*Sudanonautes*, *Liberonautes* and *Potamonautes*) or in lakes (*Platythelphusa*). In the subsequent radiation of each genus anterolateral margin teeth may have been lost as a response to a more terrestrial lifestyle. BOTT (1955) considered that the original function of the anterolateral margin teeth in the marine crab ancestors of freshwater crabs somehow prevented the animals from sinking into soft muddy substrata. It is equally likely that anterolateral margin teeth originally served to defend against attack by soft-mouthed aquatic predators (such as fish). On land, however, large anterolateral margin teeth would be less likely to deter the attacks of determined hard-mouthed terrestrial predators and may even hinder the rapid escape of the crab through dense vegetation or down a burrow. It is generally the case that burrow-digging, semi-terrestrial species of freshwater crabs (and, indeed all species of land crabs) have no anterolateral margin teeth (fig. 8B). The trend toward a round, smooth-edged carapace is, at least in part, an adaptation for moving in and out of a burrow, and in part a reflection of adaptations related to an increase in air breathing. In the intermediate condition, both the number and the size of anterolateral margin teeth are decreased (at least in the semi-terrestrial species), and in the most advanced condition the anterolateral margins of the carapace are totally smooth.

Posterolateral margin (fig. 3A)

The posterolateral margin of the carapace of the African freshwater crabs is always smooth (there are never granules or teeth) and there is an indentation to accommodate P5 close to the junction with the posterior margin. The posterior margin of the carapace is straight and is usually wider than the frontal margin.

Postfrontal crest (fig. 3A)

In all of the African freshwater crabs there is a postfrontal crest running horizontally across the carapace. The postfrontal crest in the African freshwater crabs consists of two separate components: a pair of epigastric crests and a pair of postorbital crests. In *Menippe* (fig. 8F) and *Goniopsis* (fig. 8E) the epigastric crests are distinct, but postorbital crests (that normally constitute the postfrontal crest in the African freshwater crabs) are missing in these genera. In *Gecarcinucus* (fig. 8B) the epigastric and postorbital crests are both present. Freshwater crabs with a postfrontal crest show two principle forms: either an incomplete crest, or a complete crest. In *Platythelphusa* (fig. 8A), *Potamon* (fig. 12F) and *Liberonautes* (fig. 20) the postfrontal crest is distinct, but incomplete, that is, the lateral ends of the postorbital crests do not extend to meet the carapace margins (the plesiomorphic state). In *Potamonautes* (fig. 15A-D), *Sudanonautes* (fig. 30, 31) and *Afrithelphusa* (fig. 46A-D) the postfrontal crest is complete and spans the entire carapace between the epibranchial teeth (the apomorphic state). The clarity of the postfrontal crest may be influenced by changes in carapace morphology associated with air breathing (such as an increase in carapace height) which may result in secondary changes in the appearance of the postfrontal crest. A complete postfrontal crest spanning the entire carapace, or the detectable remains of a once-complete postfrontal crest, are both treated here as the apomorphic state. For example, the broken, faint or incomplete postfrontal crest seen in *Potamonemus* (fig. 40), *Louisea* (fig. 46F-G) and *Globonautes* (fig. 45, 46E) is considered here to be the apomorphic state of the character, because in each case, when viewed under magnification, there is evidence that the ends of the crest once met the carapace margins. With proper caution, the form of the postfrontal crest can be used as a character for delimiting genera.

Carapace sidewall (fig. 3B)

The sidewalls of the carapace form the walls of the gill chambers and lie between the lateral borders of the carapace and the bases of the legs and chelipeds. All freshwater crabs have an epimeral sulcus on each sidewall that runs back from the anterolateral angle of the buccal cavity to the posterolateral angle of the carapace. This sulcus divides the sidewall into an upper part (that includes the suborbital, subhepatic and sub-branchial regions), and a lower part (the pterygostomial region). The area between the lower margin of the orbit and the pterygostomial region is the suborbital region (formed by an anterior loop of the cervical groove). In most genera of West African freshwater crabs there is a vertical (pleural) sulcus on the sidewall (between the subhepatic and sub-branchial regions) running from the anterolateral margin (between the exorbital angle and the epibranchial tooth) down to the epimeral sulcus. The vertical sulcus divides the sidewall into three parts: (1) the suborbital and subhepatic region, (2) the subbranchial region and (3) the pterygostomial region. In *Menippe* (fig. 8H) the sidewall has only a single epimeral suture that runs lengthways anterior to posterior (the plesiomorphic state). In *Gecarcinucus* (fig. 8D), *Potamon* (fig. 12G) and *Platythelphusa* (fig. 8C) and in the majority of the African freshwater crabs there is an additional vertical suture on the sidewall of the carapace running between the epimeral suture and the anterolateral margin (the apomorphic state).

Head (table VI)

The head and thorax comprise the cephalothorax which is covered by the carapace. The six segments of the head show a great deal of fusion, but the six pairs of appendages (the eyes, antennules, antennae, mandibles and the first and second maxillae) can be easily distinguished.

The first structures of the head are the stalked compound eyes that lie transversely in the orbits. The antennules (first antennae) are the second pair of head appendages and are positioned just inferior to the frontal margin.

The antennules each lie in an antennulular fossa, separated in the middle by the interantennular septum, which is a central partition formed from the union of the inferior margin of the front with the epistome. Each antennule is biramous: it consists of a two-jointed stem and an exopod and an endopod in the form of two short terminal flagella (often shaped like pine cones). The outer flagellum (the exopod) is the largest and comprises a series of little segments equipped with fine setae that test water currents.

The antennae (second antennae) are the third pair of head appendages. Each antenna is uniramous: there are three large basal segments (the peduncle) and a short flagellum (the endopod). The first segment of the antennal peduncle is a small, oval-shaped structure that is fused to the epistome. This segment bears the opening of the antennal or green gland that is involved in ionic regulation. The second and third segments of the antennal peduncle are fused together to form the basal joint of the antenna that always makes contact with margin of the front in African freshwater crabs. The terminal segments of the antenna form the flagellum that is very short, and is always much shorter than the eyestalk.

The fourth pair of appendages of the head are the mandibles. Each mandible (fig. 5) consists of a strongly calcified tooth-like structure (the protopod) that is broadened and grooved at its distal end to form the incisor and molar processes which cut and crush food. Each mandible has a curved palp (the reduced endopod) on its dorsal surface, which in brachyurans is composed of either two or three segments. The palp of the mandible of all West African freshwater crabs consists of two segments (fig. 5), never three. A two-segmented mandibular palp separates the Potamonautidae from the Potamidae (whose mandibular palp has three distinct segments). The terminal (distal) segment of the mandibular palp normally consists of a single flat oval lobe which rests on the posterior surface of the mandible (fig. 5A). In some species the mandibular palp is clearly bilobed and bears a second large flat oval structure (the anterior lobe) that overlaps the anterior surface of the mandible (fig. 5D). The number of segments of the mandibular palp and the number and size of the lobes of the terminal segment have been used in the past to assign African freshwater crabs to family and superfamily (BOTT, 1955, 1965, 1970a,b; NG, 1988).

In *Liberonautes* (fig. 33) and in *Louisea* (fig. 48E-F) there is an additional small but distinct anterior process on the terminal segment of the mandibular palp. In these genera the anterior process is a small free lobe about one quarter as big as the posterior lobe (fig. 5C). In *Liberonautes* and *Louisea* the anterior process on the mandibular palp is found in all members of each genus. However, differences in the characters of the sternum, abdomen, gonopod and carapace of *Liberonautes* and *Louisea* argue against the possibility that the anterior process on the mandibular palp of these genera is a synapomorphy. A more likely interpretation (based on a number of other characters) is that these two genera are not closely related and that this character has arisen independently in each of these genera. In *Sudanonautes* only three out of ten species have an anterior process on the terminal segment of the mandibular palp. In this genus the anterior process ranges in size from a low thickening at the base of the terminal segment (fig. 33H) to a small sharply marked ridge (fig. 33D, J). Since an anterior process is found in some, but not all, species in *Sudanonautes*, this character is not a synapomorphy that can be used to define this genus. STEWART (1997) reports the presence of a similar small anterior process on the mandibular palp of *Potamonautes brincki* (BOTT, 1960) from South Africa, and notes that this anterior process varies from conspicuous to almost completely absent in different populations of this species. It should be noted that in the present work all forms of the anterior process of the mandibular palp were found to be considerably smaller than the enlarged subequal anterior lobe seen in *Globonautes* (fig. 48D) and *Afrithelphusa* (fig. 48A-C). The small but distinct anterior process of the mandibular palp is not judged here to be an example of a bilobed mandibular palp (fig. 5D).

The fifth and sixth pairs of appendages of the head are the first and second maxillae. The first maxilla is a small, round, flattened appendage which aids in feeding and/or respiration. The second maxilla (maxillule) has a flattened exopod that forms the gill bailer (scaphognathite) which maintains the flow of respiratory water (or air) through the branchial chamber (CUMBERLIDGE, 1986).

The mandibles, maxillae and maxillules of the head, and the three pairs of maxillipeds of the thorax all lie in a square-shaped cavity (the buccal cavity) that is delimited superiorly by the lower margin of the epistome, laterally by the carapace sides, and inferiorly by the thoracic sternum. The midpoint of the epistome forms a conspicuous downward pointing triangle, while the lower margins of the epistome continue laterally to meet the sidewalls, where they form the superior wall of the exhalent (efferent) respiratory openings. The vertical sides of the buccal cavity are formed by the pterygostomial regions of the branchiostegites, the floor of the buccal cavity is formed by the upward pointing triangular tip of sternite 1 and by the roof of the buccal cavity by the endostome (palate).

Thorax (table VI)

The thorax consists of eight fused segments. The dorsal surface of the thorax is covered by the carapace, while the ventral surface is formed by the sternum. Each of the eight thoracic segments has a pair of appendages: the three anterior pairs are the maxillipeds while the five posterior pairs are the pereiopods (P1-P5). Each pair of appendages is modified for either feeding, respiration, grasping, or walking. The first, second and third maxillipeds (on sternites s1-s3) are biramous, and each usually bears a flagellum on the exopod. Each maxilliped also has a long epipod which extends back into the branchial chamber above and below the gills where its movement serves to keep the gills clean. In freshwater crabs from West Africa the distal margin of the endopod of the first maxilliped is a broad, flat triangular structure that forms the movable floor of the exhalent respiratory channel. All species of freshwater crabs from West Africa lack an extra lobe on the endopod of the first maxillipeds (the so-called portunoid lobe) seen in some of the Portunidae (RODRIGUEZ, 1992). Dramatic modifications of the endopod of the first maxilliped of the sort found in the East African Deckeniidae and in *Seychellum* from the Seychelles (NG *et al.*, 1995) are not seen in the freshwater crabs from West Africa. The third maxillipeds (fig. 4E) together form a broad cover over the buccal cavity and are the outermost and most visible of the mouthparts. In the West African freshwater crabs each third maxilliped typically has a broadened and flattened column-shaped ischium (which is longer than wide), and an equally broadened short merus, which is a rectangle, wider than long. The external angle of the merus of the third maxilliped forms a right angled corner which is the outer wall of the anterior respiratory opening. The medial margins of the meri of the third maxillipeds meet in the midline and these appendages completely close the buccal cavity. The three terminal joints of the third maxilliped (the carpus, propodus and dactylus) are small, and together form a short jointed movable palp on the medial superior margin of the merus that reaches down just beyond the merus/ischium junction. The exopod of the third maxilliped is long and robust, reaches the mid-point of the merus, and usually has a long flagellum which aids in directing water currents. A few taxa of African freshwater crabs: *Globonautes*, *Afrithelphusa* and *Louisea* (fig. 49) and *Potamonemus* (fig. 42D-F) and some species of *Liberonautes* (fig. 23D, H) show adaptations to air breathing where the flagellum of the exopod of one or more of the three maxillipeds is absent or reduced (CUMBERLIDGE, 1991b, 1993a, 1994a; CUMBERLIDGE & CLARK, 1992).

Sternum (fig. 3C, 9, table VI)

The ventral surface of the thorax consists of eight fused thoracic segments (sternites s1-s8) plus four episternites (e4-e7) and eight pairs of thoracic appendages. The first, second and third maxillipeds are attached to sternites s1-s3, while the five pairs of legs (P1-P5) are associated with sternites s4-s8. In male crabs there is a pair of sternal condyles ("boutons pressions" knobs GUINOT, 1979) on the lateral walls of the sterno-abdominal cavity of s5. The sternum of freshwater crabs shows a great deal of surface segmentation and there are potentially seven sternal sulci. The seven sulci on the sternum (here termed the sternal sulci), represent the external divisions between the eight sternites. In African freshwater crabs sternal sutures s2/s3 and s4/s5-s7/s8 are always clearly marked, while the clarity and completeness of sternal sutures s1/s2 and of s3/s4 varies between taxa. Sternal sulcus s1/s2 is horizontal and short, and runs between the posterior margin of s1 and the anterior margin of s2. Sternal suture s1 is a small triangular chip, and is the smallest of all of the sternal suture. Sternal sulcus s2/s3 is horizontal, s3/s4 (if present) is usually v-shaped, and s4/s5 continues down into the sterno-abdominal cavity but it does not meet in the mid line.

Sternite s4 is the broadest of the sternites and is adapted to support the articulation of the chelipeds. In most African freshwater crabs the anterior margin of the sterno-abdominal cavity reaches to s4 (fig. 9A, 16A-D, 21, 32, 41A-C, 47); in some species of freshwater crabs from elsewhere in the Old World the sterno-abdominal cavity may reach to s3 or even to s2 (fig. 9B). In male African freshwater crabs the anterior end of the sterno-abdominal cavity is a deep, slim depression corresponding to the shape of the telson of the abdomen. In female crabs the anterior end of the sterno-abdominal cavity forms a broad steep-sided wall that reaches laterally to episternite e4. Four sternal sutures (s4/s5, s5/s6, s6/s7 and s7/s8) cross the thoracic sternum and are of taxonomic value in brachyurans (GUINOT, 1979). These sutures may be either continuous (i.e., meeting in the midline) or discontinuous (i.e., separated medially). Sternal sulcus s5/s6 continues down into the sterno-abdominal cavity but does not meet in the mid line. Sternal sulcus s6/s7 continues down into the sterno-abdominal cavity but does not meet in the mid line. In female crabs there is a pair of sexual openings on the walls of the sterno-abdominal cavity of s6. Sternal sulcus s7/s8 runs between the posterior margin of s7 and the anterior margin of s8, and continues down into the sterno-abdominal cavity where it meets in the mid-line. In male crabs less than one half of the width of sternites s5-s7 lies in the sterno-abdominal cavity and is covered by the abdomen; the remainder of the sternum (the visible part) is formed by the rest of these sternites. In female crabs all of s5-s7 lie entirely in the sterno-abdominal cavity and the sternites are covered by the abdomen.

In both male and female crabs s8 (the last sternite) is short and most of it lies in the sterno-abdominal cavity where it is completely covered by the abdomen. In some species a small part of s8 of male crabs extends beyond the margin of the sterno-abdominal cavity and meets the coxa of P5. In female crabs all of s8 lies within the margins of the sterno-abdominal cavity, and its junction with the coxa of P5 is covered by the abdomen. In male crabs the sterno-abdominal cavity is deep and narrow and serves to protect the two pairs of gonopods. In female crabs the sterno-abdominal cavity is broad, shallow and bowl-shaped, with wide, feathery pleopods which, together with the broad abdomen, serves to retain and protect the eggs and hatchlings. The surface arrangement of the sternites and the sternal sulci reflects the underlying endophragmal skeleton. At the base of the sterno-abdominal cavity sternites s4-s6 taper medially and converge, but do not meet in the midline, leaving a long thin oval depression (fig, 9A-D). The incomplete sternites s4-s6 represent a pulling apart of the sternum and a general widening of the body associated with the repositioning of the anterior legs that brings about changes in locomotion (MAGALHÃES & TÜRKAY, 1996a). Sternites s7 and s8 curve anteriorly do not taper and meet in the midline; their junction is marked by a longitudinal sulcus (the medial line).

Sterno-abdominal cavity (fig. 3C)

In *Menippe*, *Goniopsis* and *Gecarcinucus* the sterno-abdominal cavity is deep and long, and the distal end is finger-like with long parallel sides, as is the telson, which ends in a rounded tip (the plesiomorphic state). In *Potamon*, *Platythelphusa* and the West African freshwater crabs the sterno-abdominal cavity is shallow and broad, and the distal end is triangular with long tapering sides and a rounded end. Here the telson of the abdomen is a rounded triangle with a rounded tip (the apomorphic state).

Episternites (fig. 3C)

The sternum of male and female African freshwater crabs has four crescent-shaped episternites (e4-e7) positioned laterally to s4-s8. In *Menippe*, *Goniopsis* and *Gecarcinucus* the episternites are slim (the plesiomorphic state), while in *Potamon*, *Platythelphusa* and the West African freshwater crabs the episternites are broad (the apomorphic state). The episternites lie between the bases of two adjacent walking legs and serve to support the articulations of the coxae. Episternite e4 supports the articulation of the cheliped (P1); e4 and e5 support the articulation of P2, e5 and e6 support the articulation of P3, episternites e6 and e7 support the articulation of P4, while e7, together with s8, supports the articulation of P5. The medial margin of the coxa of P1-P4 each has a condyle that articulates with two adjacent episternites. In female crabs the condyle of P5 articulates with e7 and s8. In males, the condyle of P5 bears the penis, which is positioned so that it reaches to the bases of gonopods 1 and 2 at the junction of e7 and s8.

Episternal sulci (fig. 3C)

The sulci marking the junctions between s4-s8 and e4-e7, called here episternal sulci (abbreviated to s4/e4, s5/e5, s6/e6 and s7/e7), are not always clearly marked; their presence or absence can be used to distinguish between species. All four episternal sutures (s4/e4, s5/e5, s6/e6 and s7/e7) are clearly visible in

Menippe, Goniopsis, Potamon and in *Platythelphusa* (9A, C-E), but in *Gecarcinucus* (9B) and in taxa from West Africa (21D-E, 32G-H, 41, 47) some (or all) may be absent.

Pereiopods (fig. 4, 10, 11, 17A-D, 18A-C, 24, 25, 26, 35, 36, 42A-C, 43A-C, 45A-B, 50, table VI)

The five pairs of appendages on thoracic segments s4-s8 are pereiopods 1-5 (P1-P5), which include the chelipeds (P1) and the walking legs (P2-P5). All pereiopods are uniramous and they all lack the exopod. Each pereiopod consists of seven segments: the coxa (which joins the appendage to the body), the basis and ischium (which are fused together), and the merus, carpus, propodus and dactylus. The merus of P2-P5 is always the longest segment and the carpus is always the shortest.

The chelipeds of adult male specimens of West African freshwater crabs are greatly unequal in size (heterochelous): the largest is the major cheliped and the smallest is the minor cheliped. The chelipeds of adult females and subadult and juvenile males may appear quite different from those of adult males of the same species. The major cheliped of adult males has an enlarged palm, and the cutting edges of the propodus and dactylus may have large teeth and an arched dactylus that encloses a large oval interspace (hiatus) between the closed fingers. The minor cheliped lacks dramatic enlargement and dentition, shows less differentiation between species, and is less useful for separating species.

P1 merus (fig. 4C)

The merus of the cheliped is usually long and slim and triangular in cross section. There are three distinct margins, the superior margin and the medial and lateral inferior margins. These latter two margins each have a row of teeth or granules and there is usually a single large pointed tooth (the distal tooth) at the distal end. The superior surface of the merus of the cheliped typically has a rough texture with granules and/or short carinae. In most species of African freshwater crabs the inner surface of the merus of the cheliped that is closest to the sidewall of the carapace usually has a conspicuous long, oval flat surface (the meral tympanum). The medial and lateral inferior margins of the P1 merus of *Menippe* and *Goniopsis* are completely smooth. The medial and lateral inferior margins of the merus of *Goniopsis, Gecarcinucus, Potamon* and *Platythelphusa* each have a row of granules or teeth, and there is usually a single large distal tooth (the apomorphic state). The marginal teeth are very large and pointed in *Goniopsis* and *Platythelphusa* and low and faint in other species (*Gecarcinucus*).

P1 propodus of adult male (fig. 4A)

The propodus of the major cheliped typically consists of the hand (the enlarged palm) and the elongated fixed finger (the pollex). The lower margin of the propodus usually has two downward curves separated by an upward curve or indentation. In some species (*L. latidactylus* and *L. rubigimanus*) the mid point indentation of the propodus is lacking, the entire lower margin curves downward, and both the palm and the fixed finger are very broad. The teeth on the cheliped are found on the upper edge of the fixed finger of the propodus and the lower edge of the movable finger (dactylus). Two dimensions reflect the amount of cheliped enlargement: the height of palm of the propodus, and the length of the lower margin of the propodus. While both of these dimensions change dramatically as crabs grow, and while there are obvious differences between the chelipeds of the two sexes, meaningful comparisons can still be made if they are restricted to the length and height of the major cheliped of adult male specimens. The shape of the propodus of the major cheliped of adult males varies according to species. The propodus of the major cheliped of adult males of *Menippe*, *Goniopsis*, *Gecarcinucus* and *Potamon* is short (fig. 10B-D) and is not as long as the carapace width. The propodus of the major cheliped of adult males of *Platythelphusa tuberculata*, *S. africanus*, *S. granulatus* and *Potamonautes reidi* is long (as long as, or longer than the carapace width).

P1 dactylus (fig. 4A)

The dactylus hinges on the upper distal end of the palm of the propodus and, together with the fixed finger, forms a scissors-like cutting and grasping organ. The length, width and curvature of the dactylus of the major cheliped of adult males varies according to species. The dactylus of the major cheliped of adult males of *Menippe*, *Goniopsis*, *Gecarcinucus* and *Potamon* is short, broad and curved, and when it is closed against the propodus it leaves a distinct space. The dactylus of the major cheliped of adult males of *Platythelphusa tuberculata* and of *P. reidi* (fig. 17D), *S. chavanesii* (fig. 35B) and *P. mambilorum* (fig. 42A) is long, slim and curved, and even when it is closed against the propodus it leaves a wide space (the apomorphic state). The dactylus of the major cheliped of adult males of *S. faradjensis* (fig. 35A) is long, slim and straight, and when it is closed against the propodus it leaves very little space between the fingers. In *L. rubigimanus* (fig. 24C) the dactylus of the major cheliped of adult males is long, highly curved and very broad so that when it is closed it leaves no space between the fingers.

P2-P5 merus (fig. 3A, 26)

The merus of P2-P5 is triangular in section and the superior margin of *Goniopsis*, *Gecarcinucus*, *Potamon* and *Platythelphusa* bears a distinct pointed tooth at the distal end (the subterminal tooth, the plesiomorphic state). Species of freshwater crabs in other genera show differences in the size of this tooth, which is short in some and absent in others (the apomorphic state).

P2-P5 propodus (fig. 3A, 26)

The propodus of P5 of *Menippe* and *Goniopsis* and of the lake-dwelling *Platythelphusa tuberculata* is long and narrow (the plesiomorphic state), while the propodus of P5 of fully-aquatic river-living crabs such as *S. faradjensis* and *L. chaperi* and of the lake-living *Platythelphusa armata* is short and broad (the apomorphic state). The propodus of P2-P5 has serrated margins (the plesiomorphic state) in some species and smooth margins in others (the apomorphic state).

P2-P5 dactylus (fig. 3A, 26)

In *Menippe* the dactylus of P2-P5 is either smooth or it has soft hairs or bristles (the plesiomorphic state) but it never has corneous spines. In *Goniopsis*, *Gecarcinucus*, *Potamon* and *Platythelphusa* and in all African freshwater crabs the dactylus of P2-P5 always bears four rows of short spines (the apomorphic state).

Abdomen (fig. 4F, 11E-G, 18D-G, 27, 37, 43D-F, 51, table VI)

Male abdomen

The abdomen of male African freshwater crabs is a short, flat, tapered triangular structure that covers only part of the sternum (the sterno-abdominal cavity). The first two abdominal segments (a1 and a2) of adult male freshwater crabs are narrow and wide and completely span the sternal area between the fifth pereiopods. Abdominal segment a3 is always the broadest part of the abdomen, while a7 (the telson) is always the narrowest. Abdominal segments a3-a7 together usually form a triangular shape (in juveniles and in adult males), with a3 forming the broad base and a7 forming the narrowest and most distal part. Abdominal segments a1 and a2 are normally fixed and are not capable of movement, while a3-a7 usually move as a single unit, with the hinge operating between a2 and a3. A pair of depressions on the underside of the abdomen on a6 fit tightly onto a pair of sternal condyles on s5. This mechanism serves to secure the male abdomen firmly against the sternum, and is present in all African freshwater crabs. Male freshwater crabs possess only two pairs of abdominal appendages (gonopods 1 and 2) on a1 and a2 that are highly modified for copulation.

The form of the gonopods, penis and sterno-abdominal cavity of African freshwater crabs has influenced the shape of the male abdomen: it is always triangular, never T-shaped, as is the case for some of the Asian freshwater crabs (NG, 1988). The triangular shape of the abdomen of African freshwater crabs is the result of two basic needs: (1) the abdomen must be wide enough to cover both pairs of gonopods as well as the right and left penises at the points where they join the gonopod chambers, and (2) the abdomen must be exactly the same shape as the sterno-abdominal cavity to provide a tight seal. The typical triangular shape of the male abdomen of the West African freshwater crabs reflects uniformity in the position of the male openings (always coxal and always lying above s8), in the size of the gonopods (always long), and the shape of the distal part of the sterno-abdominal cavity (always slim). In all taxa examined in this study the male abdomen completely covers the sterno-abdominal cavity. The abdominal characters used in this study are based primarily on the abdomen of adult male crabs. The abdomen of subadult male crabs often shows isometric growth during ontogeny, whereas the abdomen of subadult female crabs shows dramatic allometric growth changing in outline from a slim triangle to a broad oval (HARTNOLL, 1971).

Male abdomen: position of telson

In *Goniopsis*, *Potamon* and *Platythelphusa* (fig. 11E, G, H) and in the majority of African freshwater crabs, the telson is a rounded triangle with a rounded tip that reaches as far as s4 (the plesiomorphic state). In *Menippe* and *Gecarcinucus* (fig. 11I, F) the telson is finger-like with long parallel sides and a rounded tip that reaches as far as s2 (the apomorphic state). This character could also be expressed in terms of the position of the sterno-abdominal cavity, whose length varies according to the anteriormost sternal segment included in the cavity. In *Menippe* (fig. 11G), *Goniopsis*, *Potamon* and *Platythelphusa* (fig. 11E, G-I) and in the West African freshwater crabs, the anteriormost segment is s4 (the plesiomorphic state), while in *Gecarcinucus* (fig. 11F) it is s2 (the apomorphic state).

Female abdomen

The abdomen of juvenile female freshwater crabs is a long, slim triangle, similar to that of juvenile male crabs. The outline of the abdomen of female crabs changes with each moult from a slim triangle to a round, broad, shield-shaped structure that covers most of the sternum in adults. The first abdominal segment of adult female freshwater crabs is reduced to a thin narrow strip, and is often overlain by the posterior margin of the carapace, so that only a2-a7 can normally be seen inferiorly. Abdominal segments a2 and a3 are both broad and together they completely span the sternum between the two fifth pereiopods. Abdominal segment a5 is always the broadest and the longest segment. Abdominal segment a7 (the telson) is a broad triangle that reaches to the bases of the third maxillipeds and completely covers the anterior sternum. The entire female abdomen moves as a single unit, with the hinge operating between a1 and the posterior carapace margin. There are four pairs of biramous appendages (the pleopods), on a2-a5. The pleopods of adult female freshwater crabs are specialised for attaching and carrying eggs and hatchlings. The exopods of the female pleopods are feathery and are lined with long hairs for attachment of the eggs while the endopods are long, broad and much less hairy, and form the outer edges of the protective abdominal brood pouch in which the eggs and hatchlings are secured. The abdomen of females bearing egg masses or hatchlings bulges out away from the sternum to create a brood pouch, whose side edges are closed by the broad blades of the pleopods, which project out from under the abdomen. The female sexual openings through which the eggs are laid lie in the sterno-abdominal cavity close to the mid line on s6, and are normally covered by the abdomen. Externally, the female openings of African freshwater crabs comprise a pair of transverse holes (the vulvae) on s6. Each is oval shaped (wider than long), and in an ovigerous female of *Sudanonautes aubryi* (cw 69.6 mm) measures 3.2 mm wide by 2.1 mm long. The entire female genital duct (between the ovary and the exterior) consists of the oviduct, the spermatheca, the vagina, the vestibule and the vulva (HARTNOLL, 1968). At the surface of the sternum the lumen of the vulva is open (there is no operculum). Deep to this is a wide vestibule with flexible walls connected to the vagina which is a straight tube that gradually widens to form the spermatheca sited between the vagina and the oviduct.

Female abdomen shape

The female abdomen of *Potamon*, *Platythelphusa* and of the majority of African freshwater crabs is always a rounded shield shape, and is distinctly different from the slim triangular abdomen of the male. In contrast, the female abdomen of *Gecarcinucus* (fig. 11FF) is a slim narrow triangle that is not much broader than that of the male (fig. 11F). The shape of the female abdomen distinguishes *Gecarcinucus* from the Globonautinae and from all the other African genera.

Gonopod Terminology (fig. 6, 7)

The structure and terminology of the first and second male pleopods or gonopods of marine crabs are discussed in detail by Guinot (1979). Descriptions and illustrations of the gonopods of marine brachyurans found in West African waters are provided by Monod (1956) and by Manning & Holthuis (1981). The following account describes the structure and terminology of the first and second gonopods of the African freshwater crabs; these organs differ from those of marine crabs and from the Neotropical freshwater crabs (Rodriguez, 1982, 1992; Magalhães & Türkay, 1996a,b,c). The first and second gonopods of the African freshwater crabs are each structures with four parts, of which only the two distal parts (three and four) are of taxonomic importance. Segment 1 of gonopods 1 and 2 (the coxa) is small and serves to connect the base of the gonopod with the abdomen. Segment 2 of gonopods 1 and 2 (the basis) supports the penis as it enters the basal gonopod chamber (fig. 7A). In the present work, segment 3 of gonopods 1 and 2 (the endopod) is termed the subterminal segment of the gonopod, while part 4 (which is highly developed in most Palaeotropical freshwater crabs) is termed the terminal article of the gonopod (fig. 7B). The junctions between the two distal parts of both gonopods of freshwater crabs are usually visible in both ventral and dorsal views.

The gonopods are normally viewed by placing the crab on its back, with the specimen's anterior end furthest away from the viewer and the abdomen uppermost. When the abdomen is pulled up and straightened so that the telson is furthest from the head, the gonopods can be seen in their resting position in the sterno-abdominal cavity (fig. 6A). In this position the side of the gonopod facing the viewer is the ventral side, while the side toward the sternum that is hidden from view is the dorsal side. If the gonopods are pulled away from the sternum so that they project upward (with the animal still lying on its back), then the ventral side of the gonopod will now face in the direction of the telson of the outstretched abdomen (i.e., caudal), and the dorsal side will face toward the head (i.e., cephalic). This latter terminology (caudal side and cephalic side) was proposed as a terminology for gonopod 1 of the Neotropical freshwater crabs by Smalley (1964), and while equally valid, is not adopted in the present work in view of the great topological differences between the terminal article of gonopod 1 of the Neotropical and Afrotropical freshwater crabs.

The lateral part of the gonopod is closest to the coxae of the walking legs, while the medial part is closest to the midline (median) of the animal. The part of the gonopod that is attached to the abdomen is the proximal or basal part, while the part of the gonopod that is furthest from the point of attachment is the distal part (fig. 6A). The terminal article of gonopod 1 of African freshwater crabs is typically a short, pointed, tapered structure with a longitudinal groove dividing the segment lengthways into two parts. BOTT (1955) called these two longitudinal parts ventral and dorsal. However, since both of these features lie on the ventral side of the gonopod they are called here the lateral fold and the medial fold. This terminology is derived as follows. The topology of the ventral face of the terminal article of gonopod 1 is the result of the folding inward of the inner (medial) and outer (lateral) side edges of the segment to form a tube (like a rolled up newspaper). The two folded edges meet lengthways along their entire inner margins, and their junction forms the third major feature of the terminal article, the longitudinal groove. The part nearest to the outer margin of the gonopod is termed here the "lateral fold", and the part nearest to the inner margin of the gonopod is termed here the "medial fold". The term lateral fold corresponds to the ventral half of the terminal article of gonopod 1 in BOTT (1955) and the term medial fold corresponds to the dorsal half of the terminal article of gonopod 1 in BOTT (1955). The fusion of the two folds on the terminal article of gonopod 1 along their medial edges forms a hollow tube which is open at the tip (the apical opening) through which the spermatophores pass during copulation (fig. 7B, C). The dorsal side of both the terminal article and subterminal segment of gonopod 1 presents a smooth simple surface, and there is typically a membrane (the dorsal membrane) between the two parts that allows for limited movement of the terminal article (fig. 7E).

Gonopod structure and function

The gonopods of the Eubrachyura exhibit a somewhat uniform basic plan (gonopod 1 has at least three segments and gonopod 2 has three segments and a terminal article) but there is a great deal of diversification when the details of these structures are considered (GUINOT, 1979). The first gonopod of *Menippe* (Xanthoidea, Menippidae) is a three-segmented tubular structure that lacks a distinct terminal article (fig. 13C). In these groups segment 3 of gonopod 1 (i.e., the endopod or subterminal segment) is long, reaching up to, or even beyond, the sternal condyles, and its tip has either a small process and/or knobs or fields of bristles. This type of gonopod 1 most closely resembles that of the primitive crab families Homolidae, Dromiidae, Dynomenidae and Raninidae, as well as the Corystidae (Corystoidea) and may be close to the general brachyuran condition (the plesiomorphic state) (HARTNOLL, 1975; GUINOT, 1979; SCHRAM, 1982; NG, 1983). A similar type of gonopod 1 is also found in the Pseudothelphusidae (RODRIGUEZ, 1982) and some of the Trichodactylidae (RODRIGUEZ, 1992; MAGALHÃES & TÜRKAY, 1995). The four-part gonopod 1 with a distinct subterminal segment and an additional terminal article seen in the African freshwater crabs and in the other Old World freshwater crab families is, therefore, a derived character shared by these groups.

In all Old World freshwater crabs gonopod 2 is also divided into four parts in which segment 3 (the endopod or subterminal segment) is long, reaching up to, or even beyond, the sternal condyles, while the length and shape of the terminal article differ between genera and species (fig. 53). A gonopod 2 with four parts, in which the subterminal segment is long, the terminal article is a long flagellum, and there is a cup-shaped structure at the junction, is found in the more primitive xanthoids such as members of the Menippidae and is likely to represent the pleisiomorphic state. In *Menippe* (fig. 13G-H), *Myomenippe* and *Epixanthus* (Menippidae) the terminal article of gonopod 2 is very long and coiled (almost as long as the subterminal segment), while in *Eriphia* and in *Globopilumnus* (Menippidae) the terminal article is also long, but it is only about half as long as the subterminal segment, and is not coiled (MONOD, 1956; GUINOT, 1979; NG, 1983). In the Pilumnidae, Xanthidae, Panopeidae and Trapeziidae the subterminal segment of gonopod 2 is very short relative to gonopod 1, and the terminal article of gonopod 2 is a short stub (MONOD, 1956; GUINOT, 1979; NG, 1983).

The type of second gonopod seen in *Menippe* (with a long subterminal segment, with the terminal article a whip-like flagellum, and a cup at the junction) likely represents the ancestral condition in the Xanthoidea (NG, 1983). It is interesting to note that a similar gonopod 2 (with a long subterminal segment, and a flagellum-like terminal article) is also seen in certain primitive archaeobrachyuran (peditreme) crabs (Dromiidae and Dynomenidae), although in these families the cup is absent (GUINOT, 1979). Since the subterminal segment of gonopod 2 of the African freshwater crabs is always as long as the subterminal segment of gonopod 1 (fig. 13E, 53), and resembles the gonopod 2 of *Menippe* (fig. 13G-H), a long gonopod 2 with a long subterminal segment is considered here to represent the pleisiomorphic condition.

The two gonopods of all African freshwater crabs share a basic structure and have a common function. Both the subterminal segment and terminal article of gonopod 1 are topologically different from each other and the ventral side of each is always different from the dorsal side. The terminal article of gonopod 1 is tapered and hollow. The subterminal segment of gonopod 1 is always widest at the base and tapers to the same width as the terminal article; there is always a broad lateral flap that covers about half of the subterminal segment on the ventral side. Both distal segments of gonopod 2 are always solid, are similar on both their ventral and dorsal sides and there is a cup-like structure with concave inner surfaces at the junction between these two segments. The terminal articles of the two gonopods function together probably in locating the female sexual openings during copulation and in delivering spermatophores into these openings. The subterminal segments of gonopods 1 and 2 fit together forming a single long hollow chamber that has an opening at the base (the basal opening) into which the penis projects and another opening at the tip (the apical opening) out of which spermatophores are emitted. This single hollow channel inside the gonopods that is formed when the two gonopods are pressed tightly together is termed here the gonopod chamber. The gonopod chamber runs inside along the entire length of the subterminal segments of gonopods 1 and 2 and connects with the hollow space inside the terminal article of gonopod 1. The gonopod chamber is formed partly from the subterminal segments of gonopods 1 and 2 (the "subterminal gonopod chamber") and partly from the terminal article of gonopod 1 (the "terminal gonopod chamber").

Gonopod 1 subterminal segment

The subterminal segment of gonopod 1 has three main functions: (1) it supports and positions the terminal article of gonopod 1, (2) it secures the subterminal segment of gonopod 2, and (3) it forms the majority of the subterminal gonopod chamber. The subterminal segment of gonopod 1 is always the largest part of the gonopod, and, together with the subterminal segment of gonopod 2, forms the subterminal gonopod chamber. The features of the ventral side of the subterminal segment of gonopod 1 are the result of the inward folding of its edges. The medial part of the subterminal segment is a flattened fold that forms the broad flat floor of the segment, while the lateral part has a long wide raised lateral flap. Distally, close to the junction between the segments, the lateral flap of gonopod 1 is broad, and has a hair-fringed edge that is pressed tightly against the floor of the segment. This lateral flap forms the distal part of the subterminal gonopod chamber. The long, thin distal process of the subterminal segment of gonopod 2 is held firmly in place by the lateral flap so that it is secured inside the distal subterminal gonopod chamber. The basal (proximal) part of the subterminal segment of gonopod 1 is very broad and flat and the lateral flap here is very narrow. The basal part of the subterminal segment of gonopod 2 lies positioned against the basal part of the subterminal segment of gonopod 1. Together these two parts of the subterminal segments form the basal end of the subterminal gonopod chamber up into which the penis projects. The penis itself is a long thin membranous tubular structure that arises out of the coxa of P5 and which is partly supported by the second segment (the basis) of gonopod 1.

Gonopod 1 terminal article

The terminal article of gonopod 1 has two main functions: it connects with the female sexual openings during copulation and it forms the terminal gonopod chamber. The shape of the terminal article of gonopod 1 varies with genus and species and may be either straight or curved, or long or short. But in all African freshwater crabs the terminal article of gonopod 1 is always a closed tapering tube with an opening at the tip (the apical opening).

Gonopod 2 subterminal segment

The subterminal segment of gonopod 2 has three main functions: (1) it supports and positions the terminal article of gonopod 1, (2) it pumps the spermatophores along the length of the gonopod chamber, and (3) it forms the basal part of the subterminal gonopod chamber. The subterminal segment of gonopod 2 of West African freshwater crabs is solid and is always as long as the subterminal segment of gonopod 1. The subterminal segment of gonopod 2 has a broad rounded base and a long thin tapering process that ends in a rounded lip that supports the terminal article. This elongated part of gonopod 2 is secured under the tight-fitting lateral flap on the subterminal segment of gonopod 1. The subterminal segment of gonopod 2, together with the subterminal segment of gonopod 1, forms the subterminal gonopod chamber. The subterminal segment of gonopod 2, assisted by the cup-shaped structure at the junction, presumably functions as the pump that moves the spermatophores from the penis at the basal part of the subterminal gonopod chamber into the terminal gonopod chamber (inside the terminal article of gonopod 1) from where the spermatophores exit via the apical pore at the tip.

Gonopod 2 terminal article

The terminal article of gonopod 2 is either a long flexible flagellum (in some genera) or it is a short immovable process with a well-developed cup in other genera.

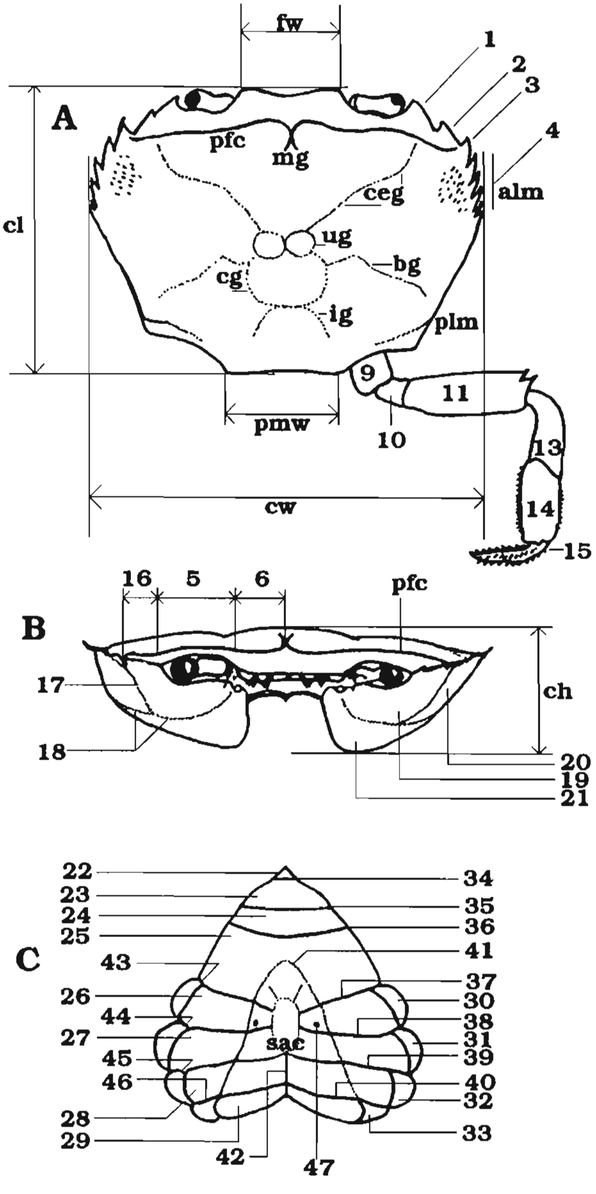
TABLE VI

Body organization of freshwater crabs

Body segment and region			**Appendages**		
HEAD					
(1)			eyes		
2			1st antennae (antennules)		
3			2nd antennae (antennae)		
4			mandibles		
5			1st maxillae (maxillules)		
6			2nd maxillae (maxillae)		
THORAX					
7 sternite 1			1st maxillipeds		
8 sternite 2			2nd maxillipeds		
9 sternite 3			3rd maxillipeds		
10 sternite 4		episternite 4	chelipeds (pereiopod 1)		
11 sternite 5	(male) sternal condyles	episternite 5	2nd walking legs		
12 sternite 6	(female) sexual openings	episternite 6	3rd walking legs		
13 sternite 7		episternite 7	4th walking legs		
14 sternite 8			5th walking legs	(male) sexual openings (penis)	
ABDOMEN			**General plan**	**Male**	**Female**
15 abdominal segment 1			1st pleopods	1st gonopods	none
16 abdominal segment 2			2nd pleopods	2nd gonopods	2nd pleopods
17 abdominal segment 3			3rd pleopods	none	3rd pleopods
18 abdominal segment 4			4th pleopods	none	4th pleopods
19 abdominal segment 5	(male) sternal condyle sockets		5th pleopods	none	5th pleopods
20 abdominal segment 6			none	none	none
21 telson		anus	none	none	none

FIG. 3.

A, Dorsal view of the carapace of a generalised potamonautid showing the right fifth pereiopod; **B**. Frontal view of the carapace of a generalised potamonautid; **C**, Inferior view of the sternum (plastron) of a generalised potamonautid. 1, exorbital angle; 2, intermediate tooth; 3, epibranchial tooth; 4, teeth on the anterolateral margin behind the epibranchial tooth; 5, postorbital region of the postfrontal crest; 6. epigastric crest of the postfrontal crest; 7; mid-groove of the postfrontal crest; 8, lateral carinae and striae on the surface of the carapace; 9, basis of pereiopod 5; 10, ischium of pereiopod 5; 11, merus of pereiopod 5; 12, subterminal tooth of the merus of pereiopod 5; 13, carpus of pereiopod 5; 14, propodus of pereiopod 5; 15, dactylus of pereiopod 5; 16, lateral extension of the postfrontal crest; 17, vertical (pleural) groove); 18, epimeral sulcus; 19, suborbital region of the sidewall of the carapace; 20, subhepatic region of the sidewall of the carapace; 21, pterygostomial region of the sidewall of the carapace; 22, sternite 1; 23, sternite 2; 24, sternite 3; 25, sternite 4; 26, sternite 5; 27, sternite 6; 28, sternite 7; 29, sternite 8; 30, episternite 4; 31, episternite 5; 32, episternite 6; 33, episternite 7; 34, sternal sulcus s1/2; 35, sternal sulcus s2/3; 36, sternal sulcus s3/4; 37, sternal sulcus s4/5; 38, sternal sulcus s5/6; 39, sternal sulcus s6/7; 40, sternal sulcus s7/8; 41, anterior margin of sterno-abdominal cavity; 42, medial vertical sulcus of the posterior sternum; 43, episternal sulcus s4/e4; 44, episternal sulcus s5/e5; 45, episternal sulcus s6/e6; 46, episternal sulcus s7/e7; 47, sternal condyle (bouton pression). alm, anterolateral margin; bg, branchial groove; cag, cardiac groove; ch, carapace height; cl, carapace width; cw, carapace width; ceg, cervical groove; cg, cardiac groove; fw front width; ig, intestinal groove; pfc, postfrontal crest; plm, posterolateral margin; pmw, posterior margin width; sac, sterno-abdominal cavity; ug, urogastric groove.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28
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42
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sac
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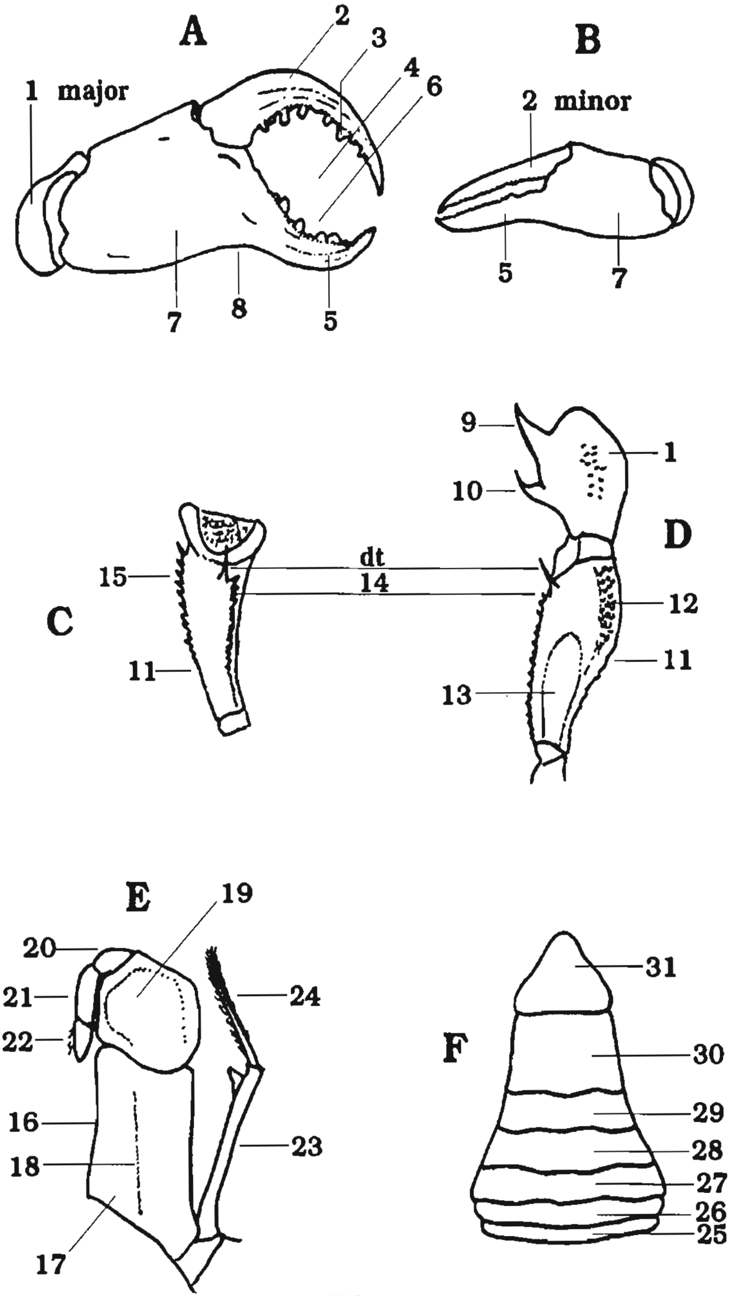
32
33

FIG. 3.

FIG. 4. A generalised African freshwater crab. **A**, frontal view of the right cheliped (pereiopod 1); **B**, frontal view of the left cheliped; **C**, inferior view of the right merus of the cheliped; **D**, superior view of the right merus of the cheliped; **E**, frontal view of the left third maxilliped; **F**, inferior view of the male abdomen. 1, carpus of the cheliped; 2, dactylus (movable finger) of the cheliped; 3, tooth on the cutting edge of the dactylus of the cheliped; 4, gape or interspace of closed cheliped; 5, fixed finger of the propodus of the cheliped; 6, tooth on the cutting edge of the fixed finger of the propodus of the cheliped; 7, palm of the propodus of the cheliped; 8, indentation on the inferior margin of the propodus of the cheliped; 9, first carpal tooth on the carpus of the cheliped; 10, second carpal tooth on the carpus of the cheliped; 11, merus of the cheliped; 12, granules and short carinae on the superior margin of the merus of the cheliped; 13, tympanum of the merus of the cheliped; 14, medial inferior margin of the merus of the cheliped (lined by small teeth) with a larger distal tooth (dt); 15, lateral inferior margin of the merus of the cheliped (lined by small teeth); 16, medial margin of the ischium of the third maxilliped; 17, ischium of the third maxilliped; 18, vertical sulcus on the ischium of the third maxilliped; 19, merus of the third maxilliped; 20, carpus of the third maxilliped; 21, propodus of the third maxilliped; 22, dactylus of the third maxilliped; 23, exopod of the third maxilliped; 24, flagellum of the exopod of the third maxilliped; 25, abdominal segment 1; 26, abdominal segment 2; 27, abdominal segment 3; 28, abdominal segment 4; 29, abdominal segment 5; 30, abdominal segment 6; 31, the telson.


A
1 major
2
3
4
6
7
8
5
B
2 minor
5
7
9
10
1
D
dt
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15
C
11
12
11
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E
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FIG. 4

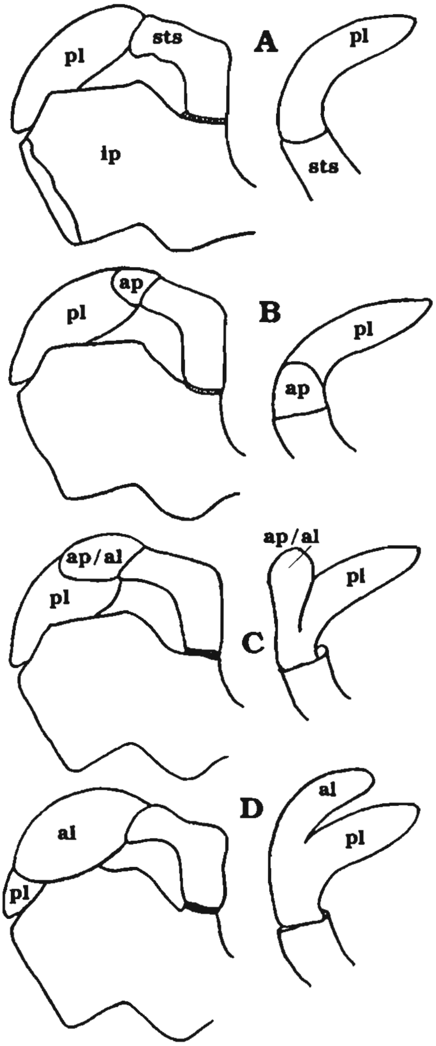


FIG. 5. Diagrams of the frontal view of the left mandible and superior view of the mandibular palp of selected African freshwater crabs showing different conditions of the mandibular palp. **A**, terminal segment consisting of the posterior lobe only; **B**, terminal segment with a large posterior lobe and a small anterior process; **C**, terminal segment with a large posterior lobe and a medium-sized anterior process; and **D**, terminal segment with a large, subequal lobular anterior process (a bilobed palp). These diagrams have not been arranged in a transformation series. al, anterior lobe of the terminal segment of the mandibular palp; ap, anterior process of the terminal segment of the mandibular palp; ip, incisor process of the mandible; pl, posterior lobe of the terminal segment of the mandibular palp; sts, subterminal segment of the mandibular palp.

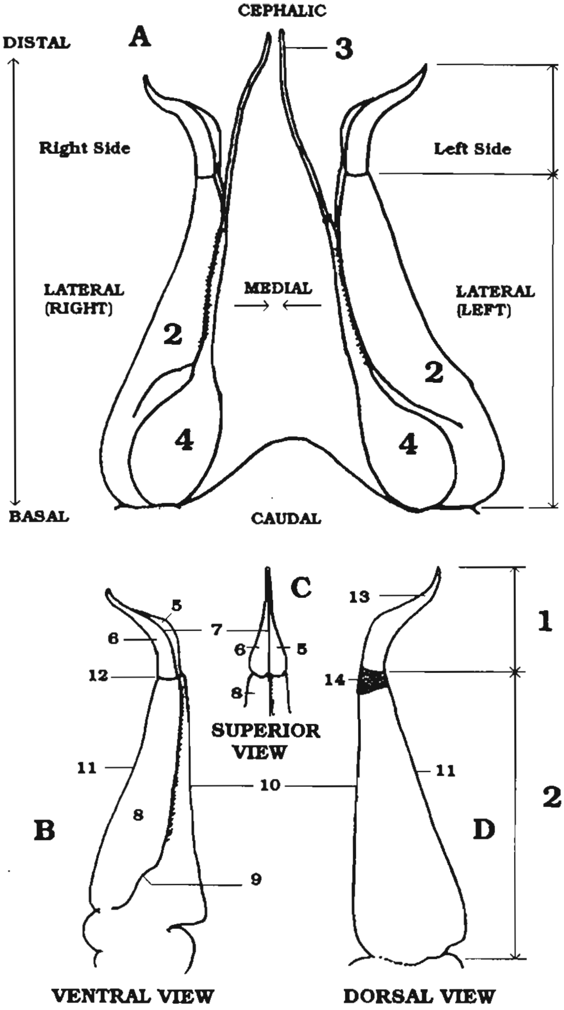


FIG. 6. A generalised African freshwater crab. **A**, ventral view of the right and left gonopods 1 and 2 shown in situ on the animal when the abdomen is pulled up to expose the gonopods lying in the sterno-abdominal cavity. The planes of reference are marked on the diagram; **B**, ventral view of the right gonopod 1; **C**, superior view of the terminal article of the right gonopod 1; **D**, dorsal view of the right gonopod 1. 1, terminal article of left gonopod 1; 2, subterminal segment of gonopod 1; 3, terminal article of left gonopod 2; 4, subterminal segment of gonopod 2; 5, medial fold of the terminal article of the right gonopod 1; 6, lateral fold of the terminal article of the right gonopod 1; 7, longitudinal groove of the terminal article of the right gonopod 1; 8, lateral flap of the subterminal segment of the right gonopod 1; 9, gonopod chamber of the subterminal segment of the right gonopod 1; 10, medial margin of the subterminal segment of the right gonopod 1; 11, lateral margin of the subterminal segment of the right gonopod 1.

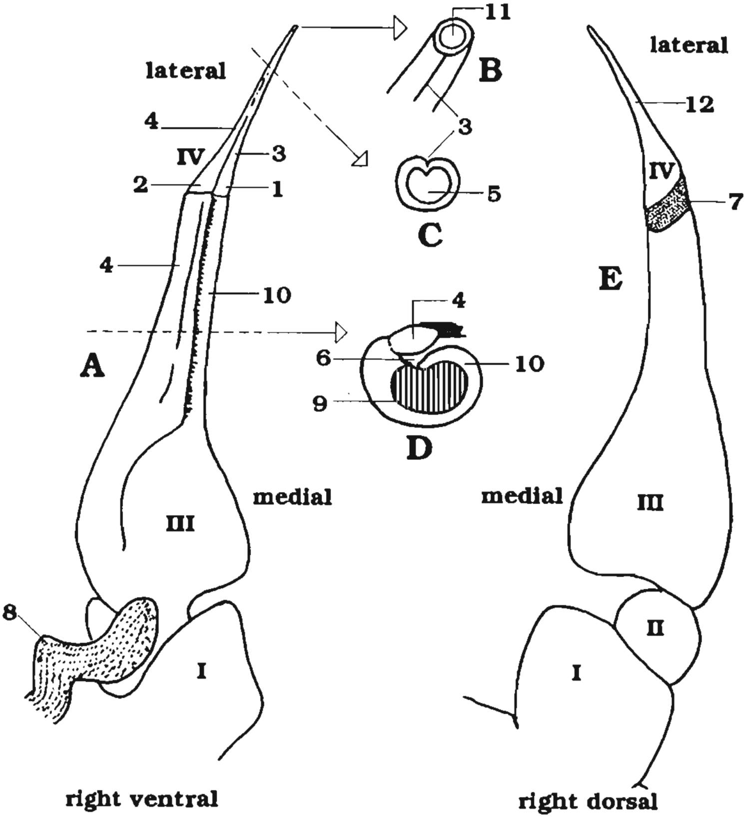


FIG. 7. *Liberonautes latidactylus*. **A**, Ventral view of right gonopod 1; **B**, ventral view of the detail of the tip of the terminal article of gonopod 1; **C**, cross section taken through the terminal article of right gonopod 1; **D**, cross section taken through the subterminal segment of right gonopod 1; **E**, dorsal view of the terminal article of right gonopod 1. The roman numerals on the diagram mark the 3 segments (I-III) and the terminal article (IV) of the gonopod. I, first segment of gonopod 1 (the coxa); II, second segment of gonopod 1 (the basis); III, third segment (the subterminal segment) of gonopod 1 (the endopod); IV, fourth part of gonopod 1 (the terminal article or process). 1, medial fold of the terminal article of the right gonopod 1; 2, lateral fold of the terminal article of the right gonopod 1; 3, longitudinal groove of the terminal article of the right gonopod 1; 4, lateral flap of the subterminal segment of the right gonopod 1; 5, gonopod chamber of the terminal article of the right gonopod 1; 6, gonopod chamber of the subterminal segment of the right gonopod 1; 7, dorsal membrane of gonopod 1; 8, penis; 9, connective tissue; 10, medial flap of the subterminal segment of gonopod 1; 11, apical opening of the terminal article of gonopod 1; 12, dorsal side of the terminal article of gonopod 1.

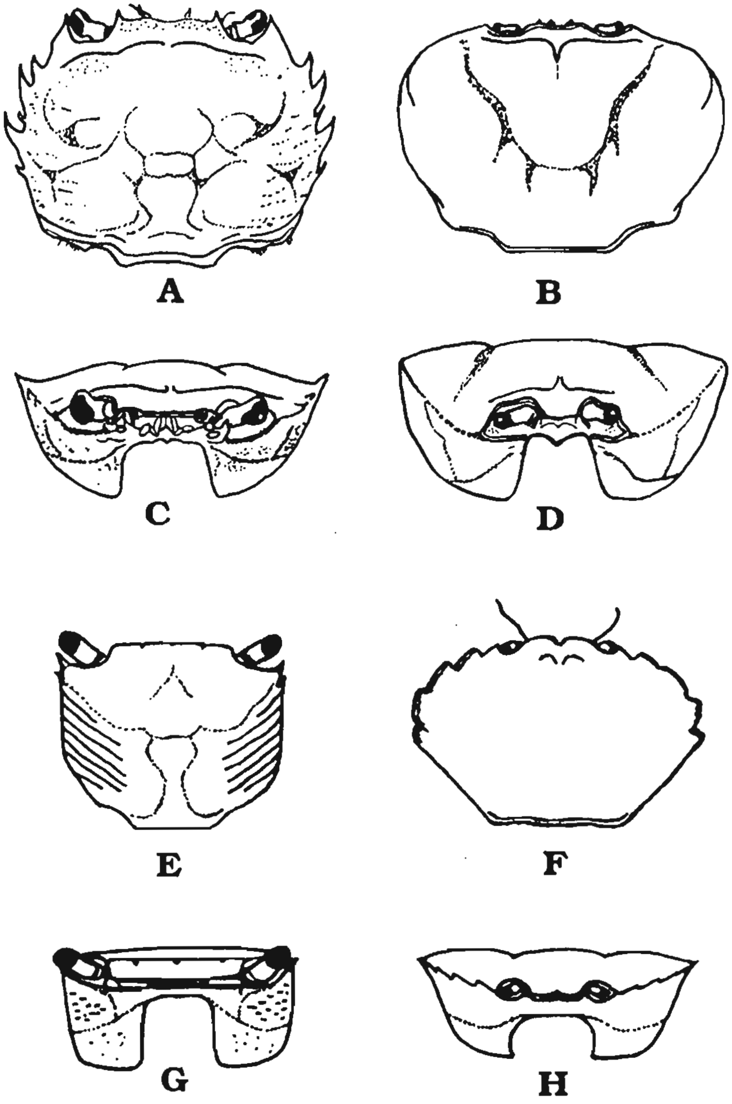


FIG. 8. Dorsal view (**A-B**, **E-F**) and frontal view (**C-D**, **G-H**) of the carapace of **A**, **C**, *Platythelphusa armata* A. MILNE-EDWARDS, 1887, adult male (cw 47.5 mm) from Lake Tanganyika, Kalémié (formerly Albertville), Zaire (NHML1952.10.23.1-10); **B**, **D**, *Gecarcinucus jacquemonti* H. MILNE EDWARDS, 1844, male (cw 38.1 mm) from Bombay, India (SMF 1763); **E**, **G**, *Goniopsis pulchra* LOCKINGTON, 1877, adult male (cw 40.2 mm) from Ecuador; **F**, **H**, *Menippe mercenaria* SAY, 1818, male (cw 22.9 mm) from the Atlantic coast of Florida, USA (Harbor Branch Oceanographic Museum 089:00423).

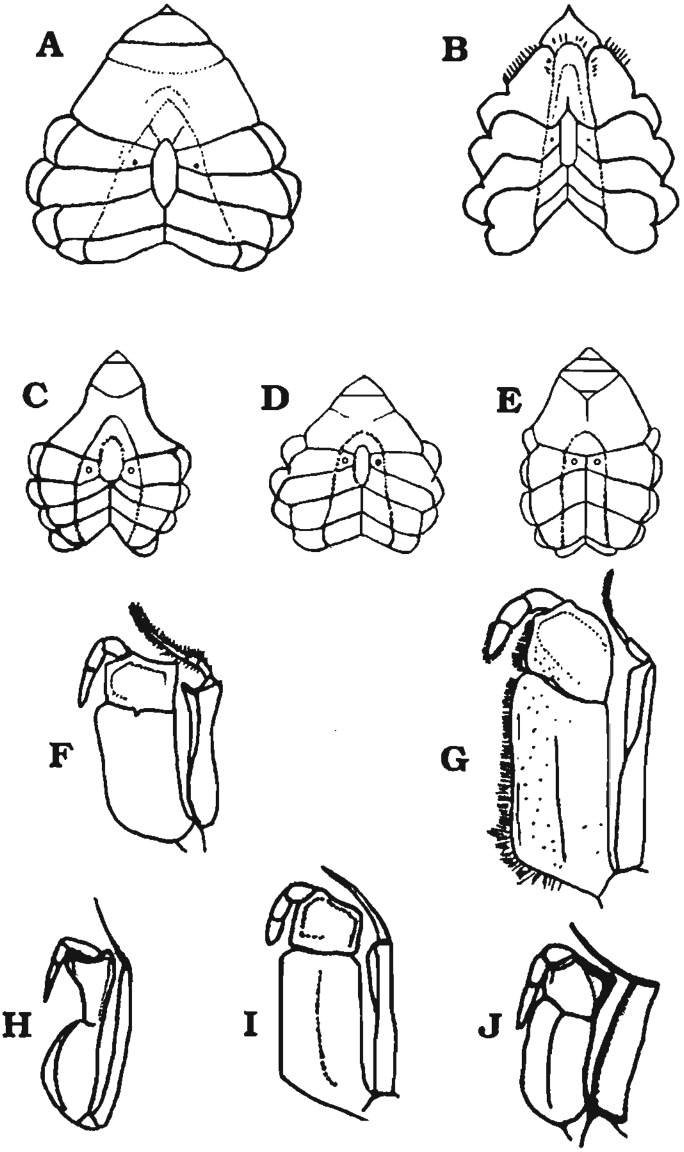


FIG. 9. Inferior view of the sternum (plastron) of **A**, *Platythelphusa*, **B**, *Gecarcinucus*, **C**, *Goniopsis*, **D**, *Potamon* and **E**, *Menippe*. Frontal view of the left third maxilliped of **F**, *Platythelphusa*, **G**, *Gecarcinucus*, **H**, *Goniopsis*, **I**, *Potamon* and **J**, *Menippe*. Specimen details (**A-C**, **E**) same as fig. 8; **D** and **I** were drawn from an adult male specimen (cw 56 mm) of *Potamon fluviatilis algeriense* BOTT, 1967, from Tunisia.

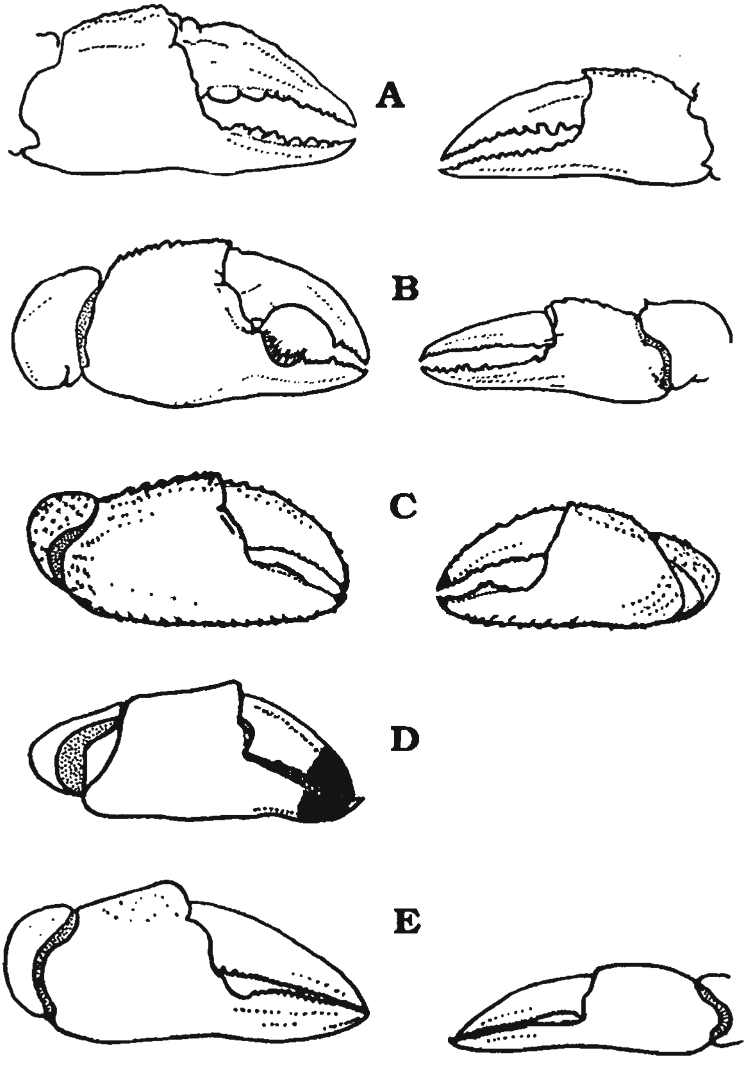


FIG. 10. Frontal view of the right and left chelipeds of **A**, *Platythelphusa*, **B**, *Gecarcinucus*, **C**, *Goniopsis*, **D**, *Menippe* and **E**, *Potamon fluviatilis algeriense* BOTT, 1967, subadult female (cw 23.2 mm) from Sebou river, El Oata (between Sefrou and El Mensel), Morocco (NMU 17.1966). The left cheliped of the specimen of *Menippe* was missing on this specimen. Specimen details for **A-D** same as fig. 8.

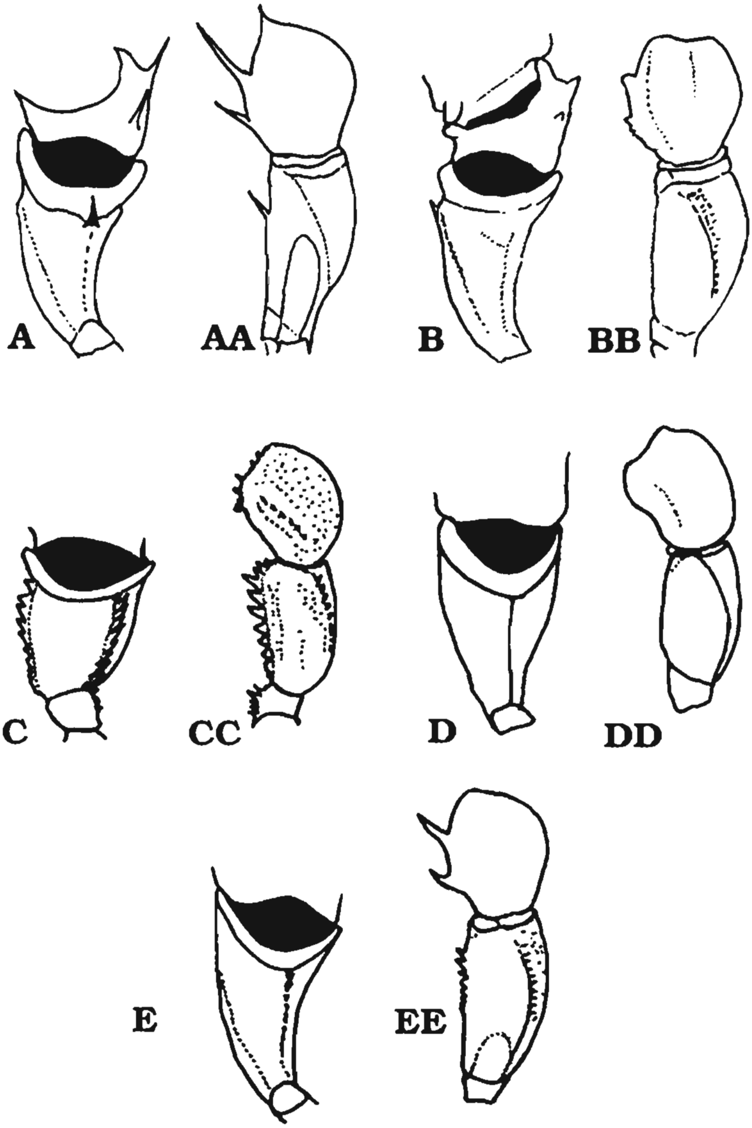


FIG. 11. Inferior view (**A-D**) and superior view (**AA-DD**) of the right carpus and merus of the cheliped of **A**. *Platythelphusa*. **B**. *Gecarcinucus*. **C**. *Goniopsis*. **D**. *Menippe* and **E**. *Potamon*. Specimen details same as fig. 10.

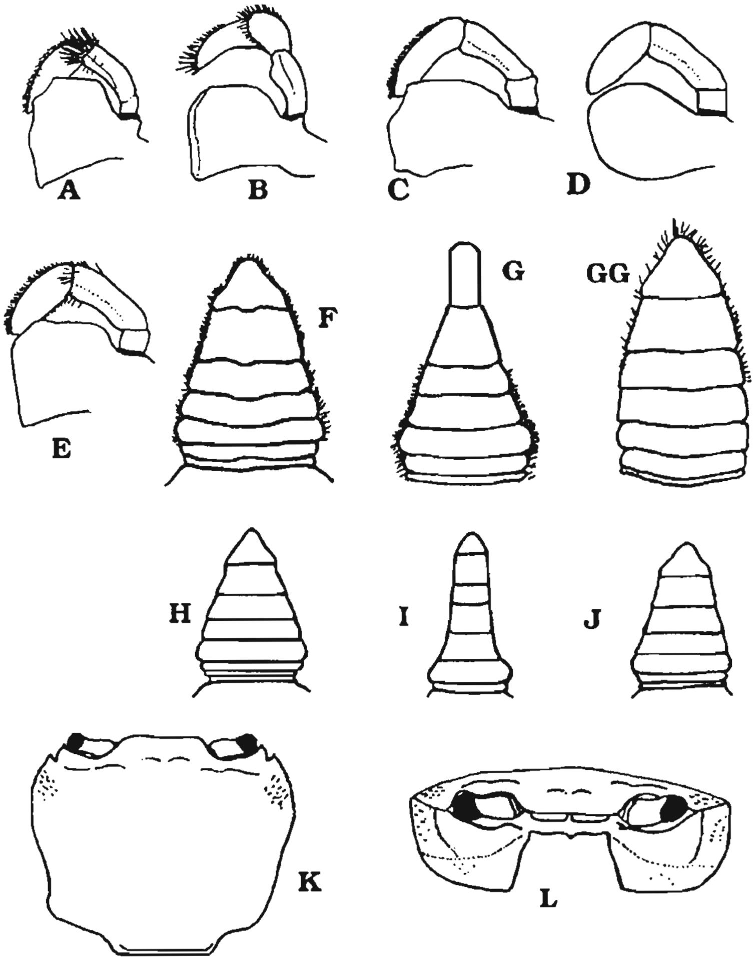


FIG. 12. Frontal view of the terminal segment of the palp of the left mandible of **A**. *Platythelphusa*. **B**. *Gecarcinucus*. **C**. *Goniopsis*. **D**. *Menippe* and **E**. *Potamon*. Inferior view of the male (**F-J**) and female (**GG**) abdomen of **F**. *Platythelphusa*. **G**. *Gecarcinucus*. **H**. *Goniopsis*. **I**. *Menippe* and **J**. *Potamon*. Dorsal view (**K**) and frontal view (**L**) of the carapace of *Potamon*. Specimen details same as fig. 10.

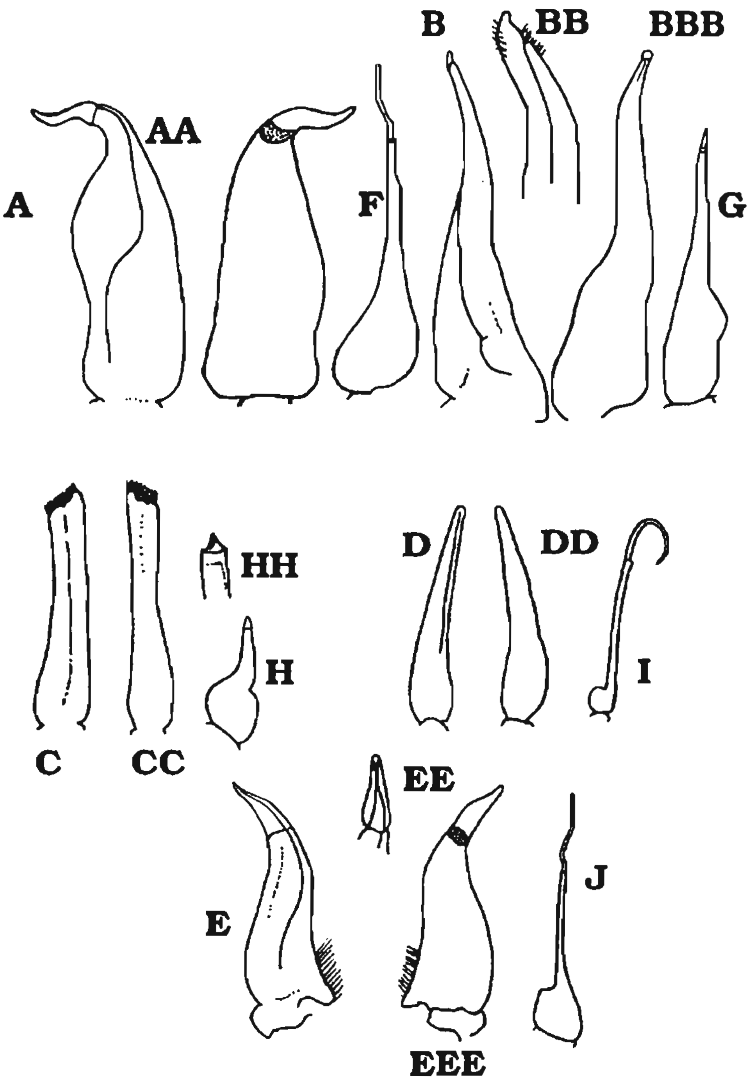


FIG. 13. Ventral view (**A-E**), dorsal view (**AA-EE**) and detail (**BBB**, **EE**) of the right gonopod 1 of **A**, *Platythelphusa*, **B**, *Gecarcinucus*, **C**, *Goniopsis*, **D**, *Menippe* and **E**, *Potamon*. Ventral view (**E-HI**) of the right gonopod 2 and detail of the terminal article (**GG**) of **E**, *Platythelphusa*, **F**, *Gecarcinucus*, **G**, *Goniopsis*, **H**, *Menippe*, and **I**, *Potamon*. Specimen details (**A-D**) same as fig. 8; **E** and **I** were drawn from a specimen of *Potamon fluviatilis algeriense*, adult male (cw 56 mm) from Tunisia.

The Systematic Position of the West African Freshwater Crabs

The only available cladistic analyses for any group of freshwater crabs are those provided by RODRIGUEZ & CAMPOS (1989), RODRIGUEZ & PEREIRA (1992) and RODRIGUEZ (1992) for the neotropical families. The new classification of the Trichodactylidae provided recently by MAGALHÃES & TÜRKAY (1996a,b,c) did not include a new cladistic analysis of the family. The systematics of the freshwater crabs of Africa has rarely been investigated within an evolutionary framework because the earlier classifications of RATHBUN (1904, 1905, 1906) and BOTT (1955, 1970a,b) were formulated without indicating genealogical relationships. BOTT (1955, 1969b, 1970a,b) assigned West African species to two families: the Potamonautidae and the Gecarcinucidae (Globonautinae) while MONOD (1977, 1980) assigned the West African species to the Potamidae and the Gecarcinucidae (Globonautinae). Both classifications imply that the West African freshwater crabs can be assigned to two different phyletic lines rather than to a single monophyletic group.

The cladistic analysis presented here is the first such analysis for any group of African freshwater crabs. It must be stressed that this is a preliminary account of the relationships between the West African taxa, and this will undoubtedly need to be updated as this work is expanded to include other genera from the rest of the African continent and elsewhere. A study of the phylogenetic relationships of the freshwater crabs of the world is currently under way (STERNBERG, CUMBERLIDGE & RODRIGUEZ, 1999) and may refine some of the provisional relationships presented here. For this reason, no taxonomic changes have been made when the relationship between groups was found to be equivocal.

The present work examines the phylogenetic history of the freshwater crabs of West Africa and the question of monophyly, and includes the results of a preliminary cladistic analysis. This study used thirty two morphological characters of the carapace, pereiopods, mandible, sternum, abdomen and gonopods to derive the most parsimonious cladograms for the group. Characters of the endophragmal system of the sternum, the location of the male and female sexual openings, the position of the penis in relation to the sternum, and the topology of the orbital region used by other authors (RODRIGUEZ, 1992; MAGALHÃES & TÜRKAY, 1996a,b,c) showed no significant differences between the genera in this study and were not used.

Taxa examined

All seven genera of freshwater crabs occurring in West Africa, Cameroon and Chad (*Potamonautes*, *Liberonautes*, *Sudanonautes*, *Potamonemus*, *Louisea*, *Globonautes* and *Afrithelphusa*) have been included in the cladistic analysis presented below. Seven outgroup genera were also included. As the monophyly of the West African freshwater crabs is one of the questions posed, and because the marine sister group of the freshwater crabs is uncertain, several outgroup taxa were used for the polarisation of characters as a test of monophyly. The outgroup taxa comprised two marine crab genera: *Menippe* (Menippidae) and *Goniopsis* (Grapsidae, Grapsinae), and three freshwater crab genera: *Potamon* from North Africa, Europe, the Middle East and Asia, *Platythelphusa* from Lake Tanganyika in East Africa and *Gecarcinucus* from Bombay, India. The primitive xanthoid *Menippe mercenaria* (Menippidae) and the grapsid *Goniopsis pulchra* (Grapsidae: Grapsinae) were included in this study to test the hypothesis allying the freshwater crabs with xanthoids versus the Grapsidae (ALCOCK, 1898, 1899, 1910). *Potamon fluviatilis* (Potamidae) was selected as a sister group to the West African freshwater crabs because some authors have linked members of this family with the African potamonautids (GUINOT *et al.*, 1997). *Platythelphusa armata* was selected as a sister group to the West African freshwater crabs because it represents a genus of African freshwater crabs that is most likely not closely related to the West African species. *Gecarcinucus jacquemonti* was selected because it is more distantly related to the African freshwater crab fauna and has been implicated in the classifications of some authors (BOTT, 1969b, 1970b; MONOD, 1977, 1980) as a close relative of the African Globonautinae. All of the ingroup and outgroup taxa all belong to the section Heterotremata (GUINOT, 1977, 1979) except for *Goniopsis pulchra* (Grapsidae, Grapsinae) which is assigned to the section Thoracotremata.

Character selection and coding

The groundplan characters for each genus were derived from the detailed examination of all thirty two ingroup species, and were based largely on the character states of the most primitive (least specialised) members of each genus. All character states were based on adult morphology. A list of characters and character states is given in table VII. The characters and their respective states are described below. The polarity of the character states was established by comparison with the outgroup taxa. Data were entered into the data matrix using MacClade version 3.06 and character analyses were carried out using PAUP version 3.1 on a Macintosh. A complete data matrix of taxon versus character states is given in table VIII. All characters were unordered. Character states are indicated in the text by numbers in parentheses, giving the character and character state where 0 = plesiomorphy and 1, or 2 = apomorphy (the 2 signifies that there is more than one apomorphic state). The analyses were run initially without a specified outgroup to permit a simultaneous unconstrained resolution of ingroup and outgroup relationships. PAUP uses the first taxon in the matrix (i.e., *Menippe*) as the default outgroup for rooting. Initially a heuristic search for the shortest trees was performed. This was then repeated using the branch and bound search option (BANDB) of PAUP to find the shortest and most parsimonious trees, otherwise default options were used. One of the five most parsimonious trees is presented (fig. 14).

Characters Examined

Gonopods (fig. 13, 19, 28, 29, 38, 39, 44, 52, 53)

Gonopod 1: overall length

(0) short (to s6/s7), (1) long (to s4)

In *Menippe*, *Goniopsis* and in *Gecarcinucus*, gonopod 1 has a relatively short total length and reaches only as far as s6/s7 (the plesiomorphic state). In *Platythelphusa* and *Potamon*, and in the majority of the African freshwater crabs, gonopod 1 has a relatively long total length and reaches as far as s4 (the apomorphic state).

Gonopod 1 terminal article length

(0) very small complex process or fields of bristles, (1) a long process, between 0.25 and 1.0 the length of the subterminal segment.

In *Menippe*, *Goniopsis* and *Gecarcinucus* gonopod 1 has three major segments, the coxa, basis and endopod (GUINOT, 1979), and there is no structure that can properly be viewed as homologous to the long terminal article seen in African freshwater crabs. In these three genera the counterpart of the terminal article of the first gonopod of freshwater crabs is either a very small complex process (*Menippe* and *Gecarcinucus*) or a short hook (*Goniopsis*); all are considered here to represent the plesiomorphic state. This latter type of gonopod 1 is also found in the Trichodactylidae and Pseudothelphusidae from the new world (RODRIGUEZ, 1982, 1992; MAGALHÃES & TÜRKAY, 1996a,b,c) and is close to the general eubrachyuran condition (plesiomorphic). In *Potamon*, *Platythelphusa* and in all seven genera of West African freshwater crabs the terminal article of gonopod 1 is a long process, measuring between 0.25 and 1.0 as long as the subterminal segment (the apomorphic state). A four-part gonopod 1 with a distinct subterminal segment and terminal article is, therefore, an apomorphic character of the African freshwater crabs and other Old World freshwater crab families. In *Potamonautes*, *Louisea*, *Globonautes* and *Afrithelphusa* the terminal article of gonopod 1 is short, measuring between 0.25 and 0.33 as long as the subterminal segment. There is a trend toward the elongation of the terminal article: in *Liberonautes* and *Sudanonautes* the terminal article of gonopod 1 is long, measuring at least 0.66 as long as the subterminal segment. In one species (*S. nigeria*) the terminal article of gonopod 1 is extremely long, measuring almost as long as the subterminal segment.

Gonopod 1: terminal article longitudinal groove

(0) not applicable, (1) distinct, (2) not visible.

In *Menippe*, *Goniopsis* and *Gecarcinucus* gonopod 1 has three major segments and the counterpart (not homologue) of the terminal article is a very small and compact structure (the plesiomorphic state). In *Potamon*, *Platythelphusa* and the West African freshwater crabs gonopod 1 has a long terminal article which is either straight and cone-shaped, curved and needle-shaped, or wide and tube-shaped. Typically, the ventral side of the terminal article of the gonopod consists of two rounded ridges (the medial and lateral folds) separated by the longitudinal groove running lengthways. The position and clarity of the longitudinal groove does not vary greatly within a genus (but the relative size of the median and lateral folds on the terminal article of gonopod 1 varies greatly between species, BOTT, 1955). In *Potamon*, *Platythelphusa*, *Potamonautes*, *Liberonautes*, *Sudanonautes* and *Potamonemus* the longitudinal groove is present and may be clearly visible or faint (an apomorphic state). In *Globonautes*, *Afrithelphusa* and *Louisea* the longitudinal groove is not visible from any view (an advanced apomorphic state).

Gonopod 1: terminal article point of curvature

(0) not applicable, (1) basal origin of curvature, (2) mid-point origin of curvature.

In *Menippe*, *Goniopsis* and *Gecarcinucus* gonopod 1 consists of three articles (the plesiomorphic state). In the African freshwater crabs the terminal article of gonopod 1 (the distal part) is long and within some genera the segment shows a trend toward a distinct curve or bend. In *Potamon, Platythelphusa* and *Potamonautes* the outward bend of the terminal article is basal and begins at the junction between the segments (an apomorphic state). In *Louisea, Globonautes* and *Afrithelphusa* the basal part of the terminal article of gonopod 1 is straight and mid-point curvature is absent (while the distal part is broad and is either weakly s-shaped or straight, an apomorphic state). In *Sudanonautes, Liberonautes,* and *Potamonemus* the basal part of the terminal article is straight while the distal part is curved, an apomorphic state).

Gonopod 1: terminal article direction

(0) not applicable, (1) curved either inward or outward (1), straight, no curvature, almost in line with the longitudinal axis of the gonopod (2).

In *Menippe, Goniopsis* and *Gecarcinucus* gonopod 1 consists of three articles (the plesiomorphic state). The terminal article of gonopod 1 of *Potamon* and *Platythelphusa* is directed outward (an apomorphic state) and this is found in *Potamonautes* and many of the African freshwater crabs. In *Liberonautes* on the other hand, the terminal article is always angled inward (towards the mid-line of the sternum, an apomorphic state). In *Louisea, Globonautes* and *Afrithelphusa* the terminal article of gonopod 1 is almost straight, in line with the longitudinal axis of the body (an advanced apomorphic state).

Gonopod 1 terminal article shape.

(0) not applicable, (1) cone shaped or needle shaped; (2) wide and hose shaped.

In *Menippe, Goniopsis* and *Gecarcinucus* gonopod 1 consists of three segments (the plesiomorphic state). In *Potamon, Platythelphusa* and the West African freshwater crab genera, the terminal article of gonopod 1 is either cone shaped (*Potamon, Potamonautes*) or needle shaped (*Sudanonautes, Potamonemus* and *Liberonautes*, an apomorphic state), or it is wide and hose shaped (*Louisea, Globonautes* and *Afrithelphusa*, an advanced apomorphic state).

Gonopod 1: subterminal segment closure.

(0) enclosed cylinder, (1) flat, broad, and only partly enclosed by the lateral flap.

In *Menippe* and *Goniopsis* the subterminal segment of gonopod 1 (the endopod) is a long thin hollow cylinder that is completely enclosed (the plesiomorphic state). In *Gecarcinucus, Potamon* and *Platythelphusa* and in most genera of West African freshwater crabs there is a hair-fringed flap on the lateral side of the subterminal segment of gonopod 1 that covers only part of the segment (the apomorphic state).

Gonopod 1: subterminal segment shape.

(0) thin cylinder, (1) broad base (no shoulder), (2) broad base (with shoulder).

Differences in the overall shape and width of the subterminal segment are seen most clearly on the dorsal face of the gonopod. In *Menippe* and *Goniopsis* the subterminal segment of gonopod 1 (the endopod) is a long thin cylinder (the plesiomorphic state). In *Gecarcinucus*, *Potamon* and *Platythelphusa* and in most genera of West African freshwater crabs the subterminal segment of gonopod 1 is broad at the base and tapers to a slim junction with the terminal article where the two parts are the same width (an apomorphic state). In *Potamonemus* and in several species of *Sudanonautes* the subterminal segment of gonopod 1 is broad and is widened considerably on the medial side by a distinct shoulder (an advanced apomorphic state).

Gonopod 1: dorsal membrane.

(0) not applicable, (1) broad membrane, (2) thin membrane.

In *Potamon* and *Platythelphusa* and in some genera of West African freshwater crabs (*Potamonautes*, *Liberonautes* and *Louisea*) there is a broad membrane on the dorsal side of the suture marking the junction between the terminal and subterminal segments of gonopod 1 that allows limited movement of the terminal article (an apomorphic state). In *Sudanonautes*, *Potamonemus*, *Globonautes* and *Afrithelphusa* the dorsal membrane is slim (an advanced apomorphic state).

Gonopod 2 terminal article length.

(0) long flagellum (0.5-0.75 as long as the subterminal segment), (1) a short cone or cup-shaped process, about 0.075 as long as the subterminal segment.

In *Menippe* the terminal article of gonopod 2 is a long coiled flagellum, about as long as the subterminal segment (the plesiomorphic state). In *Potamon*, *Platythelphusa*, *Potamonautes*, *Louisea*, *Liberonautes* and *Afrithelphusa* the terminal article of gonopod 2 consists of a long flagellum, measuring about 0.5 to 0.75 as long as the subterminal segment (the plesiomorphic state). In *Goniopsis* and *Gecarcinucus* the terminal article of gonopod 2 is present but is short (about 0.1 as long as the subterminal segment, an apomorphic state). In *Sudanonautes*, *Potamonemus* and *Globonautes* the terminal article of gonopod 2 is a short cone-shaped process about 0.075 as long as the subterminal segment of gonopod 2 (an apomorphic state).

Sternum (fig. 9A-E, 16A-D, 21, 32, 41A-C, 47)

Anterior sternum width. (0) narrow and slim, (1) broad.

In *Menippe* and *Goniopsis* the anterior region of the sternum (s1-s4) is very slim (the plesiomorphic state). In *Gecarcinucus*, *Potamon*, *Platythelphusa*, and the West African freshwater crab genera, the anterior region of the sternum (s1-s4) is a broad triangle (the apomorphic state).

Episternite width.

(0) episternite very narrow and slim, (1) episternite broad.

In *Menippe* and *Goniopsis* all four of the episternites are very slim (the plesiomorphic state). In *Gecarcinucus*, *Potamon*, *Platythelphusa*, and the West African freshwater crab genera, all four of the episternites are broad (the apomorphic state).

Mouthparts (fig. 9E-I, 12, 16E-G, 17E-H, 22, 23, 33, 34, 41D-F, 42D-F, 48, 49)

Third maxilliped: exopod length.

(0) reaches or nearly reaches the superior margin of the merus, (1) reaches only half way along the merus.

The exopod of the third maxilliped is a useful taxonomic and cladistic character. In the outgroup taxa *Menippe* and *Goniopsis* the exopod is very long and reaches, or nearly reaches, the superior margin of the merus (the plesiomorphic state). In *Gecarcinucus*, *Potamon* and *Platythelphusa* and in all of the African freshwater crab genera, the exopod reaches only half way along the merus (the apomorphic state).

Carapace outline.

(0) transversely oval, (1) subhexagonal, rounded or squarish.

In *Menippe*, *Gecarcinucus* and *Potamon*, and in the majority of the African freshwater crabs the carapace outline is transversely oval (the plesiomorphic state). In *Goniopsis* and *Platythelphusa* the carapace outline is subhexagonal, rounded or squarish (the apomorphic state).

Third maxilliped ischium width.

(0) ischium same width as merus, (1) ischium wider than merus.

In *Menippe*, *Goniopsis*, *Gecarcinucus*, *Potamon*, *Platythelphusa* and most species of African freshwater crabs, the ischium of the third maxilliped is either the same width or more narrow than the merus (the plesiomorphic state). In *Globonautes* and *Afrithelphusa* the distal part of the ischium of the third maxilliped is significantly wider than the merus (the apomorphic state).

Third maxilliped: exopod flagellum.
(0) present, (1) absent.

The presence or absence of a flagellum on the exopod of the third maxilliped is a character useful in both taxonomic and phylogenetic studies. In the outgroup taxa (*Menippe*, *Goniopsis*, *Gecarcinucus*, *Potamon* and *Platythelphusa*) and in *Potamonautes* and *Sudanonautes*, the exopod of all species possesses a long flagellum (reaching beyond the mid-point of the merus, the plesiomorphic state). In *Louisea* and in *Potamonemus* all species lack a flagellum on the exopod of the third maxilliped (the apomorphic state). In *Liberonautes* two out of eight species lack a flagellum on the exopod of the third maxilliped, while the remainder have a flagellum. The loss of the exopod flagellum is common in most groups of air-breathing crabs. Since this character is found in a number of different genera of freshwater crabs it is likely that the loss of the exopod flagellum has occurred independently in each case. It's loss is associated with a suite of adaptations of the respiratory system shown by the more terrestrial species of freshwater and land crabs. Thus the polarity of the character is clear, but the apomorphic state has most probably evolved independently several times in freshwater crabs from West Africa. The presence or absence of a flagellum on the exopod of the third maxilliped can be used to delimit genera in some cases, but its usefulness in defining higher categories is limited.

Mandibular palp: number of segments.
(0) three, (1) two.

The mandibular palp has three segments in *Menippe*, *Goniopsis*, *Potamon* and *Platythelphusa* (the plesiomorphic state). *Gecarcinucus*, and all other genera of freshwater crabs from West Africa have a mandibular palp with only two segments (the apomorphic state). The reduction of the number of segments of the mandibular palp from three to two is considered here to be irreversible.

Mandibular palp: simple or bilobed.
(0) single large posterior lobe, (1) two large subequal anterior lobes.

In *Menippe*, *Goniopsis*, *Potamon*, *Platythelphusa*, *Potamonautes* and *Potamonemus* the terminal article of the mandibular palp is simple and consists of a single large posterior lobe (the plesiomorphic state, fig. 5A).

All species with a single posterior lobe alone (fig. 5A) are considered here to represent the plesiomorphic state. A significant number of other species possess a mandibular palp with a single posterior lobe with a small but distinct anterior process (fig. 5B) this was judged here to also represent the plesiomorphic state. *Gecarcinucus* (fig. 5C) has a mandibular palp with a larger additional anterior lobe on the terminal article of the mandibular palp (about 0.5 as large as the posterior lobe). This was considered here not to be homologous with the subequal anterior lobe and was scored as the plesiomorphic state. *Globonautes* (fig. 48D) and *Afrithelphusa* (fig. 48A-C) each have a very large subequal anterior lobe on the terminal article of the mandibular palp (fig. 5D, the apomorphic state).

Mandibular palp: anterior lobe size.

(0) not applicable, (1) half size of posterior lobe, (2) subequal to posterior lobe.

In *Menippe*, *Goniopsis*, *Potamon* and *Platythelphusa* the terminal segment of the mandibular palp consists of a single posterior lobe (fig. 13A, C-E) and there is no anterior process of any kind (fig. 5A, the plesiomorphic state). This condition is also seen in *Potamonautes* (fig. 16E-G) and in *Potamonemus* (fig. 41D-F). The mandibular palp of *Gecarcinucus* (fig. 12B) consists of a terminal segment with a large posterior lobe plus an anterior lobe about half the size of the posterior lobe (the apomorphic state, fig. 5C). The mandibular palp of *Globonautes* (fig. 48D) and *Afrithelphusa* (fig. 48A-C) consists of a terminal segment with a large posterior lobe plus a very large anterior lobe almost the same size as the posterior lobe (fig. 5D, an apomorphic state). Although there is a vague topological similarity between these characters, differences in the size and shape of the anterior lobe of the mandibular palp of *Gecarcinucus* (fig. 12B) is not considered here to be homologous with the large subequal anterior lobe (fig. 5D) found in *Globonautes* and *Afrithelphusa*, that is, it is possible that these character states could have arisen independently.

Carapace (fig. 8, 15, 20, 30, 31, 40, 45B-C, 46)

Epistomal tooth.

(0) absent, (1) present.

In *Menippe* and *Goniopsis* there is no distinct triangular tooth on the epistome (the plesiomorphic state). In *Gecarcinucus*, *Platythelphusa* and *Potamon*, and in the majority of the African freshwater crabs, a distinct triangular tooth on the epistome is present (the apomorphic state).

Antennulular fossae.

(0) completely visible, (1) partly covered, (2) completely covered.

In *Menippe* and *Platythelphusa* the frontal margin projects straight out and the antennulular fossae are completely visible in the frontal view (the plesiomorphic state). In *Goniopsis* and *Potamon* and in the majority of the African freshwater crabs the frontal margin is deflexed somewhat so that the antennulular fossae are only partly completely visible in the frontal view (an apomorphic state). In *Gecarcinucus* the frontal margin is very deflexed so that the antennulular fossae are almost completely covered (an advanced apomorphic state).

Epigastric crests.

(0) advanced, in line with the orbits, (1) set back on the carapace in line with the epibranchial teeth.

In *Menippe* (fig. 8F) and in *Goniopsis* (fig. 8E) the epigastric crests are advanced anteriorly and are in line with the postorbital margins (the plesiomorphic state). In *Gecarcinucus*, *Platythelphusa* (fig. 8A-B) and in the rest of the African freshwater crabs the epigastric crests are positioned further back so that they are in line with the epibranchial teeth (the apomorphic state). Two other genera of freshwater crabs (*Potamon* from Eurasia and *Hydrothelphusa* from Madagascar) have anteriorly advanced epigastric crests that are in line with the postorbital margins. This results in a conspicuous hiatus between the epigastric crest and the postorbital crest in these genera (the plesiomorphic state). In *Platythelphusa* and in all genera of freshwater crabs from West Africa there is no hiatus between the epigastric crest and the postorbital crest (the apomorphic state).

Frontal margin dentition.

(0) toothed or granular, (1) smooth.

In *Menippe* and *Platythelphusa* the margin of the front has either a row of large teeth (*Menippe*) or small teeth or granules (*Platythelphusa*) (the plesiomorphic state). In *Goniopsis* and *Gecarcinucus* and *Potamon* and in the majority of the African freshwater crabs the margin of the front is smooth (the apomorphic state).

Postorbital crest.

(0) absent, (1) present.

In *Menippe* and *Goniopsis* the postorbital crest is absent (the plesiomorphic state). In *Gecarcinucus*, *Platythelphusa* and *Potamon*, and in the majority of the African freshwater crabs, the postorbital crest is present (the apomorphic state).

Development of the postfrontal crest.

(0) postfrontal crest either absent or incomplete (not meeting

anterolateral margins), (1) postfrontal crest meets anterolateral margin at, or behind, epibranchial tooth.

In *Menippe*, *Goniopsis* and *Gecarcinucus* there is a distinct pair of epigastric crests, but the rest of what normally constitutes the postfrontal crest in the African freshwater crabs is missing in these genera (the plesiomorphic state). In *Potamon*, *Platythelphusa* and *Liberonautes* the postfrontal crest consists of the epigastric crests and the postorbital crests but it is incomplete because the lateral ends of the postorbital crests do not extend to meet the carapace margins (the plesiomorphic state). In *Potamonautes*, *Sudanonautes* and *Afrithelphusa* the postfrontal crest is complete and spans the entire carapace between the epibranchial teeth (the apomorphic state). In most species with a complete postfrontal crest, the crest meets the anterolateral margin at the epibranchial tooth. In *S. aubryi*, however, the postfrontal crest meets the anterolateral margin at a point behind the epibranchial tooth.

Intermediate tooth.

(0) no intermediate tooth on the anterolateral margin, (1) intermediate tooth present on the anterolateral margin.

The intermediate tooth on the anterolateral margin lies between the exorbital angle and the epibranchial tooth. In *Menippe*, *Goniopsis*, *Gecarcinucus*, *Potamon* and *Platythelphusa* (fig. 8), and in the majority of African freshwater crabs (fig. 15, 46A-E), there is no intermediate tooth. An intermediate tooth is found only in three genera of African freshwater crabs: *Sudanonautes* (fig. 30, 31), *Liberonautes* (fig. 20) and *Louisea* (fig. 46F-G). The polarity of this character is clear: the absence of the intermediate tooth is the plesiomorphic state while the presence of the intermediate tooth is the apomorphic state.

Carapace: lateral carinae.

(0) absent (1) present.

In *Menippe* and in *Gecarcinucus* there are no lateral carinae or striae on the carapace (the plesiomorphic state). In *Goniopsis*, *Platythelphusa* and *Potamon*, and in the majority of the African freshwater crabs, lateral carinae or striae on the carapace are present (the apomorphic state).

Carapace sidewall: vertical sulcus

(0) absent (1) present.

In *Menippe* there is a no vertical sulcus on the sidewall of the carapace (the plesiomorphic state). In *Gecarcinucus*, *Platythelphusa* and *Potamon*, and in the majority of the African freshwater crabs, there is a vertical sulcus on the sidewall of the carapace running between the epibranchial tooth and the epimeral sulcus (the apomorphic state). In *Goniopsis* there is a vertical sulcus on the carapace sidewall, but in this genus the sulcus follows a different path to that seen in the freshwater crabs (it passes under the orbits at the suborbital region).

Pereiopods (fig. 10, 11A-D, 17A-D, 18A-C, 24, 25, 35, 36, 42, 43, 45, 50)

P1 merus: superior margin texture.

(0) the superior surface of the merus of the cheliped is smooth, (1) the superior surface of the merus of the cheliped a rough texture with granules and/or carinae.

In *Menippe* and *Goniopsis* the superior surface of the P1 merus is smooth (the plesiomorphic state). In *Gecarcinucus*, *Potamon* and *Platythelphusa* and in most genera of West African freshwater crabs the superior surface of the P1 merus is granular and has carinae positioned laterally to the sharply-defined superior margin (the apomorphic state).

P1 carpus.

(0) second carpal tooth absent, (1) second carpal tooth a granule, (2) second carpal tooth large and distinct.

The carpus of the cheliped of *Menippe* and *Goniopsis* is stout and typically bears only one large pointed tooth on the medial margin (the first carpal tooth) but the second carpal tooth is missing. In most freshwater crabs there is second carpal tooth sited behind the first which varies in size between species from a small granule (the plesiomorphic state) to a large, pointed tooth (the apomorphic state).

Abdomen (fig. 11E-I, 18D-G, 27, 37, 43D-F, 51)

Male abdomen: shape of telson.

(0) long and narrow, (1) broad and triangular.

The length of the telson (a7) relative to a6 varies. In *Menippe* and *Gecarcinucus* the telson is typically narrow and elongated, and is either the same length or longer than a6 (a7:a6 ratio >0.9, the plesiomorphic state). In *Goniopsis*, *Potamon* and *Platythelphusa* and in the majority of African freshwater crabs, the telson is shorter than a6 (a7:a6 ratio <0.75, the apomorphic state). The long, narrow telson with parallel sides found in *Gecarcinucus* has co-evolved to cover the underlying finger-shaped anterior part of the sterno-abdominal cavity, a character that is not found in any species of freshwater crab from Africa.

Male abdomen: shape of segment a6.

(0) parallel sides, (1) sides angled inward.

In *Menippe* and *Gecarcinucus* abdominal segment a6 is long and narrow and is four-sided: the proximal margin is similar in width to the distal margin and the two are joined by almost parallel lateral margins (the plesiomorphic state). In contrast, while a6 in *Goniopsis*, *Potamon* and *Platythelphusa* and in the majority of African freshwater crabs is four-sided, the distal margin is much more narrow than the proximal margin and the two are joined by lateral margins that taper inwards (the apomorphic state).

Data Analysis

The analyses of thirty two characters yielded five trees. The shortest tree was 55 steps long with a consistency index (CI) of 0.73 and retention index (RI) of 0.78 (fig. 14). The following is a compilation of synapomorphies which define the clades found on the cladogram. The character number and the character state (in parentheses) are given in table VII. Robust synapomorphies and terminal autapomorphies which are unique and unreversed (i.e., with a CI of 1.0) are given in bold. The following nineteen characters were found to be robust synapomorphies (CI 1.0): **1, 2, 3, 4, 5, 6, 7, 8, 11, 12, 13, 15, 20, 22, 24, 28, 29, 30** and **32**. The tree shown in fig. 14 is the most parsimonious explanation and the derived states in characters 9 and 19 (CI 0.67) and 14, 16, 17, 18, 23, 26, 27, 31 (CI 0.5) imply independent development.

Outgroup taxa.- The xanthoid *Menippe mercenaria* was the furthest outgroup taxon, while the grapsid *Goniopsis pulchra* was indicated as a sister group to the freshwater crab clade. *Gecarcinucus jaquemonti*, *Potamon fluviatilis* and *Platythelphusa armata* each occupy independent branches and each are sister groups to the West African freshwater crabs. Not all character states in *G. jacquemonti* and *P. armata* are plesiomorphic, indicating a certain amount of subsequent adaptation to a semi-terrestrial life, and to life in a lake respectively.

Potamon differs from the seven ingroup genera by its possession of a three-segmented mandibular palp (17,0) and forward-positioned epigastric crests (22,0). *Potamon* differs from *Platythel-*

phusa by its transversely-oval carapace outline, by a smooth frontal margin (23,1), by a frontal margin that is deflexed, and by a smooth or granular (not toothed) inferior orbital margin. *Potamon* can be distinguished from *Gecarcinucus* as follows. Gonopod 1 of *Gecarcinucus* is short and reaches only as far as s6/s7 (1,0), while that of *Potamon* reaches to s4 (1,1), and the terminal article of gonopod 2 of *Gecarcinucus* is a short stub, while that of *Potamon* is a long flagellum. In addition the mandibular palp of *Potamon* has three segments (17,0), and the terminal segment is simple (18,0), whereas the mandibular palp of *Gecarcinucus* has only two segments (17,1), and the terminal segment is bilobed (18,1).

Platythelphusa differs from the seven ingroup genera in a number of characters, almost all of which are in the pleisiomorphic state in *Platythelphusa*. These characters are: a three-segmented mandibular palp (17,0), a square carapace outline, teeth on the frontal margin (23,0), a frontal margin that projects straight out, and a toothed inferior orbital margin. Up to five teeth on the carpus of the cheliped may be a apomorphy for this genus.

Gecarcinucus is distinguished from *Platythelphusa* by the following characters: the mandibular palp has two segments (17,1); the terminal article of the mandibular palp consists of two lobes, not a single lobe (18,1); the anterior lobe on the terminal article of the mandibular palp is about half as big as the posterior lobe (19,1); the frontal margin is smooth (23,1); the frontal margin curves down; the exorbital tooth is small and low; the anterolateral margin behind the epibranchial tooth is smooth; the inferior orbital margin is smooth; episternal sutures s4/e4 and s6/e6 are not visible; the frontal margin is very narrow; and the outline of the female abdomen is a long slim triangle, not a broad oval.

Clade 1: The freshwater crabs

7(1), 8(1), 11(1), 13(1), 20(1), 24(1), 28(1), 29(1).

The monophyly of the clade that includes all of the freshwater crab genera in this study (*Gecarcinucus*, *Potamon* and *Platythelphusa* and the seven West African genera) is supported by nine robust synapomorphies that did not show reversal to pleisiomorphic conditions. These are: the subterminal segment of gonopod 1 is not a closed tube but is partly open, and is only partly enclosed by the lateral flap (**7**,1); the subterminal segment of gonopod 1 is very broad at the base (**8**,1,2); the anterior sternum (s1-s4) is relatively broad (**11**,1); the exopod of the third maxilliped only reaches to half way along the side of the merus (**13**, 1); there is a distinct epistomal tooth (**20**,1); there is a distinct postorbital crest (**24**,1); there is a vertical sulcus on the carapace sidewall (**28**,1); the superior margin of the merus of the cheliped has carinae (**29**,1); the exopod of the third maxilliped reaches only to the mid-point of the merus; and the dactylus of each of the walking legs P2-P5 has four rows of spines. In addition, a gonopod 1 with four articles (especially one with a long terminal article) appears to be a freshwater crab synapomorphy.

Clade 2: The African freshwater crabs

(Potamon* and *Platythelphusa,* plus *Potamonautes, Liberonautes, Sudanonautes, Potamonemus, Louisea, Globonautes* and *Afrithelphusa)

1(1), 2(1), 3(1), 4(1), 5(1), 6(1), 9(1), 10(1), 12(1), 22(1) and 32(1).

The monophyly of the clade that includes all of the African freshwater crab genera in this study (*Potamon and Platythelphusa* and the seven West African genera) is supported by eleven synapomorphies that did not show reversal to pleisiomorphic conditions. These are: gonopod 1 is short and reaches only as far as s6/s7 (**1**,**1**); the terminal article of gonopod 1 is a long process, ranging in length from 0.25 to 1.0 times as long as the subterminal segment (**2**,1,2); the terminal article of gonopod 1 has a longitudinal groove that is either visible, or it is faint and no longer visible (**3**,1,2); the terminal article of gonopod 1 curves either from the base or from the midpoint (**4**,1,2); the terminal article of gonopod 1 is angled either outward or inward, or it is straight (**5**,1,2); the terminal article of gonopod 1 is cone shaped, needle shaped or hose shaped (**6**,1); the subterminal segment of gonopod 2 is long and is equal in length to the subterminal segment of gonopod 1 (**10**,1); all of the episternites on the sternum are broad (**12**,1); the epigastric crest is set back on the carapace in line with the epibranchial teeth (**22**,1); and the sides of abdominal segment a6 are angled inward (**32**,1).

Clade 3: The Sub-Saharan African freshwater crabs

(*Platythelphusa, Potamonautes, Liberonautes, Sudanonautes, Potamonemus, Louisea, Globonautes* and *Afrithelphusa*)

30(1).

These eight genera of African freshwater crabs form a clade supported by one synapomorphy: the carpus of the cheliped has a second carpal tooth (30,1).

Clade 4: The West African freshwater crabs

(*Potamonautes, Liberonautes, Sudanonautes, Potamonemus, Louisea, Globonautes* and *Afrithelphusa*)

17(1).

These seven genera of West African freshwater crabs form a clade supported by one synapomorphy: the mandibular palp has two segments (17,1). The West African freshwater crabs can be further recognised by the following characters: a smooth inferior orbital margin, a transversely oval carapace outline, only two teeth on the medial margin of the carpus of the cheliped, no teeth on the frontal margin, and a frontal margin that curves down over the antennulular fossae.

Clade 5: Globonautinae BOTT, 1969b

(*Globonautes, Afrithelphusa* and *Louisea*)

5(1), 6(1) and 16(1).

The monophyly of the clade that includes *Globonautes*, *Afrithelphusa* and *Louisea* is supported by three synapomorphies (two of which are robust): the terminal article of gonopod 1 is almost straight, and is not curved (**5**,1); the terminal article of gonopod 1 is wide and tubular like a hose (**6**,2); and the exopod of the third maxilliped lacks a flagellum (16,1). In addition, the carapace is smooth and lacks carinae.

The monophyly of the clade that includes *Globonautes* and *Afrithelphusa* is supported by four synapomorphies: the dorsal membrane between the two distal segments of gonopod 1 is narrow (9,2); the ischium of the third maxilliped is distinctly wider than the merus (**15**,1); the terminal segment of the mandibular palp has two large lobes (18,1); and the anterior lobe on the terminal segment of the mandibular palp is subequal to the posterior lobe (19,2). Other characters shared by these genera include the following: the carapace is wide, cw/fw>3.6, the carapace is long cl/fw >2.6, the carapace is highly arched, ch/fw>1.5, the front is very narrow fw/cl <0.40 and sternal suture s1/s2 is not visible. *Globonautes* is distinguished from *Afrithelphusa* by a short terminal article on gonopod 2 (10,2) and by the postfrontal crest: it is incomplete in *Globonautes* (25,0) and complete in *Afrithelphusa* (25,1). *Globonautes* and *Afrithelphusa* can be distinguished from *Louisea* by comparison of the terminal article of the mandibular palp: the former two genera have a large, subequal anterior lobe (18, 1, 19,2), while the mandibular palp of

Louisea lacks a large lobe but has a much smaller anterior process (19,1). *Louisea* is distinguished from *Globonautes* and *Afrithelphusa* by sternal suture s3/s4 which is reduced to two short side notches; by the presence of an intermediate tooth on the anterolateral margin of the carapace (26,1); by spiny margins of the propodi of the walking legs P2-P5; and by the lack of a vertical suture on the ischium of the third maxilliped. These synapomorphies support the monophyly of this clade and distinguish *Louisea* from the other West African freshwater crab genera.

Clade 6: Liberonautes, Sudanonautes and Potamonemus

3(1) and 4(1)

Three of the seven genera of West African freshwater crabs under consideration here form a weakly-supported monophyletic clade. Within this clade *Liberonautes*, *Sudanonautes* and *Potamonemus* consistently group together, and are positioned separately to *Potamonautes* which exhibits a more distant relationship with these genera. These three genera are distinguished from the Globonautinae by the following characters: there is a longitudinal groove on the terminal article of gonopod 1 (**3**,1), and the terminal article of gonopod 1 is curved and sharply angled from the half way point (**4**,2). In addition, the carapace has carinae that are either clearly visible or faint, the terminal article of gonopod 1 is very long, s3/s4 is reduced to two short side notches, there is an intermediate tooth on the anterolateral margin of the carapace (23,1); the inferior margins of the merus of the cheliped are granulated or toothed; and the terminal article of the mandibular palp either completely lacks an anterior process (*Potamonemus* and some *Sudanonautes*), or has only a small anterior process (some *Sudanonautes* and all *Liberonautes*).

Liberonautes is distinguished by the following characters: the dorsal membrane on gonopod 1 is broad (9,0); the terminal article of gonopod 2 is always a long flagellum (10,0); the terminal article of gonopod 1 is angled inward; the carapace has clearly visible carinae; episternal suture s5/e5 is not visible; the postfrontal crest never meets the anterolateral margins; and the mandibular palp terminal segment always has a small but distinct anterior process. The monophyly of the clade that includes *Sudanonautes* and *Potamonemus* is supported by two synapomorphies: the dorsal membrane of gonopod 1 is narrow (9,1), and the terminal article of gonopod 2 is a short cone (10,1). *Potamonemus* is supported by one synapomorphy: the exopod of the third maxilliped lacks a flagellum (16,1). In addition, sternal suture s1/s2 is not visible and the mandibular palp terminal segment is simple and lacks a small anterior process. The monophyly of *Sudanonautes* is supported by two synapomorphies: the subterminal segment of gonopod 1 is broad based and in some species has a wide shoulder (**8**,1,2); and the postfrontal crest meets the anterolateral margin at or behind the epibranchial tooth (25,1).

These three genera and *Potamonautes* are distinguished from *Platythelphusa* (17,0) and *Potamon* (17,0) by a two segmented mandibular palp (17,1).

Potamonautes does not group closely on the cladogram with the above three genera. This genus is distinguished by the following characters: the postfrontal crest meets the anterolateral margin at the epibranchial tooth (25,1); the sterno-abdominal cavity terminates on s4 in an anterior position very close to s3/s4; the walking legs (P2-P5) have a big subterminal tooth on the superior margin; and the medial and lateral folds on the terminal article of gonopod 1 are unequal. In addition, s1/s2 and s3/s4 are always complete in this genus. The high lateral fold (and the low medial fold) on the terminal article of gonopod 1 and the anteriorly-positioned distal sterno-abdominal cavity distinguish the species of *Potamonautes* from West Africa from the other genera found in the region.

This cladistic analysis can be translated into the following taxonomic arrangement.

Family **POTAMONAUTIDAE** BOTT, 1970a
        Genus *Potamonautes*
        Genus *Liberonautes*
        Genus *Sudanonautes*
        Genus *Potamonemus*

Family Uncertain
    Subfamily **GLOBONAUTINAE** BOTT, 1969b
        Genus *Globonautes*
        Genus *Afrithelphusa*
        Genus *Louisea*

Family **PLATYTHELPHUSIDAE** COLOSI, 1920
        Genus *Platythelphusa*

This taxonomic arrangement differs in several respects from the classification used by other authors. RATHBUN (1904-1906) assigned most West African taxa to one family (the Potamonidae) and one genus (*Potamon*) and recognised differences among the fauna of the region by different subgeneric assignments (*Potamonautes* or *Parathelphusa*). This simple arrangement was used by subsequent authors with little modification until BOTT (1955), who assigned most West African species to a single family and subfamily (the Potamoninae of the Potamonidae) and to one of three genera: *Potamonautes*, *Sudanonautes* or *Liberonautes*. BOTT (1959) described *Globonautes* and, in a later work (BOTT, 1969b), that author erected the subfamily Globonautinae (Gecarcinucidae) for *Globonautes* and added another genus (*Afrithelphusa*) which he assigned to a different subfamily (the Gecarcinucinae) of the Gecarcinucidae. The major revision of the freshwater crabs of the world by BOTT (1970a,b) placed the African gecarcinucids in the superfamily Gecarcinucoidea and assigned the rest of the West African freshwater crabs to the Potamonautidae which was included in the Potamoidea. MONOD (1977, 1980) accepted the majority of BOTT's (1970a,b) taxonomic conclusions but preferred to place *Potamonautes*, *Sudanonautes* and *Liberonautes* in the Potamidae rather than the Potamonautidae.

The new classification proposed here based on the results of the above cladistic analysis assigns the ingroup taxa to three clades. Five of the seven West African freshwater crab genera in the present study (*Potamonautes*, *Liberonautes*, *Sudanonautes*, *Potamonemus* and *Louisea*) were assigned by BOTT (1955, 1959) and CUMBERLIDGE (1994a) to the Potamonautidae, while the other two (*Globonautes* and *Afrithelphusa*) were assigned by BOTT (1969b, 1970b) and CUMBERLIDGE (1996a,b) to the Gecarcinucidae (Globonautinae). The cladistic analysis shows that the seven West African genera included in this study fall into two main clades: one with three genera (*Globonautes*, *Afrithelphusa* and *Louisea*), the other with four genera (*Liberonautes*, *Sudanonautes*, *Potamonemus* and *Potamonautes*). *Potamonautes* occupies a basal position with respect to the *Liberonautes*, *Sudanonautes* and *Potamonemus* clade, indicating a more distant relationship with these genera. These two separate clades support the existing assignment of these genera into two separate groups: the Potamonautidae for *Potamonautes*, *Liberonautes*, *Sudanonautes* and *Potamonemus*, and the Globonautinae BOTT, 1969b for *Globonautes*, *Afrithelphusa* and *Louisea*. This latter genus is here transferred from the Potamonautidae to the Globonautinae.

Gecarcinucus (representing the Gecarcinucidae) does not form part of the same clade as any of the African Globonautinae or Potamonautidae. Although it is likely that the Globonautinae are not close relatives of *Gecarcinucus*, and the inclusion of this subfamily is in doubt in the Gecarcinucidae. More detailed studies on the relationships of these crabs need to be carried out. In addition, *Potamon* and *Platythelphusa* is not included in the

Potamonautidae clade. *Platythelphusa* was previously classified as a subgenus of *Potamonautes*; it is recognised here as a distinct genus (*Platythelphusa*); a number of characters do not support its inclusion in the Potamonautidae. *Platythelphusa* is therefore removed from the Potamonautidae and the Platythelphusinae COLOSI, 1920, is here revived at the family level, as the Platythelphusidae, for this endemic genus of freshwater crabs from Lake Tanganyika.

A conservative approach to changes to the existing classification has been adopted here, and so most recommendations are relatively minor in nature. This approach was used because the present study used a regional fauna, and did not include taxa from elsewhere in the Afrotropical region. A great deal more resolution of the relationships between taxa can be expected when a wider range of taxa are included in future analyses, although it is thought unlikely that the present findings will be radically altered.

Summary of Findings

(1) The present findings support the inclusion of four West African genera (*Potamonautes*, *Sudanonautes*, *Liberonautes* and *Potamonemus*) in the Potamonautidae, but the continued inclusion of *Louisea* in this family is questioned (see below). There is evidence that *Potamonemus*, *Sudanonautes* and *Liberonautes* are closely related, but *Potamonautes* does not group closely with these genera.

(2) The nature of the relationship between the Potamonautidae and the Potamidae (represented by *Potamon*) remains largely unresolved, although these two genera did not group closely on the cladogram.

(3) Three genera, *Globonautes*, *Afrithelphusa* and *Louisea*, consistently group together in a clade which is recognised here as the Globonautinae. This subfamily is expanded to include *Afrithelphusa* (which was removed from the Gecarcinucinae and reassigned to the Globonautinae by CUMBERLIDGE, 1996a,b) and *Louisea* (which was assigned to the Potamonautidae by CUMBERLIDGE, 1994a). The Globonautinae as conceived here (with *Globonautes*, *Afrithelphusa* and *Louisea*) is tentatively removed from the Gecarcinucidae, due to doubts as to this assignment. Significantly, the Globonautinae clade did not include *Gecarcinucus jacquemonti* from India, nor was this

species close to this clade on the tree. *Gecarcinucus jacquemonti* formed a separate branch on the cladogram from all of the African freshwater crabs in this study, including *Platythelphusa*.

In addition to the data from the cladistic analysis, morphological comparisons cast further doubt on the idea that the African Globonautinae and the Indian and Asian Gecarcinucidae are close relatives (as is implied by BOTT's (1969b, 1970a,b) and MONOD's (1977, 1980) classification of these two groups in the Gecarcinucidae). When *Globonautes*, *Afrithelphusa* and *Louisea* are compared with *Gecarcinucus* a number of characters show significant differences that indicate a great deal of taxonomic distance between the three genera.

Gecarcinucus can be distinguished from the Globonautinae by the following characters. The terminal article of gonopod 1 is very short (0.1 times as long as the subterminal segment) in *Gecarcinucus* (**2**,0), while this article is long (0.25-0.33 as long as the subterminal segment) in the Globonautinae (**2**,1); both the telson (31,1) and the male abdomen are triangular in the Globonautinae, while both are long and narrow in *Gecarcinucus* (31,0); the anterior lobe on the terminal segment of the mandibular palp is about half as big as the posterior lobe in *Gecarcinucus* (19,1) and larger and subequal in the Globonautinae (19,2). Other characters that distinguish *Gecarcinucus* from the Globonautinae include the following: in *Gecarcinucus* the epibranchial tooth is absent; the carapace is very wide, cw/fw>3.6; the carapace is high and arched, ch/fw>1.5; the front is extremely narrow fw/cl <0.40. In addition, the sterno-abdominal cavity is long, deep and narrow in *Gecarcinucus* and broad, shallow and wide in the Globonautinae; and the sterno-abdominal cavity terminates on s2 in *Gecarcinucus* and on s4 in the Globonautinae. This evidence, taken together with the findings of the cladistic analysis, does not support the continued assignment of *Globonautes* and *Afrithelphusa* to the Gecarcinucidae, nor does it support their assignment to another of BOTT's (1970b) subfamilies of the Gecarcinucidae. Therefore the Globonautinae are here removed from the Gecarcinucidae and reassigned tentatively to the Potamonautidae and *Louisea* is added to the African Globonautinae. It is considered likely that the Gecarcinucoidea, sensu BOTT (1969b, 1970b) and the Gecarcinucidae, sensu BOTT (1969b, 1970b) are not natural groups.

(4) *Platythelphusa armata* from Lake Tanganyika occupies an independent branch on the cladogram and is a sister group to *Potamon* and to the West African freshwater crabs. The Platythelphusidae COLOSI, 1920 is proposed here to accommodate the six species of *Platythelphusa* described in the most recent revi-

sion of this genus (CAPART, 1952; CUMBERLIDGE et *al.*, 1999). The results of the cladistic analysis cast doubt upon the present assignation of *Platythelphusa* as a subgenus of *Potamonautes* (BOTT, 1955). It is unlikely that *Platythelphusa* and *Potamonautes* are closely related and unlikely that these genera share a recent common ancestor. *Platythelphusa* has a number of distinguishing characters that sets this genus apart from *Potamonautes* and from all other African genera of freshwater crabs. These characters include a three segmented mandibular palp with a simple terminal segment, a square carapace outline, teeth on the frontal margin, a frontal margin that projects straight out and up to five teeth on the carpus of the cheliped. These distinguishing characters when considered together with the results of the cladistic analysis cast doubt upon BOTT'S (1955) assignation of *Platythelphusa* as a subgenus of *Potamonautes*. The evidence supports the view that these genera diverged a long time ago and argues for the removal of *Platythelphusa* from the Potamonautidae and for the inclusion of this genus in a separate family. A detailed revision of the Platythelphusidae is currently underway (CUMBERLIDGE *et al.*, 1999, STERNBERG *et al.*, 1999).

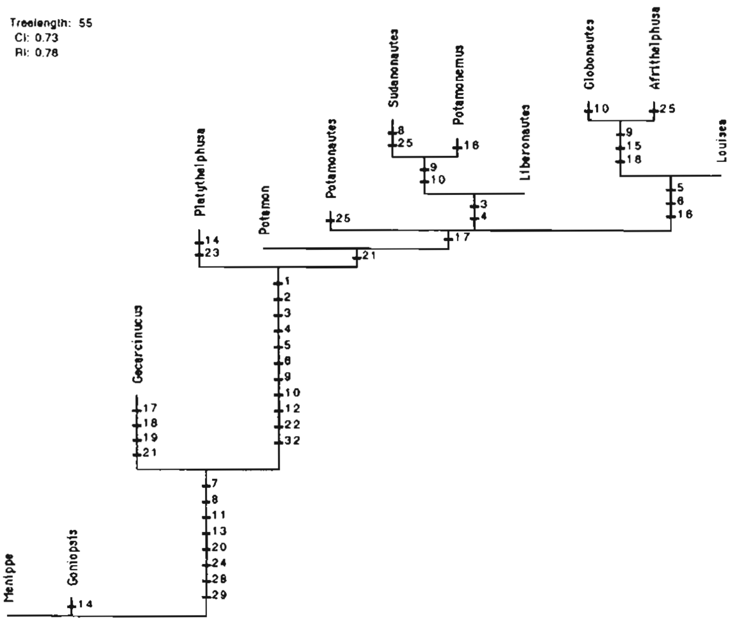


FIG. 14. Phylogram of one of the five most parsimonious arrangements obtained, with changes in the characters (numbered as in the text) marked by horizontal bars. The branch lengths are proportional to the number of characters that change unambiguously on each branch.

TABLE VII

Characters used to compare the genera of West African freshwater crabs. The first alternative for each character is considered to be pleisiomorphic.

[1]	GO1 overall length	short (reaches s6/s7) (0); long (reaches s4) (1)
[2]	GO1 terminal article length	v small process or bristles (0); long process (1)
[3]	GO1 terminal article longitudinal groove	not applicable (0); distinct (1); not visible (2)
[4]	GO1 terminal article point of curvature	not applicable (0); basal (1); halfway (2)
[5]	GO1 terminal article direction	not applicable (0); outward or inward (1); straight up (2)
[6]	GO1 terminal article shape	not applicable (0); cone or needle shape (1); wide and hose shaped (2)
[7]	GO1 subterminal segment closure	enclosed tube (0); open (lateral flap) (1)
[8]	GO1 subterminal segment shape	thin cylinder (0); broad base (no shoulder) (1); broad base (with shoulder) (2)
[9]	GO1 dorsal membrane	not applicable (0); broad membrane (1); thin membrane (2)
[10]	GO2 terminal article shape	short process (0); long flagellum (1)
[11]	sternal sulcus s6/s7 in the sac	complete (0); interrupted in the sac (1)
[12]	episternite width	slim (0); broad (1)
[13]	third maxilliped exopod length	at, or close to top of merus (0); middle of merus (1)
[14]	carapace shape	transversely oval(0); subhexagonal or square(1)
[15]	third maxilliped ischium width	narrow < merus (0); wide > merus (1)
[16]	third maxilliped exopod flagellum	present (0); absent (1)
[17]	mandibular palp: number of segments	three (0); two (1)
[18]	mandibular palp: number of lobes	single lobe (0); two lobes (1)
[19]	mandibular palp: lobe size	not applicable (0); half post lobe; (1) subequal to post lobe (2)
[20]	epistomial tooth	absent (0); present (1)
[21]	antennulular fossae	completely visible (0); partly visible (1); completely covered (2)
[22]	epigastric crests	advanced (0); set back (1)
[23]	frontal margin dentition	toothed (0); smooth (1)
[24]	postorbital crest	absent (0); present (1)
[25]	postfrontal crest development	not developed or incomplete (0); complete, meets anterolateral margins (1)
[26]	intermediate tooth	absent (0); present (1)
[27]	carapace lateral carinae	absent (0); present (1)
[28]	vertical sulcus on sidewall	absent (0); present (1)
[29]	P1 merus superior margin texture	smooth (0); carinae (1)
[30]	P1 second carpal tooth	absent (0); distinct tooth or a granule (1)
[31]	male telson shape	long & narrow (0); broad triangle (1)
[32]	abdominal segment 6 shape	parallel sides (0); sides angled inward (1)

GO1 = first gonopod; GO2 = second gonopod; sac = sterno-abdominal cavity .

TABLE VIII

Data matrix of the thirty two characters used in the cladistic analysis

	10	**20**	**30**	
Menippe	0000000000	0000000000	0000000000	00
Goniopsis	0000000000	0000000000	1010001000	10
Gecarcinucus	0000001100	1011001111	2011000110	00
Platythelphusa	1111111111	1111000001	0101001111	11
Potamon	1111111111	1111000001	1111001110	11
Potamonautes	1111111111	1111001001	1111101111	11
Liberonautes	1122111111	1111001001	1111011111	11
Sudanonautes	1122111220	1111001001	1111111111	11
Potamonemus	1122111120	1111011001	1111001111	11
Globonautes	1111221120	1111111121	1111001111	11
Afrithelphusa	1111221121	1111111121	1111101111	11
Louisea	1111221111	1111011001	1111001111	11

Systematic Study

Illustrations of the taxonomic characters of all taxa are provided (fig. 15-53), together with morphometric data (*see* "Morphometric relationships", fig. 54-62 below) and distribution data (*see* "Biogeography and biology", fig. 61-69 below).

Family POTAMONAUTIDAE BOTT, 1970a

fig. 63

Potamonautidae BOTT, 1970a, p. 327-344.-MONOD, 1977, p. 209.-MONOD, 1980, p. 380 (part).

The carapace outline is transversely oval and is widest at the anterior third. The frontal margin is smooth (not toothed) and curves down over the antennulular fossae. The anterolateral margin begins at the exorbital angle (which may be formed into a sharp tooth, or may be low and continuous with the anterolateral margin); behind the exorbital angle there is an epibranchial tooth; in some genera there is an intermediate tooth on the anterolateral margin between the epibranchial tooth and the exorbital angle. The posterior margin of the carapace is about one third as wide as the carapace. The carapace has lateral carinae.

There is a postfrontal crest consisting of the fused epigastric and postorbital crests that is either complete (meeting the anterolateral margins) or incomplete (ending just short of the anterolateral margins). The epigastric crests are set back on the carapace in line with the postorbital crests, and the entire postfrontal crest crosses the carapace in line with the epibranchial teeth. The eyestalks are long and fill the orbital cavities, and the antennae (first antennae) are very short, about a third the length of the eyestalks.

The sidewalls of the carapace are divided by two sulci (the epimeral and the vertical or pleural) into three parts (the suborbital; the subhepatic and subbranchial regions; and the pterygostomial regions). The epimeral sulcus begins medially at the lower margin of the orbit and curves backward across the sidewall, dividing the suborbital, subhepatic, and subbranchial regions (uppermost) from the pterygostomial region. The vertical (pleural) sulcus begins either at the base of the intermediate tooth or at the base of the epibranchial tooth, and separates the suborbital region from the hepatic region. The mandibular palp has two segments, the basal or subterminal segment (possibly formed from the fusion of the first two segments), and the terminal segment (a large oval lobe positioned behind the mandible). The third maxillipeds fill the entire buccal frame, except for the transversely oval efferent respiratory openings at the superior lateral corners; the merus of the third maxilliped has flanged edges; the ischium of the third maxilliped is the same width as the merus; the exopod of the third maxilliped reaches only half way along the merus; and there is a long plumose flagellum on the exopod in most species.

The sterno-abdominal cavity terminates on sternite s4, and sternal sulcus s2/s3 is clearly visible and crosses the entire sternum. Within the sterno-abdominal cavity, three of the four posterior sternal sulci (s4/s5, s5/s6, s6/s7) are discontinuous (i.e., they are separated medially) while s7/s8 is continuous (i.e., it meets in the midline). There is a short but distinct sulcus (the median line) in the posterior part of the sterno-abdominal cavity that runs perpendicular to the sternal sulci on s7 and s8, and terminates before reaching s6. Male crabs have a pair of sternal condyles within the sterno-abdominal cavity on sternite s5, and the penis meets s8 in the mid-point of the lateral margin. The male sexual openings are on the coxae of P5 and the female sexual openings are in the sterno-abdominal cavity on sternite s6 (i.e., members of this family belong to the Heterotremata sensu Guinot, 1977).

The chelipeds are unequal (i.e., heterochelous), with a major (usually the right) that is both longer and higher than the minor (usually the left). The dactylus of the major cheliped of adult males is typically highly arched, although this character varies according to species. The medial margin of the carpus of the cheliped has two teeth (the first and second carpal teeth); the first carpal tooth is usually larger than the second carpal tooth. The merus of the cheliped is triangular in cross section and has three sides - anterior, posterior and inferior. The medial and lateral margins of the inferior side of the merus of the cheliped are typically toothed and there is usually a single large pointed tooth at the distal end (the distal tooth); the superior margin of the merus of P1 (where the anterior and posterior side meet) has rows of prominent, rough grains. There is a smooth oval surface (the meral tympanum) on the posterior side of the merus of the cheliped.

The walking legs (P2-P5) are triangular in cross section; P5 is always the shortest. The dactyli of P2-P5 taper to a point, and each has four rows of downward-pointing sharp bristles; the dactylus of P4 is long and the dactylus of P5 is very short (the shortest segment of all of the walking legs).

The male abdomen is slim and the outline formed by abdominal segments a3-a7 is triangular; the telson of the male abdomen (a7) is triangular; a1-a6 are four sided; a3 is the broadest segment; the sides of a4-a7 are angled inward; the outline of the female abdomen is broad and round.

Gonopod 1 and gonopod 2 each have four distinct segments. The ventral side of the terminal article of gonopod 1 has two folds and a longitudinal groove. The dorsal side of the terminal article of gonopod 1 is smooth, and there is a distinct membrane (the dorsal membrane) at the junction between the two distal segments of gonopod 1. The terminal article of gonopod 1 is long - about one third to two thirds the length of the subterminal segment of gonopod 1; the terminal article of gonopod 1 has two lengthways folds (the medial and lateral folds) separated by a longitudinal groove; distally, the terminal article tapers strongly to a pointed or tubular tip, which has a hole (the apical opening) at the tip. The tip of the terminal article of gonopod 1 of adult males reaches further than the sternal condyles on s5.

The subterminal segment of gonopod 1 is always longer than the terminal article of gonopod 1; and the subterminal segment usually reaches as far as s5/s6. The subterminal segment of gonopod 1 is typically a simple rectangle (longer than wide), which in some species is broadened at the base; the ventral side of the subterminal segment of gonopod 1 is not completely enclosed: the medial side is exposed, while the lateral side is covered by the long lateral flap which is folded inwards across the segment from the lateral margin; this flap reaches at least halfway across the segment but never all the way across; the margin of this flap is edged lengthways by short bristles and hairs, and this margin is continuous with the longitudinal groove of the terminal article of gonopod 1.

Gonopod 2 has two principal forms: it is either the same length or longer than gonopod 1, or it is distinctly shorter than gonopod 1 (only as long as the subterminal segment of gonopod 1). The subterminal segment of gonopod 2 is long, and is always the same length as the subterminal segment of gonopod 1. The subterminal segment of gonopod 2 is widest at its base, and then tapers sharply inward to form a long, thin, rod-like, upright process which supports the terminal article; there is a rounded collar (the cup) at the junction between the terminal and subterminal segments of gonopod 2. In some genera of this family the terminal article of gonopod 2 is a long flagellum, one half to two thirds (0.5-0.67) as long as the subterminal segment of gonopod 2; in other genera the terminal article of gonopod 2 is a very short process only about one twelfth to one fifteenth (0.05-0.07) as long as the subterminal segment of gonopod 2.

Type genus.- *Potamonautes* MacLeay, 1838

The Potamonautidae are found throughout sub-Saharan Africa and their range includes the Nile valley which enables some species to extend their distribution along the river as far north as Cairo, Egypt. The only part of continental Africa where this family is absent is the Sahara desert itself and the Mediterranean fringe of north Africa in Morocco, Algeria and Tunisia (where members of the Potamidae occur). The Potamonautidae may have representatives in Madagascar (Ng & Takeda, 1994)

Bott's (1970b) major taxonomic revision of the freshwater crabs raised the number of families of freshwater crabs in the world to eleven families. This increase included the establishment of the Potamonautidae, most of whose members had previously been assigned to the Potamoninae of the Potamonidae (now corrected to Potaminae and Potamidae) (Bott, 1955, 1959, 1964, 1969b). The Potamonautidae Bott, 1970a, was established to include three African genera, *Potamonautes*, *Liberonautes* and *Sudanonautes* and was not originally divided into subfamilies. Unfortunately, Bott's (1970b) revision did not discuss the taxonomy of the Madagascan freshwater crabs, and there are, therefore, a number of taxonomic questions regarding the African and Madagascan freshwater crabs still outstanding despite Bott's (1965) work. A recent contribution to the taxonomy of the freshwater crabs of Madagascar by Ng & Takeda (1994) made a number of changes to the work of Bott (1965). Ng & Takeda (1994) included three Madagascan genera (*Hydrothelphusa*, *Madagapotamon* and *Skelosophusa*) in the Potamonautidae. These authors assigned *Hydrothelphusa* and *Skelosophusa* to the subfamily Hydrothelphusinae, but did not comment on the subfamily assignment of *Madagapotamon*, which still remains uncertain. Prior to Ng & Takeda's (1994) contribution, the Potamonautidae included no subfamilies and the assignment of the Hydrothelphusinae to the Potamonautidae raises questions regarding the subfamily status of *Madagapotamon*, as well as the large number of non-Madagascan members of this principally-African family of freshwater crabs.

Key to the African genera of Potamonautidae

1 The anterolateral margin has an intermediate tooth between the exorbital angle and the epibranchial tooth. Sternal sul-

cus s1/s2 is not visible; s3/s4 is reduced to two notches. The terminal article of gonopod 1 is long (about two thirds as long as the subterminal segment of gonopod 1). **2**

\- The anterolateral margin always lacks an intermediate tooth between the exorbital angle and the epibranchial tooth. Sternal sulcus s1/s2 is clearly visible; s3/s4 completely crosses the sternum. The terminal article of gonopod 1 is short (about one quarter to one third as long as the subterminal segment of gonopod 1). ***Potamonautes***

2 The terminal article of gonopod 1 is directed outward; the terminal article of gonopod 2 is very short (about 0.05-0.07 times as long as the subterminal segment of gonopod 2). The postfrontal crest is complete and always meets the anterolateral margins at, or behind, the epibranchial teeth. **3**

\- The terminal article of gonopod 1 is directed inward; the terminal article of gonopod 2 is a long flagellum (about 0.5-0.75 times as long as the subterminal segment of gonopod 2). The postfrontal crest is incomplete and does not meet the anterolateral margins. ***Liberonautes***

3 The flagellum on the exopod of the third maxilliped is always missing. ***Potamonemus***

\- The flagellum on the exopod of the third maxilliped is always present. ***Sudanonautes***

Potamonautes MACLEAY, 1838

fig. 64, 65

The postfrontal crest completely crosses the carapace and meets the anterolateral margins at the epibranchial teeth. The anterolateral margin always lacks an intermediate tooth between the exorbital angle and the epibranchial tooth. The mandibular palp always has two segments. The exopod of the third maxilliped always has a long flagellum. Sternal sulci s1/s2 and s3/s4 are deep and completely cross the sternum, and the sterno-abdominal cavity terminates on s4 in an advanced anterior position very close to s3/s4. The terminal article of gonopod 1 is short (about one quarter to one third as long as the subterminal segment of gonopod 1). The medial and lateral folds on the terminal article of gonopod 1 are unequal (the lateral fold is usually the larger of the two). The terminal article of gonopod 2 is a long flagellum (about 0.5-0.75 times as long as the subterminal segment of gonopod 2).

Type species.- *Thelphusa perlata* H. MILNE EDWARDS, 1837

This genus, as conceived by BOTT (1955), included thirty eight species and fourteen subspecies, all of which are found in Africa. BOTT (1955) erected fifteen subgenera to accommodate these taxa. Since that work a number of other species and subspecies have been described. These are *Potamonautes* (*Platypotamonautes*) *triangulus* BOTT, 1959, *P. brincki* (BOTT, 1960) (CUMBERLIDGE, 1994; STEWART, 1997), *P.* (*Isopotamonautes*) *anchetiae machadoi* BOTT, 1964, *P.* (*Lirrangopotamonautes*) *lirrangensis adeleae* BOTT, 1968, *P.* (*I.*) *senegalensis* BOTT, 1970a, *P. dentatus* STEWART, COKE & COOK, 1995, and *P. reidi* n. sp. in the present work. Species of *Potamonautes* can be distinguished by reference to the shape of the terminal article of the first gonopod in conjunction with characters of the carapace, sternum, pereiopods, and chelipeds. The vast majority of species of *Potamonautes* are found in continental Africa south of the Sahara, although two species are found along the Nile valley as far north as Cairo. One species (*P. margaritarius*) is found only on the island of Sao Thomé. Only four species of this genus occur in West Africa (*P. ecorssei, P. triangulus, P. senegalensis* and *P. reidi*). BOTT (1955) assigned the species of *Potamonautes* to 15 subgenera, but many of these subgenera are doubtful and the entire genus is badly in need of revision. For this reason, BOTT's subgeneric categories are not used here for the four West African species.

Key to the species of West African *Potamonautes*

1. The epibranchial tooth on the anterolateral margin is a distinct tooth. 2
- The epibranchial tooth on the anterolateral margin is not clearly visible, and is reduced to a small granule. *P. senegalensis*
2. The carapace sidewalls are divided by grooves either into three parts or into two parts. 3
- The carapace sidewalls are divided by grooves into four parts. *P. ecorssei*
3 The carapace sidewalls are divided by grooves into two parts. The medial and lateral folds of the terminal article of gonopod 1 are low and equal. *P. reidi*
- The carapace sidewalls are divided by sulci into three parts. The medial and lateral folds of the terminal article of gonopod 1 are formed into two large triangular flaps. *P. triangulus*

Potamonautes ecorssei (MARCHAND, 1902)

fig. 15A, 16A,E, 17A,E, 18C-D, 19A, 53A, 54-57, 58E, 65A, table IX.

Potamon (Potamonautes) Ecorssei MARCHAND, 1902, p. 334-342, pl. 13, fig. 2-6.-RATHBUN, 1905, p. 180.-ROUX, 1935, p. 32-34.

Potamon (Potamonautes) nigrensis RATHBUN, 1904, p. 295, pl. XII, fig. 8.

Potamon nigrensis, BALSS, 1936, p. 200.-CHACE, 1942, p. 217.- CAPART, 1954, p. 833, fig. 8, 20.

Potamon ecorssei, CHACE, 1942, p. 210

Potamonautes (Platypotamonautes) ecorssei, BOTT, 1955, p. 236-237, fig. 13, 67, pl. IV, fig. 2a-d.-BOTT, 1959, p. 1001-1002, fig. 9a-c.-MONOD, 1969, p. 78-79, fig. 4-7.-MONOD, 1977, p. 1212-1213, fig. 71-82, 86-92.-MONOD, 1980, p. 382-383, pl. VI, fig. 32.-CUMBERLIDGE, 1985a, p. 195-197, table 1.

Description

Diagnosis.- The carapace height is equal to the front width (ch/fw 1.0). The exorbital angle is small and low and the epibranchial tooth is small but distinct. The anterolateral margin between the exorbital angle and the epibranchial tooth is smooth, curves distinctly outward, and lacks an intermediate tooth; the anterolateral margin posterior to the epibranchial tooth is raised, and curves inward over the mesobranchial surface of the carapace, and is not continuous with the posterolateral margin. The sidewalls of the carapace are clearly divided by sulci into four parts. The episternal sulci s4/e4, s5/e5, s6/e6 are all clearly visible, while junction s7/e7 is without a visible groove. The merus of P5 is about as long as the fw.

Redescription.- Based on the holotype (an adult male from Mali) and on an adult male from Burkina Faso, cw 21.7 mm (MRAC 51.591). The carapace is moderately wide (cw/fw 2.83) and moderately high (the carapace height is equal to the front width, ch/fw 1.0). The entire dorsal surface of the carapace is smooth and the lateral carinae are faint. The postfrontal crest consists of fused epigastric and postorbital crests and is clear and distinct, but fades out at the lateral ends at the junctions with the anterolateral margins at the epibranchial teeth; the mid-groove on the postfrontal crest is short and flat, and is forked at its posterior end. The semi-circular and urogastric grooves are very deep; the cardiac grooves are faint; the cervical grooves are very short, and are directed anteriorly; and the transverse branchial grooves are deep and short, and do not meet the posterolateral margins. The front is straight and wide, and is nearly one third the width of the carapace (fw/cw 0.35); and the anterior margin of the front curves down. The exorbital angle is continuous with the anterolateral margin and is small and low; the epibranchial tooth is small, but distinct. The anterolateral margin between the exorbital angle and the epibranchial tooth is smooth, and curves distinctly outward and lacks an intermediate tooth; the anterolateral margin posterior to the epibranchial tooth is raised, and curves inward over the mesobranchial surface of the carapace, and is not continuous with the posterolateral margin. The posterior margin of the carapace is wide, about one half as wide as the carapace width. The suborbital, subhepatic, and pterygostomial regions are smooth. The vertical sulcus on the sidewall runs from the base of the epibranchial tooth to the epimeral sulcus and divides the suborbital region from the hepatic region; the vertical sulcus then continues down along the lateral wall of the buccal cavity (dividing the pterygostomial region into two parts), so that the sidewall is clearly divided into four parts. The ischium of the third maxilliped has a faint vertical sulcus. The third sternal sulcus s3/s4 is deep, and is angled backward so that its midpoint meets the anterior margin of the sterno-abdominal cavity. Episternal sulci s4/e4, s5/e5, s6/e6 are all clearly visible, while the s7/e7 junction does not have a visible groove.

The dactylus of both the right and left chelipeds is relatively narrow (one quarter the height of the palm), and the upper margin is smooth and the finger of the dactylus is slightly arched enclosing a long interspace; the finger of the propodus is slim (one third the height of the palm) and the lower margin of the propodus of the cheliped is indented. Both fingers of the cheliped have a series of small pointed teeth along their lengths that are interspersed with bigger teeth. The inferior margins of the merus are granular, with a single large pointed tooth at the distal end; the superior margin has rows of prominent, rough grains. The inner margin of the carpus of the cheliped has two large, slender, pointed teeth; the second is half the size of the first, and there is a series of low granules behind the second tooth. The merus of P5 is about as long as the fw. The propodus of P4 is long and thin, the propodus of P5 is short and thin, and the anterior and posterior margins of the propodi of P5 are clearly serrated.

The terminal article of gonopod 1 is short (about one third as long as the subterminal segment of gonopod 1), and the longitudinal groove is clearly visible on the ventral and superior sides, but is not visible on the dorsal side; the lateral fold of the ventral side of the terminal article is equal in height and width to the medial fold; the terminal article is directed sharply outward at a 70° angle to the vertical, and is slim, tapering strongly to a pointed tip. Gonopod 2 is longer than gonopod 1; the terminal article of gonopod 2 is a long flagellum, about one third as long as the subterminal segment.

Size.- The adult size range is from cw 24.5-36.1 mm. The carapace proportions are given in table IX. Graphs of carapace dimensions are given in fig. 58E.

Material examined

Sénégal, Gambia river, Le Parc National de Niokolo-Koba; DAGET; 1 m cw 26 mm (SMF 2659).- Gambia river, Le Parc National de Niokolo-Koba; DAGET; 2 m cw 24, 23 mm, 2 f cw 21.5, 19 mm (IFAN).- Bord du Doum fouzou? entre du Parc National de Niokolo-Koba; 29 November 1959; J. BANAIE; 1 m adult cw 30 mm, 2 f cws 25.5 (adult), 24.5 mm (subadult); (IFAN).- Bord du Sagnigui, Le Parc National du Niokolo-Koba; 27 November 1959; 1 m adult cw 31.5 mm, 1 juvenile cw 15.5 mm; (IFAN).

Mali, Manantali; 26 February 1991; 1 m cw 26 mm, 1 f adult cw 30 mm (SMF).

Côte-d'Ivoire, Pêche à la roténone, Lac de Kossou, Pont de Béoumi; 23 February 1974; R. JOCQUÉ (MRAC 55.525).

Burkina Faso, Ouagadougou, 4 May 1965; B. ROMAN; 1 m adult, cw 21.7 mm (MRAC 51.591).

Ghana, Station Ho, Ege river, tributary of the Todji; SCHRÖDER; 2 m juveniles cws 17, 16 mm, 2 f juveniles cws 14, 9 mm (ZMB 21303).

Togo, Dubul Pampamba, Mobe; THIERRY; 1 m adult cw 36.5 mm, 1 f adult cw 25 mm (ZMB 11047).- Yendi; 1901, THIERRY; 1 m adult cw 20 mm (ZMB 11048).- Ege river, tributary of Todje river near Ghana (this is probably the river Todschie (old spelling), near the border between Togo and Ghana, which flows into the lake near Keta in Ghana; SCHRÖDER; 1 m cw 22 mm, 1 f juvenile cw 15 mm (ZSM 1187/1).

Cameroon, 1 m cw 30 mm (ZSM 1187/2, donated by ZMB).- Namound Joga; 27-30 July 1969; F. PUYLAERT; 20-30 specimens (MRAC 53.102).- Namound Joga; 27-29 July 1969; F. PUYLAERT (MRAC 53.109).

Soudan (= West African savanna zone); (IFAN); 1 f adult cw 27 mm (SMF 2658).

Type and distribution

Type.- Mali, Lac Télé, near to Goundam; December 1912; Lieut. Col. ECORSSE; 1 m adult (AMNH 3346) holotype. MONOD (1969) notes that types No. 1 & No. 3 (1 m, 1 f) were deposited in the

Muséum d'Histoire naturelle de Nantes. MARCHAND indicated that paratypes No. 3 and No. 4 (both females) were in the collection of C. BORGOGNO, but they were not found in Nantes; MONOD (1969) speculates that they may have been destroyed in the bombings of 1943.

Distribution.- Mauritania (Guidimaka), eastern Sénégal, Mali (river Niger), Burkina Faso, Côte-d'Ivoire, Togo, Cameroon and Nigeria. Some of the localities in Nigeria were reported by CUMBERLIDGE (1985a), who discussed the distribution of the species. Voucher specimens of crabs from Amachi, Arochukwu, southeast Nigeria that were reported to belong to *P. ecorssei* by VOELKER & SACHS (1977) were deposited in the ZIM, Hamburg (ZIM K-30315) and have been examined by the author. These specimens are two adult females (cws 29.5 and 25 mm). Both have a very large and distinct epibranchial tooth and both have a second large tooth on the anterolateral margin behind the epibranchial tooth. These characters exclude these specimens from inclusion in *P. ecorssei*, and they place them close to *P. reidi* which is known to occur in that part of Nigeria (see below).

Remarks

Variation.- The postfrontal crest is well defined and complete in some specimens; but in others it is well defined only in the middle section and faint at the lateral ends near to the anterolateral margins. The epibranchial tooth is always small and distinct, but it is sharp and pointed in some specimens and blunt in others. The vertical sulcus on the ischium of the third maxilliped varies from clearly visible in some specimens to faint in others. BOTT (1955) described the terminal article of gonopod 1 as weakly s-shaped, in the present study this segment was found to be straight. This species does not conform to BOTT'S (1955) definition of the subgenus *Platypotamonautes* in a number of other ways. Because of this uncertainty, this subgenus category is not used here. This issue can only be resolved by a revision of the entire genus.

BOTT (1955) erected the subgenus *Platypotamonautes* (subgenotype *Potamon (Potamonautes) platynotus* CUNNINGTON, 1907 by original designation) for five species: *P. (P.) margaritarius* (A. MILNE-EDWARDS, 1969) from Sao Thomé, and *P. (P.) ecorssei* (MARCHAND, 1902) from Mali, *P. (P.) platynotus* (CUNNINGTON, 1907) from Lake Tanganyika, and *P. (P.) pilosus* (HILGENFDORF, 1898) and *P. (P.) neumanni* (HILGENDORF, 1898) both from East Africa. BOTT (1959) later added a sixth taxon, *P. (P.) triangulus* BOTT, 1959 from Ghana. *Potamonautes ecorssei* does not entirely conform to BOTT'S (1955) definition of the subgenus *Platypotamonautes*, so this category is not used for this taxon in the present work.

Potamonautes triangulus BOTT, 1959

fig. 15B, 16B, 17B,F, 18B,E, 19B, 53B, 54-57, 58F, 65B, table IX.
Potamonautes (Platypotamonautes) triangulus BOTT, 1959, p. 1002-1004, fig. 10a-b.-MONOD, 1977, p. 1212-1213, fig. 83-85.-MONOD, 1980, p. 382-383, pl. 6, fig. 35.

Description

Diagnosis.- The carapace height is equal to the front width (ch/fw 1.0). The postfrontal crest is clearly defined and complete, and meets the anterolateral margins at the epibranchial teeth. The exorbital angle is formed into a small pointed tooth; the epibranchial tooth is bigger that the exorbital angle tooth and is pointed and directed forward; the anterolateral margin between the exorbital angle and the epibranchial tooth is straight (not curved) and is edged by a row of small, even-sized granules, and this part of the anterolateral margin lacks a single large intermediate tooth; there is a series of small granules on the anterolateral margin posterior to the epibranchial tooth. The sidewalls of the carapace are clearly divided by two sulci into three parts. The ischium of the third maxilliped is smooth and lacks a vertical sulcus. The third sternal s3/s4 is deep and its midpoint is indented but does not quite meet the anterior margin of the sterno-abdominal cavity. Episternal sulci s4/e4, s5/e5, s6/e6, and s7/e7 are all clearly visible. The merus of P5 is shorter than the fw. The medial and lateral folds of the terminal article of gonopod 1 are each formed into a conspicuous triangular raised flap.

Redescription.- Based on an adult male paratype from a stream near Kibi, Ghana, cw 23.2 mm (SMF 2817). The carapace is moderately wide (cw/fw 3.08) and moderately high (the carapace height is equal to the front width, ch/fw 1.0). The entire dorsal surface of the carapace is smooth and there are no visible carinae. The postfrontal crest is almost straight and its lateral ends curve forward to meet anterolateral margins at the epibranchial teeth; the mid-groove on the postfrontal crest is short and wide, and is forked at its posterior end. The semi-circular and urogastric grooves are very deep; the cardiac grooves are faint; the cervical grooves are long and are directed anteriorly and do not meet the postfrontal crest; and the transverse branchial grooves are deep and short, and do not meet the posterolateral margins. The front is straight and wide (about one third the width of the carapace, cw/fw 3.08) and the anterior margin of the front curves down. The exorbital angle is formed into a small pointed tooth; the epibranchial tooth is bigger than the exorbital angle tooth and is pointed and directed forward; the anterolateral margin between the exorbital angle and the epibranchial tooth is straight (not curved) and is edged by a row of small, even-sized granules, and lacks a single large intermediate tooth; there is a series of small granules on the anterolateral margin posterior to the epibranchial tooth. The suborbital and pterygostomial regions are smooth, and the subhepatic regions are granular. The vertical sulcus on the sidewall begins at the base of the epibranchial tooth and divides the suborbital region from the hepatic region; the sidewalls are divided into three parts.

The ischium of the third maxilliped is smooth and lacks a vertical sulcus. The first sternal sulcus s1/s2 is distinct; the second sulcus s2/s3 is deep, and runs horizontally across the sternum; the third sternal sulcus s3/s4 is complete and is angled backward; its midpoint is indented anteriorly and almost meets the anterior edge of the sterno-abdominal cavity. Episternal sulci s4/e4, s5/e5, s6/e6, and s7/e7 are all clearly visible. The dactylus of the right and left chelipeds is relatively wide (one third the height of the palm), the upper margin is smooth, and the finger of the dactylus is slightly arched and encloses a long oval interspace; the finger of the propodus is broad (one half the height of the palm) and the lower margin of the propodus of the cheliped is indented. Both fingers of the cheliped have a series of small pointed teeth along their lengths that are interspersed with bigger teeth. The inferior margins of the merus have rows of small pointed teeth, and there is a single large pointed tooth at the distal end; the superior margin of the merus has rows of prominent, rough grains. The inner margin of the carpus of the cheliped has two large, slender, pointed teeth, the second is almost as big as the first, and there are small granules behind the second carpal tooth. The merus of P5 is shorter than the fw. The propodus of P4 and P5 is long and broad, and the anterior and posterior margins of propodi of P4 and P5 are clearly serrated.

The terminal article of gonopod 1 is short (about one third as long as the subterminal segment of gonopod 1), and the longitudinal groove is clearly visible on the ventral and superior sides, but is not visible from the dorsal side; the medial and lateral folds of the terminal article of gonopod 1 are each formed into a conspicuous triangular raised flap; the terminal article of gonopod 1 is directed sharply outward at a 70° angle to the vertical, and is slim, tapering strongly to pointed tip. Gonopod 2 is longer than gonopod 1; the terminal article of gonopod 2 is a long flagellum, about one half as long as the subterminal segment.

Size.- The adult size range is from cw 23-25 mm. The carapace proportions are given in table 1X. Graphs of carapace dimensions are given in fig. 58F.

Material examined

West Africa, Ghana, stream near Kibi; 20 May 1950; R. Bassindale; 2 m cws 19.5, 17 mm, 2 f subadults cws 18, 17 mm (IFAN), paratypes.- Stream near Kibi; 20 May 1950; R. Bassindale; 26 f and 46 m, cws 10-24.5 mm (IFAN).- Schülters; 1 f adult cw 23 mm (ZMB 7527).

Type and distribution

Type.- West Africa, Ghana, stream near Kibi; 20 May 1950; R. Bassindale; 1 m adult, cw 23.2 mm (SMF 2817), paratype.

Type locality.- The type and paratypes come from a stream about 9 km (5 miles) north of Kibi, which is about 90 km (50 miles) north of Accra, and which is near to Puso Puso, about 7 km (4 miles) west of Asiakwa, Ghana.

Remarks

This small species of river crab is endemic to the rivers of Ghana. This species does not entirely conform to Bott's (1955) definition of the subgenus *Platypotamonautes*. Because of this uncertainty, this subgenus category is not used here. This issue can only be resolved by a revision of the entire genus.

Potamonautes senegalensis Bott, 1970a

fig. 15C, 16C, 17C,G, 18F, 19C, 53C, 54-57, 58G, 65C, table IX.

Potamonautes (Isopotamonautes) senegalensis Bott, 1970a, p. 340-341, pl. 1, fig. 1-6

Description

Diagnosis.- The carapace is very wide (cw/fw 3.65), and is high and arched, so that the carapace height is greater than the front width (ch/fw 1.56); the carapace texture is smooth and glossy. The postfrontal crest is straight, and it is distinct and completely spans the carapace; its lateral ends curve forward to meet anterolateral margins at the epibranchial teeth. The exorbital angle is small and low; the epibranchial tooth is reduced to a granule; the anterolateral margin between the exorbital angle and epibranchial tooth is edged with small granules, but there is no intermediate tooth; the anterolateral margin posterior to the epibranchial tooth is marked by a series of small granules; the anterolateral margin does not curve inward over the mesobranchial surface of the carapace, and is continuous with the posterolateral margin. The sidewalls of the carapace are divided into three parts. The ischium of the third maxilliped has a vertical sulcus. The third sternal sulcus s3/s4 is angled backward, and the midpoint almost meets the anterior margin of the sterno-abdominal cavity. The superior margin of the merus is smooth.

Redescription.- The carapace is very wide (cw/fw 3.65), and is very high (the carapace height is greater than the front width, ch/fw 1.56); the carapace texture is smooth and glossy. The semi-circular and urogastric grooves are very deep; the cardiac grooves are faint; the cervical grooves are long, and are directed anteriorly, and do not meet the postfrontal crest; and the transverse branchial grooves are deep and short, and do not meet the posterolateral margins. The postfrontal crest is straight, and it is distinct and completely spans the carapace; its lateral ends curve forward to meet anterolateral margins at the epibranchial teeth. The exorbital angle is small and low; the epibranchial tooth is reduced to a granule and is no bigger than the other granules along the anterolateral margin; the anterolateral margin between the exorbital angle and epibranchial tooth is edged with small granules, but there is no intermediate tooth; the anterolateral margin posterior to the epibranchial tooth is marked by a series of small granules; the anterolateral margin does not curve inward over the mesobranchial surface of the carapace, and is continuous with the posterolateral margin. The front is straight and narrow (nearly one quarter of the carapace width, cw/fw 3.65), and the anterior margin of the front curves down. The posterior margin of the carapace is about one third as wide as the carapace. The suborbital, subhepatic, and pterygostomial regions of the sidewall are smooth. The vertical sulcus on the sidewall begins at the base of the epibranchial tooth and runs parallel with the anterolateral margin before curving down to meet the epimeral sulcus, so dividing the suborbital region from the hepatic region; the sidewalls of the carapace are thus divided into three parts. The ischium of the third maxilliped has a vertical sulcus. The first sternal sulcus s1/s2 is complete and distinct; the second sulcus s2/s3 is deep, and runs horizontally across the sternum; the third sternal sulcus s3/s4 is angled backward, and the midpoint almost meets the anterior margin of the sterno-abdominal cavity.

The dactylus of the right and left chelipeds is relatively narrow (one quarter the height of the palm), and its upper margin is smooth, and the finger of the dactylus is slightly arched and encloses a long oval interspace; the finger of the propodus is slim (one third the height of the palm) and the lower margin of the propodus of the cheliped is indented. Both fingers of the cheliped have a series of small pointed teeth along their lengths interspersed with two or three bigger teeth. The inferior margins of the merus are granular with a single large pointed tooth at the distal end; the superior margin of the merus is smooth. The inner margin of the carpus of the cheliped has two large, slender, pointed teeth, the second is half the size of the first. The merus of P5 is shorter than the fw. The propodus of P4 and P5 is long and broad, and the anterior and posterior margins of propodi of P4 and P5 are clearly serrated.

The terminal article of gonopod 1 is short (about one third as long as the subterminal segment of gonopod 1), and the longitudinal groove is clearly visible on the ventral and superior sides, but is not visible from the dorsal side; the lateral fold of the terminal article of gonopod 1 is much higher than the medial fold; the terminal article of gonopod 1 is directed slightly outward (at a 30° angle to the vertical); the segment is slim, and tapers strongly to a pointed tip. Gonopod 2 is longer than gonopod 1; the terminal article of gonopod 2 is a long flagellum, about one half as long as the subterminal segment.

Size.- Only an adult male (cw 58.5 mm) and an adult female are known. The carapace proportions are given in table IX. Graphs of carapace dimensions are given in fig. 58G.

Material examined

Type.- West Africa, Sénégal; 1 m, cw 58.5, cl 38.5, ch 25, fw 16, holotype (NHMG).- West Africa, Sénégal; 1 f, paratype.

Type and distribution

Type.- West Africa, Sénégal; 1 m, cw 58.5, holotype (NHMG).- West Africa, Sénégal; 1 f, paratype.

Type locality.- West Africa, Sénégal.

Distribution.- West Africa, Sénégal river, Sénégal.

Remarks

BOTT (1955) erected the subgenus *Isopotamonautes* (subgenotype *Telphusa anchetiae* BRITO-CAPELLO, 1871 by original designation) for two taxa, *P.* (*I.*) *anchetiae* (BRITO-CAPELLO, 1871) from Angola and the lower Congo, and *P.* (*I.*) *macrobrachii*, BOTT, 1953 from Angola. *Potamonautes senegalensis* from Sénégal was the third species to be assigned to this subgenus by BOTT (1970a). However, this latter species does not entirely conform to BOTT's (1955) definition of the subgenus *Isopotamonautes*, so this category is not used for this taxon in the present work.

Potamonautes senegalensis is known only from the male and female types. A description with photographs of the types is available in BOTT (1970a). *Potamonautes senegalensis* bears a superficial resemblance to other savanna freshwater crabs (such as *S. monodi*), but the long terminal article on gonopod 2, the short terminal article of gonopod 1, and the lack of an intermediate tooth clearly place this species in *Potamonautes*.

Potamonautes reidi n. sp.

fig. 15D, 16D,G, 17D,H, 18B,G, 19D, 53D, 54-57, 58H, 65D, table IX.

Description

Diagnosis.- The postfrontal crest is not quite complete, and the lateral ends do not quite meet the anterolateral margins. The exorbital angle is produced into a small, low, blunt tooth; the epibranchial tooth is large and thin, and points forward; the anterolateral margin between the exorbital angle tooth and the epibranchial tooth is smooth, curves distinctly outward, and lacks an intermediate tooth; the anterolateral margin posterior to the epibranchial tooth has a single large, sharp, forward-pointing tooth; the margin is otherwise smooth and is raised and curves inward over the mesobranchial surface of the carapace, and is not continuous with the posterolateral margin. The front is very broad, measuring almost one half the width of the carapace (fw/cw 0.45). The sidewall of the carapace lacks a vertical sulcus and so it is only divided into two parts by the epimeral sulcus. The ischium of the third maxilliped has a clear vertical sulcus. Sternal sulcus s3/s4 is deep and is angled backward and its midpoint has a slight vertical groove; s3/s4 meets the anterior margin of the sterno-abdominal cavity. Episternal sulci s6/e6 and s7/e7 are clearly visible, and the junctions between s4/e4 and s5/e5 are not marked by complete and visible grooves. The inner margin of the carpus of the cheliped has two large, slender, pointed teeth, the second is the same size as the first. The medial and lateral inferior margins of the merus of the cheliped are smooth, and there is a single large pointed tooth at the distal end; the superior margin of the merus is smooth.

Description.- The carapace is very wide (cw/fw 2.6) and is quite flat (the carapace height is less than front width, ch/fw 0.94). The entire dorsal surface of the carapace is smooth. The semicircular and urogastric grooves are very deep; the cardiac grooves are faint; the cervical grooves are short, and are directed anteriorly, and terminate well short of the postfrontal crest; and the transverse branchial grooves are deep and short, and do not meet the posterolateral margins. The postfrontal crest is not complete, and the ends do not quite meet the anterolateral margins and fade out before meeting the epibranchial teeth; the mid-groove on the postfrontal crest is short, flat, and wide, and is not forked at its posterior end. The exorbital angle forms a small, low, blunt tooth; the epibranchial tooth is large and thin, and points forward; the anterolateral margin between the exorbital angle and the epibranchial tooth is smooth and curves distinctly outward, and lacks an intermediate tooth; the anterolateral margin posterior to the epibranchial tooth has a single large, sharp, forward-pointing tooth; the margin is otherwise smooth and is raised, curving inward over the mesobranchial surface of the carapace, and is not continuous with the posterolateral margin. The frontal region is very broad, measuring almost one half the cw (fw/cw 0.45). The suborbital, subhepatic, and pterygostomial regions of the sidewall smooth and the sidewall of the carapace lacks a vertical sulcus so that it is divided into just two parts: the suborbital and subhepatic regions (uppermost) and the pterygostomial region.

The ischium of the third maxilliped has a vertical sulcus. The first sternal sulcus s1/s2 is distinct; the second sulcus s2/s3 is deep and runs horizontally across the sternum; the third sternal sulcus s3/s4 is angled backward, and the midpoint (which has a slight vertical grove) almost meets the anterior edge of the sterno-abdominal cavity. Episternal sulci s6/e6 and s7/e7 are clearly visible, and the junctions between s4/e4 and s5/e5 are not marked by visible grooves.

The dactylus of the right cheliped is relatively narrow (one quarter the height of the palm), the upper margin is smooth, and the finger of the dactylus is highly arched and encloses a wide oval interspace; the finger of the propodus is slim (one third the height of the palm) and the lower margin of the propodus of the cheliped is indented; the lower margin of the propodus of the cheliped is longer than the width of the carapace. Both fingers of the cheliped have a series of small pointed teeth along their lengths interspersed with several bigger teeth. The medial and lateral inferior margins of the merus are smooth, and there is a single large pointed tooth at the distal end; the superior margin of the merus is smooth. The inner margin of the carpus of the cheliped has two large, slender, pointed teeth, the second is the same size as the first. The merus of P5 is as long as the fw. The propodus of P4 and P5 is long and thin, and the anterior and posterior margins of propodi of P4 and P5 are clearly serrated.

The terminal article of gonopod 1 is short (about one third as long as the subterminal segment of gonopod 1), and the longitudinal groove is clearly visible on the ventral and superior sides, but is not visible from the dorsal side; the lateral fold of the terminal article of gonopod 1 is low and is about the same size as the medial fold; the terminal article of gonopod 1 is directed slightly outward at a 45° angle to the vertical, and is slim, tapering strongly to a pointed tip. Gonopod 2 is longer than gonopod 1; the terminal article of gonopod 2 is a long flagellum, about one half as long as the subterminal segment.

Size.- The adult size range is from cw 24-36.5 mm. The carapace proportions are given in table IX. Graphs of carapace dimensions are given in fig. 58H.

Material examined

Nigeria, Cross River State, Addy Arbour, about 8 km north of Calabar, off Murtala Mohammed Highway, about 2 km along a dirt road; 11 May 1979; J. C. REID; 1 m cw 33 mm, permanent stream with a sand bed with *Nymphe*, clear white water, crab found under a cement block (NMU 11.V.1979, donated by J. C. REID, #18).- Cross River State, Adaibo Bridge, Palmol Estate near Calabar; 6 April 1983; J. C. REID & N. CUMBERLIDGE; 2 m juveniles cws 24, 32.5 mm, 3 f juveniles cws 27, 30, 32 mm; caught in overhanging vegetation with a sweep net in a small stream (NMU 6.IV.1983).- Bendel State, Sombreiro River at Agoada; 1 April 1977; B. POWELL; 1 m cw 30 mm (NMU 1.IV.1977 donated by B. POWELL).

Type and distribution

Types (examined).- Nigeria, Cross River State, Palmol Estate near Calabar; B. D. BARRETT; 30 April 1982; 1 m adult cw 42 mm, caught clinging to overhanging vegetation at the sides of a small, slow-flowing freshwater stream (NMU 30.IV.1982a) designated here the holotype.-Cross River State, Palmol Estate near Calabar; B. D. BARRETT; 30 April 1982; 1 m juvenile cw 24.5 mm, 1 f juvenile cw 21.5 mm (NMU 30.IV.1982b), paratypes.

Type locality.- West Africa, Nigeria, Cross River State, Palmol Estate near Calabar.

Etymology.- This species is named for the late Dr. Jonathan C. REID in recognition of his remarkable talent for collecting animals of all kinds from the rainforests of southeast Nigeria. A substantial part of his collection of freshwater crabs from this region which he complied over a period of ten years was kindly donated to the author for identification and further study and is included here.

Remarks

This species is close to *Potamonautes paecilei* (A. MILNE-EDWARDS, 1886). I have examined one of the types of *P. paecilei* held in the

MNHN, Paris (MNHN-B 263) (an adult male cw 32 mm) which was collected from the Congo, Alima, Latéké by DE BRAZZAE. Another of the male types of *P. paecilei* (cw 22.7 mm) is figured by CAPART (1954). *Potamonautes reidi* and *P. paecilei* share the following characters. Both species have a large forward-pointing epibranchial tooth; a large tooth (or teeth) behind the epibranchial tooth on the anterolateral margin; an enlarged major cheliped in adult males with a widely arched dactylus and a propodus that is longer than the carapace width; a long sharp distal spine on the merus of the cheliped; and two large pointed teeth on the inner margin of the carpus of the cheliped. The two species can be distinguished by the following characters: the exorbital angle of *P. reidi* is a low, blunt angle, while that of *P. paecilei* is formed into a strong sharp pointed tooth; the anterolateral margin behind the epibranchial tooth of *P. reidi* has only one large tooth, whereas this margin in *P. paecilei* has at least two large sharp pointed teeth followed by one smaller tooth. The carapace of *P. reidi* is entirely smooth whereas that of *P. paecilei* has granules or carinae. The lateral ends of the postfrontal crest of *P. reidi* do not meet the anterolateral margins, whereas those of *P. paecilei* do. The fingers of the chelipeds of adult males of *P. reidi* have several small teeth but no large teeth, whereas in *P. paecilei* the cheliped fingers have small teeth and one large tooth. The sidewalls of the carapace in *P. reidi* are clearly divided into two parts (the vertical sulcus is lacking or so faint it cannot be detected), whereas the sidewalls of *P. paecilei* are divided into three parts by a distinct vertical sulcus. Finally, the ischium of the third maxilliped of *P. reidi* has a distinct vertical sulcus, whereas that of *P. paecilei* is smooth and this sulcus is lacking.

BOTT (1955) assigned *Potamonautes paecilei* to the subgenus *Longipotamonautes* BOTT, 1955, which also includes a number of other species of rainforest river crabs from Central Africa which have elongated chelipeds and teeth on the anterolateral margins (*P. vandenbrandeni* (BALSS, 1936), *P. schubotzi* (BALSS, 1914), *P. punctatus* BOTT, 1955, and *P. ballayi* (A. MILNE-EDWARDS, 1886)). *Potamonautes reidi* is close to these species in many respects, but it is not assigned here to the subgenus *Longipotamonautes* pending further taxonomic work on the genus.

Liberonautes BOTT, 1955

fig. 64C

There is an intermediate tooth on the anterolateral margin between the epibranchial tooth and the exorbital angle. The postfrontal crest is prominent, almost horizontal, but not complete (the lateral ends never meet the anterolateral margins). The sidewall is divided by two sulci into three parts. The mandibular palp has two segments; the terminal segment consists of a large oval posterior lobe, with a small but distinct anterior process at the junction between the segments. There is a long, plumose flagellum on the exopod of the third maxilliped in all species except for two (*L. rubigimanus* and *L. lugbe*). Sternal sulcus s3/s4 is represented only by two short notches at the lateral ends. Episternal sulcus s7/e7 is missing. The terminal article of gonopod 1 curves inward, not outward, when viewed from the ventral side. The dorsal side of the terminal article of gonopod 1 is smooth, and the dorsal membrane at the junction between the two distal segments is very broad. The medial and lateral folds on the ventral side of the terminal article of gonopod 1 are low and of equal size; they are separated lengthways by the distinct longitudinal groove. The terminal article tapers strongly to a pointed or tubular tip, which has a hole (the apical opening) at the tip. The subterminal segment of gonopod 1 is a long, slim rectangle. The flagellum on the terminal article of gonopod 2 is long, two thirds as long as the subterminal segment of gonopod 2.

Type species.- *Potamon (Potamonautes) latidactylum* DE MAN, 1903

Members of this genus are restricted to the western part of West Africa from Sénégal to Ghana. The genus includes eight species: *L. latidactylus*, *L. chaperi*, *L. rubigimanus*, *L. paludicolis*, *L. nanoides*, *L. nimba*, *L. lugbe*, and *L. grandbassa*. All members of this genus are found in rainforest habitats, and occupy different ecological niches including lowland streams (*L. latidactylus*, *L. lugbe* and *L. grandbassa*), mountain streams (*L. rubigimanus* and *L. nimba*), surface water sources (*L. paludicolis*), and major rivers (*L. chaperi* and *L. nanoides*). *Liberonautes latidactylus* is the only member of the genus that also occurs in drier savanna habitats from northern Ghana to Sénégal.

From 1955 until 1985 *Liberonautes* was considered to be a monotypic genus, and all specimens that resembled *L. latidactylus* were identified as this species. As the knowledge of the taxonomy of the genus has increased (CUMBERLIDGE, 1985b, 1999; CUMBERLIDGE & SACHS, 1989a,b; 1999) the process of identification has become increasingly more complex. Species of *Liberonautes* can be distinguished by reference to the shape of the terminal article of the first gonopod in conjunction with characters of the carapace, sternum, pereiopods, and chelipeds. An important part of this process of identification is the precise distribution of the species, together with a knowledge of its habitat. Parasitologists working on human lung fluke disease (paragonimiasis) in Liberia focused a lot of their attention on the easily accessible freshwater crab second intermediate hosts of the parasite. A species of crab is considered to be a second intermediate host of the parasite if the metacercariae of *Paragonimus uterobilateralis* or *P. africanus* have been isolated from any specimens. In this way, four of the eight species of the genus *Liberonautes* have been shown to host *Paragonimus* (CUMBERLIDGE & SACHS, 1989a,b; SACHS & CUMBERLIDGE, 1990, 1991), while the status of *L. rubigimanus*, *L. nimba*, *L. lugbe*, and *L. grandbassa* is at present unknown.

Key to the species of *Liberonautes*

1 The anterolateral margin of the carapace behind the epibranchial tooth is smooth or consists of small granulations; the intermediate tooth and the epibranchial tooth are small. 2

- There are three or more large pointed teeth on the anterolateral margin of the carapace behind the epibranchial tooth; the intermediate tooth is large, triangular, and pointed; the epibranchial tooth is large and pointed. (This species is found only in major rivers, never in creeks or on nearby land. The common name is the spiny river crab). *L. chaperi*

2 The exopod of the third maxilliped has a long flagellum. 3

- The exopod of the third maxilliped lacks a flagellum. 7

3 The carapace height is equal to the front width (ch/fw 1.0). 4

- The carapace height is greater than the front width (ch/fw 1.11). 5

4 Episternal sulci s4/e4, s5/e5, and s6/e6 are all clearly visible; specimens in the size range cw 25-33 mm are adult. (This species is found only in major rivers, and never in creeks or on nearby land. The common name is the dwarf river crab). *L. nanoides*

- Episternal sulci s4/e4 and s5/e5 are missing, s6/e6 is clearly visible; specimens in the size range cw 25-33 mm are subadult. (This species is found only in creeks or on nearby land, never in major rivers. The common name is the common creek crab). *L. latidactylus*

5 Episternal sulci s4/e4, s5/e5, and s6/e6 are not visible; specimens in the size range cw 20-24.5 mm are adult. (This species is found only on Mount Nimba). *L. nimba*

- Episternal sulci s4/e4, s5/e5, and s6/e6 are all clearly visible. 6

6 A large species, specimens in the size range cw 31-32 mm are subadult. (This species is found on land or in nearby creeks, never in major rivers. The common name is the swamp crab). *L. paludicolis*

- A small species, specimens in the size range cw 31-32 mm are adult. *L. grandbassa*

7 Length of the inferior margin of the propodus of the major cheliped of adult males is shorter than the carapace width; the carapace has carinae in the branchial and subbranchial regions; the carapace is not wide (cw/fw < 3.5); the carapace is not long (cl/fw < 2.4). *L. lugbe*

- The dactylus and propodus of the cheliped are flattened and broad; the length of the inferior margin of the propodus of the major cheliped of adult males is longer than the carapace width; the carapace is completely smooth; the carapace is very wide (cw/fw > 3.5); the carapace is very long (cl/fw >2.4). (This species is found only in mountain streams, never in major rivers. The common name is the lobster claw crab). *L. rubigimanus*

Liberonautes chaperi (A. MILNE-EDWARDS, 1887)

fig. 20F, 21F, 22F, 23F, 24F, 25F, 26F, 27F, 28C, 53J, 54-57, 59F, 66E, table IX.

Parathelphusa chaperi A. MILNE-EDWARDS, 1887, p. 144, pl. 18, fig. 4a.-RATHBUN, 1900, p. 284-285.

Potamon (Parathelphusa) chaperi, RATHBUN, 1905, p. 262-263, pl. 12, fig. 6.

Potamon chaperi, CHACE, 1942, p. 209.-CAPART, 1954, p. 828.

Sudanonautes (Sudanonautes) africanus chaperi, BOTT, 1955, p. 298-299 (not *Potamon (Acanthothelphusa) faradjensis* RATHBUN, 1921).-MONOD, 1977, p. 1216.-MONOD, 1980, p. 384.

Liberonautes chaperi, CUMBERLIDGE, 1987, p. 2703-2706, fig. 1; CUMBERLIDGE & SACHS, 1989a, p. 224, fig. 1a-f.

Redescription

Diagnosis.- The exorbital angle is small and low and is continuous with the anterolateral margin, and the intermediate and epibranchial teeth are large, sharp and triangular, and both point forward. The anterolateral margin posterior to the epibranchial tooth has three large forward-pointing teeth. The finger of the propodus of the major cheliped has a large flattened (fused) tooth in the proximal region. The propodus of P4 is long (longer than the fw).

Redescription.- The carapace is not wide (about half as wide as long, cw/cl 1.46) and it is very flat (the carapace height is less than front width, ch/fw 0.87). The front is relatively narrow, about one quarter of the carapace width (fw/cw 0.3). The surface of the carapace has rows of granules in the epibranchial and mesobranchial regions. The cardiac and urogastric grooves are distinct; and the cervical grooves are deep and short and are directed laterally toward the anterolateral margins. The exorbital angle is small and low and is continuous with the anterolateral margin, and the intermediate and epibranchial teeth are large, sharp and triangular, and both point forward. The anterolateral margin posterior to the epibranchial tooth has three large forward-pointing teeth. The suborbital, subhepatic, and pterygostomial regions of the sidewall are smooth. The vertical sulcus on the sidewall begins at the base of the epibranchial tooth, and then runs forward (parallel with the anterolateral margin) as far as the base of the intermediate tooth, when it turns sharply down to meet the epimeral sulcus. The ischium of the third maxilliped is smooth and lacks a vertical sulcus. Episternal sulci s5/e5, and s6/e6 are distinct; but s4/e4 and s7/e7 are not visible.

The dactylus of the right and left chelipeds is rounded, narrow (one third the height of the palm), and the upper surface is smooth; the finger is very arched and encloses a wide interspace; the finger of the propodus is narrow, and the lower margin of the propodus of the cheliped is indented. The finger of the propodus of the major cheliped has a large flattened (fused) tooth in the proximal region. The inferior margins of the merus of the chelipeds is granular, with a single small pointed tooth at the distal end; the superior margin has a row of prominent, rough grains. There is a smooth oval surface (the meral tympanum) on the inner surface of the merus of the cheliped. The inner margin of the carpus of the cheliped has two teeth, the first is large, thin, and pointed, and is directed forward, the second is about one third the size of the first tooth, and there is a small tooth behind this tooth. The merus of P5 is short, only as long as the fw. The propodus of P4 is thin and long (longer than the fw), the propodus of P5 is wide and short, and the anterior and posterior margins of the propodi of P5 are clearly serrated; the dactyli of P2-P5 taper to a point, and each has rows of downward-pointing sharp bristles; the dactylus of P4 is long, the dactylus of P5 is very short, the shortest of the walking legs.

The terminal article of gonopod 1 is long (about two-thirds as long as the subterminal segment), and the longitudinal groove is clearly visible from both ventral and superior views, but is not visible on the dorsal side; the segment is directed inward at a 50° angle to the vertical, and is slim, tapering strongly to pointed tip; the lateral fold of the terminal article is as wide as the medial fold. The inner margin of the subterminal segment of gonopod 1 is long and wide, and tapers only slightly up to the junction with the distal part of the subterminal segment.

Size.- The adult size range is from cw 35-49.5 mm. The carapace proportions are given in table IX. Graphs of carapace dimensions are given in fig. 59F.

Colour

The following description is based on a living adult male from Liberia. The dorsal carapace is a uniformly dark (either black, dark brown, or dark green). The postfrontal crest is usually the same colour as the carapace. The pterygostomial region is yellow-orange, the sternum pale orange, and the abdomen off-white or cream. The dorsal propodus of the cheliped is dark and mottled, while the underside of the propodus is off-white or cream. The dorsal sides of P2-P5 are dark and mottled, and the undersides cream, while the tips of P2-P5 are always orange.

Material examined

Liberia, Lofa County, St. Paul river near Beyan town (= Beyanta); 19 July 1970; 1 f subadult cw 38 mm (SMF 22187, donated by ZIM). For other material see CUMBERLIDGE (1985a), and (SACHS & CUMBERLIDGE, 1991).

Type and distribution

Type.- Assini, Côte-d'Ivoire; M. CHAPER; 1 f adult cw 53 mm, dried specimen (MNHN-B 2401-82), holotype. Since the type is a dried specimen, this species was redescribed by CUMBERLIDGE (1985a) from an adult male (cw 55 mm) from Iuofoam, Ghana (NHML 1902.3.22.0(1-3)).

Type locality.- Assini, Côte-d'Ivoire.

Distribution.- Côte-d'Ivoire, Ghana, Liberia.

Remarks

Liberonautes chaperi is found in the major rivers of the rainforest zones of Liberia, Côte-d'Ivoire and Ghana (CUMBERLIDGE, 1985a; CUMBERLIDGE & SACHS, 1989a); it has never been found in small streams. *Liberonautes chaperi* serves as second intermediate host to *Paragonimus uterobilateralis* in Liberia (SACHS & CUMBERLIDGE, 1991). However, the incidence of infection in that country is low indicating that this species does not play an important role in the transmission of the parasite to humans. The common name for *L. chaperi* in Liberia is the spiny river crab.

Liberonautes latidactylus (DE MAN, 1903)

fig. 20C, 21D, 22D, 23D, 24D, 25D, 26D, 27A, 28A, 53H, 54-57, 56A, 66A, table IX.

Potamon (Potamonautes) latidactylum DE MAN, 1903. p. 41-47, pl. 9, fig. 1-6.

Liberonautes latidactylus, BOTT, 1955, p. 306-308, pl. 29, fig. 102, 103.- MONOD, 1977, p. 1219, fig. 96-97, 117-131.- MONOD, 1980, p. 385, fig. 31.

Liberonautes latidactylus latidactylus, CUMBERLIDGE & SACHS, 1989a, p. 221-230, fig. 2n-u.-CUMBERLIDGE & SACHS, 1989b, p. 425-431, 436-437, fig. 1a, table 1.

Redescription

Diagnosis.- The exorbital angle tooth and the intermediate and epibranchial teeth are small and low. The anterolateral margin behind the epibranchial tooth is raised, granular, and curves inward over the carapace at the posterior end. The dactylus and propodus of the major cheliped are very broad, the lower margin of the propodus of the cheliped curves downward, making the entire cheliped appear to be broad and flat. The propodus of P4 is long (longer than the fw). The ischium of the third maxilliped has a clear vertical sulcus. The terminal article of gonopod 1 is long (about two thirds as long as the subterminal segment), the longitudinal groove is clearly visible on the ventral and superior sides (but not on the dorsal side); the entire terminal article is directed inward at a 30° angle to the vertical, and is slim, and tapers strongly to the tip (which is like a thin pointed stylus); the lateral fold on the terminal article is a little wider and higher than the medial fold.

Redescription.- The carapace is relatively wide (cw/cl 1.54) and of moderate height (ch/fw 1.0). The front is slightly indented and relatively narrow (between one third and one quarter of the carapace width, fw/cw 0.30). The epibranchial regions of the carapace have rows of short granular ridges (carinae) and the rest of the surface of the carapace is smooth. The semi-circular and urogastric grooves are very deep; the cardiac grooves are faint; the cervical grooves are long and are directed anteriorly and do not meet the postfrontal crest; and the transverse branchial grooves are deep. The mid-groove of the postfrontal crest is short and is forked at its posterior end. The exorbital angle tooth and the intermediate and epibranchial teeth are small and low. The anterolateral margin behind the epibranchial tooth is raised, granular, and curves inward over the carapace at the posterior end, and is not continuous with the posterolateral margin. The posterior margin of the carapace is about one third as wide as the carapace. The suborbital, subhepatic, and pterygostomial regions of the sidewall are smooth. The vertical sulcus on the sidewall begins at the base of the epibranchial tooth. The ischium of the third maxilliped has a distinct vertical sulcus. Episternal sulci s5/e5, and s6/e6 are distinct, while s4/e4 and s7/e7 are not visible.

The dactylus of the right and left chelipeds is relatively broad (one half the height of the palm), and the upper margin is smooth; the finger is slightly arched and encloses a long interspace; the finger of the propodus is very broad (one half the height of the palm), and the lower margin of the propodus of the cheliped curves downward (and is not indented), making the entire cheliped appear broad. Both fingers of the cheliped have a series of small pointed teeth along their lengths interspersed with two big teeth. The inferior margins of the merus of the chelipeds are faintly granular, with a single large pointed tooth at the distal end; the superior margin has rows of prominent, rough grains. There is a smooth oval surface (the meral tympanum) on the inner surface of the merus of the cheliped. The inner margin of the carpus of the cheliped has two teeth, the first is large and blunt and is directed forward, the second is about one third the size of the first tooth, and there is a small tooth behind this tooth. The merus of P5 is long, and is longer than the fw. The propodus of P4 is thin and long (longer than the fw), the propodus of P5 is wide and short, and the anterior and posterior margins of the propodi of P5 are clearly serrated; the dactylus of P4 is long, the dactylus of P5 is very short, the shortest of the walking legs.

The terminal article of gonopod 1 is long (about two thirds as long as the subterminal segment), the longitudinal groove is clearly visible on the ventral and superior sides (but not on the dorsal side); the entire terminal article is directed inward at a 30° angle to the vertical, and is slim, and tapers strongly to the tip which is like a thin pointed stylus; the lateral fold on the terminal article is a little wider and higher than the medial fold.

Size.- The adult size range is from cw 45-50 to 76 mm. The carapace proportions are given in table 1X. Graphs of carapace dimensions are given in fig. 59C.

Colour

The following description is based on a living adult male from Liberia. The dorsal carapace is a uniform dark colour (either black, dark brown, or dark green), although some specimens bear a pale yellow M-shaped marking on the carapace centred on the cardiac region. The carapace of subadult crabs (cw 25-

45 mm) is dark only in the anterior region, with a mottled appearance in the hepatic and branchial regions. The postfrontal crest is usually the same colour as the carapace, except in the populations from Margibi and Grand Gedah Counties in Liberia which have a contrasting yellow postfrontal crest. The pterygostomial region is yellow-orange, the sternum pale orange, and the abdomen off-white or cream. The merus of the third maxilliped is cream with a round purple patch, while the carpus, propodus, and dactylus of the third maxillipeds are purple, and the ischium and exopodite cream. The epistome and subantennular region are orange. The eyestalks are dark yellow with black corneas. The fingers of the cheliped are orange with purple mottling, the teeth on the fingers cream, while the arthrodial membranes between the propodus/carpus, the carpus/merus, the merus/ischium, and the ischium/coxa are a transparent, pale yellow. The dorsal propodus of the cheliped is dark and mottled, while the underside of the propodus is off-white or cream. The dorsal sides of P2-P5 are dark and mottled, are the undersides cream, while the tips of P2-P5 are always orange.

Material examined

Sénégal, Dakar, Yoff (= Yof); IFAN; 1 f subadult cw 38 mm (SMF 2654).

Guinea, Fenaria; 1943, E. Lutten; 1 m adult cw 76 mm (SMF 2652 donated by the Dundo museum).- Seredou; 1958; R. Pugol; 5 juveniles cws 30, 26, 28, 24, 24 mm, 1 f subadult cw 50 mm, 4 m subadults cws 47, 46, 40, 26, 1 f adult ovigerous cw 64 mm, in freshwater (SMF, donated by MNHN).- north Zida; (IFAN); 1 m adult cw 62 mm (SMF 5655).- Mount Nimba; Lamotte; 6 juveniles (SMF 12024).

Sierra Leone, Moyamba District, Gambi-Gambia town (about 6-8 km after Sudan, towards Strenge); 7 November 1986; K. O. Nagel; 1 m subadult cw 34 mm, 1 f subadult cw 37 mm (SMF 14964).

Liberia, Yoefallé; IFAN: 1 f subadult cw 52 mm (SMF 2661).- Grand Gedah County, Balloon (Balu?) creek; 20 November 1969; R. Garms; 1 f adult, cw 56 mm (together with *L. rubigimanus*) (SMF 6590).- Grand Gehah County, Balloon creek; 20 November 1969; R. Garms; 1 f adult, cw 68 mm (together with *L. rubigimanus*) (SMF 6591).- Grand Gehah County, Balloon creek; 26 June 1969; R. Garms; 1 m adult cw 69 mm, 1 f adult, cw 69 mm (together with *L. rubigimanus*) (SMF 6592).- Grand Gedah County, Putu range; 20 November 1969; R. Garms; 1 m juvenile cw 18 mm (SMF 6608).- Grand Gedah County, Dorne creek, Kuma town; 10 December 1970, R. Garms; 1 m juvenile cw 20 mm (SMF 6609).-Nimba County, Dehn creek near Lugbai

400 m; 20 August 1969; R. GARMS; 1 m subadult cw 36 mm (SMF 6593).-Nimba County, Dehn creek near Lugbai 400 m; 20 August 1969; R. GARMS; 1 f adult cw 53 mm, 2 m juveniles cws 37, 20 mm (SMF 6602).- Gibi district, Mount Gibi, 160 m; 24 September 1969; R. GARMS; 1 juvenile cw 16 mm (SMF 6595).- Gibi District, Mount Gibi, 160 m; 12 June 1969; R. GARMS; 1 f juvenile cw 12 mm (SMF 6612).- Grand Cape Mount County, mountain creek near Fono; 19 April 1969; R. GARMS; 1 m adult cw 50 mm (SMF 6604).- Montserrado County, Farmington river; 16 August 1969; R. GARMS; 1 m subadult cw 39 mm (SMF 6597).- Bong County, Mauwa creek, 120 m; 1 August 1969; R. GARMS; 1 f subadult cw 36 mm (SMF 6598).- Bong County, waterfall near Bong Iron Mine, 160 m; 29 July 1969; R. GARMS; 1 f subadult cw 53 mm (SMF 6599).- Lofa County, Garbayea creek, 480 m; 27 June 1969; R. GARMS; 3 juveniles cws 23, 22, 19 mm (SMF 6594).- Lofa County, Lofa river, 430 m; 26 June 1969; R. GARMS; 1 f subadult cw 59 mm (SMF 6600).- Lofa County, Garbayea creek, 480 m; 27 June 1969; R. GARMS; 1 f adult cw 69 mm, 1 m subadult cw 36 mm (SMF 6601).- Bong County, Bong Range, waterfall Mount Zaweah (= Za Wea), 160 m; 29 July 1969; R. GARMS; 1 m adult cw 57 mm (SMF 6603).- Lofa County, Toiyah creek near Gorlu, 480 m; 1 m juvenile cw 21 mm (SMF 6606).- Lofa County, Kolahun district; 20 March 1971; R. GARMS; 1 juvenile cw 14 mm (SMF 6610).- Sinoe County, Juarzon district, 130 m, Slaneboe creek; 17 May 1970, R. GARMS; 2 m juveniles cws 14, 12 mm (SMF 6611).- Fulba? August 1908; SCHERER; 1 m juvenile cw 20 mm, 1 f juvenile cw 33 mm; (ZSM 1527/1 (ex 1174/1)).- Millsburg, St. Paul river near Monrovia; SCHERER; 2 m juveniles cws 14, 11 mm (ZSM 1527/2 (ex 1174/3)).- SCHERER; 3 f adults cws 58, 50, 62 (hatchlings), 1 f subadult cw 46 mm, 3 m subadults cws 50, 42, 48 mm (ZSM 1527/3 (ex 1174/4)).- Wreppoosta, 150 km northeast of Monrovia; SCHULTZ-KAMPFHENKEL; 1 m adult cw 65 mm, 3 juveniles cws 33, 256, 14 mm (ZMB 23558).- Nimba County, Mount Nimba; 1 f subadult cw 30 mm (SMF).

Côte-d'Ivoire, B. HOLAS; 1 m adult cw 79 mm, 1 f adult cw 61 mm, 2 juveniles cws 24, 24 mm (SMF 2656).- 2 m adults cws 55, 58 mm, 3 f subadults cws 43, 51, 47 mm, 3 m subadults cws 43, 48, 54 mm; IFAN Dakar; (SMF). For other localities see CUMBERLIDGE (1998, 1999).

Type and distribution

Types (examined).- Ghana, Ashante, Prah river; 1 m, cw 58.5 (NHML 1905.1.17.21-23), lectotype.- Ghana, Ashante, Prah river (NHML 1905.1.17.21-23), syntypes.

Type locality.- Ghana, Ashante, Prah river.

Distribution.- *Liberonautes latidactylus* is a widespread species occurring in an area of West Africa bounded by the Sahara desert and the Atlantic ocean from Sénégal to Ghana. The species has been recorded in the rainforest zone from localities in Sierra Leone, Liberia, Guinea, Côte-d'Ivoire and Ghana, and in the savanna zone from localities in Sénégal, Guinea, Sierra Leone, Liberia and Côte-d'Ivoire (BOTT, 1955, 1959; MONOD, 1977, 1980; CUMBERLIDGE, 1997, 1999; CUMBERLIDGE & SACHS, 1989a, b).

Remarks

Liberonautes latidactylus is the most common and most frequently caught freshwater crab in small streams throughout the rainforest and savanna zones of West Africa. It is also encountered from time to time on land adjacent to streams. During the day these crabs remain inactive, lying hidden under stones or in crevices in the stream bed. At night crabs leave their resting places to feed on dead organic material or on small aquatic animals, such as molluscs, which they find in the creeks. Crabs also eat vegetable matter, and are attracted into traps baited with cassava, palm nuts, or red papaya. Meat, in the form of live or freshly-killed toads or tinned dog food, also attracts crabs into the traps. Occasionally *L. latidactylus* is found on land adjacent to creeks, feeding on the abundant vegetable matter and small invertebrates on the forest floor. *Liberonautes latidactylus* is the predominant second intermediate host of the human lung fluke *Paragonimus uterobilateralis* in Liberia, Guinea (SACHS & VOELKER, 1982), and Côte-d'Ivoire (NOZAIS *et al.*, 1980). This species plays a very important role in the transmission of this parasite to humans. The vernacular name of *L. latidactylus* in Liberia is the common creek crab.

Liberonautes paludicolis CUMBERLIDGE & SACHS, 1989b

fig. 20A, 21A, 22A, 23A, 24A, 25A, 26A, 27D, 28B, 53I, 54-57, 59A, 66B, table IX.

Liberonautes latidactylus paludicolis CUMBERLIDGE & SACHS, 1989b, p. 431-433, fig 1b, table 1.

Redescription

Diagnosis.- The carapace is of medium height (ch/fw 1.11); and the ch is always greater than the fw. The intermediate and epibranchial teeth are small and low. The anterolateral margin behind the epibranchial tooth is raised, but smooth. The ischium of the third maxilliped has a clear vertical sulcus. The terminal article of gonopod 1 is directed inward at a 45° angle to the vertical, the lateral fold of the terminal article is much wider than the medial fold. The propodus of P4 is wide and short (equal to the fw).

Redescription.- The carapace is relatively wide (cw/fw 3.35) and slightly arched (ch/fw 1.11). The front is slightly indented and relatively narrow (about one quarter of the carapace width, fw/cw 0.27). The surface of the carapace is smooth except for a few short granular ridges (carinae) in the epibranchial regions. The semi-circular and urogastric grooves are very deep; the cardiac grooves are faint; the cervical grooves are long and are directed anteriorly and almost meet the postfrontal crest; and the transverse branchial grooves are deep. The mid-groove of the postfrontal crest is short and is not forked at its posterior end. The exorbital angle and the intermediate and epibranchial teeth are small and low. The anterolateral margin behind the epibranchial tooth is raised and smooth, curves inward over the carapace at the posterior end, and it is not continuous with the posterolateral margin. The posterior margin of the carapace is about one third as wide as the carapace. The suborbital, subhepatic, and pterygostomial regions of the sidewall are smooth. The vertical sulcus on the sidewall begins at the base of the intermediate tooth and divides the suborbital region from the hepatic region, so that the sidewall is divided into three parts. The ischium of the third maxilliped has a distinct vertical sulcus. Episternal sulci s4/e4, s5/e5, and s6/e6 are distinct, while s7/e7 is not visible.

The dactylus of the right and left chelipeds is relatively broad (one half the height of the palm), and the upper margin is serrated; the finger is slightly arched and encloses a long interspace; the finger of the propodus is very broad (one half the height of the palm), and the lower margin of the propodus of the cheliped curves downward (and is not indented), making the entire cheliped appear broad. Both fingers of the cheliped have a series of small pointed teeth along their lengths interspersed with three big teeth. The inferior margins of the merus of the chelipeds are faintly granular, with a single large pointed tooth at the distal end; the superior margin has rows of prominent, rough grains. There is a smooth oval surface (the meral tympanum) on the inner surface of the merus of the cheliped. The inner margin of the carpus of the cheliped has two teeth, the first is large and blunt, and is directed forward, the second is small, and there are two small granules behind this tooth. The merus of P5 is long, and is longer than the fw. The propodi of P4 and P5 are short and wide (shorter than the fw), and the anterior and posterior margins of the propodi of P5 are clearly serrated; the dactylus of P4 is long, the dactylus of P5 is very short, the shortest of the walking legs.

The terminal article of gonopod 1 is long (about two thirds as long as the subterminal segment), the longitudinal groove is clearly visible on the ventral and superior sides (but not on the dorsal side); the entire terminal article is directed inward at a 45° angle to the vertical, and is slim, and tapers strongly to the tip which is like a thin pointed stylus; the lateral fold on the terminal article is a little wider and higher than the medial fold.

Size.- The adult size range is from cw 50-74 mm. The carapace proportions are given in table IX. Graphs of carapace dimensions are given in fig. 59A.

Colour

The following description is based on a living adult male from Liberia. The carapace, sternum, abdomen, chelipeds and legs are all uniformly pale brown, pale yellow, or pale orange. The eyestalks are pale orange with black corneas. The third maxillipeds are pale brown and show no colour contrasts; the segments of P2-P5 are orange. Hatchlings recovered from the abdominal brood pouches of two adult females were uniformly orange, indicating that the light colour may be a genetically fixed character rather than a character acquired during ontogeny or through the diet.

Material examined

Liberia, Nimba County, Yeplue creek west of Saniquellie; 4 April 1988; R. SACHS; 1 m cw 51.5 mm, 1 f cw 44.5 mm (NMU 4.IV.1988).- BÜTTIKOFER; 1 m adult cw 52 mm (ZMB 6837).

Côte-d'Ivoire, Mt. Nimba; 25 January 1959, H. LOUDA & R. ROY; 1 M adult (SMF 2262).

Type and distribution

Type.- Liberia, Nimba County, near Saniquellie, Paygweli creek, St. John river basin; 2 April 1988; R. SACHS, J. MOMO & G. DUNCAN; 1 m adult cw 56 mm, 1 f adult cw 56 mm (NMU 2.IV.1988), paratypes.

Type locality.- Bong County, Liberia

Distribution.- *Liberonautes paludicolis* is known only from the rainforest zone of Liberia (see CUMBERLIDGE & SACHS, 1989b for details).

Remarks

Liberonautes paludicolis was originally described by CUMBERLIDGE & SACHS (1989b) as a subspecies of *L. latidactylus*, but is recognised here as a valid species based on the results of a more detailed study undertaken as part of the present revision of the genus.

Ecology.- *Liberonautes paludicolis* is found in or near forest streams, or in low-lying areas of cleared forest which have permanent surface water, such as fish farm excavations, swamp rice farms, and ditches. Crabs also occur in other sites which become inundated with shallow water only during the rainy season (May to October). Crabs spend a good deal of time resting in burrows dug into the banks of streams, swamps, marshy land, or the forest floor. Burrows are usually sited next to, or in the vicinity of water and are usually absent from those parts of the forest where there is no nearby surface water. Swamp crabs have often been encountered crossing the road during daytime rain storms or at night, when they leave their resting places to look for food on the nearby land. Sometimes *L. paludicolis* ventures into streams (as evidenced by the occasional collection of specimens in basket traps set in creeks). The common name of *L. paludicolis* in Liberia is the swamp crab.

Comparisons.- *Liberonautes paludicolis* is closest to *L. latidactylus* and is distinguished from *L. latidactylus* by two main characters: carapace height and colour. The ch of *L. paludicolis* always measures greater than the fw, and the carapace and legs are coloured light brown or light yellow. The relative ch (mean ch/fw 1.11) of *L. paludicolis* is significantly greater ($P < 0.001$) than that of *L. latidactylus* (mean ch/fw 1.00). In most other respects the cheliped and carapace characters of *L. paludicolis* resemble those of *L. latidactylus*. For example, the front width (mean fw/cl 0.44), and the carapace width (mean cw/fw 3.35) of *L. paludicolis* are not significantly ($P > 0.05$) different from those of *L. latidactylus* (where these ratios are 0.44 and 3.36 respectively). The ecology of the swamp crab is distinct from that of *L. latidactylus*, but there is an area of overlap, because the two species are both found in the small streams of the rainforest zone of Liberia (*L. latidactylus* always, *L. paludicolis* occasionally). The swamp crab has only so far been recorded to occur in Liberia. This species is an important second intermediate host to *Paragonimus uterobilateralis* in Liberia and plays an key role in the transmission of the parasite to humans (CUMBERLIDGE & SACHS, 1989b).

Liberonautes nanoides CUMBERLIDGE & SACHS, 1989b

fig. 20B, 21B, 22B, 23B, 24B, 25B, 26B, 27C, 28D, 53K, 54-57, 59B, 66F, table IX.

Liberonautes latidactylus nanoides CUMBERLIDGE & SACHS, 1989b, p. 433-434, fig. 1c, table 1.

Redescription

Diagnosis.- *Liberonautes nanoides* is a small species that matures at body sizes beginning at cw 33 mm. The propodus of the cheliped bears two large teeth. The closed fingers of the cheliped do not touch along their entire length, leaving a wide interspace. The ischium of the third maxilliped is smooth and lacks a vertical sulcus. Episternal sulci s5/e5, and s6/e6 are distinct, s4/e4 is faint and s7/e7 is missing.

Redescription.- The carapace is relatively wide (cw/fw 3.46) and flat (ch/fw 0.99). The front is slightly indented and relatively narrow (about one third of the carapace width, fw/cw 0.30). The surface of the carapace is smooth except for a few short granular ridges (carinae) in the epibranchial regions. The semicircular groove is very deep; the cardiac and urogastric grooves are faint; the cervical grooves are long and are directed laterally toward the anterolateral margins; and the transverse branchial grooves are deep. The mid-groove of the postfrontal crest is short and is not forked at the posterior end. The exorbital angle tooth and the intermediate and epibranchial teeth are small but distinct. The anterolateral margin from the exorbital angle to the region posterior to the epibranchial tooth is edged by a series of small teeth. The posterior margin of the carapace is about one third as wide as the carapace. The suborbital, subhepatic, and pterygostomial regions of the sidewall are smooth. The vertical sulcus on the sidewall begins at the base of the epibranchial tooth and divides the suborbital region from the hepatic region, so that the sidewall is divided into three parts. The ischium of the third maxilliped is smooth and lacks a vertical sulcus. Episternal sulci s5/e5, and s6/e6 are distinct, s4/e4 is faint and s7/e7 is missing.

The dactylus of the right and left chelipeds is relatively broad (one half the height of the palm), and the upper margin is smooth; the finger is arched and encloses an oval interspace; the finger of the propodus is broad (one third the height of the palm), and the lower margin of the propodus of the cheliped is straight and is not indented. Both fingers of the cheliped have a series of small pointed teeth along their lengths interspersed with two big teeth. The inferior margins of the merus of the chelipeds are very granular, with a single large pointed tooth at the distal end followed by a row of smaller teeth; the superior margin has rows of prominent, rough grains. There is a smooth oval surface (the meral tympanum) on the inner surface of the merus of the cheliped. The inner margin of the carpus of the cheliped has two teeth, the first is large, pointed and thin, and is directed forward, the second is smaller, and there are two small teeth behind this tooth. The merus of P5 is short, and is equal to the fw. The propodus of P4 is long and thin (equal to the fw), the propodus of P5 is short and wide, and the anterior and posterior margins of the propodi of P5 are clearly serrated.

The terminal article of gonopod 1 is long (about two thirds as long as the subterminal segment), the longitudinal groove is clearly visible on the ventral and superior sides (but not on the dorsal side); the entire terminal article is directed inward at a 45° angle to the vertical, and is slim, and tapers strongly to the tip which is pointed; and the lateral fold on the terminal article is wider than the medial fold.

Size.- The adult size range is from cw 35-42.5 mm. The carapace proportions are given in table IX. Graphs of carapace dimensions are given in fig. 59B.

Colour

All living specimens of *L. nanoides* from the St. Paul River in Liberia were dark brown-green, and a similar colour to that described for *L. latidactylus*.

Type and distribution

Type.- Liberia, Bong County, St. Paul River, at the Bong Mine Fishing Club near Haindi; 13 December 1988; SACHS, CUMBERLIDGE, MOMO, & DUNCAN; 1 M (holotype), 1 f (paratype) (NMU 13.XII.1988).

Type locality.- Liberia, Bong County, St. Paul River, at the Bong Mine Fishing Club near Haindi.

Distribution.- *Liberonautes nanoides* is known only from the above locality on the St. Paul River, Bong County, Liberia. See CUMBERLIDGE & SACHS (1989b) for details.

Remarks

Liberonautes nanoides was originally described by CUMBERLIDGE & SACHS (1989b) as a subspecies of *L. latidactylus*, but is recognised here as a valid species based on the results of the more detailed study undertaken here as part of the revision of the genus.

Ecology.- Populations of *L. nanoides* are found only in the rocky parts of the fast-flowing waters of the St. Paul river, which during the rainy season was up to 100 m wide and 1-3 m deep at the collecting stations. *Liberonautes nanoides* is found in the major rivers of the rainforest zones of Liberia, and is rarely, if ever, found in small streams. This species has only so far been recorded to occur in Liberia. The dwarf river crab serves as the second intermediate host to *Paragonimus uterobilateralis* in Liberia, but the incidence of infection is low indicating that this species does not play an important role in the transmission of the parasite to humans (CUMBERLIDGE & SACHS, 1989b).

Comparisons.- *Liberonautes nanoides* resembles *L. latidactylus* in colour and relative carapace dimensions, but differences in body size, carapace proportions, and characters of the third maxilliped and cheliped set the two species apart. *Liberonautes nanoides* reaches sexual maturity at a relatively small body size, and the moult of puberty in this species occurs between cw 33-35 mm. This contrasts with that of its larger relatives, where the moult of puberty occurs between cw 52-55 mm. Neither the front width (mean fw/cl 0.44), nor the carapace width (mean cw/fw 3.46) of *L. nanoides* is significantly different ($P > 0.05$) from those of *L. latidactylus* (where these values are 0.44 and 3.36 respectively). *Liberonautes nanoides* lacks a vertical sulcus on the ischium of the third maxilliped, while this sulcus is distinct in *L. latidactylus*.

Liberonautes rubigimanus CUMBERLIDGE & SACHS, 1989b

fig. 20D, 21C, 22C, 23C, 24C, 25C, 26C, 27C, 28C, 29A, 53L, 54-57, 59D, 66C, table IX.

Liberonautes latidactylus rubigimanus CUMBERLIDGE & SACHS, 1989b, p. 434-436, fig. 1d, table 1.

Liberonautes rubigimanus, CUMBERLIDGE, 1999.

Redescription

Diagnosis.- The dactylus of the cheliped of *L. rubigimanus* is flattened and broad (the height of the dactylus is half the width of the palm), while the propodus of the cheliped of adult males is longer than the carapace width. The teeth on both fingers of the dactylus are small, even, and cream coloured. The ventral margin of the propodus of the cheliped is straight, and is not indented. The fingers of the cheliped almost touch when they are closed, and do not leave a space. The front is relatively narrow, about one quarter cw (fw/cw 0.25). The carapace is relatively wide (cw/fw 3.77) and it is moderately high (ch/fw 1.07). The exopod of the third maxilliped always lacks a flagellum. All four episternal sulci (s4/e4, s5/e5, s6/e6, and s7/e7) are missing. The dactylus of the right and left chelipeds is flattened and broad (one half the height of the palm), and the upper margin is smooth; the finger is slightly arched and encloses a long narrow interspace; the finger of the propodus is flattened and broad (one third the height of the palm), and the lower margin of the propodus of the cheliped is straight and is not indented.

Redescription.- The carapace is relatively wide (cw/fw 3.77) and moderately high (ch/fw 1.07). The front is slightly indented and relatively narrow (about one quarter of the carapace width, fw/cw 0.25). The surface of the carapace is smooth all over. The semi-circular groove is very deep; the cardiac and urogastric grooves are very faint; the cervical grooves are deep and long and are directed toward (but do not meet) the postfrontal crest; and the transverse branchial grooves are deep. The mid-groove of the postfrontal crest is short and it is not forked at the posterior end. The exorbital angle tooth and the intermediate and epibranchial teeth are small but distinct. The anterolateral margin is smooth. The posterior margin of the carapace is about one third as wide as the carapace. The suborbital, subhepatic, and pterygostomial regions of the sidewall are granulated. The vertical sulcus on the sidewall begins at the base of the intermediate tooth and divides the suborbital region from the hepatic region, so that the sidewall is in three parts. The ischium of the third maxilliped is smooth and has a deep vertical sulcus. All four episternal sulci (s4/e4, s5/e5, s6/e6, and s7/e7) are missing.

The dactylus of the right and left chelipeds is flattened and broad (one half the height of the palm), and the upper margin is smooth; the finger is slightly arched and encloses a long narrow interspace; the finger of the propodus is flattened and broad (one third the height of the palm), and the lower margin of the propodus of the cheliped is straight and is not indented. Both fingers of the cheliped have a series of small pointed teeth along their lengths interspersed with three big teeth. The inferior margins of the merus of the chelipeds are smooth, with a single large pointed tooth at the distal end; the superior margin has rows of prominent, rough grains. The meral tympanum on the inner surface of the merus of the cheliped is lacking. The inner margin of the carpus of the cheliped has two teeth, the first is large, pointed and thin, and is directed forward, the second is smaller, and there is a small blunt tooth behind this tooth. The merus of P5 is long, and is longer than the fw. The propodus of P4 is long and thin (equal to the fw), the propodus of P5 is short and wide, and the anterior and posterior margins of the propodi of P5 are clearly serrated.

The terminal article of gonopod 1 is long (about two thirds as long as the subterminal segment), the longitudinal groove is clearly visible on the ventral and superior sides (but not on the dorsal side); the entire terminal article is directed inward at a 45° angle to the vertical, and is slim, with long bristles, and tapers strongly to the tip which is pointed; the lateral fold on the terminal article is wider than the medial fold.

Size.- The adult size range is from cw 50-66 mm. The carapace proportions are given in table IX. Graphs of carapace dimensions are given in fig. 59D.

Colour

The following description is based on a living adult male from Liberia. The carapace of *L. rubigimanus* is brick red (deep orange-red). The merus, carpus, propodus, and dactylus of the third maxilliped are pale orange-red, while the ischium and exopod are cream. The walking legs (P2-P5) are pale orange from the ischium to the merus, while the dactyli are red with yellow tips. The flattened fingers (propodus and dactylus) of the chelipeds and the brick red colour gives the claws the appearance of a cooked lobster. The base of the palm of the propodus of the cheliped is cream.

Material examined

Liberia, Margibi County, Gibi District, Mount Gibi, 160 m; 12 June 1969; R. GARMS; 1 f subadult cw 62 mm, 2 juveniles cws 16, 14 mm (SMF 6605).- Margibi County, Sengbe creek, near the waterfall on the slopes of Mount Gibi, this stream is a tributary of the Farmington river; 18 March 1989; SACHS, CUMBERLIDGE, MOMO, & DUNCAN; 4 m, 3 f (NMU 18.III.1989a).- Margibi County, Mount Gibi; 18 March 1989; SACHS, GARMS, MOMO, & DUNCAN; 11 specimens cws 48.5-60.2 mm (NMU 18.III.1989b).- Grand Gedah County, Balloon (Balu?) creek; 20 October 1969; R. GARMS; subadult female cw 60 mm, 1 m adult cw 65 mm, together with *L. latidactylus* (SMF 6590).- Grand Gedah County, Balloon creek; 20 October 1969; R. GARMS; 1 f adult cw 68 mm, together with *L. latidactylus* (SMF 6591).

Guinea. Vallée du Ya, Nimba 600 m, forêt, 30 July 1992**?**; LAMOTTE; 1 m subadult cw 48.9 mm; (MNHN-B 25579).

Type and distribution

Type- Liberia, Margibi County, Sengbe Creek, near the waterfall on the slopes of Mount Gibi, this stream is a tributary of the Farmington river; 23 June 1988; SACHS, CUMBERLIDGE, MOMO, & DUNCAN; 3 m, 1 f (NMU 23.VI.1988), types.

Type locality.- Liberia, Margibi County, Sengbe Creek, near the waterfall on the slopes of Mount Gibi.

Distribution.- *Liberonautes rubigimanus* is known from only three localities: two are in Liberia (Mount Gibi, Margibi County, and Balloon creek, Grand Gedah County) and one is in Guinea (Mount Nimba) (CUMBERLIDGE, 1999).

Remarks

Liberonautes rubigimanus was originally described by CUMBERLIDGE & SACHS (1989b) as a subspecies of *L. latidactylus*, but is recognised here as a valid species based on the results of the more detailed study undertaken here as part of the revision of the genus.

Ecology.- *Liberonautes rubigimanus* is found in fast-flowing mountain streams in Liberia (Mount Gibi) and Guinea (Mount Nimba), and at lower elevations in forest streams in Grand Gedah County, Liberia. The specimen from Mount Nimba was collected in forest at 600 m altitude. This is a large species, with an adult size range between cw 62-75 mm. This species is sympatric with *L. latidactylus* and *L. paludicolis*. The common name for *L. rubigimanus* in Liberia is the lobster claw crab.

Comments.- The scarcity of available specimens of *L. rubigimanus* means that the tests of significance reported here may lack accuracy. Nevertheless, these tests have been carried out, but their limitations must be bourne in mind. The front width of *L. rubigimanus* (mean fw/cl 0.41) measures less than the carapace height, and is significantly shorter ($P < 0.001$) than that of *L. latidactylus* (mean fw/cl 0.44). The status of *L. rubigimanus* as a host of *Paragonimus* is at present unknown. No metacercariae of *P. uterobilateralis* have ever been recovered from any specimens of *L. rubigimanus*, although only a few individuals have been examined so far (CUMBERLIDGE & SACHS, 1989b). It is possible that this species may host the parasite, since specimens from the same locality as the type material could have been found to be infected (VOELKER, 1973), for at that time all freshwater crabs from Liberia were identified simply as *L. latidactylus*.

Liberonautes nimba CUMBERLIDGE, 1999

fig. 20E, 21E, 22E, 23E, 28G, 24E, 25E, 26E, 27F, 29B, 53M, 54-57, 59E, 66D, table IX.

Liberonautes nimba CUMBERLIDGE, 1999, fig. 1, pl. 1.

Description

Diagnosis.- The terminal article of gonopod 1 is straight and is directed inward at a 45° angle to the longitudinal axis of the gonopod, and is wide and tube-like, tapering strongly to a rounded tip which has a conspicuous apical opening. The exorbital angle is low and is continuous with the anterolateral margin and the intermediate and epibranchial teeth are small and low. The carapace height is approximately equal to the front width. The dactylus and propodus of the major cheliped are curved and slim and the lower margin of the propodus of the cheliped is indented. The ischium of the third maxilliped has a distinct vertical sulcus. None of the episternal sulci (s4/e4-s7/e7) are visible.

For a detailed description see CUMBERLIDGE (1999)

Size.- This is a small species with an adult size range between cw 20 and 24.5 mm. The carapace proportions are given in table IX. Graphs of carapace dimensions are given in fig. 59E.

Material examined

West Africa, Guinea, Mt. Nimba 1600 m, camp III; 29 April 1962; LAMOTTE; 2 m adults cw 24.3 mm, 21.4 mm (MNHN-B 25581).- Mt. Nimba 1300 m; 22 August 1992; 1 f adult cw 17.4 mm (MNHN-B 25582).- Mt. Nimba; LAMOTTE; 1 m juvenile cw 11.8 mm, MNHN-B 25588.- Mt. Nimba; LAMOTTE; 1 m adult cw 19.5 mm (MNHN-B 25589).- Mt. Nimba; LAMOTTE; 1 m adult cw 21.1 mm (SMF 2663).

Type and distribution

Types (examined).- West Africa, Guinea, Mt. Nimba, altitude 1580 m, fissures in rocks; 7-8 May 1960; VOGELI; 1 m adult cw 24.1 mm (MNHN-B 25580) holotype; Mt. Nimba 1580 m, fissures in rocks; 7-8 May 1960; VOGELI; 1 f subadult cw 19.2 mm; (MNHN-B 25587), paratype; Mt. Nimba 1580 m, fissures in rocks; 7-8 May 1960; VOGELI; 1 m 18.6 mm, 1 f adult cw 20.1 mm, 1 juvenile cw 10.9 mm; (SMF) all paratypes.

Type locality.- West Africa, Guinea, Mt. Nimba, altitude 1580 m.

Distribution.- *Liberonautes nimba* is known only from the slopes of Mount Nimba in Guinea.

Remarks

Mount Nimba reaches 1752 m at its summit and is second only in altitude to the highest peak of the Loma mountains (1850 m). The vegetation cover on the slopes of Mount Nimba includes lowland forest and savanna (up to altitudes of 500 m), high evergreen forest (from 900-1200 m), and high altitude grassland (above 1200 mm). Species diversity for many groups of animals and plants on Mount Nimba is exceptionally high, and this mountain range is known to support a large number of endemic species (CURRY-LINDHAL & LAMOTTE 1964; LAMOTTE 1983). *Liberonautes nimba* was collected in cracks in rocks in high altitude grassland, above the upper limit of montane forest. This species may therefore be semi-terrestrial in habit.

Comparisons.- *Liberonautes nimba* is distinguished from the other species in the genus as follows. *Liberonautes nimba* is the smallest species of *Liberonautes* with an adult size range from cw 20 to 24.5 mm: specimens of most other species in the genus measuring cw 24.5 mm would not be adult (except for *L. lugbe*, which can be distinguished from *L. nimba* by the lack of a flagellum on the exopod of the third maxilliped in the former species). *Liberonautes nimba* is most likely to be confused with *L. nanoides*, the other small species found in Liberia. Any specimens measuring more than 30 mm across the carapace would most likely belong to *L. nanoides*, rather than to *L. nimba*. *Liberonautes nimba* can be further distinguished from *L. nanoides* by the body size at maturity: specimens of *L. nimba* measuring 20 mm across the carapace could be adult, whereas specimens of *L. nanoides* of this size would be juvenile or subadult. In addition, the tip of the terminal article of gonopod 1 of *L. nimba* is wide, straight and tube like, whereas that of *L. nanoides* is a thin pointed stylus. Finally, episternal sulci s4/e4, s5/e5, s6/e6 of *L. nimba* are completely absent, whereas these sulci in *L. nanoides* are all clearly visible.

Characters of the carapace of *L. nimba* are similar to those of *L. latidactylus*, and small specimens of the latter species may be confused with *L. nimba*. As a rule, any specimens measuring more than 30 mm across the carapace would most likely belong to *L. latidactylus*, rather than to *L. nimba*. *Liberonautes nimba* can also be distinguished from *L. latidactylus* by body size at maturity: specimens of *L. latidactylus* in the adult size range of *L. nimba* (cw 20-24.5 mm) would all be clearly juvenile. In addition, the tip of the terminal article of gonopod 1 of *L. nimba* is wide and tube-like, whereas that of *L. latidactylus* is a thin pointed stylus. While the front width and the carapace height of both *L. nanoides* and *L. latidactylus* are approximately equal, the carapace of *L. nimba* is distinctly higher (ch/fw 1.10) than that of *L. latidactylus* (ch/fw 1.00), and the front of *L. nimba* is distinctly wider (fw/cl 0.50) than that of *L. latidactylus* (fw/cl 0.44). Finally, s6/e6 of *L. nimba* is missing, whereas this sulcus is clearly marked in *L. latidactylus*.

Liberonautes grandbassa n. sp.

fig. 20G, 21G, 22G, 23G, 24G, 25G, 26G, 27H, 29C, 53O, 54-57, 59G, 66F, table IX.

Description

Diagnosis.- The terminal article of gonopod 1 curves inward at a 45° angle to the longitudinal axis of the gonopod, and is narrow and needle-like, tapering strongly to a pointed tip. At the junction between the two distal segments of gonopod 1 there is a sulcus on the ventral face and a broad membrane on the dorsal face. The exorbital angle is produced into a small tooth; the intermediate tooth is small and pointed, and the epibranchial tooth is a small granule. The carapace is high and arched (the ch is greater than the front width, ch/fw 1.15). The dactylus and propodus of the major cheliped are highly curved and broad with overlapping tips, and the lower margin of the propodus of the cheliped is clearly indented. The ischium of the third maxilliped has a clear vertical sulcus; the exopod of the third maxilliped has a long flagellum. Sternal sulcus s1/s2 is small but distinct. Episternal sulci s4/e4-s6/e6 are clearly visible; s7/e7 is not visible.

Description.- The carapace is less than one and a half times as wide as long (cw/cl 1.44), and the carapace is high and arched (ch/fw 1.15). The front is slightly indented, and measures between one third and one quarter of the carapace width (fw/cw 0.30). The branchial region of the carapace has rows of carinae, and the rest of the surface of the carapace is smooth. The semi-circular, urogastric, cardiac, cervical, and transverse branchial grooves are deep and distinct. The postfrontal crest is prominent and is almost straight, and consists of fused epigastric and postorbital crests; it does not span the entire carapace because the lateral ends fade out before meeting the anterolateral margins; the mid-groove of the postfrontal crest is short and forked. The exorbital angle is produced into a small tooth; the intermediate tooth is small and pointed, and the epibranchial tooth is a small granule. The anterolateral margin posterior to the epibranchial tooth is raised, and is marked by a line of small granules; the posterior end of the anterolateral margin curves inward over the surface of the carapace and is not continuous with the posterolateral margin. The posterior margin of the carapace is a little wider than the front, about one third as wide as the carapace. The suborbital, pterygostomial and subhepatic regions of the sidewall are smooth. Each sidewall is divided into three parts by the epimeral sulcus and the vertical sulcus: the latter is straight and is clearly aligned to meet with the base of the intermediate tooth, but the tip curves back to meet the epibranchial tooth. The ischium of the third maxilliped is as wide as the merus, and the ischium has a clear vertical sulcus; the exopod of the third maxilliped is longer than the ischium, reaching to halfway along the merus; the exopod of the third maxilliped has a long flagellum.

Sternal sulcus 1 (s1/s2) is short but distinct; sternal sulcus 2 (s2/s3) is deep, straight, and completely crosses the sternum; sternal sulcus 3 (s3/s4) is reduced to two short notches at its lateral ends. Episternal sulci s4/e4-s6/e6 are clearly visible; s7/e7 is not visible.

The chelipeds are unequal, the major (left) is longer and higher than the minor. The dactylus of the major cheliped is broad (it is one third as high as the palm), the upper margin is smooth, the finger is arched and encloses a long interspace; the finger of the propodus is broad (one third the height of the palm) and the lower margin of the propodus of the cheliped is almost straight, with only a small curved indentation, and is faintly serrated. The dactylus of the minor cheliped is relatively slim (its width is one quarter the height of the palm), the upper margin is faintly serrated, the finger is slightly arched enclosing a long interspace. Both fingers of the cheliped have two small pointed teeth along their lengths interspersed with several larger teeth. The first carpal tooth on the inner margin of the carpus of the cheliped is large and pointed, the second carpal tooth is low and blunt, and behind this there are a few small granules. The lateral inferior margin of the merus of the cheliped is smooth, the medial inferior margin of the merus has a row of small raised granules, and there is a single larger granule at the distal end; the superior margin of the merus of the cheliped has a row of small raised granules. There is a large, smooth, oval-shaped meral tympanum on the inner face of the merus of P1. P2-P5 are smooth with a slightly serrated superior margin. The merus of P5 is longer than the fw. The propodus of P4 is long and thin, the propodus of P5 is short and wide, and the anterior and posterior margins of propodus of P5 are slightly serrated.

Abdominal segments a1-a6 are four sided; a7 (the telson) is triangular, with a rounded distal margin; a3 is broadest, a3-a7 form a slim triangle with indented sides, which tapers towards the telson. The terminal article of gonopod 1 is long (about two thirds as long as the subterminal segment), and is distinctly curved, tapering gradually so that the distal part is long and narrow; the lateral and medial folds on the terminal article are both narrow and low; there is a longitudinal groove on the ventral face which is not visible on the dorsal face; the entire terminal article is directed inward. The subterminal segment of gonopod 1 is long and slim; the lateral margin has a distinct inward curve, and the base is very broad. Gonopod 2 is longer than gonopod 1, and the difference in length is due to the long flagellum of the terminal article of gonopod 2, which is almost as long as the subterminal segment. The subterminal segment of gonopod 2 is as long as the subterminal segment of gonopod 1.

Size: The species is known only from two adults (cw 31.3 and 31.4 mm). The carapace proportions are given in table IX. Graphs of carapace dimensions are given in Fig 59G.

Type and distribution

Type.- Liberia, Grand Bassa County, Weeni creek; 4 August 1988; George DUNCAN; 1 m adult, cw 31.4 (NMU 4.VIII.1988), is designated here as the holotype.- Grand Bassa County, Weeni creek; 4 August 1988; George DUNCAN; 1 f adult, cw 31.3 (NMU 4.VIII.1988), is designated here as the paratype.

Type locality.- West Africa, Liberia, Grand Bassa County, Weeni creek.

Distribution.- *Liberonautes grandbassa* is known only from Grand Bassa County in Liberia.

Etymology.- The species is named for Grand Bassa County in Liberia, where it was first collected. The species name *grandbassa* is a noun in apposition.

Remarks

Liberonautes grandbassa is assigned to the genus *Liberonautes* on the basis of the following characters. The terminal article of gonopod 1 is long and curves inward; the terminal article of gonopod 2 is a long flagellum; the postfrontal crest is incomplete and does not meet the anterolateral margins; there is an intermediate tooth on the anterolateral margin between the epibranchial tooth and the exorbital angle; each sidewall is divided into three parts by the epimeral and vertical sulci; the mandibular palp has two segments and the terminal article is a single, undivided lobe, with a small hard hair-fringed flap at the junction between the segments; sternal sulcus 2 (s2/s3) is deep, straight, and completely crosses the sternum; sternal sulcus 3 (s3/s4) is represented only by two short notches at the lateral ends; and episternal sulcus s7/e7 is missing.

Comparisons.- *Liberonautes grandbassa* is most similar to the other small species of the genus (*L. nanoides*, *L. nimba*, and *L. lugbe*). *Liberonautes grandbassa* can be distinguished from *L. nimba* and *L. lugbe* by the body size at maturity. *Liberonautes nimba* and *L. lugbe* are the smallest species of *Liberonautes*, with an adult size range from cw 20-24.5 mm: specimens of all other species in the genus (including *L. nanoides* and *L. grandbassa*) measuring cw 25 mm would not be adult. *Liberonautes grandbassa* is distinguished from *L. lugbe* by the exopod of the third maxilliped: *L. grandbassa* has a flagellum on the exopod, while *L. lugbe* lacks a flagellum. In addition, in *L. grandbassa* episternal sulci s4/e4, s5/e5, and s6/e6 are all clearly marked and visible; in *L. lugbe* these sulci are all faint and incomplete. The first carpal tooth of the carpus of the cheliped is large and pointed in *L. grandbassa* whereas in *L. lugbe* it is small, blunt and low. *Liberonautes grandbassa* is distinguished from *L. nimba* by the anterolateral margin: the posterior end curves inward and is not continuous with the posterolateral margin in *L. grandbassa*, whereas in *L. nimba* the anterolateral margin does not curve inward and is continuous with the posterolateral margin. In addition, in *L. grandbassa* episternal sulci s4/e4, s5/e5, and s6/e6 are all clearly marked and visible, whereas in *L. nimba* these sulci are all completely absent. The first carpal tooth of the carpus of the cheliped is large and pointed in *L. grandbassa* whereas in *L. nimba* it is small, blunt and low. *Liberonautes grandbassa* is distinguished from *L. nanoides* by the carapace height: the carapace height is greater than the front width in *L. grandbassa*, whereas the carapace height is equal to the front width in *L. nanoides*.

Liberonautes lugbe n. sp.

fig. 20H, 21H, 22H, 23H, 24H, 25H, 26H, 27G, 29D, 53N, 54-57, 59H, 66D, table IX.

Description

Diagnosis.- The terminal article of gonopod 1 is directed inward at a 45° angle to the longitudinal axis of the gonopod, and is narrow and needle-like, tapering strongly to a pointed tip. At the junction between the two distal segments of gonopod 1 there is a sulcus on the ventral face and a broad membrane on the dorsal face. The exorbital angle and the intermediate tooth are small and pointed, and the epibranchial tooth is small but is a distinct tooth. The carapace is moderately high (ch/fw 1.05). The dactylus and propodus of the major cheliped are highly curved and broad with overlapping tips, and the lower margin of the propodus of the cheliped is only slightly indented. The ischium of the third maxilliped has a clear vertical sulcus; the exopod of the third maxilliped lacks a flagellum. Sternal sulcus s1/s2 is small but distinct. Episternal sulci s4/e4-s6/e6 only partly cross the junction; s7/e7 is not visible.

Description.- The carapace is transversely oval about one and a half times as wide as long (cw/cl 1.51), and is moderately high; the carapace height is approximately equal to the front width (ch/fw 1.05). The front is slightly indented, and is not narrow, measuring between one-third and one quarter of the carapace width (fw/cw 0.29). Both the epibranchial and the branchial regions of the carapace have rows of carinae, the rest of the surface of the carapace is smooth. The semi-circular, urogastric, cardiac, the cervical, and transverse branchial grooves are deep and clearly visible. The postfrontal crest is prominent and almost straight, and consists of fused epigastric and postorbital crests; it does not span the entire carapace because the lateral ends fade out in the fields of carinae before meeting the anterolateral margins; the mid-groove on the postfrontal crest is short and forked. The exorbital angle and the intermediate tooth are small and pointed, and the epibranchial tooth is small, but distinct. The anterolateral margin posterior to the epibranchial tooth is raised, and is marked by a line of small granules; the anterolateral margin curves inward over the carapace at its posterior end and is not continuous with the posterolateral margin. The posterior margin of the carapace is a little wider than the front, about one third as wide as the carapace. The suborbital, pterygostomial and subhepatic regions of the sidewall are smooth. Each sidewall is divided into three parts by the epimeral sulcus and the vertical sulcus: the latter running between the base of the epibranchial tooth and the epimeral sulcus. The ischium of the third maxilliped is as wide as the merus, and the ischium has a clear vertical sulcus; the exopod of the third maxilliped is longer than the ischium, reaching to halfway along the merus; the exopod of the third maxilliped lacks a flagellum. The mandibular palp has two segments with a single, undivided terminal segment which has a small hard, hair-fringed flap-like anterior process at the junction between the segments.

Sternal sulcus 1 (s1/s2) is short but distinct; sternal sulcus 2 (s2/s3) is deep, straight, and completely crosses the sternum; sternal sulcus 3 (s3/s4) is reduced to two short notches at the lateral ends. Episternal sulci s4/e4-s6/e6 are clearly visible; s7/e7 is not visible.

The chelipeds are unequal; the major (left) is longer and higher than the minor. The dactylus of the major cheliped is broad (its width is one third the height of the palm), the upper margin is smooth, the dactylus is arched and encloses a wide interspace; the finger of the propodus is broad (one third the height of the palm), the lower margin of the propodus of the cheliped is almost straight, with only a small curved indentation, and is faintly serrated. The dactylus of the minor cheliped is relatively slim (its width is one quarter the height of the palm), the upper margin is faintly serrated, the finger is slightly arched enclosing a long interspace. Both fingers of the cheliped have two small pointed teeth along their lengths interspersed with several larger teeth. The first carpal tooth on the inner margin of the carpus of the cheliped is small and blunt, and is directed forward, the second carpal tooth is very small, not much larger than the row of small granules behind it. Both the lateral and medial inferior margins of the merus of the cheliped have a row of small pointed granules and there is a single large conical tooth at the distal end; the superior margin of the merus of the cheliped has a row of small raised granules. There is a large, smooth, oval-shaped meral tympanum on the inner face of the merus of P1. P2-P5 are smooth and have slightly serrated superior margins. The merus of P5 is the same length as the fw. The propodus of P4 is long and thin, the propodus of P5 is short and wide, and the anterior and posterior margins of propodus of P5 are slightly serrated.

Abdominal segments a1-a6 are four sided; a7 (the telson) is triangular, with a rounded distal margin; a3 is broadest, a3-a7 form a slim triangle with indented sides, which tapers towards the telson. The terminal article of gonopod 1 is long (about two thirds as long as the subterminal segment), and is distinctly curved, tapering gradually so that the distal part is long and narrow; the lateral and medial folds on the terminal article are both narrow and low; there is a longitudinal groove on the ventral face which is not visible on the dorsal face; the entire terminal article is directed inward. The subterminal segment of gonopod 1 is long and slim; the lateral margin has a distinct inward curve, and the base is very broad. Gonopod 2 is longer than gonopod 1, and the difference in length is due to the long flagellum of the terminal article of gonopod 2, which is almost as long as the subterminal segment. The subterminal segment of gonopod 2 is as long as the subterminal segment of gonopod 1.

Size.- The species is known only from two adults (cw 22.7 and 23.2 mm). The carapace proportions are given in table IX. Graphs of carapace dimensions are given in fig. 59H.

Type and distribution

Type.- Liberia, Nimba County, from farmland near Lugbe; 20 July 1988; Paye BELLAH; 1 m adult, cw 22.7 (NMU 20.VII.1988), is designated here as the holotype.- Nimba County, from farmland near Lugbe; 20 July 1988; Paye BELLAH; 1 f adult, cw 23.2 (NMU 20.VII.1988), is designated here as the paratype.

Type locality.- West Africa, Liberia, Nimba County, from farmland near Lugbe.

Distribution.- *Liberonautes lugbe* is known only from Lugbe in Nimba County in Liberia. The specimens were captured by hand out of the water, when the crabs were walking on land close to a stream.

Etymology.- The species is named for the village of Lugbe (sometimes spelled "Lugbai") in Nimba County in Liberia, where it was first collected. The species name *lugbe* is a noun in apposition.

Remarks

Comparisons.- *Liberonautes lugbe* is most similar to the other small species of the genus (*L. nimba*, *L. grandbassa* and *L. nanoides*). *Liberonautes lugbe* is distinguished from *L. nimba* and *L. grandbassa* by its body size at maturity. *Liberonautes nimba* and *L. lugbe* are the smallest species of *Liberonautes* with an adult size range from cw 20-24.5 mm: specimens of all other species in the genus (including *L. nanoides* and *L. grandbassa*) measuring cw 25 mm would not be adult. *Liberonautes lugbe* is distinguished from *L. grandbassa* by the exopod of the third maxilliped: *L. grandbassa* has a flagellum on the exopod, while *L. lugbe* lacks a flagellum. In addition, in *L. grandbassa* episternal sulci s4/e4, s5/e5, and s6/e6 are all clearly marked and visible; in *L. lugbe* these sulci are all faint and incomplete. The first carpal tooth of the carpus of the cheliped is large and pointed in *L. grandbassa* whereas in *L. lugbe* it is small, blunt and low. *Liberonautes lugbe* is distinguished from *L. nimba* by the anterolateral margin of the carapace: the posterior end curves inward and is not continuous with the posterolateral margin in *L. lugbe*, whereas in *L. nimba* the anterolateral margin does not curve inward and is continuous with the posterolateral margin. In addition, in *L. lugbe* episternal sulci s4/e4, s5/e5, and s6/e6 are all faint and incomplete, whereas in *L. nimba* these sulci are all completely absent. *Liberonautes grandbassa* is distinguished from *L. nanoides* by the carapace height: the carapace height is greater than the front width in *L. lugbe*, whereas the carapace height of *L. nanoides* is equal to the front width.

Sudanonautes Bott, 1955

fig. 64B

Sudanonautes Bott, 1955: 295.

There is an intermediate tooth on the anterolateral margin between the epibranchial tooth and the exorbital angle tooth. The postfrontal crest is prominent, almost horizontal, and complete (the lateral ends meet the anterolateral margins). The sidewall is divided by two sulci into three parts. The mandibular palp has two segments; the terminal segment consists of a large oval posterior lobe (in three species there is a small but distinct anterior process at the junction between the segments). There is a long, plumose flagellum on the exopod of the third maxilliped in all species. Sternal sulcus s3/s4 is represented only by two short notches at the sides of the sternum. The terminal article of gonopod 1 is very long (at least two-thirds as long as the subterminal segment, and even longer in some species). The terminal article of gonopod 1 curves outward and the curvature begins half way along the segment. The medial and lateral folds on the ventral side of the terminal article of gonopod 1 are low and of equal size; they are separated lengthways by the distinct longitudinal groove. The terminal article is either slim and needle-like (where the longitudinal groove is not visible) or broadened in the middle (which is the result of a higher medial fold), where the longitudinal groove is visible at least for part of its length. The dorsal side of the terminal article of gonopod 1 is smooth, and there is a broad membrane (the dorsal membrane) at the junction between the two distal segments. The subterminal segment of gonopod 1 is either a long, slim rectangle (in some species) or it is broadened significantly at the base (in other species). The terminal article of gonopod 2 is very short (one fifteenth the length of the subterminal segment).

Type species.- *Thelphusa africana* A. Milne-Edwards, 1869; by original designation, juvenile male.

Distribution

The genus is present in Côte-d'Ivoire, Ghana, Togo, Benin, Nigeria, Cameroon, Gabon, Bioko (Fernando Po), Central African Republic, Congo, Democratic Republic of Congo, northern Angola, and southwest Sudan. The ten species of *Sudanonautes* are found in the inland waters of West and Central Africa in a region bounded by Côte-d'Ivoire, southwest Sudan, and northern Angola. This area includes the Upper Guinea rainforests, the Lower Guinea forest together with the savannas of the eastern part of West Africa, and the offshore island of Bioko. Species of *Sudanonautes* comprise the dominant element of the freshwater crab fauna in the rivers and streams from Côte-d'Ivoire to Cameroon; here seven species occur (*S. africanus* (A. MILNE-EDWARDS, 1869), *S. aubryi* (H. MILNE EDWARDS, 1853), *S. floweri* (DE MAN, 1901), *S. granulatus* (BALSS, 1929), *S. monodi* (BALSS, 1929), *S. kagoroensis* CUMBERLIDGE, 1991, and *S. nigeria* n. sp.). In other parts of the range of this genus in Central Africa (in an area bounded by the Republic of the Congo, Gabon, Democratic Republic of Congo, northern Angola, and south-western Sudan) species of *Sudanonautes* share the rivers and forests with species of *Potamonautes*, *Potamonemus*, and *Louisea*. This region includes five species of *Sudanonautes*: *S. africanus*, *S. aubryi*, *S. floweri*, *S. chavanesii* (A. MILNE-EDWARDS, 1886) and *S. faradjensis* (RATHBUN, 1921). *Sudanonautes* is absent from the western part of West Africa (from Liberia to Sénégal) where the predominant species of freshwater crabs belong to *Liberonautes*. Some species of *Sudanonautes* are found exclusively in rainforest habitats (*S. africanus*, *S. granulatus*, *S. orthostylis* BOTT, 1955, *S. chavanesii*, *S. nigeria* and *S. faradjensis*) while others are found in both rainforest and woodland savanna (*S. aubryi* and *S. floweri*). One species (*S. kagoroensis*) occurs only in woodland savanna, while the semi-terrestrial air-breathing *S. monodi* is the only species found in both woodland savanna and in dry sudan savanna. Those species found in rainforest habitats divide the available niches between the lowland streams (*S. africanus*, *S. granulatus*, *S. orthostylis*, and *S. aubryi*), the mountain streams (*S. granulatus*), the surface water sources (*S. floweri*, *S. aubryi*, and *S. nigeria*), and the major rivers (*S. africanus*, *S. chavanesii* and *S. faradjensis*). In the savanna regions *S. floweri*, *S. aubryi*, and *S. monodi* live in temporary aquatic habitats during the rainy season, and dig burrows down to the water table in the dry season. *Sudanonautes kagoroensis* lives in streams in the guinea savanna region associated with the Jos plateau in central Nigeria.

Remarks

The first three species of *Sudanonautes* to be described were *S. aubryi* and *S. africanus* from Gabon, and *S. chavanesii* from the Congo. In the early 20th Century a further three species were added, these were *S. floweri* from the Sudan, *S. faradjensis* from Democratic Republic of Congo, and *S. granulatus* and *S. monodi* from Cameroon. More recently, three other species have been described, these are *S. orthostylis* from Cameroon, and *S. kagoroensis* and *S. nigeria* from Nigeria.

When Bott (1955) established the genus *Sudanonautes* (type species by original designation, *Thelphusa africana* A. Milne-Edwards, 1869), he recognised two subgenera, *Sudanonautes* s. str., and *Convexonautes* Bott, 1955 (type species by original designation, *Thelphusa aubryi* H. Milne Edwards, 1853). The genus as first conceived by Bott (1955) included eight taxa assigned to two subgenera and three species: *S.* (*S.*) *africanus*, *S.* (*S.*) *d. decazei* (A. Milne-Edwards, 1886), and *S.* (*C.*) *aubryi*, and five subspecies: *S.* (*S.*) *africanus chaperi*, *S.* (*S.*) *a. chavanesii*, *S.* (*S.*) *decazei orthostylis*, *S.* (*C.*) *aubryi floweri*, and *S.* (*C.*) *a. monodi*. Bott (1955) included in synonymy a further four taxa: *P.* (*P.*) *faradjensis*, *P.* (*P.*) *pobeguini* Rathbun, 1904, *P.* (*P.*) *regnieri* Rathbun, 1904, and *P.* (*P.*) *decazei granulata*.

Bott (1964) later judged *S.* (*S.*) *d. decazei* to be a synonym of *S.* (*S.*) *p. pelii* (Herklots, 1861) and the latter became the prioritised name. Thus, according to Bott (1955, 1964) *Sudanonautes* included three species: *S.* (*S.*) *africanus*, *S.* (*S.*) *pelii*, and *S.* (*C.*) *aubryi*. However, *S.* (*S.*) *decazei orthostylis* was not accounted for when Bott (1964) synonymized *S.* (*S.*) *decazei* with *S.* (*S.*) *pelii*. This rather confusing and inconsistent version of the taxonomy of the genus (*S.* (*S.*) *a. africanus*, *S.* (*S.*) *a. chaperi*, *S.* (*S.*) *a. chavanesii*, *S.* (*S.*) *p. pelii*, *S.* (*C.*) *aubryi aubryi*, *S.* (*C.*) *a. floweri*, and *S.* (*C.*) *a. monodi*) was adopted by Monod (1977, 1980). Until recently the works of Bott (1955, 1959, 1964) and Monod (1977, 1980) provided the only identification keys for this genus. Subsequent contributions to the taxonomy of the genus (Cumberlidge, 1991a, 1993b,c, 1994b, 1995a,b,c,d, present work) have now raised the number of valid species in the genus from three to ten. Two of Bott's (1955) species, *S. aubryi* and *S. africanus*, have been recognised but each has been completely redescribed (Cumberlidge, 1994b, 1995a). Two new species (*S. kagoroensis* and *S. nigeria*) have since been added, and four of Bott's subspecies, *orthostylis*, *chavanesii*, *floweri*, and *monodi*, have been recognised as valid species (Cumberlidge, 1993c, 1995b,c, present work). Two other species (*S. granulatus* and *S. faradjensis*) which Bott (1955) suppressed as junior synonyms have since been recognised as valid species (Cumberlidge, 1993b; 1995d). In summary, the number of species in *Sudanonautes* has been increased from three to ten, and none of Bott's (1955) five subspecies are recognised. In addition, Bott's division of the genus into two subgenera for three species is inconsistent with the new data and has been omitted from this revision.

Ecology.- Species of *Sudanonautes* show distinct ecological preferences in their distribution. For example, crabs collected in the rainforest zone of West Africa are likely to belong to *S. granula-*

tus, *S. floweri*, *S. orthostylis*, *S. africanus*, *S. chavanesii*, *S. aubryi*, or *S. faradjensis*. Crabs collected in the guinea savanna zone are likely to belong to *S. kagoroensis*, *S. aubryi*, *S. monodi*, or *S. floweri*, while crabs collected in the sudan savanna zone are likely to belong to *S. monodi* or *S. aubryi*.

Colour

The colour of live specimens offers a useful means of distinguishing between the species of *Sudanonautes* in the field. The dorsal carapace of male adult *S. kagoroensis* is dark brown with dull yellow patches, and the postfrontal crest is also dark brown. *Sudanonautes kagoroensis* is clearly distinguished from *S. aubryi*, *S. floweri* and *S. monodi* which all have a uniformly red-brown carapace with a contrasting yellow postfrontal crest. Both *S. kagoroensis* and *S. granulatus* have a dark carapace, but the two taxa can be distinguished by the colour of the major cheliped: it is brick-red yellow in *S. granulatus* but dull brown in the former species. In *S. kagoroensis* the arthrodial membranes between the sternum and coxae of the walking legs, and between the dactylus and the index of the cheliped is brown-yellow while in *S. granulatus* these membranes are brick-red-yellow. Furthermore, the carapace of both *S. africanus* and *S. aubryi* is uniformly dark green-brown, and lacks patches of yellow colour as seen in *S. kagoroensis*, and the arthrodial membrane of *S. africanus* and of *S. aubryi* is crimson, while that of *S. kagoroensis* is a dull yellow.

Key to the species of *Sudanonautes*

1. The median fold of the terminal article of gonopod 1 is higher than the lateral fold, and the longitudinal groove is clearly visible; the intermediate tooth on the anterolateral margin is reduced to an inconspicuous notch 7
- The median fold of the terminal article of gonopod 1 is the same size as the lateral fold (both are low); the segment is slim and needle-like, and the longitudinal groove is faint or not detectable; the intermediate tooth on the anterolateral margin is large and triangular. 2
2. There is a row of sharp teeth on the anterolateral margin behind the epibranchial tooth. *S. faradjensis*
- The anterolateral margin behind the epibranchial tooth is smooth. 3
3. The epibranchial tooth is large, triangular and pointed, and is directed outward; the distance between the epibranchial tooth and the intermediate tooth is twice the distance between the

intermediate tooth and the exorbital angle tooth. *S. chavanesii*

- The epibranchial tooth is small and blunt, and points forward; it is positioned in line with the mid groove of the postfrontal crest, so that the distance between the epibranchial tooth and the intermediate tooth is the same as the distance between the intermediate and the exorbital angle tooth 4

4. Much of the surface of the carapace is granular and warty; the carapace is very flat (ch/fw <1.10). *S. africanus*

- The surface of the carapace is smooth; the carapace is of medium height or it is high and arched (ch/fw >1.11). 5

5. The postfrontal crest always meets the anterolateral margins at the epibranchial teeth. 6

- The postfrontal crest always meets the anterolateral margins behind the epibranchial teeth. *S. aubryi*

6. The vertical sulcus on the sidewall meets the anterolateral margin at the intermediate tooth. *S. nigeria*

- The vertical sulcus on the sidewall meets the anterolateral margin at the epibranchial tooth. *S. orthostylis*

7. The longitudinal groove on the terminal article of gonopod 1 fades out one-third of the distance along the segment; the subterminal segment of gonopod 1 is slim, and tapers to the junction with terminal article. *S. kagoroensis*

- The longitudinal groove on the terminal article of gonopod 1 fades out two-thirds of the distance along the segment; the subterminal segment of gonopod 1 is distinctly widened, and is broad at the junction with the terminal article. 8

8. The medial fold of the terminal article of gonopod 1 is wider than the lateral fold. *S. monodi*

- The medial fold of the terminal article of gonopod 1 is not wider than the lateral fold. 9

9. There is a small hard anterior process on the mandibular palp at the junction between the two segments; there are conspicuous raised ridges on the sternum at the points where the chelipeds insert. *S. floweri*

- There is no small hard anterior process on the mandibular palp at the junction between the two segments; there are no raised ridges on the sternum at the points where the chelipeds insert. *S. granulatus*

Sudanonautes aubryi (H. MILNE EDWARDS, 1853)

fig. 30A, 32A, 33A, 34A, 35D, 36H, 37D, 38A, 53Q, 54-57, 60A, 67B, table IX.

Thelphusa aurantia Herklots, 1851, p. 5, pl. 1, fig. 2.

Thelphusa aubryi H. Milne Edwards, 1853, p. 210.- A. Milne-Edwards, 1887, p. 122.-Aurivillius, 1899, p. 8-9.

Thelphusa pelii Herklots, 1861, p. 13.

Thelphusa decazei A. Milne-Edwards, 1886, p. 150.- A. Milne-Edwards, 1887, p. 127, pl. 8, fig. 7.

Potamon (Potamonautes) decazei, Rathbun, 1900, p. 283; 1904, VI, pl. 16, Potamidae (VIII), fig. 3 (type, Franceville); 1905, p. 195.-Sendler, 1912, p. 199.

Potamon (Potamonautes) pelii, de Man, 1901, p. 99-100.- Rathbun, 1905, p. 162, 191-193.

Potamon (Potamonautes) pobeguini, Rathbun, 1904, VI, pl. 16, Potamidae (VIII), fig. 8 (type, Batah).-Rathbun, 1905, p. 195-197.

Potamon (Potamonautes) aubryi, Rathbun, 1900, p. 283 (not p. 282).-de Man, 1901, p. 94, 98-100; Rathbun, 1904, VI, pl. 17, Potamidae (IX), fig. 4 (type, Gabon).-Rathbun, 1905 VII, p. 191, part, only the female from Gabon, not the specimens from Cabinda (Landana), or from the Republic of the Congo (Batah and Mayumba).-Roux, 1927, p. 237.

Potamonautes decazei, Balss, 1914a, p. 104; 1929, p. 118 (part).

Potamonautes decazei granulata Balss, 1929, p. 122 (part).

Potamonautes pobeguini Rathbun, 1905, p. 195-197.- Balss, 1914a, p. 104; Balss, 1929, p. 116, 120 (part).

Potamon aubryi, Chace, 1942, p. 206.

Potamon decazei, Chace, 1942, p. 209; Capart, 1954, p. 830, fig. 12, 15.

Potamon pobeguini, Chace, 1942, p. 220; Capart, 1954, p. 842-843, fig. 10, 39.

Sudanonautes (Convexonautes) aubryi aubryi.-Bott, 1955, p. 303-304 (part, only type from Gabon, not specimens from Democratic Republic of Congo, not fig. 1a-d, 64, 99a,b).

Sudanonautes (Sudanonautes) pelii pelii-Bott, 1964, p. 32-33, pl. 2, fig. 1, 2; Monod, 1977, p. 1217, fig. 98-101, 110-115; Monod, 1980, p. 384-385, fig. 29.

Sudanonautes (Sudanonautes) africanus africanus.-Bott, 1959, p. 1004 (part).-Lutz, 1969, p. 469-470.-Ejike, 1972, p. 33-34.-Bertrand, 1979, p. 27.

Sudanonautes pelii.-Cumberlidge, 1989, p. 242-243.- Cumberlidge, 1993b, p. 813-814.-Cumberlidge, 1993c, p. 520, table 2.

Sudanonautes aubryi.-Cumberlidge, 1994b, p. 225-241.

Diagnosis

The terminal article of gonopod 1 is robust, rounded, and long (two thirds as long as the subterminal segment); the first half is a straight continuation of the subterminal segment, and the second half curves outward, and tapers to a pointed tip; the longitudinal groove is obscure and is not visible from either ventral or dorsal views; the subterminal segment of gonopod 1 is slim. The terminal article of gonopod 2 is extremely short. The dactylus is long and narrow, and it is not arched; it encloses a long thin interspace. There is a large triangular intermediate tooth on the anterolateral margin between the exorbital angle and the epibranchial tooth; the intermediate tooth is almost as big as the exorbital angle; the epibranchial tooth is small. The vertical sulcus on the sidewall of the carapace meets the anterolateral margin at the epibranchial tooth. The anterolateral margin behind the epibranchial tooth is raised, faintly granulated, and curves inward over the surface of the carapace. The postfrontal crest always meets the anterolateral margins behind the epibranchial teeth; the carapace is moderately high (ch/fw 1.29). The arthrodial membranes of the chelipeds are scarlet. This is a large species, with a moult of puberty between cw 45-50 mm, and a maximum size up to cw 89.5 mm.

For a detailed description see CUMBERLIDGE (1994b).

Size.- The adult size range is from cw 45-50 mm to cw 89.5 mm (the largest known specimen, a male from Cameroon). The carapace proportions are given in table IX. Graphs of carapace dimensions are given in fig. 60A. Growth in this species is discussed by EJIKE (1972). Voucher specimens of "*S.* (*S.*) *a. africanus*" deposited by EJIKE in the NHML, London (NHML 1966.10.17.5.6) belong to *S. aubryi* and are clearly not *S. africanus*.

Colour

The following is based on living adult specimens of *S. aubryi* from Gwarzo, northern Nigeria. The dorsal carapace is green-brown; the postfrontal crest is white-cream; the sidewalls are light green; the eyestalks are brown, the cornea is scarlet; the epistome is burnt brown-orange; the edges of the orbits and the frontal margin are white-cream; the sternum and abdomen are white-cream; the arthrodial membranes between the joints of the chelipeds and the pereiopods are scarlet red; the dorsal surface of the chelipeds and pereiopods are dark green, and the ventral surface is white-cream. The eggs of an ovigerous female were orange. The specimens from Owo, southern Nigeria showed the following variations: the postfrontal crest is green brown; the sidewalls are light brown with purple under the edges; the eyestalks are brown and the cornea is black; the abdomen, sternum, undersides of legs, and chelipeds are white-cream with a pink-mauve wash.

Material examined

Ghana, October 1964; IFAN; 1 m adult cw 54 mm (SMF 2653).

Togo, February 1905; Graf Zech; 1 m adult, cw 65 mm (with *S. granulatus*) (ZSM 1525/6 (ex 1214/9)).- Sokodé, flowing water; Schröder; 2 m subadults cws 40, 37 mm, 7 juveniles, cws 12.5-29 mm; (ZSM 1525/7 (ex 1214/2) donated by ZMB 1928).- Misahöhe, near Palimé, north of Klouto; Baumann; 1 m cw 26 mm; (ZSM 1525/8 (ex 1214/8) caught together with 6 *S. granulatus*.- Bismarkberg, near Blitta; February 1905; Büttner; 1 f adult cw 73 mm (ZSM 1525/9 (ex 1214/10) donated by ZMB 1928).

Nigeria, Ibadan; 5 February 1966; Peter L. Lutz; 2 m adults cws 74.8, 71.6 mm (SMF 2816).- Ibadan; 17 December 1966; C. Ejike (NHML 1966.10.17.5.6).- Lake Tiga, Kano; 26 October 1982; N. Cumberlidge; 1 m adult cw 61 mm (SMF).

Cameroon, Yaounde; von Carnap; 1 f adult cw 56 mm, ovigerous (ZSM 1525/4 (ex 1214/5)).- Mfiende river near Enongal; 15 October 1977; Ripert; 1 m juv cw 30 mm (SMF 9301).- Mfiende river near Enongal; 8 April 1978; Ripert; 1 m adult cw 49 mm (SMF 9304).- Waterfall at Broto near to Kumba; 15 March 1978, Ripert; 1 m subadult cw 32 mm (SMF 9306).- Enyumu river near Afanengong; 25 February 1978; Ripert; 1m juvenile cw 17 mm (SMF 9309).- Mfiende river near Ebolowa; October 1977; Ripert; 1 f adult cw 52 mm (SMF 9311).- Bipindi, Lokoundié river; Zenker; 1 m adult cw 51 mm (together with *S. granulatus*) (ZSM 1525/5 (ex 1214/3), donated by ZMB 1928).- Barombi station by Barombi lake, near Kumba, north of Mount Cameroon, captured in rice field; Preuss; 1 f adult cw 51 mm, 1 f subadult cw 34 mm (ZSM 1525/1 (ex 1214/4), donated by ZMB, 1928).- Victoria south of Mount Cameroon; 6 November 1912; E. Fickenday; 1 f subadult cw 36 mm (ZSM 1525/3 (ex 1214/6)).- 1908; Haberer; 1 f subadult cw 38 mm, 1 juvenile damaged (ZSM 1525/2 (ex 1214/7)).

Bioko, Molla, 1300 m; 8 December 1957; Monod; 1 m subadult cw 23 mm (SMF 2660).

For other material see Cumberlidge (1994b, 1999).

Type and distribution

Types (examined).- *Thelphusa aubryi* H. Milne Edwards, 1853; Gabon; 31 May 1854; M. Aubry Lecomte; 1 m adult cw 58, cl 40 mm, preserved dry (MNHN-B 3805) "C'est l'exemplaire appelé *aubryi* par DE MAN, 1901, p. 94".- Gabon; M. AUBRY LECOMTE; 1 f cw 36, cl 26 mm, preserved dry (MNHN-B 3792). - *Thelphusa pelii* Herklots, 1861; Ghana, St. George d'Elmina (= Elmina); H. S. PEL; 1 m cw 64, cl 49.5 mm (NNH D322), lectotype. *Thelphusa decazei* A. MILNE-EDWARDS, 1886; Gabon, Alima river, at Franceville; M. DE BRAZZA (USNM 30009), cotype. - *Potamon* (*Potamonautes*) *pobeguini* RATHBUN, 1905; Gabon, Batah (or Bata in Equatorial Guinea?); September 1890; M. POBEGUIN; 1 m cw 46.5, cl 33 mm (BP 278 [= B5278]).- 1 m cw 31, cl 23 mm (USNM 30011), cotype.- *Potamon* (*Potamonautes*) *floweri* DE MAN, 1901; Sudan, Bahr el Gebel, 26 August 1901; Capt. S. S. FLOWER; syntype (NHML 1901.8.26.2). - *Potamonautes aubryi monodi* BALSS, 1929; between Tschamba and Laro, Cameroon, T. MONOD. *Potamon* (*Potamonautes*) *regnieri* RATHBUN, 1905; Sanaga river basin; 1899; E. REGNIER; 1 f cw 35, cl 24.5 mm, ovigerous (MNHN-B 5239). - *Thelphusa africana* A. MILNE-EDWARDS, 1869; Gabon; M. AUBRYI LECOMTE; 1 juvenile. - *Potamon decazei granulata* BALSS, 1929; Togo, Misahöhe, near Palimé, north of Klouto; 1 f (ZMB 11257), cotype.

Type localities.- *Thelphusa aubryi*, Gabon; *T. pelii*, St. George d'Elmina, Ghana; *T. decazei*, Alima river, at Franceville, Gabon; *Potamon* (*Potamonautes*) *pobeguini*, Batah, Gabon.

Distribution.- This species is found in Côte-d'Ivoire, Ghana, Togo, Benin, Nigeria, Cameroon, and Gabon. It is likely that *S. aubryi* is also present in Equatorial Guinea. CUMBERLIDGE (1994b) extended the range of this species westward to include Côte-d'Ivoire and Ghana, and removed the Republic of the Congo and Democratic Republic of Congo from the range. According to BOTT (1955) and MONOD (1977, 1980) this species is present in Democratic Republic of Congo, but this was not found to be the case in the present study.

Remarks

Sudanonautes aubryi was redescribed in detail by CUMBERLIDGE (1994b). The gonopods illustrated by BOTT (1955, fig. 64) and labelled to be those of *Sudanonautes* (*Convexonautes*) *aubryi aubryi*, and the position of the vertical sulcus on the carapace sidewall shown in BOTT (1955, fig. 99 a-b and in pl. 28, fig. 1 a-d) both clearly identify these specimens as belonging to *S. floweri* (DE MAN, 1901) rather than to *S. aubryi* (H. MILNE-EDWARDS, 1853).

Variation.- The carapace height depends on locality, whereby the carapace of specimens from rainforest regions (southern Nigeria, southern Cameroon and Gabon) is flatter than that of specimens from savanna regions (Ghana, Togo, northern Nigeria, and northern Cameroon). Distinct patches of granulations on the sidewalls in the suborbital region are present in some specimens (Nigeria and Ejura, Ghana) while others (Bitye, Cameroon) have almost smooth sidewalls. The postfrontal crest is wavy in some specimens (Ja river, Bitye, Cameroon) and straight in others (Kribi river, Cameroon); the postfrontal crest is granulated in some specimens (Obubra district, Nigeria) and smooth in others (Ja river, Bitye, Cameroon); the postfrontal crest behind the intermediate tooth has a distinct notch in some specimens (Côte-d'Ivoire, southern Nigeria and Edea, Cameroon) and is straight in others (Bitye and Kribi, Cameroon). Both the medial and lateral inferior margins of the merus of the cheliped are granulated in specimens from Ibadan, Nigeria; whereas only one of these margins is granulated in specimens from Bitye, Cameron. The specimen from Kribi River, Cameroon has only faint granules on the anterolateral margin, and the terminal of the anterolateral margin doesn't curve inward over the carapace.

Ecology.- *Sudanonautes aubryi* is found in the guinea and woodland savanna regions from Côte-d'Ivoire to northern Cameroon, and in tropical rainforest from south-east Nigeria to Gabon. This large species inhabits streams, rivers, and ponds, and digs burrows near waterways; it is often found on land at night, since it is capable of breathing air. The habitat of *S. aubryi* in wooded savanna fringing a forested area in Côte-d'Ivoire has been described by BERTRAND (1979), whose specimens were misidentified as *Sudanonautes* (*S.*) *a. africanus* (A. MILNE-EDWARDS, 1869). Voucher specimens deposited by BERTRAND in the MNHN and in the SMF following his study have been examined by the author and clearly belong to *S. aubryi*.

Sudanonautes africanus (A. MILNE-EDWARDS, 1869)

fig. 30B, 32B, 33B, 34B, 35C, 36E, 37C, 53P, 54-57, 60B, 67A, table IX.

Thelphusa africana A. MILNE-EDWARDS, 1869: p. 186, pl. XI, fig. 2, 2a,b.-A. MILNE-EDWARDS, 1887, p. 124-126, pl. IV, fig. 8.

Potamon (Potamonautes) africanus, DE MAN, 1903: p. 41, pl. IX, fig. 7-9.-RATHBUN, 1904, pl. 16, fig. 6.-RATHBUN, 1905, p. 188-190, fig. 47.-BALSS, 1929, p. 124-125, fig. 5-7.-BALSS, 1936, p. 166.

Potamon (Potamonautes) africanum, COLOSI, 1920, p. 34.-COLOSI, 1924, p. 21, fig. 16.-ROUX, 1927, p. 237.

Potamon africanus, CHACE, 1942, p. 204.-CAPART, 1954, p. 824, fig. 1, 6.

Sudanonautes (Sudanonautes) africanus africanus, Bott, 1955, p. 295-298, fig. 61, 93-95, 103 a-d, pl. 24, fig. 2a-c, 3.-Bott, 1959, p. 1004-1005.-Monod, 1977, p. 1216 (not fig. 93-95, 102).-Monod, 1980, p. 384, pl. V, fig. 27.

Sudanonautes africanus, Cumberlidge, 1995a, p. 588-598, fig. 1-3, table 1.

Diagnosis

The terminal article of gonopod 1 is thin and needle-like and the subterminal segment of gonopod 1 is slim. The carapace is relatively flat (ch/fw 1.06). The postfrontal crest is smooth and is almost straight; it spans the entire carapace and meets the anterolateral margins at the epibranchial teeth; the posterior surface of the carapace in the cardiac and branchial regions has patches of raised circular blisters, and the lateral parts have fields of raised short lines (carinae); the semi-circular, cardiac, and urogastric grooves are very deep. The proximal region of the pollex of the propodus of the major cheliped of adults has a large, conspicuously flattened tooth. The exorbital angle tooth is large and triangular; the intermediate tooth is large, triangular and blunt, and is as big as the exorbital angle tooth. The epibranchial tooth is small, about half the size of the intermediate tooth and the exorbital angle tooth. The anterolateral margin behind the epibranchial tooth is smooth.

For a detailed description see Cumberlidge (1995a).

Size.- This is the largest species in Africa. The adult size ranges from the size at pubertal moult (cw 70-75 mm) to the largest known specimen (cw 113 mm). The carapace proportions are given in table IX. Graphs of carapace dimensions are given in fig. 60B.

Colour

The following description is based on a living adult male from Cross River State, Nigeria. The dorsal carapace and postfrontal crest are dark brown black and the sidewalls are pale brown; the eyestalks are brown dorsally and white ventrally and the cornea is black; the sternum is white-cream, and the abdomen is white. The arthrodial membranes between the joints of the chelipeds and pereiopods are bright red; the ventral surface of the chelipeds is purple and dark green; the pereiopods and chelipeds are dark green.

Material examined

Cameroon, Yaounde; Zenker; 1 juvenile cw 18 mm (ZSM 1209/1, donated by MRAC 19357).- Barombi station at

Barombi lake near Kumba, north of Mount Cameroon; PREUSS; 2 f subadults cw 57, 49 mm (ZSM 1209/2, ZMB exchange 1911/4379).- Victoria; 1907, O. VALLEY; 2 m adults, cws 85, 90 mm, 4 f adults, cws 90, 98, 86, 86 mm, 4 f subadults, cws 80, 70, 74, 55 mm (SMF 1784/1785).- Mfiende river near Enongal; 15 October 1977; RIPERT; 1 m adult cw 75 mm (SMF 9300).- Mfiende river near Enongal; 8 April 1978; RIPERT; 1 f adult cw 86 mm (SMF 9303).- Mfiende river near Ebolowa; October 1977; RIPERT; 1 f subadult cw 62 mm, 1 m subadult cw 49 mm (SMF 9304).- Waterfall near Broto near Kumba; 15 March 1978, RIPERT; 1 m subadult cw 62 mm, 3 m juveniles cws 39, 33, 32 mm (SMF 9305).

Congo, Kai Bumba, Mayumbe district, between Boma and Tshela, lower Zaire river, tributary of the river Chilongo; 10 October 1920; SCHOUTEDEN; 1 m subadult cw 39 mm (ZSM 1209/4, donated by MRAC 1935).- Ganda Sundi; 30 May 1951; VLEEREHAUWUS; 3 m subadults cws 61, 58, 44 mm, 1 f subadult 35 mm (SMF 2406).

Democratic Republic of Congo, Lower Congo, Kidada near Kitobola, river Lukunga, lower Zaire river, southwest of Mbanza-Ngungu (Thysville); 15 February 1922; SCHOUTEDEN; 1 juvenile cw 28 mm (ZSM 1209/3, donated by MRAC 1935).- Lukula; 1937; J. E. DARTEVELLE; 1 m subadult cw 58 mm (SMF 2386).- In the vicinity of Mbanza-Ngungu (Thysville); 1954; LA BARRE; 1 m subadult cw 62 mm (SMF 2387, donated by MRAC 1942).- Kindambo, north Goma, river Shiloango; J. E. DARTEVELLE; 1 m subadult cw 62 mm, 2 m juveniles, cws 34, 19 mm (SMF 2402, donated by MRAC T47/1567).-Gabon, Ivindo river, Makokon; 9 December 1975; right cheliped only (112 mm long x 47 mm high) (SMF 8345). "Africa"; 1 subadult cw 69 mm (ZSM 1209/5).

See Cumberlidge (1995a, 1997) for more localities.

Type and distribution

Type.- The specimen used by A. MILNE-EDWARDS (1869) to describe *Thelphusa africana* was a small juvenile (MNHN) (cw 17 mm) collected from Gabon by M. AUBRY-LECOMTE. A more detailed description (A. MILNE-EDWARDS, 1887) was based on a larger, but still subadult, female (MNHN) (cw 53 mm) collected from the river Ogoué, Congo (= Gabon). Since neither of these specimens was suitable to select as a lectotype (one is a juvenile and the other a subadult female), and no topotypes were available, the species was redescribed by CUMBERLIDGE (1995a) from an adult male (cw 83 mm) from Cross River State, Nigeria (NMU 9.IV.1983), and an adult female (cw 108 mm) from a tributary of the Ikpan river, Cross River State, Nigeria (NMU 5.IV.1983).

Type locality.- Gabon.

Distribution.- *Sudanonautes africanus* occurs in the coastal rainforest regions of Nigeria and Central Africa. *Sudanonautes africanus* is found in southeast Nigeria to the east of the river Niger: this species is not known from the rest of the West African region (from western Nigeria to Sénégal). In CUMBERLIDGE (1995a), the locality of the specimens listed under "NNH 31618 several juveniles, Tussen Creek, Eagle Island west of the College (now University) of Science and Technology, Port Harcourt, 30 Jan 1977, donated by C. B. POWELL" is almost certainly incorrect (C. B. POWELL, pers comm.). This may mean that the correct western boundary for *S. africanus* is further east, closer to the Cross river than to the Niger river. In Central Africa *S. africanus* occurs in south Cameroon, the Republic of the Congo, and Gabon (the San Benito, Ogoué and Alima rivers), and in the lower reaches of the river Zaire basin. It is likely that this species is also found in Equatorial Guinea and Cabinda. For more details see CUMBERLIDGE (1995a).

Remarks

Sudanonautes africanus was redescribed by CUMBERLIDGE (1995a).

Ecology.- *Sudanonautes africanus* is restricted to the more humid areas of the coastal rainforest belt from south-east Nigeria to lower Democratic Republic of Congo. *Sudanonautes africanus* is capable of breathing air, and is often found on land at night. The species is also common in streams and rivers draining mature forest, and also digs burrows near waterways. *Sudanonautes africanus* occurs in a range of permanent aquatic habitats from large rivers and small streams (with both fast and slow flowing water) to ponds. This crab also occurs in temporary water sources such as drainage culverts and ditches. Most aquatic habitats were found to be shaded by overhanging climbing palms or by emergent vegetation. For more details see CUMBERLIDGE (1995a). *Sudanonautes africanus* serves as an important second intermediate host to the human lung flukes *Paragonimus uterobilateralis* and *P. africanus* in Nigeria and Cameroon (VOELKER & SACHS, 1977).

Sudanonautes chavanesii (A. MILNE-EDWARDS, 1886)

fig. 30C, 32C, 33C, 34C, 35B, 36G, 37B, 38C, 53R, 54-57, 60D, 67I, table IX.

Thelphusa chavanesii A. MILNE-EDWARDS, 1886: p. 150.

Parathelphusa chavanesii, A. MILNE-EDWARDS, 1887, p. 145-146, pl. 7, fig. 3a, b.-RATHBUN, 1900, p. 285.

Potamon (Potamonautes) chavanesi, ORTMANN, 1897, p. 305, 309.

Potamon (Parathelphusa) chavanesii, RATHBUN, 1905, p. 232, pl. 11, fig. 1.-BALSS, 1929, p. 127.-BALSS, 1936, p. 166.

Potamon chavanesi, CHACE, 1942, p. 209.-CAPART, 1954, p. 829-830, fig. 7, 11.

Sudanonautes (Sudanonautes) africanus chavanesii, BOTT, 1955, p. 299, fig. 97.-BOTT, 1959, p. 1005.-MONOD, 1977, p. 1217 (not fig. 103-107).-MONOD, 1980, p. 384.

Sudanonautes chavanesii, CUMBERLIDGE, 1995b, p. 238-246, fig. 1-3.

Diagnosis

The exorbital angle tooth and the intermediate tooth are large, sharp, and point forward; the epibranchial tooth is large and points outward. The epibranchial tooth is set back behind the mid-point of the postfrontal crest and this tooth is positioned in line with the widest part of the carapace; the distance between the epibranchial tooth and the intermediate tooth is twice the distance between the intermediate tooth and the exorbital angle tooth. The postfrontal crest spans the entire carapace, and curves sharply backward before meeting the epibranchial tooth; there is a distinct notch in the postfrontal crest behind the exorbital angle tooth; the anterolateral margin posterior to the epibranchial tooth is smooth. The semi-circular, urogastric, cardiac, and transverse branchial grooves are very deep. The vertical sulcus on the sidewall of the carapace forms a y-shaped depression beneath the intermediate tooth. The carapace is very flat (ch/fw 1.09). The mandibular palp has two segments; the terminal segment is single and undivided, and there is a small hard, hair-fringed anterior process at the junction between the segments. The terminal article of gonopod 1 is thin and needle-like; the subterminal segment of gonopod 1 is slim. The dactylus of the major cheliped is highly arched and forms an oval interspace; there are two or three large fused teeth in the proximal regions of both fingers of the cheliped, and the rest of the cutting edges are lined with rows of rounded teeth.

For a detailed description see CUMBERLIDGE (1995b).

Size.- The adult size range is from the pubertal moult (cw 35-45 mm) to the largest known specimen (cw 81 mm). The carapace proportions are given in table IX. Graphs of carapace dimensions are given in fig. 60D.

Material examined

Cameroon, Boedou, near Banyo; RIGGENBACH; 1 f subadult cw 47 mm, 1 m adult cw 49 mm (ZSM 1526/1 (ex 1201/1), donated by ZMB 1928).- Foumban, vicinity of Dschang; Th. MONOD; 1 m subadult cw 47 mm, 1 m juvenile cw 28 mm (ZSM 1526/2 (ex 1201/2)). For details of other localities see CUMBERLIDGE (1995b, 1997).

Type and distribution

Type.- Gabon, vicinity of Franceville on the Alima river; MISSION DE BRAZZA; 1 M adult cw 54, cl 39 mm (MNHN-B 5079) type.- Gabon, Lac de Franceville; MISSION DE BRAZZA; 1 M adult cw 54 mm (USNM 30034) cotype.

Type locality.- Gabon, vicinity of Franceville on the Alima river.

Distribution.- This species is found in the coastal rainforest of Central Africa from south Cameroon to Gabon, including the forested parts of the Central African Republic. The presence of this species in southern Cameroon and northern Gabon make it likely that *S. chavanesii* is also present in Equatorial Guinea. For more details on distribution see CUMBERLIDGE (1995b).

Remarks

Sudanonautes chavanesii was redescribed by CUMBERLIDGE (1995b).

Sudanonautes floweri (DE MAN, 1901)

fig. 30D, 32D, 33D, 34D, 35H, 36A, 37D, 38A, 53T, 54-57, 60E, 67C, table IX.

Potamon (Potamonautes) floweri DE MAN, 1901, p. 94-98, 100-101, pl. X (fig. 1-7).-RATHBUN, 1904, pl. 17 (figs 2, 6).-RATHBUN, 1905, p. 193-195; RATHBUN, 1921:406-410, fig. 6, pl. 10 (fig. 2); PARISI, 1925, p. 99.

Potamon (Potamonautes) aubryi; BALSS, 1914a, p. 405 (except ZIM K13557 from Mukonje farm, Cameroon, not *Potamon aubryi* H. MILNE EDWARDS, 1853).

Potamonautes floweri, BALSS, 1936, p. 171, fig. 6.

Potamon floweri, FLOWER, 1931, p. 734.-CHACE, 1942, p. 211.-CAPART, 1954, p. 834, fig. 21.

Sudanonautes (Convexonautes) aubryi floweri, BOTT, 1955, p. 304-306, fig. 64, 65, 99 a-b, 100, a-b, pl. 28 (fig. 1 a-d, 2 a-d).-MONOD, 1977, p. 1218.-MONOD, 1980, p. 384-385.

Sudanonautes floweri, CUMBERLIDGE, 1995c, p. 111-119, fig. 1-3, table 1.

Diagnosis

The mandibular palp has two segments; the terminal segment consists of the single large posterior lobe, plus a small hard, hair-fringed anterior process at the junction between the segments. The terminal article of gonopod 1 has a conspicuously raised medial fold which is separated from the smaller lateral fold by a distinct longitudinal groove; the subterminal segment of gonopod 1 is distinctly broadened on the inner margin by a wide shoulder at the junction between the segments. There are conspicuous raised ridges on the sternum at the points where the chelipeds articulate. The carapace is high and arched (ch/fw 1.68) and very wide (cw/fw 4.18). The vertical sulcus on the sidewall separates the sub-hepatic and suborbital regions and meets the anterolateral margin at the base of the intermediate tooth.

For a detailed description see CUMBERLIDGE (1995c).

Size.- The adult size range is from the pubertal moult (cw 33-42 mm) to the largest known specimen (cw 60.4 mm). The carapace proportions are given in table IX. Graphs of carapace dimensions are given in fig. 60E.

Colour

The following description is based on a live adult from Ogoja, Nigeria. The carapace is a dark purplish brown, with a contrasting yellow-orange postfrontal crest and a yellow orbital border. The sidewalls of the carapace are light brown, the third maxillipeds are pale brown with a purple tinge, the eyestalks are white cream and the cornea is black; the sternum and abdomen are light brown with a purple tinge. The arthrodial membranes between the joints of the chelipeds and pereiopods are dark brown; the dorsal surface of the chelipeds and pereiopods is light brown and the ventral surface is light brown. Specimens from the Ogoué river, in the Fang forest, Gabon have a brown-pink carapace, shading into neutral orange in the middle and their walking legs are orange-vermilion.

Material examined

Nigeria, Benue State, Otta, pond near tributary of the river Niger (20 km east of the river); 30.IV.1984; JOHN IYAGE; 1 f cw 54 mm (NMU 30.IV.1984).

Cameroon, 1 f subadult cw 28 mm (ZSM 1174/2).- Victoria; 1907; O. VALLEY; 1 m adult cw 40 mm (SMF 1787).- Bibundi; JUSTUS WEIL; 1 m subadult cw 37 mm, 1 f adult cw 33.5 mm (SMF 2868).- Bibundi; 20 August 1918; JUSTUS WEIL; 1 m juvenile cw 28 mm, 1 f subadult cw 34 mm (SMF 2889, donated by ZIM K 3553).- 1 f subadult cw 28 mm (ZSM 1524-6 (ex 1174/2)).- Victoria; 1898-1899; VALDIVIA; 1 f subadult cw 33 mm (ZSM 1524/4 (ex 1211/2)).- Bibundi, west of Mount Cameroon; RETZLAFF; 2 m adults cws 46, 45 mm, 1 f adult cw 38 mm, 1 f subadult cw 30 mm, 1 m juvenile cw 32 mm (ZSM 1524/5 (ex 1211/3)).

Congo, Ganda Sundi; 1 f adult cw 41 mm (SMF 2398).

Democratic Republic of Congo, Duma; SCHUBOTZ; 2 m subadults cws 39, 27 mm, 1 f adult cw 45 mm (SMF 1782).- Fort Krampel; SCHUBOTZ, Inner Afrika Expedition; 2 f juveniles cws 19, 16 mm (SMF 1789).- Bambesa; VRYDAGH; 1 m adult cw 45 mm, 1 f adult cw 54 mm, 1 f subadult cw 30 mm, 1 m subadult cw 36 mm (SMF 2383).- Faradje, Haute Uele; May 1925; SCHOUTEDEN; 1 m adult cw 51 mm (MRAC 1079), 1 f adult cw 45 mm (MRAC 1083) (SMF 2385).- Luki, lower Congo; DARTEVELLE; 1 f adult cw 38 mm (SMF 2405).- Bambesa, Upper Uele river; 14 October 1933, H. BREDO; 2 m adults cws 46, 45 mm, 2 f adults, cws 42, 38 mm, 2 m juveniles cws 32, 22 mm (ZSM 1524/1 (ex 1212/1), donated by MRAC 1935/1).- Monbuttu? (near the upper Uele) between Kibali and the Ituri river, west of Lake Albert southeast of the river Uele; SCHWEINFURTH; 1 f subadult cw 29 mm (ZSM 1524/2 (ex 1212/2)).- Monbuttu? (near the upper Uele) between Kibali and the Ituri river, west of Lake Albert southeast of the river Uele; SCHWEINFURTH; 1 f subadult cw 34 mm (ZSM 1524/3 (ex 1211/1), donated by ZMB, 1928).

For a list of other material examined see CUMBERLIDGE (1995c, 1997)

Type and distribution

Type.- Bahr el Gebel, Sudan; 26 August 1901; Capt. S. S. FLOWER; 1 m cw 48.5, cl 30.5, ch 17.8, fw 11.7 mm (NHML 1901.8.26.2), lectotype.

Type locality.- Bahr el Gebel, Sudan.

Distribution.- This species is found in Nigeria, Cameroon, Bioko, Central African Republic, Sudan, Zaire, Congo, Gabon, Cabinda, and Angola. It is likely that *S. floweri* is also present in Equatorial Guinea. RATHBUN (1921) and BALSS (1936) provided details of the distribution of the species in Zaire. MONOD (1980) reported *S. floweri* from the basins of the Nile, Zaire, Chari, and Lake Chad. CUMBERLIDGE (1995) added several new localities in Nigeria, Bioko, and northern Angola.

Remarks

Sudanonautes floweri was redescribed by CUMBERLIDGE (1995c).

Variation.- The anterolateral margin is raised and is marked by a series of granules or small teeth in some specimens (from Juba, Shambe, and Kojo-Kaji, Sudan; from Ituri forest, Banana, and Faradje, Zaire; and from Ogoja, Kaduna, and Bendel State, Nigeria). In other specimens (from Poko, Zaire; Bioko, and Luali, Angola) the anterolateral margin is completely smooth. In specimens from Oban, Nigeria, the anterolateral margin is smooth except for the epibranchial tooth (which is the size of a large granule), followed by two smaller granules. It is possible that the above variations of the anterolateral margin are due to changes associated with growth. For example, the adult male (cw 53.5 mm) from Juba, Sudan (FMC) was the only one in which the anterolateral margin was smooth, out of 25 specimens of all sizes. This margin was toothed or serrated in all the other specimens which measured cw 48 mm or less. A similar observation was made in the series of specimens from Cameroon (MRAC 53.389), where the anterolateral margin of a large male (cw 60.4 mm) was completely smooth, but that of smaller specimens was granulated. Some specimens from Juba, Sudan have rough granulations on the dorsal surface of the dactylus of the cheliped while other specimens from Juba and from Nepoko, Zaire lack these granulations.

Ecology.- *Sudanonautes floweri* is a common species of freshwater crab widely distributed in Nigeria and Central Africa. It is found in the moister regions of the woodland and guinea savanna zones from central Nigeria to southern Sudan. This species is also found in the humid tropical rainforest habitats in southeast Nigeria, south Cameroon, Bioko, Central African Republic, Zaire, Congo, and Gabon. *Sudanonautes floweri* is common in shallow streams, rivers, and ponds, and digs burrows near waterways. This species is also found on land either next to water or some distance away, since it is capable of breathing air, and functions well for long periods out of water. The widened and highly arched carapace, and the lack of teeth on the anterolateral margins of the carapace of *S. floweri* are features often associated with air-breathing and burrow-living. This body shape contrasts with the more flattened, deeply-grooved and spiny carapace of the more aquatic river-living species such *S. faradjensis* (RATHBUN, 1921).

Sudanonautes floweri has the widest carapace of any species of African freshwater crab (cw/fw 4.18), and the carapace is among the most highly arched (ch/fw 1.68) on the continent. *Sudanonautes floweri* serves as an important second intermediate host to the human lung flukes *Paragonimus uterobilateralis* and *P. africanus* in Nigeria and Cameroon (VOELKER & SACHS, 1977).

Sudanonautes faradjensis (RATHBUN, 1921)

fig. 30F, 32E, 33E, 34E, 35A, 36F, 37A, 38E, 53S, 54-57, 60C, 67D, table IX.

Potamon (Acanthothelphusa) faradjensis RATHBUN, 1921, p. 428-430, pl. 31, fig. 13.

Potamon (Potamonautes) faradjensis, BALSS, 1929, p. 126, fig. 8.-BALSS, 1936, p. 166-7, fig. 1.

Potamon faradjensis, CHACE, 1942, p. 211.-CAPART, 1954, p. 833, fig. 8, 20.

Sudanonautes (Sudanonautes) africanus chaperi, BOTT, 1955, p. 298-299 (part), pl. 27, fig. 1a-c, 2; fig. 62, 96a,b.-MONOD, 1977, p. 1216 (part). Not *Parathelphusa chaperi* A. MILNE-EDWARDS, 1887.

Sudanonautes faradjensis, CUMBERLIDGE, 1995d, p. 629-636, fig. 1-3.

Diagnosis

The postfrontal crest spans the entire carapace, and there is a shallow notch in the postfrontal crest behind the exorbital angle; there is a series (from seven to eight) of sharp teeth on the anterolateral margin posterior to the epibranchial tooth. The posterior lateral surface of the carapace has fields of raised short lines (carinae); the cervical, semi-circular, cardiac, urogastric grooves are very deep. The epibranchial and intermediate teeth, and the exorbital angle tooth are all large, sharp, and point forward. The terminal article of gonopod 1 is long, thin and needle-like, and the subterminal segment of gonopod 1 is slender. The carapace is very flat (ch/fw 1.09).

For a detailed description see CUMBERLIDGE (1995d).

Size.- The adult size range is from cw 35-43 mm to cw 90 mm (the largest known specimen, a male from Cameroon). The carapace proportions are given in table IX. Graphs of carapace dimensions are given in fig. 60C.

Colour

The following is based on a living adult from Kinshasa, Zaire. The dorsal carapace and postfrontal crest are dark brown-black, the sidewalls are pale brown; the eyestalks are brown and the cornea is black; and the sternum and abdomen are light brown. The arthrodial membranes between the joints of the chelipeds and pereiopods are light brown; the chelipeds and pereiopods are light brown.

Material examined

Cameroon, Bipindihof; ZENKER; 1 m adult cw 34 mm, 2 f adults cws 34, 33.8 mm (ZMB 10359).- Boedou stream, subdivision of Banyo; RIGGENBACH; 1 m, 1 f (ZSM 1526/1 (ex 1210/1)).- Foumban, Dschang district; Th. MONOD; 1 m (ZSM 1526/2 (ex 1210/2)).

Gabon, Ivindo river, Makokon; 9 December 1975; 1 f subadult cw 65 mm (SMF 7296).

Democratic Republic of Congo, Lisala; DE HEYN; 1 m subadult male cw 47 mm (SMF 2382, donated by MRAC 32071).

Type and distribution

Types (examined).- Zaire, Faradje; December 1912; H. LANG & R. CHAPIN; 1 m adult cw 71.5, cl 51 mm (AMNH 3346), holotype.- Zaire, Faradje, December 1912; H. LANG & R. CHAPIN; 1 m, 2 f (AMNH 3351) paratypes, photographed and illustrated by RATHBUN, 1921.- Zaire, Gombari (van Kerckhovenville); April 1912; H. LANG & R. CHAPIN; MRAC 836) paratype.

Type locality.- Faradje, Democratic Republic of Congo.

Distribution.- *Sudanonautes faradjensis* is found in the rivers of the rainforest regions of Cameroon, Central African Republic, Gabon and Zaire. It occurs in the middle reaches of the Zaire river basin, and in the rivers Ubangui and Uele, and in the tributaries of the Zaire river. The distribution of this species in Zaire is described by RATHBUN (1921) and BALSS (1936), and the distribution in Cameroon by BALSS (1929).

Remarks

Sudanonautes faradjensis was redescribed in detail by CUMBERLIDGE (1995d).

Ecology.- *Sudanonautes faradjensis* is restricted to the more humid areas of the rainforest from south Cameroon to Zaire. This species occurs in permanent aquatic habitats from large rivers to small streams. The following notes are based on the observations of HERBERT LANG, the leader of the US Congo Expedition, as reported by RATHBUN (1921). *Sudanonautes faradjensis* is one of the largest river-living crabs of the Uele district in the Zaire basin. The species is found under stones in quiet portions of the river near rapids, where it is reportedly preyed upon by small crocodiles and carnivorous fish.

Sudanonautes monodi (Balss, 1929)

fig. 32F, 33F, 34F, 35I, 36C, 37F, 39A, 53U, 54-57, 60F, 67E, table IX.

Potamonautes aubryi monodi Balss, 1929, p. 123, fig. 4 (Laro).

Potamon monodi, Chace, 1942, p. 217.-Capart, 1954, p. 823, figs 9, 29.

Sudanonautes (Convexonautes) aubryi monodi, Bott, 1955, p. 306, fig. 101.-Monod, 1977, p. 1281, figs 108-109.-Monod, 1980, p. 385.-Cumberlidge, 1986.

Redescription

Diagnosis.- The mandibular palp has two segments; the terminal segment consists only of the single posterior lobe and there is no additional small anterior process or lobe. The medial fold on the terminal article of gonopod 1 is higher than the lateral fold, and the two folds are separated by the conspicuous longitudinal groove that runs to the tip of the segment; the subterminal segment of gonopod 1 is distinctly broadened on the inner margin by a wide shoulder at the junction between the segments. The carapace is high and arched (ch/fw 1.46) and very wide (cw/fw 3.82). The vertical sulcus on the sidewall of the carapace meets the anterolateral margin at the base of the epibranchial tooth. The carapace is completely smooth except for small fields of granules in the anterolateral corners close to where the postfrontal crest meets the anterolateral margins. There is a small (but distinct) intermediate tooth on the anterolateral margin between the exorbital angle and the epibranchial tooth; the anterolateral margin behind the epibranchial tooth is completely smooth.

Redescription of male holotype.- The carapace is ovoid and is extremely wide (cw/fw 3.82), and is widest in the anterior third; the carapace is extremely high (ch/fw 1.46), with a maximum height in the anterior region. The anterior margin of the front is straight and curves down; the front is relatively narrow (about one quarter the carapace width, fw/cw 0.25). The surface of the carapace is smooth with no deep grooves except for small fields of granules in the anterolateral corners close to where the postfrontal crest meets the anterolateral margins. The postfrontal crest consists of fused epigastric and postorbital crests, and the lateral ends of the postfrontal crest meet, or almost meet, the anterolateral margins of carapace close to each epibranchial tooth; the mid-groove is broad and shallow; the postfrontal crest is yellow (while the rest of the carapace is red-brown), and is positioned very close to, almost touching, the superior margins of the orbits. The exorbital angle is produced into a small low pointed tooth and the intermediate tooth is smaller than the exorbital angle tooth; the epibranchial tooth is a small, low granule. The anterolateral margin of the carapace behind the epibranchial tooth is smooth. The posterior margin of the carapace is wider than the front (about two-thirds as wide as the cw). The vertical sulcus on the sidewall of the carapace is marked by a row of small rounded granules which begin at the base of the epibranchial tooth and which separate the suborbital from the hepatic regions, dividing the sidewall into three parts. The third maxillipeds fill the entire oral field except for the transversely oval efferent respiratory openings at the superior lateral corners; there is a long flagellum on the exopod of the third maxilliped; the ischium of the third maxilliped is smooth and has a faint vertical sulcus; the merus of the third maxilliped has flanged edges. The mandibular palp has two segments, the terminal segment consists of a single undivided (posterior) lobe, and there is no anterior process or thickening present. Sternal sulcus 1 (s1/s2) is absent; s2/s3 is complete and crosses the sternum; and s3/s4 is reduced to two small notches at the sides of the sternum. All four episternal sulci (s4/e4-s7/e7) are very faint and are almost missing. The penis meets s8 in the midpoint of the lateral margin.

The chelipeds are unequal, and the right is longer and higher than the left. The dactylus of the right cheliped is not arched, and the closed fingers enclose a long interspace, the palm of the propodus is swollen. The fingers of the right cheliped have four larger teeth on the lower digit and four larger teeth on the upper digit, interspersed with a series of smaller pointed teeth along their lengths. The inferior and medial superior margins of the merus of P1 have rows of small teeth, and there is a cluster of granules surrounding the larger distal tooth. The carpus of the cheliped has two large pointed teeth on the inner margin, and the second is smaller than the first. The left cheliped is similar to the right, but is smaller in all respects. The walking legs (P2-P5) are long, P3 is the longest, and P4 the shortest. The posterior margin of the carapace of the propodus of P2-P5 is serrated and the dactyli taper to a point, each bearing four rows of downward-pointing sharp spines; the dactylus of P5 is the shortest.

Abdominal segments a1-a6 are four sided, the telson (a7) is triangular and its sides are longer than the base and they taper toward the rounded terminal margin; a1-a2 are fixed and occupy the entire area between the coxae of P5; a3-a7 is triangular, moving as one piece (hinging between segments 2 and 3), and a3 is the broadest segment. The terminal article of gonopod 1 is long (two-thirds as long as the subterminal segment), the first half is a straight continuation of the subterminal segment, while the second half curves outward and tapers to a pointed tip; the medial fold is raised and is clearly higher than the lateral fold, and the longitudinal groove is distinct in the ventral view, but is not visible in the dorsal side. The subterminal segment of gonopod 1 is broadened conspicuously on its outer margin, and is fringed with bristles; the medial flap extends halfway across the segment in the distal part, and tapers diagonally to meet the junction with the terminal article; the lateral floor of the subterminal segment is broad. Gonopod 2 is shorter than gonopod 1 (reaching only to the junction between last two segments of gonopod 1). The terminal article of gonopod 2 has a pointed tip and is extremely short, only 1/15 as long as the subterminal segment of gonopod 2.

Adult female.- The right and left chelipeds are the same proportions as in a male of the same size; they are heterochelous and are unequal in both length and height. The abdomen of adult females is very wide and reaches the coxae of P2-P5. The distal segments of the abdomen of adult females are long and wide, and the abdomen is widest at the a4/a5 sulcus; the telson is semicircular.

Growth.- Sexual maturity can be judged by the amount of development of the female abdomen: that of mature females is round and wide, and overlaps the bases of the coxae of the walking legs, and the pleopods are broad and hair-fringed. The moult of puberty in *S. monodi* occurs between cw 33-42 mm, and the adult size range is between cw 33-42 and 60.4 mm. In the sudan and guinea savanna zones of northern Nigeria, females produce eggs in February, and hatchlings are present in early April. The dimensions of the carapace vary with age. The relative proportions of the carapace width (cw/fw) and carapace height (ch/fw) of juvenile and subadult *S. monodi* are significantly different ($P < 0.001$) from adults. The carapace length cl/fw of adult *S. monodi* is not significantly longer ($P > 0.05$) than that of juvenile and subadult animals.

Size.- A medium-sized species. The adult size ranges from cw 33-42 to 60.4 mm. The carapace proportions are given in table IX. Graphs of carapace dimensions are given in fig. 60F.

Colour

The following description is based on living adults from Tiga, Nigeria. The dorsal carapace is a dark purplish brown, and has a contrasting yellow-cream postfrontal crest and yellow orbital border. The sidewalls of the carapace are light brown, the third maxillipeds are pale brown with a purple tinge, the epistome is orange/red, the eyestalk is white cream, the cornea is black, and the sternum and abdomen are pale cream with a purple tinge. The arthrodial membranes between the joints of the chelipeds and pereiopods are pale white-yellow. The dorsal surface of the chelipeds and pereiopods ranges from light brown to mauve-pink, while the ventral surface is light brown to mauve-pink. The cheliped teeth are yellow, and the tips of the chelipeds are yellow-cream. The pereiopods are uniformly light brown.

Material examined

Togo, Tamboursan; 21 December 1982; N. CUMBERLIDGE; 1 f (NMU 21.XII.1982).

Republic of Benin (formerly Dahomey), locality, date & collector unrecorded; 1 specimen (MNHN).

Nigeria, Hadejia; 3 December 1981; (NMU 3.XII.1981), 3 m, 4 f.-Tiga Lake, 1 m; 5 May 1982; (NMU 5.IV.1982).-Anadaryia, 10 May 1982; (NMU 10.V.1982); 2 juveniles.-Yola, 1 m; 12 May 1982 (NMU 12.V.1982).-Falgore; July 1982; (NMU VII.1982); 1 m.-14 May 1982; (NMU 14.V.1982); 1 m, 1 f with hatchlings.-8 April 1982; (NMU 8.IV.1982); 4 m, 3 f (1 with hatchlings).-Maigwado; 1 February 1983; (NMU 1.II.1983); 2 m, 7 f.-2 February 1983.-2 f; 17 February 1983; (NMU 17.II.1983); 6 m, 12 f.-20 February 1983; (NMU 20.II.1983); 7 m, 25 f.-20 April 1983; (NMU 20.IV.1983); 10 m, 12 f.-31 May 1983; (NMU 31.V.1983); 18 m, 21 f.-2 July 1983; (NMU 2.VII.1983); 20 m, 29 f.-31 July 1983; (NMU 31.VII.1983); 11m, 14f.- 2 September 1983; (NMU 2.IX.1983); 14 m, 13 f;.-1 October 1983; (NMU 1.X.1983); 9 m, 13 f.-26 November 1983 (NMU 26.XI.1983); 23 m, 22 f.-14 April 1984; (NMU 14.IV.1984); 16 m, 18 f.-Gwarzo; 12 May 1983; (NMU 12.V.1983); 1 m, 1 f.-July 1983; (NMU VII.1983); 2 m, 1 f.-1 October 1983; (NMU 1.X.1983); 6 m, 3 f.-Kogar-Kasa, 15 March 1984; (NMU 15.III.1984); 4 m, 3 f.-Dabar Kwari, 24 March 1984; (NMU 24.III.1984); 4 m, 11 f.-Badeggi, 13 April 1984; (NMU 13.IV.1984); 2 m, 2 f. All above specimens collected by N. CUMBERLIDGE. North east Bauchi State, approximately 20 km east of Ningi; 7 September 1980; 1 m; (NMU 7.IX.1980).- 1 m.-Gadan (= Gadau); 18 September 1933; (NHML 18.9.1933.1); 1 f.- Near Yola, Benue river; 20 December 1904; Dr. J. H. ASHWORTH; (NHML 1904.12.20.1); 1 m.-Ibi, Benue river; 17 November 1916; A. L. FRANCIS; (NHML 1916.11.17.1); 1 specimen.-Bauchi Province; 31 May 1935; (NHML 1935.5.31.1-3); 3 specimens.-Northern Nigeria; 17 August 1934; T. A. GLOVER; (NHML 1934.8.17 (1-5); 5 specimens.

Cameroon, Satche; 8 October 1905, RIGGENBACH; (ZMB 20208); 1 m, 1 f with hatchlings.- Garoua, 8 October 1905; LANGHOLD; (ZMB 20219); 2 f.- Mobe; THIERRY; (ZMB).-Aledjo, 19 July 1969; F. PUYLAERT; (MRAC 53.108); 3 specimens.-Waza; 24 August 1972; E. GERAERT; (MRAC 53.971); 4 specimens.-near Maroua, north Cameroon; 3 September 1964; B. DE WILDE-DUYFJER; (NNH 21162).

Chad, southern region, river Chari; 1 August 1977, G. PUELLA; 3 specimens (MRAC 54.665).

Type and distribution

Types (examined).- Cameroon, Laro, between Tschamba and Laro; 1929; Th. MONOD; 1 m adult (MNHN-B 5299), lectotype.- Cameroon, Laro; 1929; Th. MONOD; MNHN-B 5044); 1 f juvenile, syntype.- Cameroon, Laro by the river Deo; 1929; Th. MONOD; 2 m adults cws 43, 40 mm (ZSM 1213/1), syntypes.

Type locality.- Cameroon, Laro, between Tschamba and Laro.

Distribution.- Distributional data and ecological notes are based on nearly 400 new specimens from a large number of new localities in West Africa (most are in Nigeria, but there is one each in Togo, the Republic of Benin and Chad). *Sudanonautes monodi* is found only in the sudan and guinea savanna zone of West Africa, in Chad, Cameroon, Nigeria, Republic of Benin and Togo. The species is not found in the Sahel savanna regions and in the tropical rainforest zone. In Nigeria *S. monodi* is associated with three major river systems draining the savanna region: the Benue river basin, the Hadejia-Jama'are river/ Lake Chad basin, and the Kaduna river/ Niger river basin. In Togo and Benin *S. monodi* occurs in the upper reaches of the Volta river basin which drains savanna country. Prior to the present study *S. monodi* was known only from six localities in northern Cameroon. These reports increase our knowledge of the distribution of *S. monodi* in several important ways. The present records are the first new records of the occurrence of *S. monodi* since its original description in 1929, and the first records of its occurrence in Nigeria, the Republic of Benin and Togo. The lack of new records of this species since its first description is due partly to the severe undercollection of the freshwater crab fauna of the region and partly to difficulties in distinguishing this species from its close relatives.

Sudanonautes monodi is locally common throughout a wide area of savanna in West Africa from Togo to Chad, and is particularly abundant in Nigeria. The majority of new localities are in the sudan savanna zone, while the rest are in the guinea savanna zone. This species was previously known only from sudan savanna in West Africa, and this is the first time it has been reported to occur in guinea savanna. Data presented here also allow discussion of the distribution of this species in terms of ecological zones. The most northerly record is from Hadejia in northern Nigeria, a locality close to the border between the sudan savanna and Sahel regions. It would appear that the Sahel savanna region, which lies close to the southern edge of the Sahara desert forms the northern boundary for this species. *Sudanonautes monodi* has not been recorded from the tropical rainforests of Nigeria and Cameroon despite regular surveys of the decapod fauna in southeast Nigeria over a number of years by the author. This species is also absent from collections of freshwater crabs from sites in woodland savanna as well as the rainforest. It would appear that the southern boundary of the distribution lies between the guinea savanna and woodland savanna zones.

It is difficult to be precise about the eastern and western limits of the range of this species. The present data indicate a range from Togo to Chad. However, the savanna region of West Africa (from Sénégal to southern Sudan) is an apparently uniform environment which presents few obvious geographical or ecological barriers to the distribution of its fauna. At the present state of our knowledge, however, it would be premature to make firm conclusions about the distribution of this species until data from thorough, systematic faunal surveys of West Africa are available.

Remarks

Ecology.- Until the present work *S. monodi* was known only from a few specimens collected from six localities in the Benue river basin of northern Cameroon (BALSS, 1929). Studies using new material collected mainly in Nigeria have led to a preliminary description of the respiratory physiology and ecology of *S. monodi* (CUMBERLIDGE, 1986). That work remains one of the few studies on the respiratory physiology of any freshwater crab from Africa, and underlines the need for more field work on all aspects of the biology of these interesting animals. The following account is based on field observations of the species in northern Nigeria. In the guinea and sudan savanna regions of West Africa the dry season lasts from October to April. To survive in this arid environment, each crab digs a burrow. Tunnels and burrows up to one metre long are dug into dried stream banks, waterless swamp beds and cracked water holes, which are all sited in low-lying areas where the water table is close to the surface. This species is found living in colonies of up to a hundred, with one crab per burrow. The purpose of digging a burrow is to avoid exposure to high temperatures, and to create a makeshift aquatic environment at the bottom. This habitat offers the crab little more than a shallow layer of mud-brown tepid water, which collects by seepage through the soil. This water is usually sufficient to only partly immerse the resident crab, but it is enough to keep the crab alive in the dry season, by maintaining body fluid levels and by keeping respiratory surfaces moist. Crabs spend the hot daytime hours of the dry season resting semi-submerged in their tepid underground habitations, where the air is cooler and damper than at the surface. Later, in the colder nocturnal air, crabs emerge from their burrows, scavenging nearby land for vegetable matter or plant and animal remains. This is the pattern of *S. monodi's* behaviour during the dry season: daytime inactivity in the burrow, nocturnal activity on land. The first storms of the wet season inundate the burrows and prompt crabs to move onto land in the daylight hours, as well as the night. The night air is cooler and more humid, and the new undergrowth provides crabs both concealment from predators and shade from the sun. Once the wetlands develop, crabs congregate in great numbers in the muddy, shallow waters of the newly-formed pools and marshes. This is the pattern of *S. monodi's* behaviour during the wet season: it is active both day and night, either under water, on land, or it may rest in its burrow.

Taxonomic remarks.- *Sudanonautes monodi* was formerly considered by both BOTT (1955) and MONOD (1977, 1980) to be a subspecies of *S. aubryi*. *Sudanonautes monodi* is judged here to be a valid species, and is redescribed from a male syntype from Cameroon (MNHN-B 5299]) which is here designated the lectotype. Gonopod 1 of *S. monodi* is unique to the species, and when considered in conjunction with other characters of the carapace and sternum and mandibles, can be used to identify the species unequivocally. However, the ambiguous descriptions of *S. monodi*, *S. floweri* and *S. aubryi* in the literature (A. MILNE-EDWARDS, 1853; DE MAN, 1901; BOTT, 1955; MONOD, 1977, 1980) have led to the misidentification of specimens of *S. monodi* as *S. (C.) a. aubryi* (MONOD, 1977, fig. 108-110).

Sudanonautes monodi appears in BOTT (1955) as *Sudanonautes (Convexonautes) aubryi monodi*, and was one of three subspecies of *S. aubryi* recognised in that work (the others being *S. (C.) a. aubryi* and *S. (C.) a. floweri*). BOTT's (1955) classification was followed in most part by MONOD (1977, 1980). Comparison of the male type of *Potamon (Potamonautes) aubryi monodi* from Cameroon with the male type of *Potamon (Potamonautes) floweri* from the Sudan indicates that these taxa are significantly different from each other, and each is distinct from the type of *S. aubryi*. For this reason, *S. monodi* and *S. floweri* are considered here to be valid species. BOTT's (1955) subgenus *Convexonautes* is not recognised, since under the present classification this subgenus would include *S. floweri* and *S. monodi* but would exclude *S. aubryi* (the type species of this subgenus).

Sudanonautes monodi was first described by BALSS (1929) as *Potamon* (*Potamonautes*) *aubryi monodi*, a geographical subspecies of *P.* (*P.*) *aubryi* (H. MILNE EDWARDS, 1853). BALSS (1929) distinguished *S. monodi* mainly by the clusters of granules on the anterolateral corners of the dorsal carapace (which *S. floweri* lacks), and noted (correctly) that *S. monodi* occurs in savanna regions. In the absence of any new studies on *S. monodi* BOTT (1955, 1959) and MONOD (1977, 1980) simply updated BALSS's nomenclature. Both BALSS (1929) and BOTT (1955) provided only a brief description of *S. monodi* and each gave a simple sketch of the dorsal carapace. The illustrations in MONOD (1977, fig. 108-109) labelled "*Sudanonautes pelii*" clearly depict *S. monodi*. CAPART (1954, fig. 9, 29) illustrated gonopod one and the dorsal carapace of the type of *S. monodi*, which correspond well with the figures provided here.

Comparisons.- *Sudanonautes monodi* is the only species of freshwater crab found in dry sudan savanna from Nigeria to Sudan. In the guinea savanna zone of Nigeria, *S. monodi* occurs together with *S. aubryi* and *S. floweri*. These taxa can be distinguished from *S. floweri* as follows. *S. monodi* has a raised medial fold on the terminal article of gonopod 1 which is considerably higher than that of *S. floweri* and *S. aubryi*. *Sudanonautes monodi* has patches of granules on the anterior corners of the carapace behind the postfrontal crest, while *S. floweri* and *S. aubryi* lack these granules. The carapace height of both *S. monodi* and *S. floweri* is significantly ($P < 0.001$) higher (ch/fw *S. monodi* and *S. floweri* 1.46 and 1.68 respectively) than *S. aubryi* (ch/fw 1.29). The carapace of *S. monodi* is significantly ($P < 0.001$) wider (cw/fw *S. monodi* 3.82) than that of *S. aubryi* (cw/fw 3.52). Finally, *S. floweri* has a small hard anterior process on the mandibular palp at the junction between the two segments, and conspicuous raised ridges on the sternum at the points where the chelipeds insert: both *S. monodi* and *S. aubryi* lack these features.

Sudanonautes granulatus (BALSS, 1929)

fig. 31B, 32G, 33G, 34G, 35G, 36J, 37G, 39B, 53W, 54-57, 60G, 67H, table IX.

Potamonautes decazei granulata BALSS, 1929, p. 119-120.

Potamon granulata, CHACE, 1942, p. 211

Sudanonautes (Sudanonautes) decazei decazei BOTT, 1955, p. 300-301 (part).

Sudanonautes orthostylis, CUMBERLIDGE, 1989, p. 231-237, fig. 1a-g, 2a-c; tables 1, 2 (part).-CUMBERLIDGE, 1991a, p. 1943, fig. 2f.

Sudanonautes granulatus, CUMBERLIDGE, 1993b, p. 805-816, fig. 1a-d. 2a-d, 3a-m, 4a-j, 6a-b, 7.

Diagnosis

The mandibular palp has two segments and the terminal segment consists of a single large posterior lobe; there is no additional small anterior process. The exopod of the third maxilliped has a flagellum; the terminal article of gonopod 2 is extremely short. The dactylus of the right cheliped of adult males is narrow and is arched so that it encloses a wide, ovoid interspace. The propodus of the major cheliped of adult males is longer than the carapace width. The medial fold of the terminal article of gonopod 1 is higher than the lateral fold in the mid section of the segment and there is a distinct longitudinal groove. The anterolateral margin of the carapace of adult males is smooth. The frontal margin is relatively wide (about one-third of the carapace width). The exorbital angle and epibranchial tooth are small and low and the intermediate tooth is small but distinct. The vertical sulcus on the sidewall of the carapace meets the anterolateral margin at the base of the intermediate tooth.

For a detailed description see CUMBERLIDGE (1993b).

Size.- The size at maturity varies between populations: specimens from Nigeria and Cameroon are adult between cw 22-25 to 45 mm; those from Côte-d'Ivoire are adult between cw 45-58 mm. The carapace proportions are given in table IX. Graphs of carapace dimensions are given in fig. 60G.

Colour

The following description is based on a living adult male from Nigeria. The dorsal carapace is brown with a purple, cream pattern, the sternum is white with a purplish tinge, the arthrodial membranes between the joints of the chelipeds and the pereiopods are brick-red and yellow; and the tips of the chelipeds are brown-red. In adult females and juveniles the carapace, chelipeds, and dorsal pereiopods are dark brown and the sternum and the undersides of P2-P5 are light brown.

Material examined

Togo, Misahöhe, near Palimé, north of Klouto; BAUMANN; 6 m cw 25-16 mm; (ZSM 1525/8 (ex 1214/8)) caught together with 1 m *S. aubryi*.- February 1905; Graf ZECH; 1 m adult cw 25 mm, collected with *S. aubryi* (ZSM 1523/3 (ex 1214/9)).

Cameroon, Victoria; 1907; O. VALLEY; 1 f adult cw 38 mm, 1 m subadult cw 23 mm (SMF 1786).- Bipindi near the Lokoundié river, northwest of Ebolowa; ZENKER; 1 m adult cw 31 mm, 1 f adult ovigerous cw 35 mm, 4 subadults cws 25, 15, 12, 9 mm, collected with *S. aubryi* (ZSM 1523/5 (ex 1214/3), donated by ZMB 1928).- Bipindihof; ZENKER; 1 m adult cw 34 mm, 2 f adults cws 34, 33. 8 mm (ZMB 10359).- Bafia near the Mban river, northwest of Yaounde; LEIDERER; 1 m subadult cw 21 mm (ZSM 1523/4 (ex 657)).

For other material see CUMBERLIDGE (1993b).

Type and distribution

Types (examined).- BALSS (1929) did not designate a holotype for *Potamon* (*Potamonautes*) *decazei granulata*. The museum label of a specimen from Lome (Bismarksburg), Togo collected by BÜTTNER (ZMB 8977) indicates that this specimen is a paratype. BOTT (1955) selected a female lectotype (ZMB 11257, cw 26 mm) from Misahöhe, near Palimé, north of Klouto, Togo (collected by SMEND) from the syntype series. Since the lectotype is a female, and since *S. granulata* shows variation in body size between populations in the two parts of its disjunct distribution, CUMBERLIDGE (1993b) redescribed the species from the largest male specimens from the two parts of its range - an adult male (cw 58.1 mm NNM 35246) from Côte-d'Ivoire, and an adult male (cw 41.5 mm NMU 28.IV.1979) from Nigeria. The female lectotype (ZMB 11257) from Togo, and a subadult male (cw 34.2 mm NMU 5.VI.1979) from Nigeria were also described.

Type locality.- Misahöhe, Togo.

Distribution.- Côte-d'Ivoire, Ghana, Togo, Nigeria, Cameroon, Bioko, and the Central African Republic.

Remarks

Sudanonautes granulatus was redescribed by CUMBERLIDGE (1993b). This is the only species in this genus with a disjunct distribution, and characters of the carapace, chelipeds, and gonopods vary according to geographic locality as well as ontogeny.

Ecology.- The following account also draws upon field notes kindly supplied by J. C. REID. This species is restricted to the tropical rainforest zone of West Africa from Côte-d'Ivoire to Cameroon, including the island of Bioko. In the Oban Hills northeast of Calabar, Nigeria, *S. granulatus* occurs in streams flowing through mature rainforest. Crabs were collected by hand from small streams (1-10 m wide, 20-50 cm deep), with fast, medium or slow flowing water, and even from a dried-up stream bed. The stream beds varied from mudstone to sand, together with either clay or yellow silt. These streams usually lacked vegetation (although one collection was made in a grass swamp). Crabs were collected from a variety of habitats: lodged among grass, under stones, burrowing among root material in the centre of the stream, hiding among stones, or burrowing in the moist bed of a dried up stream. One locality was a roadside ditch, with rust-red algae and grass in the water.

Sudanonautes orthostylis BOTT, 1955

fig. 31C, 32H, 33H, 34H, 35F, 36I, 37E, 39C, 53V, 54-57, 60H, 67F, table IX.

Sudanonautes (Sudanonautes) decazei orthostylis BOTT, 1955: p. 301, fig. 63a, b; pl. 29 fig. 2a-d.

Sudanonautes (Sudanonautes) pelii pelii, BOTT, 1964, p. 2 (part) (not *Cancer (Thelphusa) pelii* HERKLOTS, 1861).

Sudanonautes orthostylis, CUMBERLIDGE, 1989, p. 230 (part), fig. 1a-g, 2a-c.-CUMBERLIDGE, 1993c, p. 514-522, fig. 1-3, table 1.

Diagnosis

The terminal article of gonopod 1 is straight for most of its length then it curves sharply outward just before the tip; the medial and lateral folds are both equal and low and are fused into a tube; the longitudinal groove is undetectable. The subterminal segment of gonopod 1 is slim. The terminal article of gonopod 2 is extremely short. The major cheliped of adult males is longer and higher than the minor cheliped. The dactylus of the major cheliped of adult males is broad and flat and the fingers enclose a long narrow interspace. The carpus of the cheliped has two large pointed teeth; the second carpal tooth is smaller than the first carpal tooth. The carapace is flat (ch/fw 1.07) and the front is unusually wide (fw/cl 0.45), : it is the widest of any species in this genus. The carapace, anterolateral margins, the inferior orbital margin and the postfrontal crest are all smooth. The intermediate tooth on the anterolateral margin between the exorbital angle and the epibranchial tooth is small.

The vertical sulcus on the sidewall meets the anterolateral margin at the epibranchial tooth.

For a detailed description see CUMBERLIDGE (1993c).

Size.- This is a small species. The adult size range is between cw 22-28 mm. The carapace proportions are given in table IX. Graphs of carapace dimensions are given in fig. 60H.

Type and distribution

Types (examined).- Cameroon, Bipindihof; ZENKER; 1 m cw 25.8 mm (ZMB 11093), holotype.- Bipindihof; 7 m, 2 f, 3 juveniles (ZMB 11093), paratypes.- Bipindihof; 1 m (SMF 2439), paratype.

Type locality.- Cameroon, Bipindihof. This locality is most likely Bipindi (3° 08'N, 10° 30'E).

Distribution.- *Sudanonautes orthostylis* is known only from the rivers and streams of the rainforests of south west Cameroon.

Remarks

Sudanonautes orthostylis was described by BOTT (1955) and was redescribed by CUMBERLIDGE (1993c).

Sudanonautes kagoroensis CUMBERLIDGE, 1991a

fig. 31D, 32I, 33I, 34I, 35E, 36B, 37J, 39D, 53X, 54-57, 61A, 67G, table IX.

Sudanonautes kagoroensis CUMBERLIDGE, 1991a, p. 1938-1944, fig. 1-3.

Diagnosis

The postfrontal crest spans the entire carapace, and meets the anterolateral margins at the epibranchial teeth; the anterolateral margin posterior to the epibranchial tooth is completely smooth. The exorbital angle is continuous with the anterolateral margin, and the epibranchial and intermediate teeth are all low, small, and blunt. The carapace is flat (ch/fw 1.07). The surface of the carapace is smooth; the cervical, semi-circular, cardiac, and urogastric grooves are all faint and shallow. The vertical sulcus on the sidewall meets the anterolateral margin at the epibranchial tooth. The terminal article of gonopod 1 is long (two-thirds as long as the subterminal segment) and is slim; the segment is straight at the base and curves sharply outward at the halfway point; the medial fold is raised and is wider than the lateral fold at the midpoint; the longitudinal groove is visible in the basal half but is not otherwise visible on the ventral face; the subterminal segment of gonopod 1 is slim; the terminal article of gonopod 2 is extremely short. The dactylus of the major cheliped of adult males is slim and long and is not arched; the fingers enclose a long narrow interspace. The carpus of the cheliped has two large pointed teeth, the second is smaller than the first.

For a detailed description see CUMBERLIDGE (1991a).

Size.- This is a medium sized species. The adult size ranges from the pubertal moult (cw 40-50 mm) to cw 63.5 mm. The carapace proportions are given in table IX. Graphs of carapace dimensions are given in fig. 61A.

Colour

The following account is based on a living adult male. The dorsal carapace and postfrontal crest are dark brown and the sidewalls are pale brown. The branchial regions of the carapace are marked by distinct pale yellow patches. The carapace of females and juveniles lacks these pale yellow patches. The third maxillipeds are pale brown with a purple tinge; the epistome is orange/red, and the cornea of the eye is black. The sternum is pale brown-yellow. The arthrodial membranes between the joints of the chelipeds and pereiopods are pale-white/yellow. The ventral surface of the chelipeds is pale-brown/pink-mauve; the teeth of the cheliped are yellow; the tips of the chelipeds are yellow-cream. Pereiopods P2-P5 are uniformly light brown. The colour of specimens preserved in alcohol is uniformly light brown, regardless of sex and age.

Type and distribution

Type.- Nigeria, Kaduna State, Kagoro, Agban River, tributary of the Mada river; 11 April 1984; N. CUMBERLIDGE; 1 m adult 63 mm (NHML 1.12.6.1984), holotype.

Type locality.- Nigeria, Kaduna State, Kagoro, Agban river, tributary of the Mada river.

Distribution.- *Sudanonautes kagoroensis* is locally common in streams and rivers of the guinea savanna zone of west central Nigeria on the western slopes of the Jos plateau. The species occurs in the rivers on the top of the plateau, in the fast-flowing streams which drain the western escarpment, and in the rivers close to the western base of the plateau. All seven localities from which *S. kagoroensis* has been collected are associated with the Mada river, which collects water from the Jos plateau and which eventually joins the Benue/Niger river.

Remarks

Sudanonautes kagoroensis was described by CUMBERLIDGE (1991a).

Sudanonautes nigeria n. sp.

fig. 31E, 32J, 33J, 34J, 35J, 36D, 37I, 39E, 53Y, 54-57, 61B, 67G, table IX.

Description

Diagnosis.- The postfrontal crest spans the entire carapace, and meets the epibranchial teeth; the anterolateral margin posterior to the epibranchial tooth is raised and granular. The carapace is high and arched (ch/fw 1.46). The surface of the carapace is smooth; the cervical, semi-circular, cardiac, and urogastric grooves are all distinct. The exorbital angle tooth and the intermediate tooth are small and pointed; and the epibranchial tooth is reduced to a small granule. The vertical sulcus on the sidewall of the carapace meets the anterolateral margin at the intermediate tooth. The mandibular palp has two segments; the terminal segment of the mandibular palp has a small but distinct anterior process at the junction between the segments. The dactylus of the major cheliped of adult males is slim and straight and is not arched; the fingers enclose a long narrow interspace. The carpus of the cheliped has two large pointed teeth; the second carpal tooth is smaller than the first carpal tooth. The terminal article of gonopod 1 is very long (almost as long as the subterminal segment), and is slim, curved and needle-like (the medial and lateral folds are low and even); the longitudinal groove is visible in superior view. The basal half of the terminal article of gonopod 1 is straight; it then curves outward at the halfway point. The subterminal segment of gonopod 1 is broad and is widened medially; it has a distinct medial shoulder close to its junction with the terminal article. The terminal article of gonopod 2 is extremely short. This is a medium sized species, which reaches maturity at cw 45 mm.

Description of male holotype.- The carapace is transversely oval, and is extremely wide (it is widest in the anterior third, cw/fw 4.02), and it is extremely high, with a maximum height in the anterior region (ch/fw 1.46). The anterior margin of the front is slightly indented, and curves down so that it partly covers the antennulular fossae; the front is narrow (about one quarter of the carapace width, fw/cw 0.25). The carapace is high and arched (ch/fw 1.46). The surface of the carapace is smooth; the cervical, semi-circular, cardiac, and urogastric are grooves all distinct. The postfrontal crest consists of the fused epigastric and postorbital crests and the lateral ends of the postfrontal crest meet the anterolateral margins at each epibranchial tooth; the postfrontal crest is in an advanced anterior position very close to the superior orbital margins; the mid-groove of the postfrontal crest is broad, shallow, and forked. The exorbital angle tooth and the intermediate tooth are small and pointed and the epibranchial tooth is reduced to a small granule; the anterolateral margin posterior to the epibranchial tooth is raised and granular. The posterior margin of the carapace is wider than the front (about two-thirds as wide as the carapace). The vertical sulcus on the sidewall of the carapace is marked by a row of small rounded granules; it begins at the base of the intermediate tooth and separates the suborbital region from the hepatic region, and divides the sidewall into three parts. There is a long flagellum on the exopod of the third maxilliped; the ischium of the third maxilliped is smooth and has a distinct vertical sulcus; the merus of the third maxilliped has flanged edges. The mandibular palp has two segments and the terminal segment consists of a single large posterior lobe; there is a small but distinct anterior process at the junction between the segments. Sternal sulcus 1 (s1/s2) is visible; s2/s3 completely crosses the sternum; s3/s4 is reduced to two small notches at the sides of the sternum. All four episternal sulci (s4/e4-s7/e7) are clearly visible.

The major cheliped of adult males is longer and higher than the minor cheliped. The dactylus of the major cheliped of adult males is slim, straight and is not arched so that the fingers enclose a long narrow interspace. The fingers of the right cheliped have six larger teeth on the lower digit and four larger teeth on the upper digit and these are interspersed with a series of smaller pointed teeth. The medial margin of the carpus of the cheliped has two large pointed teeth; the first carpal tooth is larger than the second carpal tooth. The inferior and medial inferior margins of the ventral face of the merus of P1 have rows of small teeth, and a singe large distal tooth. The inner surface of the merus of P1 has a clear meral tympanum; the superior margin of the merus of P1 is rough, and has rows of carinae. Walking legs (P2-P5) are long; P3 is the longest and P4 is the shortest. The meri of P2-P5 have a low, almost indistinguishable, subterminal tooth. The propodi of P5 are long and slim. The posterior margin of the carapace of the propodus of the walking legs is smooth.

Abdominal segments a1-a6 are four sided; the sides of taper inward; the telson (a7) is triangular: its sides are of equal length and they taper toward the rounded terminal margin; a1-a2 are narrow and fixed, and occupy the entire area between the coxae of P5; a3-a7 has a triangular outline and moves as one piece (hinging between segments a2 and a3); a3 is the broadest segment. The terminal article of gonopod 1 is very long (almost as long as the subterminal segment), and is slim, curved and needle-like and the medial and lateral folds are low and even; the longitudinal groove is visible, but only in the superior view. The basal half of the terminal article of gonopod 1 is straight before curving outward at the halfway point; the subterminal segment of gonopod 1 is widened medially and has a distinct medial shoulder. Gonopod 2 is shorter than gonopod 1 (reaching only to the junction between last two segments of gonopod 1). The terminal article of gonopod 2 is extremely short (only 1/15 as long as subterminal segment) and has a pointed tip. The subterminal segment of gonopod 2 is as long as the terminal article of gonopod 2; it is widest at the base; it then tapers sharply inward to form a long, thin, pointed, upright process that supports the short terminal article.

Adult female.- The right and left chelipeds of adult females are heterochelous (unequal in both length and height); they have the same proportions as those of adult males of the same size. The abdomen of adult females is rounded and wide and reaches the coxae of P2-P5. The distal segments of the abdomen of adult females are long and wide, and the abdomen is widest at the a4/a5 sulcus; the telson (a7) is semicircular.

Size.- A medium-sized species. The adult size range is from cw 33-42 to 60.4 mm. The carapace proportions are given in table IX. Graphs of carapace dimensions are given in fig. 61B.

Type and distribution

Type.- West Africa, Nigeria, Uzombe, southeastern Nigeria; 26 March 1973; VOELKER; 1 m adult cw 54 mm, 1 f adult cw 44 mm (SMF 6905, donated by ZIM).- Uzombe, southeastern Nigeria; 26 March 1973; VOELKER; 1 m adult cw 54 mm, 1 f adult cw 44 mm (ZIM K30303). Largest male (cw 54 mm) from Uzombe (SMF 6905) is designated here as the holotype. The female (SMF 6905) and the other two specimens (ZIM K30303) are paratypes.

Type locality.- West Africa, Nigeria, Uzombe, southeastern Nigeria.

Etymology.- The species is named for the country of Nigeria where it is endemic. The species name *nigeria* is a noun in apposition.

Remarks

Comparisons.- *Sudanonautes nigeria* is known only from four specimens collected in the rainforest zone of southeast Nigeria in the western part of the Lower Guinea forest. This species is most similar to *S. floweri*, *S. monodi* and *S. aubryi*. *Sudanonautes nigeria* can be distinguished from *S. monodi* and *S. aubryi* as follows. First, the vertical sulcus on the sidewall of *S. nigeria* meets the anterolateral margin at the intermediate tooth, whereas this sulcus meets this margin at the epibranchial tooth in *S. monodi* and *S. aubryi*. Second, the terminal article of gonopod 1 of *S. monodi* and *S. aubryi* has a raised medial fold, whereas that of *S. nigeria* is slim and lacks a raised medial fold. *Sudanonautes nigeria* has conspicuous raised ridges on the sternum at the points where the chelipeds insert, whereas in *S. monodi* and *S. aubryi* this part of the sternum is smooth. *Sudanonautes nigeria* is closest to *S. floweri*. Both species have a small hard anterior process on the mandibular palp at the junction between the two segments, both have conspicuous raised ridges on the sternum at the points where the chelipeds insert, and the vertical sulcus on the sidewall meets the anterolateral margin at the intermediate tooth. *Sudanonautes nigeria* can be distinguished from *S. floweri* as follows. *Sudanonautes floweri* has a raised medial fold on the terminal article of gonopod 1, whereas the terminal article of gonopod 1 of *S. nigeria* lacks a raised medial fold. Furthermore, the carapace of *S. floweri* is very high and arched (ch/fw for *S. floweri* is 1.68) compared to that of *S. nigeria* (ch/fw 1.46).

Potamonemus CUMBERLIDGE & CLARK, 1992

fig. 64D

Potamonemus CUMBERLIDGE & CLARK, 1992, p. 149, fig. 1-3, tables 1-2, pl. 1.

The carapace is moderately high (ch/fw 1.06-1.10). There is no intermediate tooth on the anterolateral margin between the epibranchial tooth and the exorbital angle. The postfrontal crest is prominent, almost horizontal, and complete (the lateral ends meet the anterolateral margins). The sidewall is divided by two sulci into three parts. The mandibular palp has two segments; the terminal segment consists of a large oval posterior lobe. There is no flagellum on the exopod of the third maxilliped in all species. Sternal sulcus s3/s4 is represented only by two short notches at the sides of the sternum. The terminal article of gonopod 1 is very long (at least two-thirds as long as the subterminal segment). The terminal article of gonopod 1 curves outward and the curvature begins half way along the segment. The medial and lateral folds on the ventral side of the terminal article of gonopod 1 are low and of equal size; they are separated lengthways by the distinct longitudinal groove. The terminal article is broadened in the middle, which is the result of a high medial fold, and the longitudinal groove is visible at least for part of its length. The dorsal side of the terminal article of gonopod 1 is smooth, and there is a broad membrane (the dorsal membrane) at the junction between the two distal segments. The subterminal segment of gonopod 1 is broadened significantly at the base (in other species). The terminal article of gonopod 2 is very short (one fifteenth the length of the subterminal segment).

Type species.- *Potamonemus mambilorum* CUMBERLIDGE & CLARK, 1992

The genus comprises three closely related species all of which are found in the rainforest region of southwest Cameroon. One species (*P. sachsi*) is also found in the rainforests of southwestern Togo.

Key to the species of *Potamonemus*

1. The length of the lower margin of the propodus of the major cheliped of adult males is greater than the carapace width; the dactylus of the major cheliped is narrow and is greatly arched; the interspace between the closed fingers of the major cheliped is ovoid. *P. mambilorum*

\- The length of the lower margin of the propodus of the major cheliped of adult males is less than the carapace width; the dactylus of the major cheliped is broad and is not arched; the interspace between the closed fingers of the major cheliped is long and narrow. 2

2 The longitudinal groove on the terminal article of gonopod 1 follows a twisting path along the ventral side of th segment, but it is not visible on the dorsal side; this groove reaches to the tip of the segment; there are no bristles along the margins of the terminal article of gonopod 1. The vertical sulcus on the sidewall of the carapace meets the anterolateral margin between the exorbital angle and the epibranchial tooth. The carapace has patches of short hair along the anterolateral and posterolateral margins. *P. sachsi*

\- The longitudinal groove on the terminal article of gonopod 1 is visible on the dorsal side of the segment, but it is not

visible on the ventral side; this groove is not visible at the tip of the segment; there are bristles along the margins of the terminal article of gonopod 1. The vertical sulcus on the sidewall of the carapace meets the anterolateral margin at the epibranchial tooth. The carapace is completely smooth.
P. asylos

Potamonemus mambilorum CUMBERLIDGE & CLARK, 1992

fig. 40A, 41A,D, 42A,D, 43A,D, 44A, 53E, 54-57, 61C, 65E, table IX.

Potamonautes anchetiae, BALSS, 1929, p. 117 (part).

Potamonemus mambilorum CUMBERLIDGE & CLARK, 1992, p. 149, fig. 1-3, tables 1-2, pl. 1.-CUMBERLIDGE, 1993a, p. 582-584, fig. 5e-f, 6g-i, table 3.

Diagnosis

The major (right) cheliped of adult males is longer and higher than the minor (left) cheliped, the dactylus of the cheliped is highly arched forming an ovoid interspace; the terminal article of gonopod 1 has a twisting longitudinal groove on the ventral side; the exorbital angle and the epibranchial tooth are small and low; the vertical sulcus on the sidewall meets the anterolateral margin at the base of the epibranchial tooth; the carapace is smooth all over, and has no deep grooves, granulations or hairs.

For a detailed description see CUMBERLIDGE & CLARK (1992) and CUMBERLIDGE (1993a).

Size.- The adult size range is from cw 29 mm to cw 38.1 mm. The carapace proportions are given in table IX. Graphs of carapace dimensions are given in fig. 61C.

Material examined

Cameroon, Foumban, region of Dschang; MONOD; 2 f adults cw 34, 28 mm, 1 f subadult cw 22.5 mm (ZSM 1520/1 (ex 1176/1)).

Type and distribution

Type.- Cameroon, Somié village, Tikow plain 760 m; 7 January 1987; Dr. David ZEITLIN; 1 m, cw 34.5 mm (NHML 1991: 183); holotype. Fifteen specimens are held in the ZMB (all are paratypes).

Type locality.- Somié Village, Tikow Plain, southwest Cameroon.

Distribution.- This species is found in the forested highlands of southwest Cameroon (Bamenda, Bambulae and Nfom Grasslands), and in the forested lowlands of south Cameroon (Douala and Yaounde).

Remarks

Most of the material in the ZMB was formerly identified as *Potamonautes anchetiae* BRITO-CAPELLO, 1871 by Dr. H. BALSS (see CUMBERLIDGE & CLARK, 1992 and CUMBERLIDGE, 1993a for details).

Ecology.- The collector of the type specimen (Dr. David ZEITLIN) provided the following comments. *Potamonemus mambilorum* is a riverine crab and is eaten by the Mambila people especially during the dry season when crabs are caught by villagers who bail out drying sections of river bed. The Mambila people call this species the "Kap" crab. *Sudanonautes faradjensis* is sympatric with *P. mambilorum*. The local name for *S. faradjensis* is the "Nyar" crab.

Potamonemus sachsi CUMBERLIDGE, 1993a

fig. 40B, 41B,E, 42B,E, 43B,E, 44B, 53F, 54-57, 61D, 65F, table IX.

Potamonemus sachsi CUMBERLIDGE, 1993a, p. 571-576, fig. 1, 2, 5c-d, 6d-f, 7; tables 1, 3.

Diagnosis

The carapace has patches of short hairs along the anterolateral and posterolateral margins that continue around to the sidewalls in the subhepatic and pterygostomial regions. There is a twisting longitudinal groove on the ventral side of the terminal article of gonopod 1, this groove is not visible on the dorsal side; the longitudinal groove reaches to the tip of the segment; there are no hairs or bristles on the terminal article. The vertical sulcus on the sidewall of the carapace meets the anterolateral margin between the exorbital angle and the epibranchial tooth. The inferior medial margin of the merus of the right cheliped has two large distal teeth. This is a small species, and reaches maturity between cw 23-28 mm.

For a detailed description see CUMBERLIDGE (1993a).

Size.- The adult size range is from the pubertal moult (cw 23-28 mm) to the largest known specimen (cw 28 mm). The carapace proportions are given in table IX. Graphs of carapace dimensions are given in fig. 61D.

Colour

The following description is based on living specimens of *P. sachsi* from Nigeria. The carapace is dark brown or pale purple, the pereiopods and the sternum are light brown or pale purple; the abdomen is light brown; the undersides of P2-P5 are pale purple or light brown-purple. The chelipeds of adult males are pink-red; the chelipeds of juveniles lack the pink-red colour.

Material examined

Cameroon, Bamenda; 21 April 1975; 1 m adult cw 33 mm, 1 f adult cw 32 mm (SMF 7272).- Buea, Tole; 10 November 1980; SCHLEGEL & FERRARA; 1 f adult cw 20 mm ovigerous (SMF 11715).- Bura; BIGGE; 1 f adult cw 22 mm (ZSM 1521/1 (ex 1176/3)).

Nigeria, Obudu plateau; 30.18.1968, Peter VOLSPE; 2 m adults cws 28, 29 mm (SMF).

Type and distribution

Types (examined).- Cameroon, Bamenda; 1 m, cw 33.1 mm (ZIM K30395) holotype.- Cameroon, Bamenda; 7 specimens (ZIM K30395) paratypes.

Type locality.- Bamenda highlands, southwest Cameroon.

Distribution.- This species is known only from the Bamenda highlands in southwest Cameroon, and from the Obudu plateau in southeast Nigeria, which is continuous with the Bamenda highlands.

Remarks

Ecology.- There are no ecological notes available for the specimens from Cameroon. The following notes refer to the specimens from the Obudu plateau in Cross River State, Nigeria which were collected by the author. The steep-sided plateau is some 1,000 m above sea level rising steeply out of the rainforest zone of southeast Nigeria. This Nigerian highland region continues across the nearby border with Cameroon (where it is known as the Bamenda highlands), and this latter region is where the specimens in the ZIM, Hamburg were collected. The climate on top of the plateau is cooler, but still humid, and supports a tropical montane vegetation, including extensive grasslands. The streams and rivers where the specimens of *P. sachsi* from Nigeria were collected drain south into the Cross River, just to the east of the Nigeria-Cameroon border. These streams are about 2 m wide and 10 cm deep, with a medium flow, and a gravel-sand bed. The crabs were all caught by hand, from under boulders in stretches of the stream that were shaded by overhanging vegetation and the forest canopy.

Potamonemus asylos CUMBERLIDGE, 1993a

fig. 40C, 41C,F, 42C,F, 43C,F, 44C, 53G, 54-57, 61E, 65F, table IX.

Potamonemus asylos CUMBERLIDGE, 1993a, p. 576-584, fig. 3, 4, 5a-b, 6a-c, 8a-b; tables 2, 3.

Diagnosis

The dactylus of the major (right) cheliped of the adult male is broad and flat and is not arched. The terminal article of gonopod 1 has distinct bristles along the margins; the terminal article is widest in the mid section and the longitudinal groove ends before reaching the tip; this groove is only visible on the dorsal side, and is not seen on the ventral side, the entire groove can only be seen only when the gonopod is viewed along its medial edge. The inferior margins of the merus of the cheliped are lined by conspicuous teeth. The vertical sulcus on the sidewall of the carapace meets the anterolateral margin at the epibranchial tooth. This is a small species that matures at cw 20 mm.

For a detailed description see CUMBERLIDGE (1993a).

Size.- The adult size ranges from the moult of puberty (cw 20.1 mm) to the largest known specimen (cw 27.7 mm). The carapace proportions are given in table IX. Graphs of carapace dimensions are given in fig. 61E.

Type and distribution

Type.- Cameroon, Buea / Kumba area; 1969; R. H. L. DISNEY, donated by TREFOR WILLIAMS; 1 m, cw 27.7 mm (NHML 1994.587 donation from NMU 1969/1991), holotype.- Buea / Kumba; 1969; R. H. L. DISNEY, donated by TREFOR WILLIAMS; 6 specimens (NHML 1994.588-591, donation from NMU 1969/1991), paratypes.

Type locality.- Cameroon, Buea, southwest Cameroon.

Distribution.- Buea and Victoria, southwest Cameroon.

Remarks

Two male specimens (cws 21.3, 20.1 mm) from Victoria, Cameroon (ZIM K3607), collected 6 February 1912, by Dr. E. FICKENDAY, were described as “Essbare Landkrabben” (edible land crabs).

Family Uncertain

Subfamily GLOBONAUTINAE Bott, 1969b

fig. 63B

Gecarcinucinae Rathbun, 1904, p. 247 (part).-Bott, 1959, p. 995 (part).-1970b, p. 25 (part).-Chace, 1942, p. 226 (part).

Gecarcinucidae Bott, 1969b, p. 359 (part).-1970b, p. 22 (part).-Monod, 1977, p. 209.-Monod, 1980, p. 380 (part).

Globonautinae Bott, 1969b, p. 359.-Bott, 1970b, p. 23.-Cumberlidge, 1987, p. 2210.-Cumberlidge, 1996a, p. 681-695.-Cumberlidge, 1996b, p. 809-820.

The vertical sulcus on the sidewall of the carapace meets the anterolateral margin at the epibranchial tooth. The terminal segment of the mandibular palp consists of a single large posterior lobe with either a large subequal anterior lobe or a small anterior process. The terminal article of gonopod 1 is short (one third as long as the subterminal segment of gonopod 1), and tube-like with a broad tip. The carapace is smooth and lacks visible lateral carinae. The sidewall is divided by two sulci into three parts. The exopod of the third maxilliped lacks a flagellum. All species in the Globonautinae are small animals, and do not grow larger than cw 32 mm.

Type genus.- *Globonautes* Bott, 1959

The Globonautinae is a wholly West African subfamily with a disjunct distribution. Members of this subfamily are found in the western Upper Guinea forest of West Africa, from Guinea to Liberia, and in the eastern Lower Guinea forest in southwest Cameroon. All species in the Globonautinae are endemic to West African rainforests, most have a restricted distribution within this area, and most are known only from a small type series or from a single locality. Included are *G. macropus*, four species of *Afrithelphusa* (*A. gerhildae, A. afzelii, A. monodosus*, and *A. leonensis*) and two species of *Louisea* (*L. edeaensis* and *L. balssi*). Bott (1969b, 1970b) originally assigned *Afrithelphusa* to the Gecarcinucinae (together with *Gecarcinautes* Bott, 1960, and four Indian genera (*Barytelphusa* Alcock, 1909, *Gecarcinucus* H. Milne Edwards, 1844, *Cylindrotelphusa* Alcock, 1909 and *Ingletelphusa* Bott, 1970b). Later, Cumberlidge (1996a,b) removed *Afrithelphusa* from the Gecarcinucinae and included it together with *Globonautes* in the Globonautinae, but did not change the family assignment of this subfamily to the Gecarcinucidae. In the present work *Louisea* (which was assigned to the Potamonautidae by CUMBERLIDGE, 1994a) is now included in the Globonautinae. *Globonautes macropus*, the four species of *Afrithelphusa* (*A. gerhildae*, *A. afzelii*, *A. monodosus* and *A. leonensis*) and *Louisea edeaensis* are all listed in the IUCN red list of threatened and endangered animals (IUCN, 1996).

Key to the genera of the Globonautinae

1. The terminal segment of the mandibular palp is clearly bilobed, with a large subequal anterior lobe, almost as big as the posterior lobe. There is no intermediate tooth on the anterolateral margin between the exorbital angle and the epibranchial tooth. There is a clear vertical sulcus on the ischium of the third maxilliped. **2**

\- The terminal segment of the mandibular palp has an anterior process that is only about one quarter as big as the posterior lobe. There is an intermediate tooth on the anterolateral margin between the exorbital angle and the epibranchial tooth. There is no sulcus on the ischium of the third maxilliped. ***Louisea***

2. The terminal article of gonopod 2 is very short (1/15 the length of the subterminal segment); the terminal and subterminal segments of gonopod 1 are fused, and the junction between the segments on the ventral side is smooth and there is no visible sulcus; there is no dorsal membrane at the junction between the segments on the dorsal side. The postfrontal crest is incomplete: only the epigastric crests are distinct, while the rest of the postfrontal crest is faint and is broken in places. ***Globonautes***

\- The terminal article of gonopod 2 is a long flagellum (just a little shorter than the subterminal segment of gonopod 2); the terminal and subterminal segments of gonopod 1 are not fused, and the junction between the segments on the ventral face is clearly marked by a distinct sulcus; there is a broad dorsal membrane at the junction between the segments on the dorsal side. The postfrontal crest is sharp edged and complete, and runs unbroken across the carapace to meet the anterolateral margins. ***Afrithelphusa***

Globonautes BOTT, 1959

fig. 64E

Globonautes BOTT, 1959, p. 995, fig. 1-3.-BOTT, 1969b, p. 359.-MONOD, 1977, p. 1209.-MONOD, 1980, p. 380.-CUMBERLIDGE, 1987, p. 2215.-CUMBERLIDGE, 1996a, p. 683-684.

The carapace is very wide (cw/fw 3,94); very long (cl/fw 3,04); and very high and convex (ch/fw 1.69). The postfrontal crest is incomplete and is broken in places, so that only the epigastric crests are distinct, while the rest of the postfrontal crest is faint. The anterolateral margin always lacks an intermediate tooth between the exorbital angle and the epibranchial tooth. The antero- vertical sulcus on the sidewall of the carapace meets the lateral margin at the epibranchial tooth. The mandibular palp always has two segments. The exopod of the third maxilliped always lacks a flagellum. Sternal sulci s1/s2, s2/s3 and s3/s4 are deep and completely cross the sternum; the sterno-abdominal cavity terminates halfway along on s4. The terminal article of gonopod 1 is short (about one third the length of the subterminal segment of gonopod 1) almost straight, and tapers to a tubular tip, which has a hole (the apical opening) at the tip. The medial and lateral folds on the terminal article of gonopod 1 are equal and low, and the longitudinal groove is not visible. The subterminal segment of gonopod 1 is a long, slim rectangle. The terminal and subterminal segments of gonopod 1 are fused and the junction between the segments on the ventral face is smooth and the sulcus between the segments is not visible; there is no dorsal membrane at the junction between the segments on the dorsal side. The terminal article of gonopod 2 is very short (one fifteenth the length of the subterminal segment).

Type species.- *Potamon (Geothelphusa) macropus* RATHBUN, 1898

Globonautes is a monotypic genus found only in the western Upper Guinea forest of West Africa from Guinea to Liberia. *Globonautes* was originally established by BOTT (1959) to accommodate three species, *G. macropus*, *G. monodosus*, and *G. balssi* BOTT, 1959. In later works (BOTT, 1969b, 1970b) the genus was conceived of as a single species, with three subspecies, *G. m. macropus*, *G. m. balssi*, and *G. m. edeaensis* BOTT, 1969b. *Globonautes macropus* has long been recognised as a unique species (CUMBERLIDGE, 1987, 1991b, 1996a,b) that is entirely distinct from BOTT'S (1969b, 1970b) other two subspecies (*G. m. edeaensis* and *G. m. balssi*). CUMBERLIDGE (1994a) reassigned *G. m. edeaensis* to *Louisea* as *L. edeaensis*, and recorded *G. m.*

balssi as incertae sedis. In the present work these two taxa are included as *Louisea edeaensis* and *L. balssi*. Although *G. monodosus* was omitted by BOTT (1969b, 1970a) the species was recognised by other workers (MONOD, 1977, 1980; CUMBERLIDGE, 1987, 1996a,b). In addition, CUMBERLIDGE (1987) described *G. leonensis* from new material from Sierra Leone. CUMBERLIDGE (1996a,b) reassigned both *G. monodosus* and *G. leonensis* to *Afrithelphusa*, and recognised *Globonautes* as a monotypic genus with *G. macropus* as the type species of the genus. BOTT (1969b, 1970a) assigned *Globonautes* to the Globonautinae and *Afrithelphusa* to the Gecarcinucinae RATHBUN, 1904; CUMBERLIDGE (1996a,b) included both *Globonautes* and *Afrithelphusa* in the Globonautinae.

Globonautes macropus (RATHBUN, 1898)

fig. 45, 46E, 47E, 48D, 49E, 50E, 51E, 52A, 53Z, 54-57, 62E, 68A, table IX.

Potamon (Geothelphusa) macropus RATHBUN, 1898, p. 29, pl. 2, fig. 1-4.-RATHBUN, 1900, p. 284.-RATHBUN, 1905, p. 221-222, pl. 18 [1904], fig. 1.

Cylindrothelphusa macropus, RATHBUN, 1921, p. 385.-CHACE, 1942, p. 226.-BOTT, 1955, p. 213.

Globonautes macropus, BOTT, 1959, p. 996-997, fig. 1-3.-CUMBERLIDGE, 1987, p. 2214-2215, fig. 2c-e, tables 1,2.-CUMBERLIDGE, 1991b, p. 69-80.-CUMBERLIDGE & SACHS, 1991, p. 55-68.-CUMBERLIDGE, 1996a, p. 682-684, table 1.-CUMBERLIDGE, 1996b, p. 813-814.

Globonautes macropus macropus, BOTT, 1970b, p. 23-24, pl. 1, fig. 1-2.-MONOD, 1977, p. 1209.-MONOD, 1980, p. 380.

Diagnosis

As for genus.

For more detailed descriptions see RATHBUN (1898); BOTT (1959, 1970a); MONOD (1977); CUMBERLIDGE (1987, 1991b, 1996a,b), and CUMBERLIDGE & SACHS (1991).

Size.- The adult size range is from cw 25-32 mm. The carapace proportions are given in table IX. Graphs of carapace dimensions are given in fig. 62E.

Distribution and types

Type.- West Africa, Liberia, Monrovia, mouth of the Mesurado river; 1 m, cw 32 mm (USNM 20643), holotype.

Type locality.- West Africa, Liberia, Monrovia, mouth of the Mesurado river.

Distribution.- Liberia and Guinea.

Remarks

From 1898 to 1959 *G. macropus* was known only from the holotype from Liberia. The next significant find was a series of seven specimens from Guinea which were used by BOTT (1959) to describe the genus *Globonautes*. The species was subsequently made the type genus of the subfamily Globonautinae BOTT, 1969b. More recently, CUMBERLIDGE (1987) redescribed gonopods 1 and 2 of the holotype of *G. macropus*, and found the gonopods to differ significantly from that described by BOTT (1959), and from those of the other species assigned by these authors to *Globonautes*. In 1988-89 a new series of specimens of *G. macropus* were collected from Liberia and the ecology, distribution, and respiratory system of this species were described for the first time (CUMBERLIDGE, 1991b; CUMBERLIDGE & SACHS, 1991). CUMBERLIDGE (1996a,b) revised the taxonomy of the West African globonautids, and those conclusions are followed here.

Afrithelphusa BOTT, 1969b

fig. 64F

Globonautes BOTT, 1959, p. 997-999.-BOTT, 1969b, p. 360.-MONOD, 1977, p. 1209.-MONOD, 1980, p. 380.-CUMBERLIDGE, 1987, p. 2210-2214.

Afrithelphusa BOTT, 1969b, p. 359.-BOTT, 1970a, p. 25-27.-MONOD, 1977, p. 1208-1210.-MONOD, 1980, p. 380.-CUMBERLIDGE, 1996a, p. 684-688, table 1.-CUMBERLIDGE, 1996b, p. 814.

The carapace is high and convex (ch/fw 1.44-1.83). The postfrontal crest is sharp edged and complete, and runs unbroken across the carapace to meet the anterolateral margins. The anterolateral margin always lacks an intermediate tooth between the exorbital angle and the epibranchial tooth. The vertical sulcus on the sidewall of the carapace meets the anterolateral margin at the epibranchial tooth. The mandibular palp always has two segments. The exopod of the third maxilliped always lacks a flagellum. Sternal sulci s1/s2, s2/s3 and s3/s4 are deep and completely cross the sternum; the sterno-abdominal cavity terminates half-way along on s4. The terminal article of gonopod 1 is short (about one third the length of the subterminal segment of gonopod 1) almost straight, and tapers to a tubular tip, which has a hole (the apical opening) at the tip. The medial and lateral folds on the terminal article of gonopod 1 are equal and low, and the longitudinal groove is visible. The subterminal segment of gonopod 1 is a long, slim rectangle. The terminal and subterminal segments of gonopod 1 are not fused and there is a groove marking the junction between the segments on the ventral side; there is a dorsal membrane at the junction between the segments on the dorsal side. The terminal article of gonopod 2 is a long flagellum (just a little shorter than the subterminal segment of gonopod 2).

Type species.- *Afrithelphusa gerhildae* BOTT, 1969b.

This genus is found only in the Upper Guinea forests of West Africa from Guinea to Sierra Leone. According to CUMBERLIDGE (1996a,b) *Afrithelphusa* includes four species, *A. gerhildae, A. afzelii, A. monodosus*, and *A. leonensis*. The latter two species were assigned to *Afrithelphusa* in recognition of significant differences between *G. macropus* and the other West African globonautines with respect to characters of the gonopods and carapace. For example, the terminal article of gonopod 2 of *G. macropus* is extremely short, while that of the other four species is a long flagellum. Differences in characters of gonopod 2 of this magnitude have warranted the separation of other African freshwater crab genera. For example, the gonopod 2 with a very short terminal article distinguishes *Sudanonautes* from *Potamonautes* and *Liberonautes* (both genera have a gonopod 2 with a very long terminal article), and a gonopod 2 with a very short terminal article distinguishes *Potamonemus* from *Louisea* (gonopod 2 with a long terminal article). In addition, the postfrontal crest of *G. macropus* is interrupted in places and is poorly defined, while that of the other four species is sharp-edged and runs uninterrupted across the carapace. When BOTT (1969b) established *Afrithelphusa* he separated it from *Globonautes* according to differences in gonopod 1, making *A. gerhildae* from Guinea the type species of the genus. The next year, BOTT (1970a) added a second species, *A. afzelii* from Sierra Leone, to the genus. *Afrithelphusa monodosus* and *A. leonensis* share a number of characters with *A. gerhildae* and *A. afzelii* - all four have a long terminal article of gonopod 2, a straight terminal article of gonopod 1, a clearly visible sulcus between the terminal and subterminal segments of gonopod 1, and a sharp-edged postfrontal crest running unbroken across the carapace to meet the anterolateral margins. The long terminal article of gonopod 2 and the unbroken postfrontal crest of these taxa preclude their inclusion in *Globonautes*.

Key to the species of *Afrithelphusa*

1. There are patches of dense short hair on the sidewalls of the carapace in the pterygostomial region; the walking legs P2-P5

are very short (only 1.1 to 1.5 times cw); the flagellum of the terminal article of gonopod 2 is relatively short, only as long as the terminal article of gonopod 1. *A. gerhildae*

- The sidewalls of the carapace in the pterygostomial region are smooth; the walking legs P2-P5 are very long (almost two times the cw); the flagellum of the terminal article of gonopod 2 is long, about twice as long as the terminal article of gonopod 1. 2

2. The terminal article of gonopod 2 ends in a barbed tip *A. monodosus*

- The terminal article of gonopod 2 ends in a rounded tip 3

3. The subterminal segment of gonopod 1 is broadened at the distal end by a prominent shoulder on the medial margin close to the junction between the segments. *A. afzelii*

- The subterminal segment of gonopod 1 is slim, and lacks a prominent shoulder close to the junction between the segments. *A. leonensis*

Afrithelphusa gerhildae Bott, 1969b

fig. 46A, 47A, 48A, 49A, 50A, 51B, 52B, 53AA, 54-57, 62A, 68B, table IX, plate 1

Afrithelphusa gerhildae Bott, 1969b, p. 360.-Bott, 1970a, p. 26-27, pl. 2, fig. 9-11, pl. 26, fig. 9.-Monod, 1977, p. 1210.-1980.-Monod, p. 380.-Cumberlidge, 1996a, p. 688-690, table 1.

Diagnosis

There are patches of dense short hair on the sidewalls of the carapace in the pterygostomial region; the walking legs P2-P5 are very short (the total length is only 1.1 to 1.5 times the cw); the flagellum of the terminal article of gonopod 2 is short, only about as long as the terminal article of gonopod 1. The carapace is high and arched (ch/fw 1.48) and the front is narrow (fw/cw 0.30).

For descriptions see Bott (1959, 1969b, 1970b); Monod (1977); Cumberlidge (1987, 1991b, 1996a,b); Cumberlidge & Sachs, 1991.

Size.- The adults range between cw 21 and 22.5 mm. The carapace proportions are given in table IX. Graphs of carapace dimensions are given in fig. 62A.

Types and distribution

Types.-West Africa, Guinea, Voile de la Mariée, Kindia, near Conakry; Marchal; 8 July 1957; 1 m cw 21 mm (SMF 2619a),

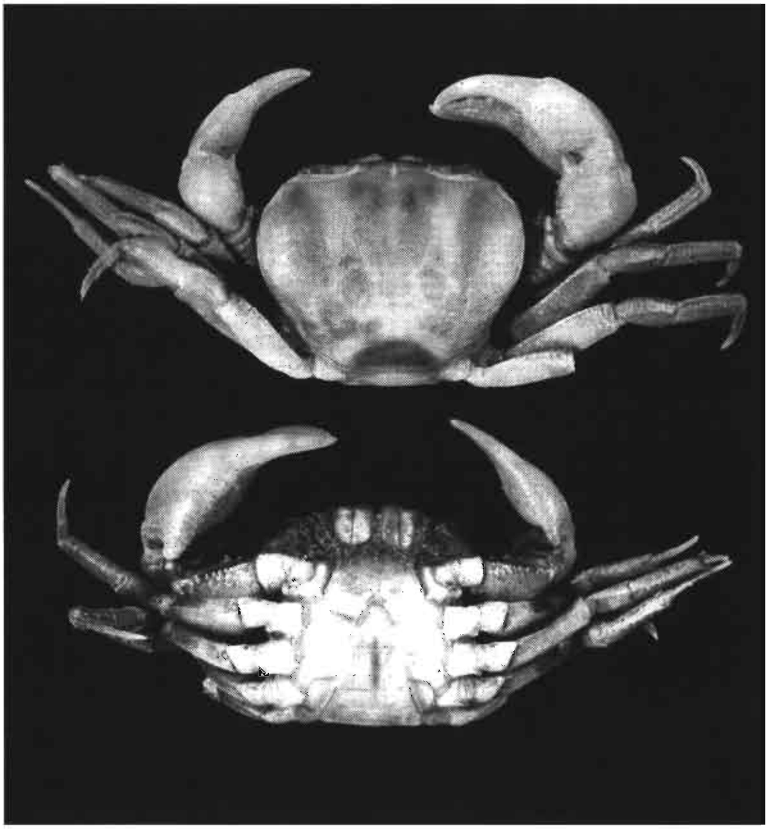


PLATE 1. *Afrithelphusa gerhildae* BOTT, 1969, adult male holotype (cw 21 mm) from Kindia, Guinea (SMF 2619a), dorsal and ventral views. Dr. Michael Türkay (SMF) is kindly thanked for supplying the photograph.

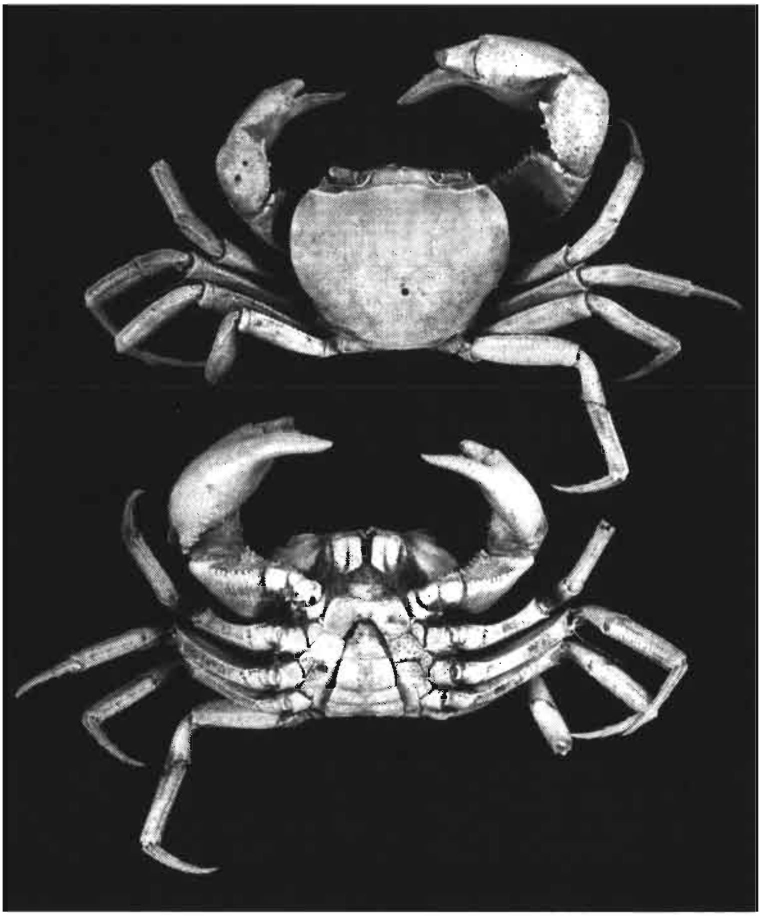


PLATE 2. *Afrithelphusa afzelii* (COLOSI, 1924), adult male lectotype (cw 29.5 mm) from Sierra Leone (SSN 168), dorsal and ventral views. Dr. Michael Türkay (SMF) is kindly thanked for supplying the photograph.

holotype.-Voile de la Mariée, Kindia, near Conakry; MARCHAL; 8 July 1957; 1 m cw 22.5 mm (SMF 2619a), paratype, 1 f, cw 22 mm (SMF 2619b), paratype.

Type locality.- West Africa, Guinea, Voile de la Mariée, Kindia, near Conakry.

Distribution.- The western portion of the Upper Guinea rainforest zone of West Africa in Guinea.

Remarks

The flagellum of the terminal article of gonopod 2 of the male paratype is shorter than that of *A. monodosus*, *A. leonensis*, and *A. afzelii*, but it is still much longer than the short stub-like terminal article of *G. macropus*. BOTT (1959) apparently included the type series of *A. gerhildae* from Voile de la Mariée, Guinea under *G. macropus*. His illustrations of *G. macropus* (BOTT, 1959, fig. 1-3) were based on one of these specimens from Guinea (a male cw 22.5 mm, SMF 2619a), rather than on the holotype of *G. macropus*. This would explain why the text and the figure of gonopod 2 (BOTT, 1959, fig. 3) describes a medium-length terminal article (as in *A. gerhildae*), rather than the short stub-like terminal article of gonopod 2 characteristic of *G. macropus*. This species was redescribed by CUMBERLIDGE (1996a,b).

Afrithelphusa afzelii (COLOSI, 1924)

fig. 46B, 47B, 49B, 50B, 54-57, 62B, 68C, table IX, plate 2

Parathelphusa (Barythelphusa) afzelii COLOSI, 1924, p. 19-21, figs 14a-b.

Para-Barythelphusa afzelii BALSS, 1936, p. 200.

Parathelphusa afzelii, CHACE, 1942, p. 226.-BOTT, 1955, p. 213.

Afrithelphusa afzelii, BOTT, 1970a, p. 27.-MONOD, 1977, p. 1210.-MONOD, 1980, p. 380.-CUMBERLIDGE, 1996a, p. 690-692, table 1.

Diagnosis

The subterminal segment of gonopod 1 is broadened at the distal end by a prominent shoulder on the medial margin close to the junction between the segments. The flagellum of the terminal article of gonopod 2 is long, about twice as long as the terminal article of gonopod 1 and it ends in a rounded tip. The carapace is high and arched (ch/fw 1.44), the front is very narrow (fw/cw 0.27), and the postfrontal crest is sharp edged and crosses the entire carapace, meeting the anterolateral margins. The walking legs (P2-P5) are very long (1.8 times cw).

For a detailed description see Colosi (1924), Bott (1955, 1970a), Monod (1977, 1980), Cumberlidge (1996a).

Size.- Adult sizes include cw 29 and 29.5 mm. The carapace proportions are given in table IX. Graphs of carapace dimensions are given in fig. 62B.

Type and distribution

Types (examined).- West Africa, Sierra Leone; 1790-1800; Adam Afzelius; 1 m cw 29.5 mm (SMNH 168), lectotype.- West Africa, Sierra Leone; 1790-1800; Adam Afzelius; 1 f cw 29.5 mm, dried specimen (SMNH 168), paratype.

Type locality.- West Africa, Sierra Leone.

Distribution.- West Africa, Sierra Leone.

Remarks

Bott (1969b, 1970a) did not illustrate *A. afzelii*. The description of gonopod 1 provided here is based on information provided by Dr. M. Türkay (SMF, pers. comm.); the description of the mandible is taken from Colosi (1924). *Afrithelphusa afzelii* is still only known from the type specimens. Bott (1969b, 1970a) and Monod (1977, 1980) distinguished between *A. afzelii* and *A. gerhildae* on the basis of differences in the length and width of P2-P5 (those of *A. afzelii* are long and thin, those of *A. gerhildae* are short and wide). This difference in limb lengths between the species was also observed by Cumberlidge (1991b). When the size difference between the two animals is taken into account, the total length of P2-P5 measured between 1.6 and 1.8 times cw (*A. afzelii*) and between 1.1 and 1.5 times cw (*A. gerhildae*). Bott's (1970a) description of *A. afzelii* noted that the third maxilliped had a flagellum on the exopod, but in the present study no flagellum was found. This species was redescribed by Cumberlidge (1996a,b).

Afrithelphusa monodosus (Bott, 1959)

fig. 46C, 47C, 48C, 49C, 50C, 51A, 52E, 53BB, 54-57, 62C, 68D, table IX.

Globonautes monodosus Bott, 1959, p. 997, fig. 4a-b, 5, 6a-b.-Monod, 1977, p. 1209.-Monod, 1980, p. 380.-Cumberlidge, 1987, p. 2212-2214, fig. 1a-d, 2a-b, tables 1,2.-Cumberlidge, 1996a, p. 692-693, fig. 1, 2, table 1.

Diagnosis

The terminal article of gonopod 1 is almost straight and curves slightly outward away from the midline; the final two-thirds are tube-like; the segment ends in a blunt, rounded tip. The subterminal segment of gonopod 1 is slim and lacks a prominent shoulder close to the junction between the segments. The flagellum of the terminal article of gonopod 2 is long, about twice as long as terminal article of gonopod 1, and ends in a barbed tip. The carapace is high and arched (ch/fw 1.83), the front is very narrow (fw/cw 0.25), and the walking legs (P2-P5) are very long (the total length is 1.7-1.8 times the cw).

For detailed descriptions see BOTT (1959) and CUMBERLIDGE (1987, 1996a).

Size.- Adult at cw 21.5 mm The carapace proportions are given in table IX. Graphs of carapace dimensions are given in fig. 62C.

Type and distribution

Type.- West Africa, Guinea, Boké; 1 April 1947; 1 m cw 21.5 mm (MNHN-B 5302), holotype.

Type locality.- West Africa, Guinea, Boké.

Distribution.- The western part of the Upper Guinea rainforest block of West Africa in Guinea.

Remarks

This species was redescribed by CUMBERLIDGE (1996a,b). The carapace is the most highly arched (ch/fw 1.83) of any species of freshwater crab from West Africa.

Afrithelphusa leonensis (CUMBERLIDGE, 1987)

fig. 46D, 47D, 48C, 49D, 50D, 51D, 52C, 53CC, 54-57, 62D, 68E, table IX.

Globonautes leonensis CUMBERLIDGE, 1987, p. 2210-2215, fig. 1e-h, 2f-g, tables 1, 2.-CUMBERLIDGE, 1996a, p. 693-694, table 1.

Diagnosis

The terminal article of gonopod 1 is almost straight and tapers to a rounded tip; the subterminal segment of gonopod 1 is slim and lacks a prominent shoulder close to the junction between the segments; the flagellum of the terminal article of gonopod 2 is long, about twice as long as the terminal article of gonopod 1; the segment ends in a rounded tip. The carapace is high and arched (ch/fw 1.55); the front is very narrow (fw/cw 0.25); and the walking legs (P2-P5) are very long (the total length is two times the cw).

For a detailed description see CUMBERLIDGE (1987; 1996a).

Size.- The adult size range is from cw 26.5-27 mm. The carapace proportions are given in table IX. Graphs of carapace dimensions are given in fig. 62D.

Type and distribution

Types (examined).- West Africa, Sierra Leone, Sugar Loaf Mountain; 7 October 1955; T. S. JONES; 1 m cw 26.4 mm (NHML 1955.10.7.42-43), lectotype.- West Africa, Sierra Leone, Sugar Loaf Mountain; 7 October 1955; T. S. JONES; 2 f cws 21, 27 mm(NHML 1955.10.7.42-43), paratypes.

Type locality.- West Africa, Sierra Leone, Sugar Loaf Mountain.

Distribution.- The western Upper Guinea rainforest of West Africa in Sierra Leone.

Remarks

Afrithelphusa leonensis was originally assigned to *Globonautes* by CUMBERLIDGE (1987). This species was later reassigned by CUMBERLIDGE (1996a,b) to *Afrithelphusa* in the Globonautinae.

Louisea CUMBERLIDGE, 1994a

fig. 64E

Globonautes BOTT, 1959, p. 995, pl. 1, fig. 1-6.-BOTT, 1969b, p. 359.-BOTT, 1970b, p. 23.

The carapace is of medium height (ch/fw 1.14-1.20). The carapace surface, anterolateral margin, lower margin of orbit, and postfrontal crest are smooth. The exorbital angle is small and low and the epibranchial tooth is almost undetectable; there is a small but distinct intermediate tooth between the exorbital angle and the epibranchial tooth. The postfrontal crest is sharp edged and complete, and runs unbroken across the carapace to meet the anterolateral margins. The vertical sulcus on the sidewall of the carapace meets the anterolateral margin at the epibranchial tooth. The mandibular palp always has two segments; the terminal segment consists of a large posterior lobe with a much smaller anterior process. The exopod of the third maxilliped always lacks a flagellum, and there is no vertical sulcus on the ischium of the third maxilliped. Sternal sulci s1/s2, s2/s3 and s3/s4 are deep and completely cross the sternum; the sterno-abdominal cavity terminates half-way along on s4. The terminal article of gonopod 1 is short (about one third the length of the subterminal segment of gonopod 1) slightly s-shaped, and is tube-like with a blunt and rounded tip; the medial and lateral folds on the terminal article of gonopod 1 are equal and low, and the longitudinal groove is not visible. The subterminal segment of gonopod 1 is a long, slim rectangle that is very wide at the base. The terminal and subterminal segments of gonopod 1 are not fused and there is a groove marking the junction between the segments on the ventral side; there is a dorsal membrane at the junction between the segments on the dorsal side. The terminal article of gonopod 2 is a long flagellum (just a little shorter than the subterminal segment of gonopod 2). Members of this genus are small animals, adult at cw 17-18 mm.

Type species.- *Globonautes macropus edeaensis* Bott, 1969b.

The genus is endemic to southwest Cameroon. Edea and Yabassi are 90 km apart, and both are in the rainforest zone of the Littoral Province of south west Cameroon. Edea lies on the Sanaga river, while Yabassi lies on the Wouri river.

Key to the species of *Louisea*

1. The first carpal tooth of the cheliped is larger than the second carpal tooth. The postfrontal crest is well defined, and is complete and meets the anterolateral margins. *L. balssi*
- The first carpal tooth of the cheliped is smaller than the second carpal tooth. The postfrontal crest is poorly defined, and is incomplete and does not meet the anterolateral margins. *L. edeaensis*

Louisea edeaensis (Bott, 1969b)

fig. 46F, 47E, 48E, 49F, 51F, 52F, 53DD, 54-57, 62F, 68F, table IX, plate 3

Globonautes macropus edeaensis Bott, 1969b, p. 360.- Bott, 1970, p. 24, pl. 1, fig. 3-5, pl. 26, fig. 8.-Cumberlidge, 1987, p. 2215, table 2.

Louisea edeaensis, Cumberlidge, 1994a, p. 124-125, fig. 1, table 1.

Diagnosis

The carapace is moderately high (mean ch/fw 1.14). The postfrontal crest is poorly defined, and is incomplete and does not meet the anterolateral margins. The carapace surface, anterolateral margins, lower margins of the orbits, and the postfrontal crest are all smooth. The exorbital angle is small and low and is continuous with the anterolateral margin; the epibranchial tooth is almost undetectable; there is a small but distinct intermediate tooth between the exorbital angle and the epibranchial tooth. The vertical sulcus on the sidewall of the carapace meets the anterolateral margin at the epibranchial tooth. The dactylus of the right cheliped of adult males is slim. The propodus of the cheliped is very long, as long as the carapace width, and has a large three-peaked proximal tooth. The first carpal tooth of the cheliped is smaller than the second carpal tooth. The medial inferior margin of the merus of the cheliped has a large jagged tooth at the end close to the carpus, and has rows of small pointed teeth along the rest of the margin. The terminal article of gonopod 1 is directed outward; it is broad at the base and narrows sharply so that the final two-thirds are tube-like; the tip is blunt and rounded; the terminal article completely lacks a visible longitudinal groove; the subterminal segment of gonopod 1 is very wide at the base. The flagellum of the terminal article of gonopod 2 is long, almost as long as the subterminal segment of gonopod 2. A small species, mature at cw 17.5 mm.

For a detailed description see CUMBERLIDGE (1994a).

Size.- Adult size cw 17.5-22.5 mm. The carapace proportions are given in table IX. Graphs of carapace dimensions are given in fig. 62F.

Material examined

Cameroon, Yaounde; 1907; HABERER; 1 m adult cw 19.3 mm, 2 f adults cws 19.4, 17.5 mm (NHMW 1877).

Type and distribution

Type.- Cameroon, Edea; January 1910; 1 m adult, cw 22.5 mm (ZSM 1118/1), holotype.

Type locality.- Cameroon, Edea.

Distribution.- Between the Wouri and Sanaga rivers in the rainforest zone of southwest Cameroon.

Remarks

This species was originally known only from the holotype. Two additional specimens assigned by CUMBERLIDGE (1994a) to this species from Yabassi, Cameroon are here included under *L. balssi*. The number of known specimens of *L. edeaensis* now stands at four, with the discovery of three additional specimens

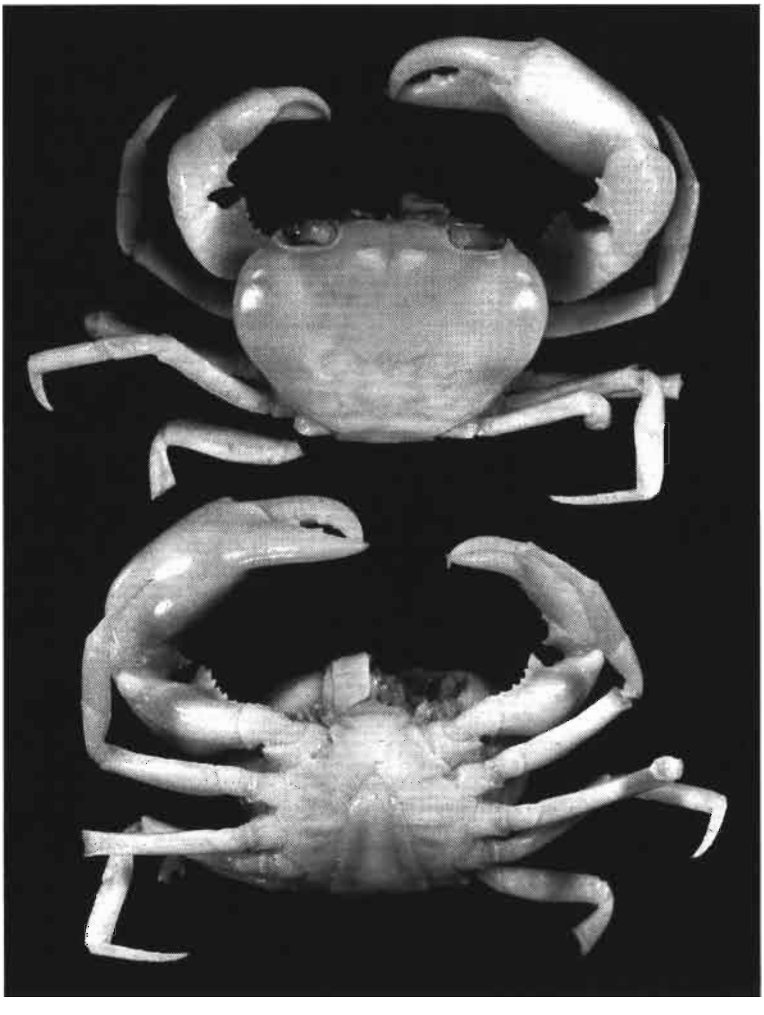


PLATE 3. *Louisea edeaensis* (BOTT, 1969) male holotype (cw 12.5 mm) from Eosung, Bakossi highlands, Kumba (Johann-Albrechthöhe), 1060 m, Cameroon (ZIM K3506), dorsal and ventral views. Dr. Michael Türkay (SMF) is kindly thanked for supplying the photograph.

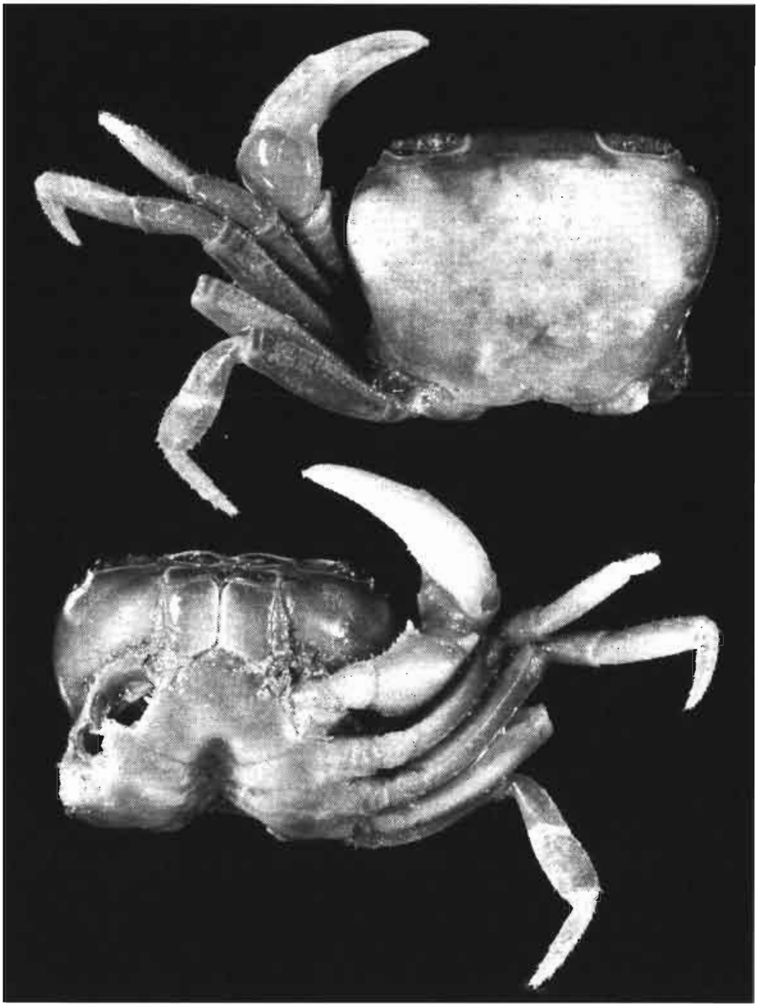


PLATE 4. *Louisea balsii* (BOTT, 1969) male holotype (cw 12.5 mm) from Eosung, Bakossi highlands, Kumba (Johann-Albrechthöhe), 1060 m, Cameroon (ZIM K3506), dorsal and ventral views. Dr. Michael Türkay (SMF) is kindly thanked for supplying the photograph.

in the NHMW, Vienna (CUMBERLIDGE, 1997). For comparisons see below under *L. balssi.*

Louisea balssi (BOTT, 1959)

fig. 46G, 48F, 49G, 52G, 53EE, 54-57, 62G, 68F, table IX, plate 4

Geothelphusa macropus BALSS, 1914a, p. 406.-BALSS, 1936, p. 200.

Globonautes balssi BOTT, 1959, 999-1000, fig. 7.-CUMBERLIDGE, 1987, p. 2210-2212.

Globonautes macropus balssi, BOTT, 1969b, p. 360.-BOTT, 1970, p. 24, pl. 1, fig. 3-5, pl. 26, fig. 8.

Louisea edeaensis, CUMBERLIDGE, 1994a, p. 127, 130, fig. 2, 3, tables 1, 2.

Redescription

Diagnosis.- The carapace is moderately high (ch/fw 1.2). The postfrontal crest is well defined, complete, and meets the anterolateral margins. The carapace surface, anterolateral margins, lower margins of the orbits, and the postfrontal crest are all smooth. The exorbital angle is small and low and is continu-continuous with the anterolateral margin, and the epibranchial tooth is almost undetectable; there is a small but distinct intermediate tooth between the exorbital angle and the epibranchial tooth. The vertical sulcus on the sidewall of the carapace meets the anterolateral margin at the epibranchial tooth. The dactylus of the right cheliped of adult males is slim. The propodus of the cheliped is very long, and is as long as the carapace width. The first tooth on the medial margin of the carpus of the cheliped (the first carpal tooth) is larger than the second carpal tooth. The medial inferior margin of the merus of the cheliped has a large jagged tooth at the end clost to the carpus, and there are rows of small pointed teeth along the rest of this margin. The terminal article of gonopod 1 is directed outward and it is broad at its base before narrowing sharply so that the distal half is a slim rounded cylinder with a blunt and rounded tip; the terminal article completely lacks a visible longitudinal groove; the base of the subterminal segment of gonopod 1 is very wide. The flagellum of the terminal article of gonopod 2 is long, almost as long as the subterminal segment of gonopod 2. This is a small species, mature at cw 18.1 mm.

Size.- Adult size cw 18.1-22.5 mm. The carapace proportions are given in table IX. Graphs of carapace dimensions are given in fig. 62G.

Material examined

Cameroon, Eosung, Bakossi region, Kumba (= Johann-Albrechthöhe), 1060 m; CARL RATHKE; 1 f adult cw 21 mm (ZSM 1117/1).- Eosung, Bakossi region, Kumba (= Johann-Albrechthöhe), 1060 m; 10 September 1909, CARL RATHKE; 1 adult female cw 21 mm (SMF 5093, donated by ZIM K3506).- Yabassi; RIGGENBACH; 2 m, cws 18.1, 13.7 mm (ZMB 21575).

Type and distribution

Types (examined).- Cameroon, Eosung, Bakossi highlands, Kumba (Johann-Albrechthöhe), 1060 m; 10 September 1909; CARL RATHKE; 1 m juvenile cw 12.5 mm (ZIM K3506), holotype.- Eosung, Bakossi highlands, Kumba (Johann-Albrechthöhe), 1060 m; 10 September 1909; CARL RATHKE; 2 f cws 22 ovigerous, 13.5 mm (ZIM K3506), paratypes.

Type locality.- Cameroon, Eosung, Bakossi highlands, Kumba (Johann-Albrechthöhe), 1060 m. Johann-Albrechthöhe is today known as Kumba, which is situated north of Mount Cameroon on the road to Mamfe.

Distribution.- The Lower Guinea forest of southwest Cameroon.

Remarks

This species was first identified as *Potamon (Geothelphusa) macropus* by BALSS (1914a, 1936). BOTT (1959) recognised that these specimens belonged to a separate species which he redescribed as *Globonautes balssi* BOTT, 1959. Later, that author BOTT (1969b, 1970b) reclassified this taxon as *Globonautes macropus balssi*. In 1994 (CUMBERLIDGE, 1994a) established *Louisea* for *G. m. edeaensis* and listed *G. balssi* as *incertae sedis*. This decision was taken in view of the shortage of material, because the species was described by BOTT (1959) from a juvenile male which was missing gonopod 2 on both sides. A knowledge of the terminal article of gonopod 2 is necessary to distinguish *Potamonemus* (in which the terminal article of gonopod 2 is extremely short) from *Louisea* (in which the terminal article of gonopod 2 is a long flagellum). The new material from the ZMB, Berlin included an adult male with both of its gonopods intact, and confirmed the assignment of *G. balssi* to *Louisea*. The two males of *L. balssi* from Yabassi, Cameroon were first considered by CUMBERLIDGE (1994a) to be representatives of a variable population of *L. edeaensis*; these specimens are recognised here as the valid species *L. balssi*, which is redescribed.

Comparisons.- The distal tooth on the medial inferior margin of the merus of the cheliped of *L. balssi* is smaller than that of

L. edeaensis. The first tooth on the medial margin of the carpus of the cheliped (the first carpal tooth) of *L. balssi* is larger than the second carpal tooth, while in *L. edeaensis* the first carpal tooth is smaller than the second carpal tooth. In *L. balssi* the postfrontal crest is well defined and meets the anterolateral margins, while in *L. edeaensis* the postfrontal crest is poorly defined, incomplete, and does not meet the anterolateral margins. BOTT (1959) reported *L. balssi* to have a distinct vertical sulcus on the ischium of the third maxilliped, and clearly visible cervical grooves. In fact, both *L. edeaensis* and *L. balssi* lack a vertical sulcus on the ischium of the third maxilliped, and the cervical grooves in both species are almost undetectable.

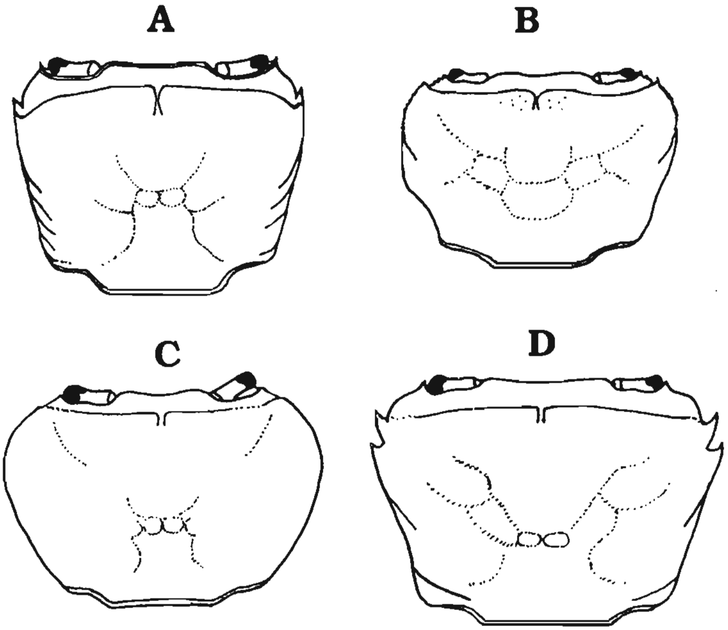


FIG. 15. Dorsal view of the carapace of **A**, *Potamonautes ecorssei* MARCHAND, 1902, adult male (cw 21.7 mm) from Burkina Faso (MRAC 51.591). **B**, *P. triangulus* BOTT, 1959, adult male paratype (cw 23.2 mm) from a stream near Kibi, Ghana (SMF 2817). **C**, *P. senegalensis* BOTT, 1970a, adult male holotype (cw 58.5 mm) from Sénégal (NHMG). **D**, *P. reidi* n. sp. adult male holotype (cw 42 mm) from Cross River State, Nigeria (NMU 30.IV.1982a).

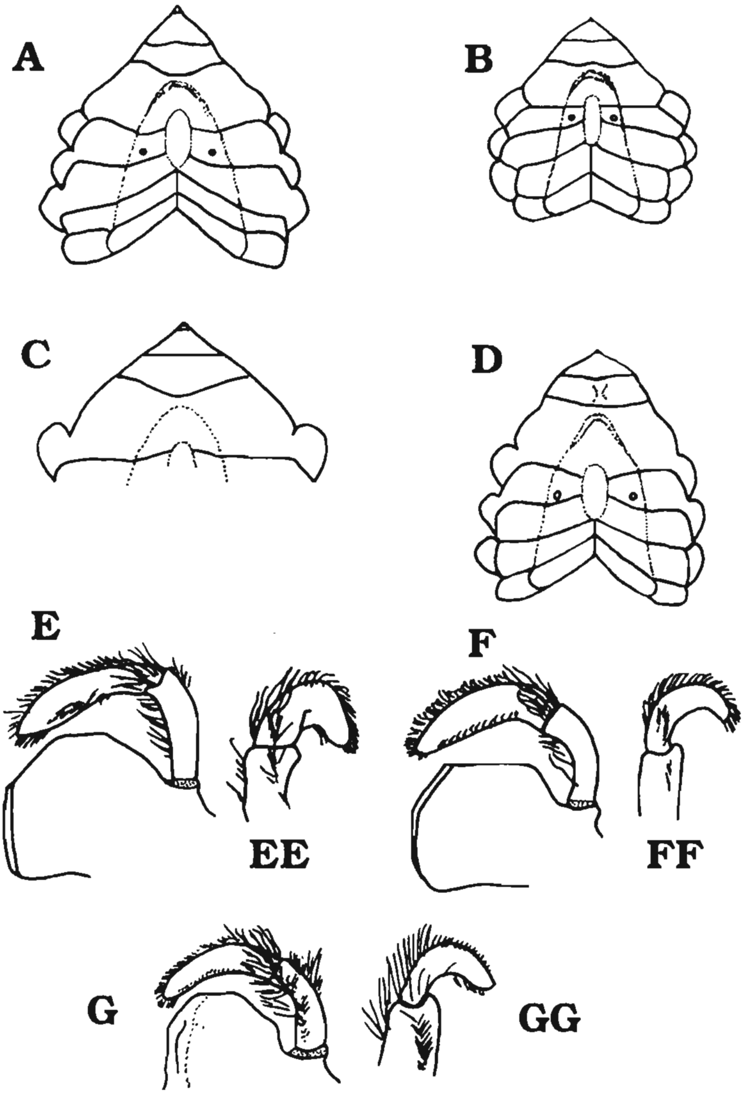


FIG. 16. Inferior view of the sternum (plastron) of **A**, *Potamonautes ecorssei*, **B**, *P. triangulus*, **C**, *P. senegalensis* and **D**, *P. reidi*. Frontal view (**E-G**) and superior view of terminal segment (**EE-GG**) of the left mandible of **E**, *Potamonautes ecorssei*, **F**, *P. triangulus* and **G**, *P. reidi*. Specimen details same as fig. 15.

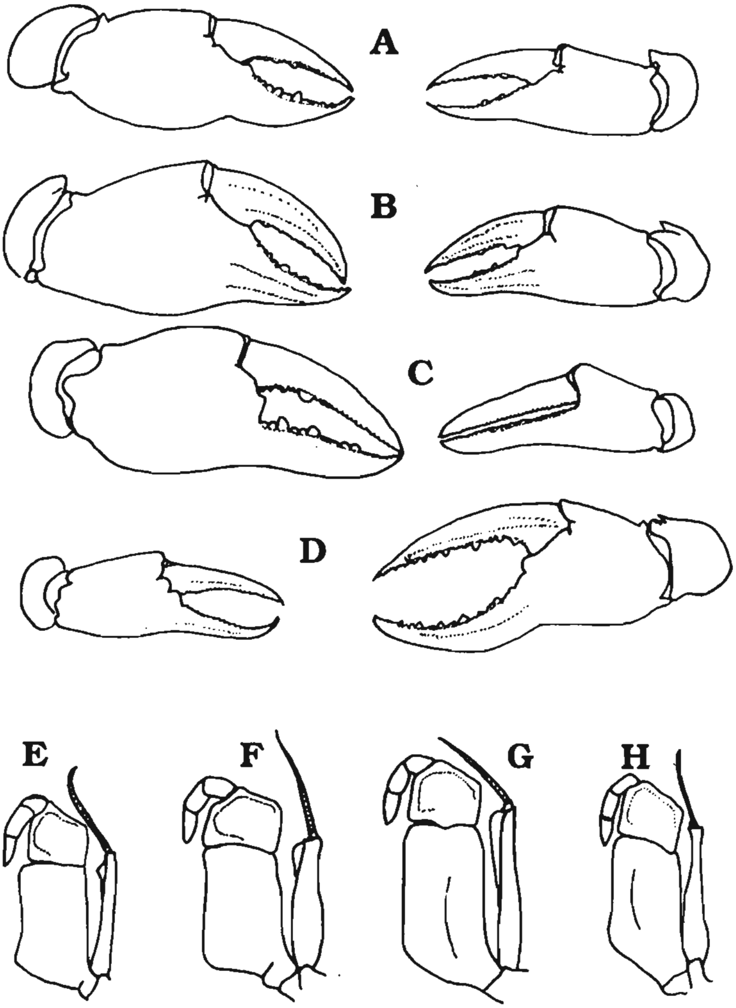


FIG. 17. Frontal view of the right and left chelipeds of **A**, *Potamonautes ecorssei*, **B**, *P. triangulus*, **C**, *P. senegalensis* and **D**, *P. reidi*. Frontal view of the left third maxilliped of **E**, *Potamonautes ecorssei*, **F**, *P. triangulus*, **G**, *P. senegalensis* and **H**, *P. reidi*. Specimen details same as fig. 15.

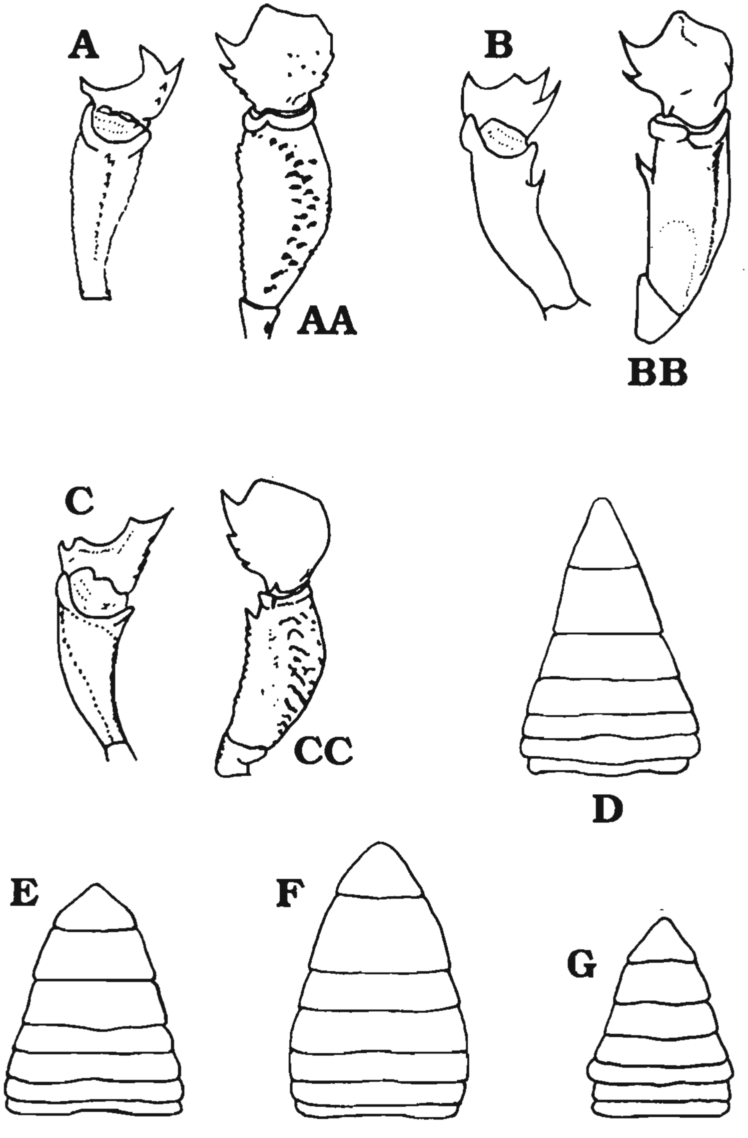


FIG. 18. Inferior view (**A-C**) and superior view (**AA-CC**) of the right carpus and merus of the cheliped of **A**, *Potamonautes ecorssei*, **B**, *P. triangulus* and **C**, *P. reidi*. Inferior view of the male abdomen of **D**, *Potamonautes ecorssei*, **E**, *P. triangulus*, **F**, *P. senegalensis* and **G**, *P. reidi*. Specimen details same as fig. 15.

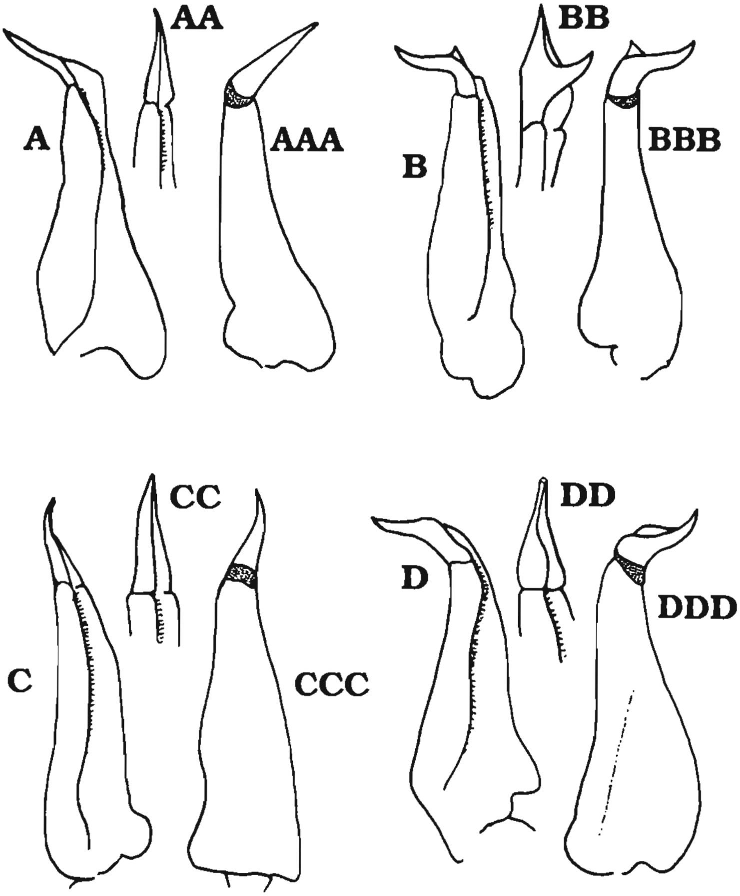


FIG. 19. Ventral view (**A-D**), superior view (**AA-DD**) and dorsal view (**AAA-DDD**) of the right gonopod 1 of **A**, *Potamonautes ecorssei*, **B**, *P. triangulus*, **C**, *P. senegalensis* and **D**, *P. reidi*. Specimen details same as fig. 15.

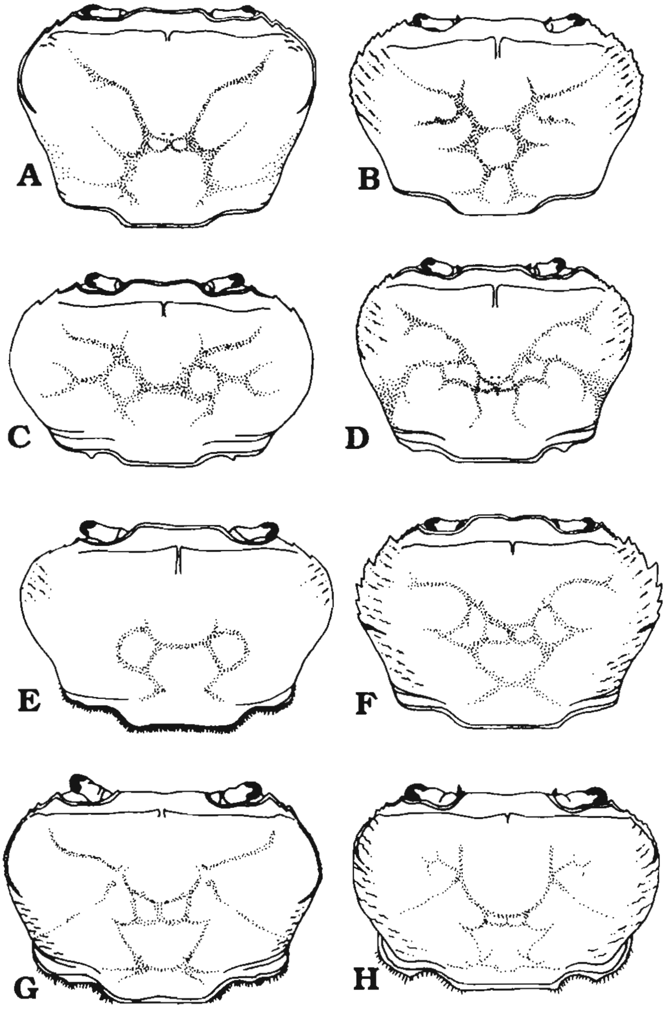


FIG. 20. Dorsal view of the carapace of **A**, *Liberonautes paludicolis* CUMBERLIDGE & SACHS, 1989a, adult male paratype (cw 56 mm) from Nimba County, Liberia (NMU 2.IV.1988). **B**, *L. nanoides* CUMBERLIDGE & SACHS, 1989a, adult male paratype (cw 42.5 mm) from Haindi, Liberia (NMU 13.XII.1988). **C**, *L. rubigimanus* CUMBERLIDGE & SACHS, 1989a, adult male paratype (cw 66 mm) from Mount Gibi, Liberia (NMU 23.VI.1988). **D**, *L. latidactylus* DE MAN, 1903, adult male (cw 46 mm) from Lofa County, Liberia (NMU 24.IX.1986). **E**, *L. nimba* CUMBERLIDGE, 1999, adult male holotype (cw 24.1 mm) from Mount Nimba, Guinea (MNHN-B 25582). **F**, *L. chaperi* A. MILNE-EDWARDS, 1886, adult male (cw 45.5 mm) from Grand Gedah County, Liberia (NMU 19.XII.1988). **G**, *L. grandbassa* n. sp., adult male holotype (cw 31.4 mm) from Grand Bassa County, Liberia (NMU 4.VIII.1988). **H**, *L. lugbe* n. sp., adult male holotype (cw 22.7 mm) from Lugbe, Nimba County, Liberia (NMU 20.VII.1988).

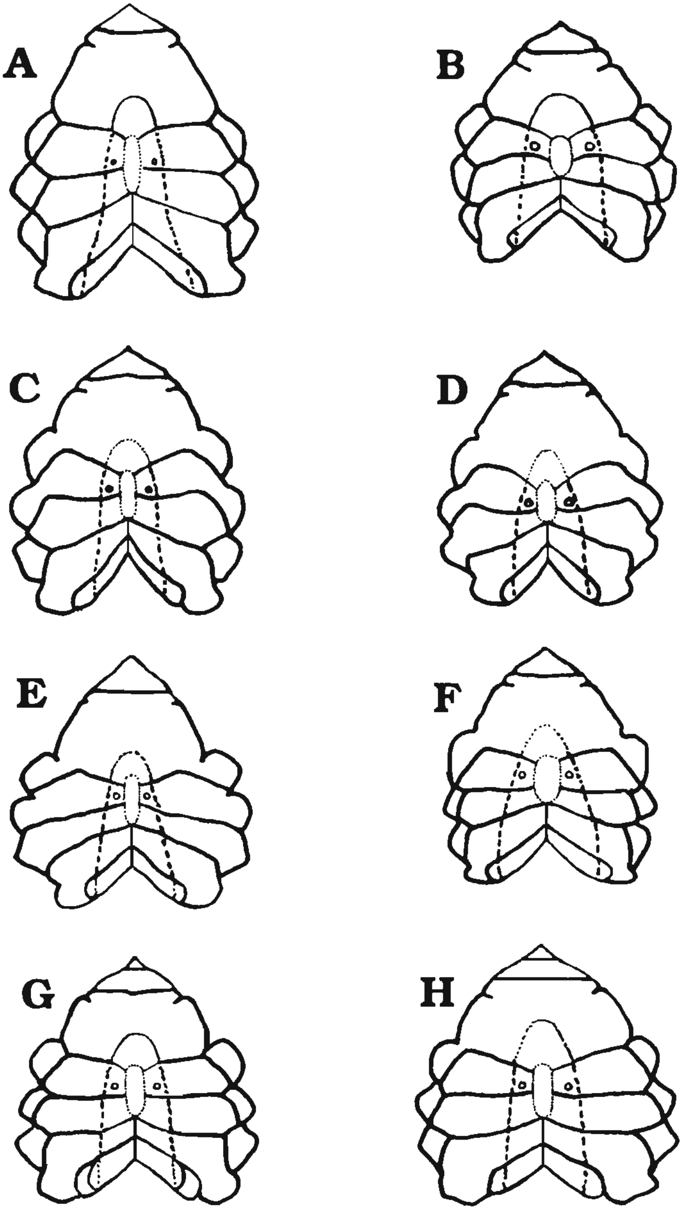


FIG. 21. Inferior view of the sternum (plastron) of **A**, *Liberonautes paludicolis*, **B**, *L. nanoides*, **C**, *L. rubigimanus*, **D**, *L. latidactylus*, **E**, *L. nimba*, **F**, *L. chaperi*, **G**, *L. grandbassa* and **H**, *L. lugbe*. Specimen details same as fig. 20.

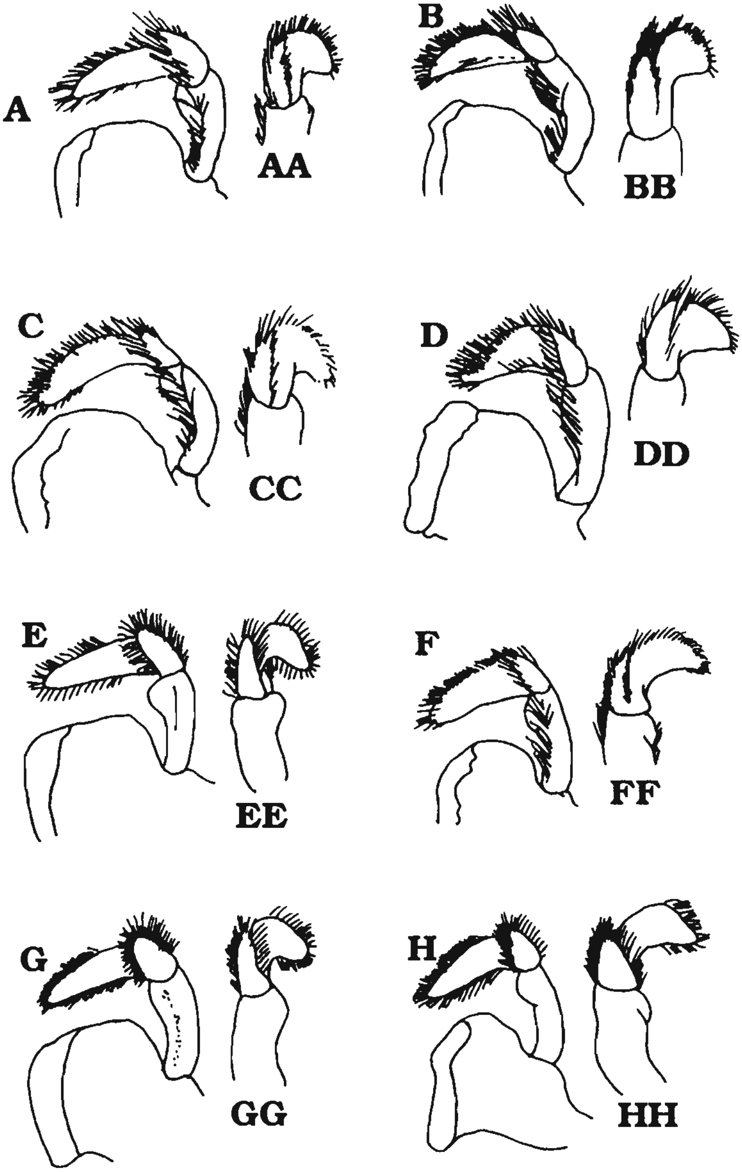


FIG. 22. Frontal view (**A-H**) and superior view of the terminal segment (**AA-HH**) of the left mandible of **A**, *Liberonautes paludicolis*, **B**, *L. nanoides*, **C**, *L. rubigimanus*, **D**, *L. latidactylus*, **E**, *L. nimba*, **F**, *L. chaperi*, **G**, *L. grandbassa* and **H**, *L. lugbe*. Specimen details same as fig. 20.

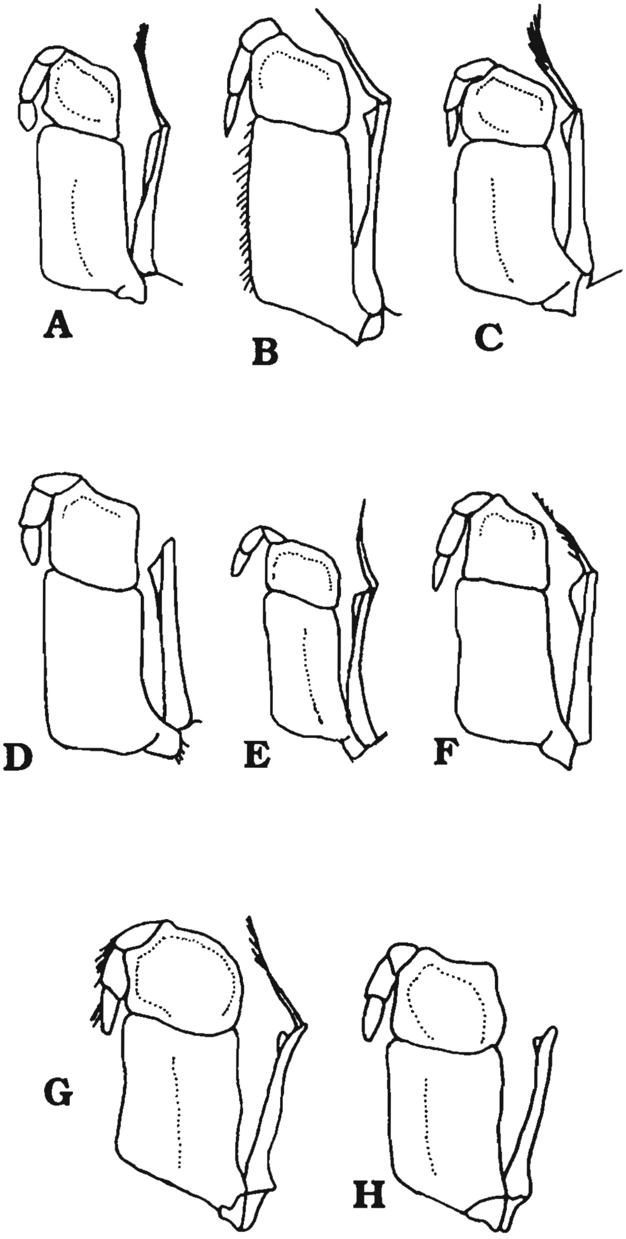


FIG. 23. Frontal view of the left third maxilliped of **A**, *Liberonautes paludicolis*, **B**, *L. nanoides*, **C**, *L. rubigimanus*, **D**, *L. latidactylus*, **E**, *L. nimba*, **F**, *L. chaperi*, **G**, *L. grandbassa* and **H**, *L. lugbe*. Specimen details same as fig. 20.

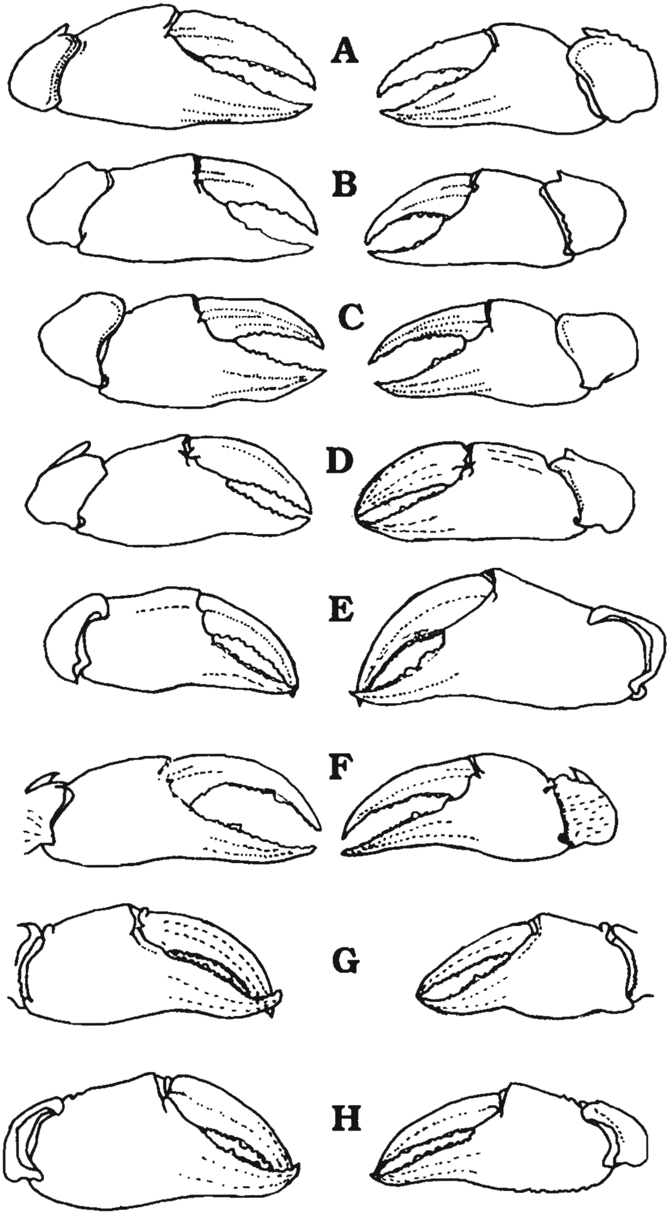


FIG. 24. Frontal view of the right and left chelipeds of **A**, *Liberonautes paludicolis*, **B**, *L. nanoides*, **C**, *L. rubigimanus*, **D**, *L. latidactylus*, **E**, *L. nimba*, **F**, *L. chaperi*, **G**, *L. grandbassa* and **H**, *L. lugbe*. Specimen details same as fig. 20.

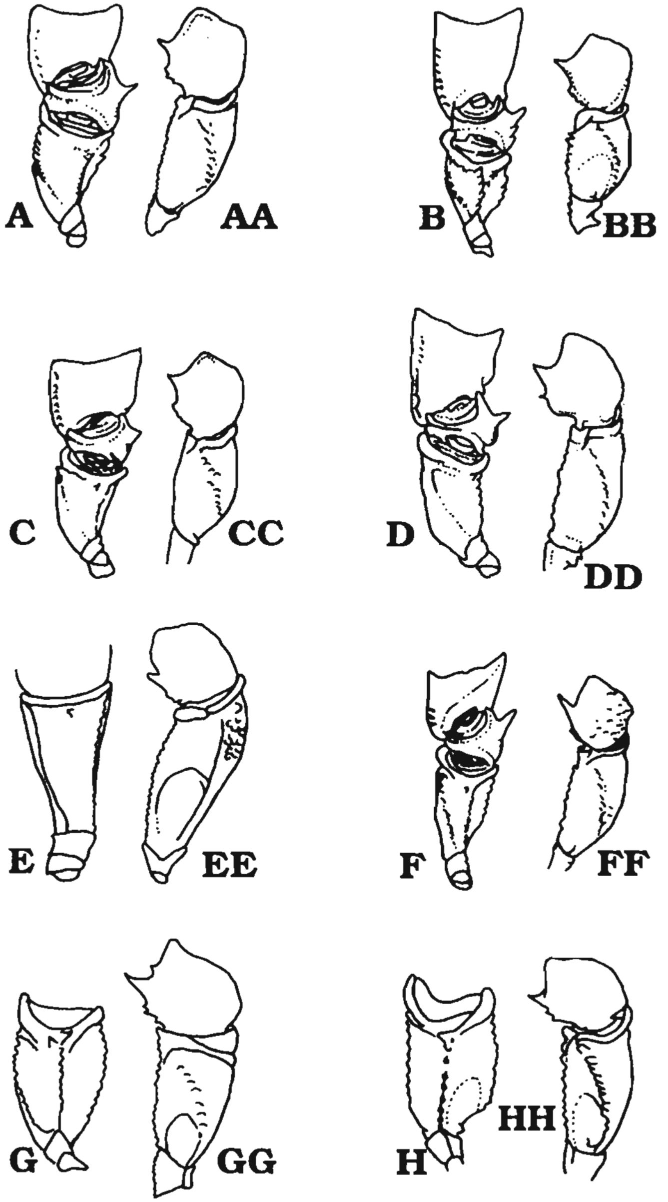


FIG. 25. Inferior view (**A-H**) and superior view (**AA-HH**) of the right carpus and merus of the cheliped of **A**, *Liberonautes paludicolis*, **B**, *L. nanoides*, **C**, *L. rubigimanus*, **D**, *L. latidactylus*, **E**, *L. nimba*, **F**, *L. chaperi*, **G**, *L. grandbassa* and **H**, *L. lugbe*. Specimen details same as fig. 20.

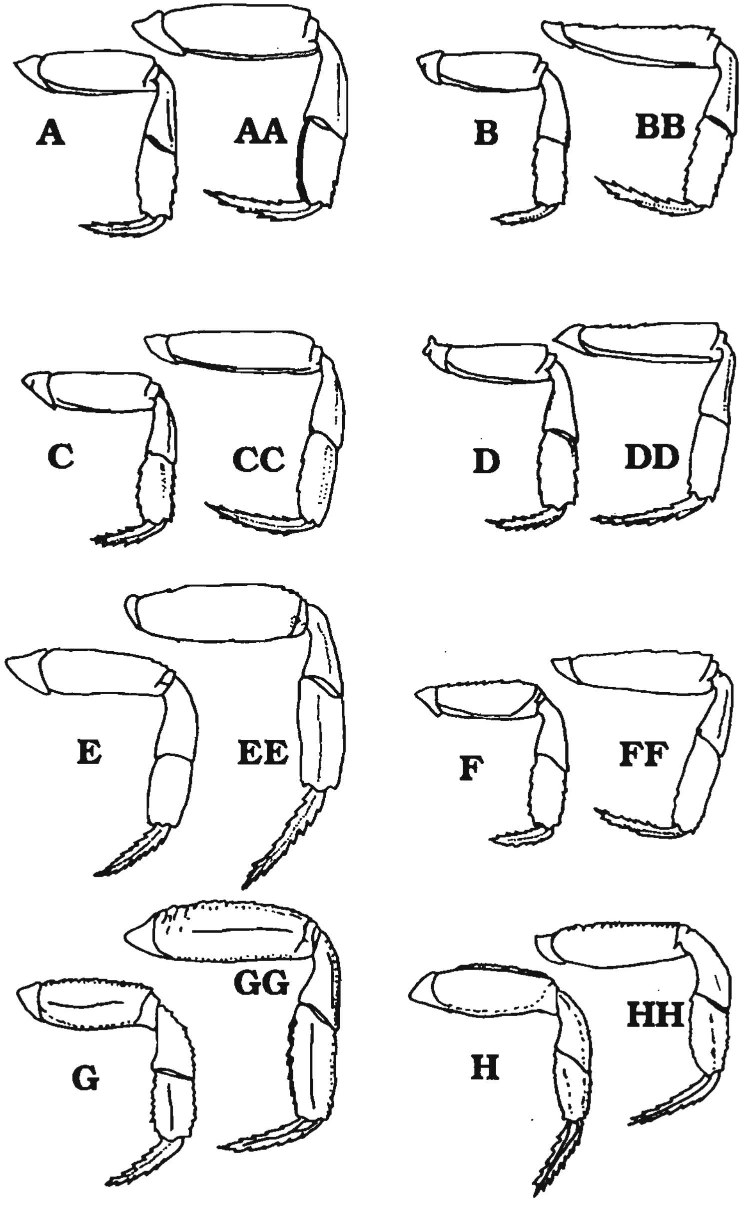


FIG. 26. Posterior view of right pereiopod 5 (P5, **A-H**) and right pereiopod 4 (P4, **AA-HH**) of **A**, *Liberonautes paludicolis*, **B**, *L. nanoides*, **C**, *L. rubigimanus*, **D**, *L. latidactylus*, **E**, *L. nimba*, **F**, *L. chaperi*, **G**, *L. grandbassa* and **H**, *L. lugbe*. Specimen details same as fig. 20.

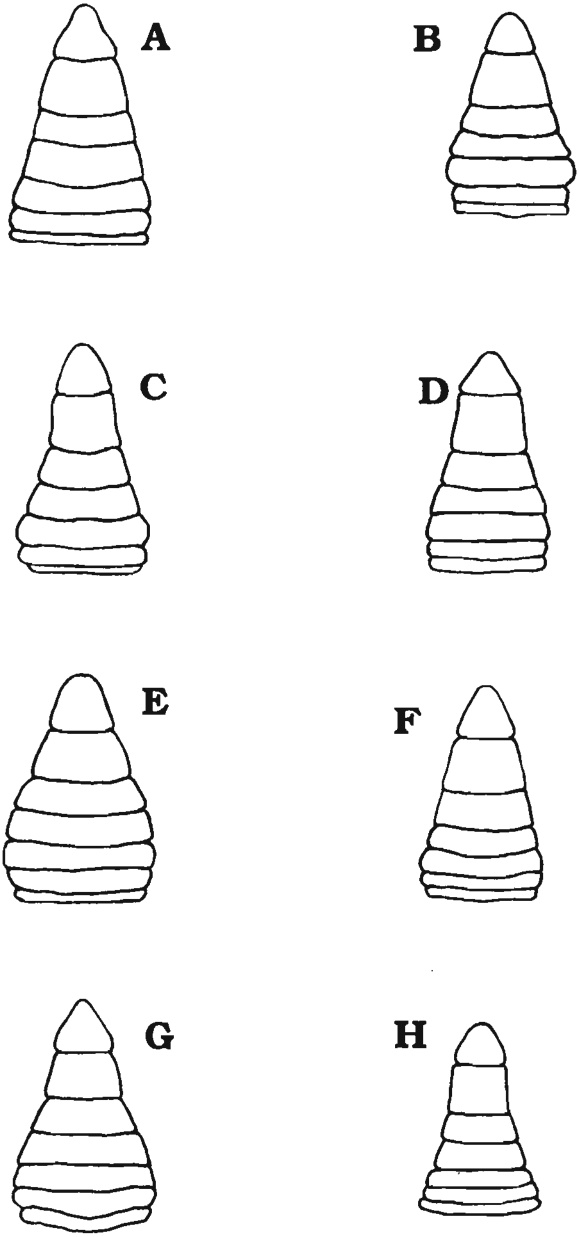


FIG. 27. Inferior view of the male abdomen of **A**, *Liberonautes latidactylus*, **B**, *L. rubigimanus*, **C**, *L. nanoides*, **D**, *L. paludicolis*, **E**, *L. chaperi*, **F**, *L. nimba*, **G**, *L. lugbe* and **H**, *L. grandbassa*. Specimen details same as fig. 20.

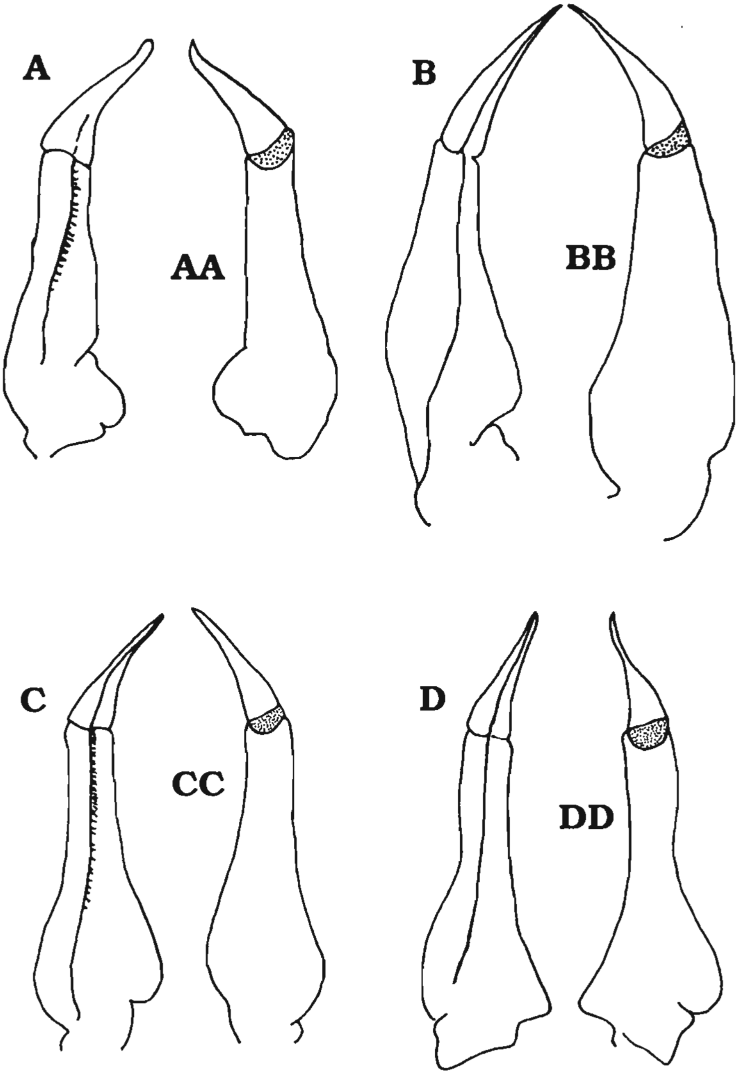


FIG. 28. Ventral view (**A-D**) and dorsal view (**AA-DD**) of the right gonopod 1 of **A**, *Liberonautes latidactylus*, **B**, *L. paludicolis*, **C**, *L. chaperi* and **D**, *L. nanoides*. Specimen details same as fig. 20.

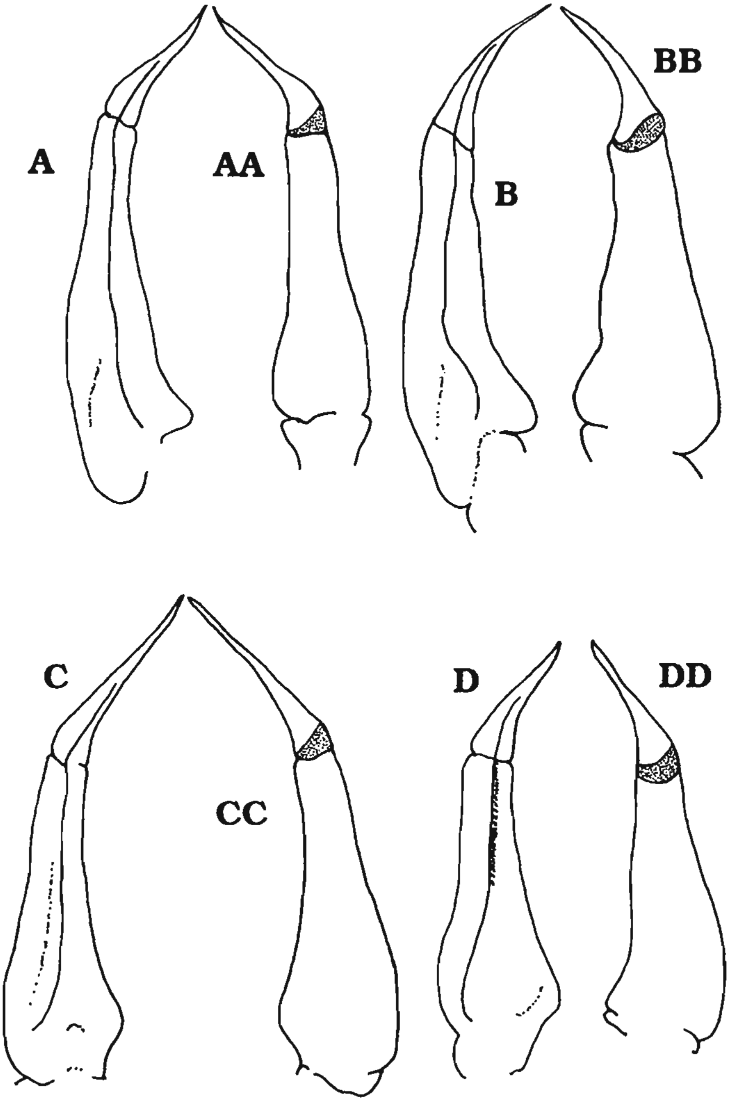


FIG. 29. Ventral view (**A-D**) and dorsal view (**AA-DD**) of the right gonopod 1 of **A**, *L. rubigimanus*, **B**, *L. nimba*, **C**, *L. grandbassa* and **D**, *L. lugbe*. Specimen details same as fig. 20.

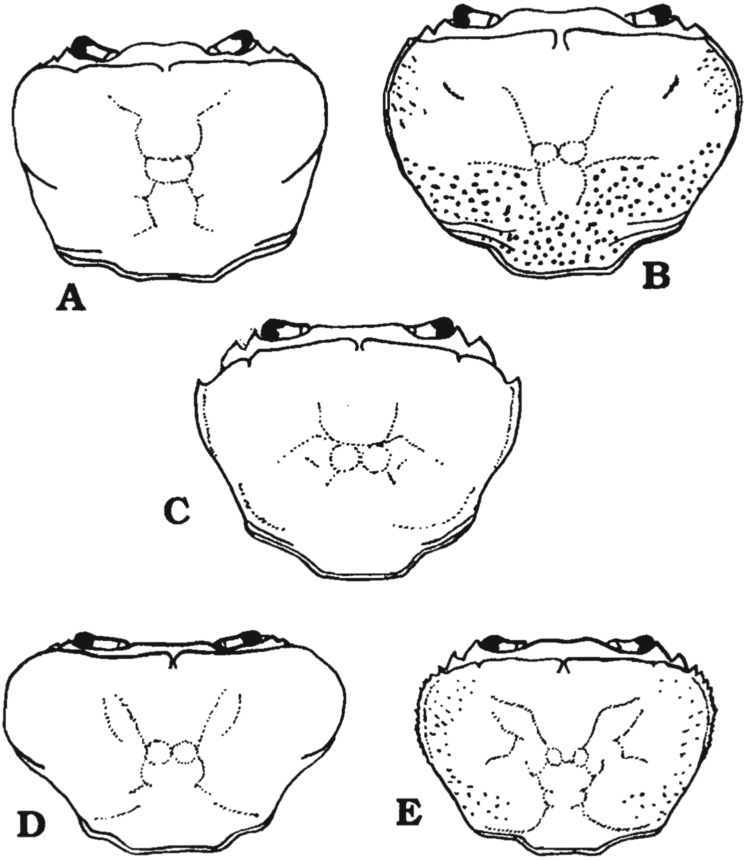


FIG. 30. Dorsal view of the carapace of **A**, *Sudanonautes aubryi* H. Milne Edwards, 1853, adult male (cw 65 mm) from Tiga Dam, Nigeria (NMU 6.XI.1982). **B**, *S. africanus* A. Milne-Edwards, 1869, adult male (cw 83 mm) from Cross River State, Nigeria (NMU 9.IV.1983). **C**, *S. chavanesii* A. Milne-Edwards, 1886, adult male (CW 72.7 mm) from Ebogo, Cameroon (MRAC 53.291). **D**, S. *floweri* De Man, 1901, adult male lectotype (CW 48.5 mm) from Bahr el Gebel, Sudan (NHML 1901.8.26.2). **E**, *S. faradjensis* Rathbun, 1921, adult male holotype (CW 71.5 mm) from Faradje, Zaire (AMNH 3346).

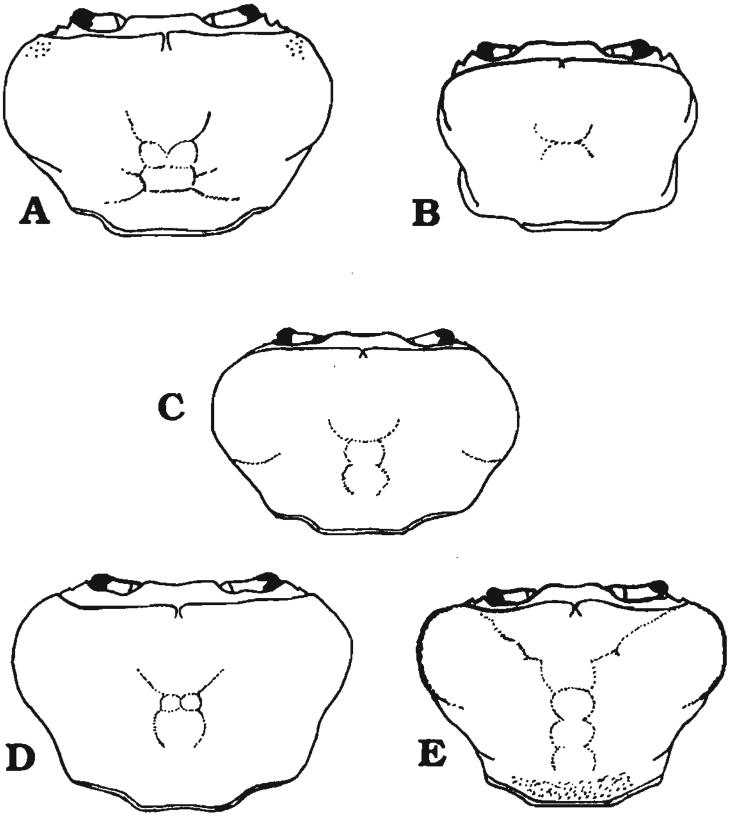


FIG. 31. Dorsal view of the carapace of **A**, *Sudanonautes monodi* Balss, 1929, adult male (cw 55 mm) from Tiga Dam, Nigeria (NMU 6.XI.1982). **B**, *S. granulatus* Balss, 1929, adult male (cw 41.5 mm) from Cross River State, Nigeria (NMU 28.IV.1979). **C**, *S. orthostylis* Bott, 1955, adult male holotype (cw 25.8 mm) from Bipindihof, Cameroon (ZMB 11093). **D**, *S. kagoroensis* Cumberlidge, 1991, adult male holotype (cw 63 mm) from Kagoro, Nigeria (NHML 1.12.6.1984). **E**, *S. nigeria* n. sp., adult male holotype (cw 54 mm) from Uzombe, Nigeria (SMF 6905).

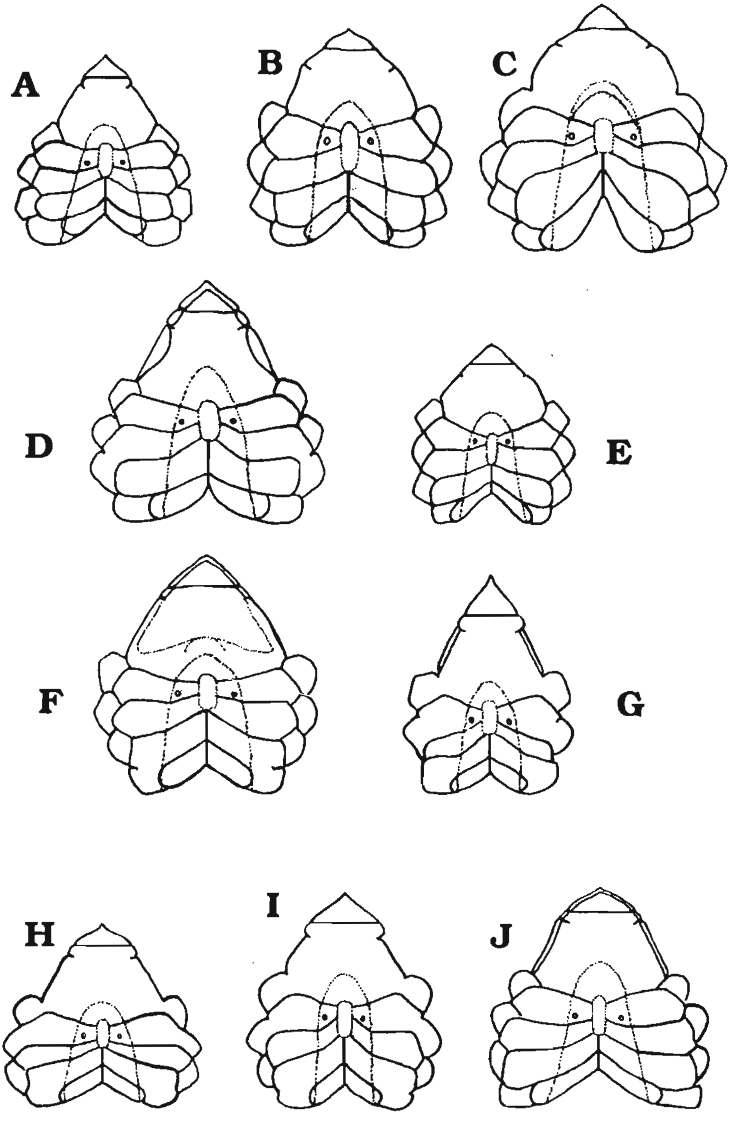


FIG. 32. Inferior view of the sternum (plastron) of **A**, *Sudanonautes aubryi*, **B**, *S. africanus*, **C**, *S. chavanesii*, **D**, *S. floweri*, **E**, *S. faradjensis*, **F**, *S. monodi*, **G**, *S. granulatus*, **H**, *S. orthostylis*, **I**, *S. kagoroensis* and **J**, *S. nigeria*. Specimen details same as fig. 30, 31.

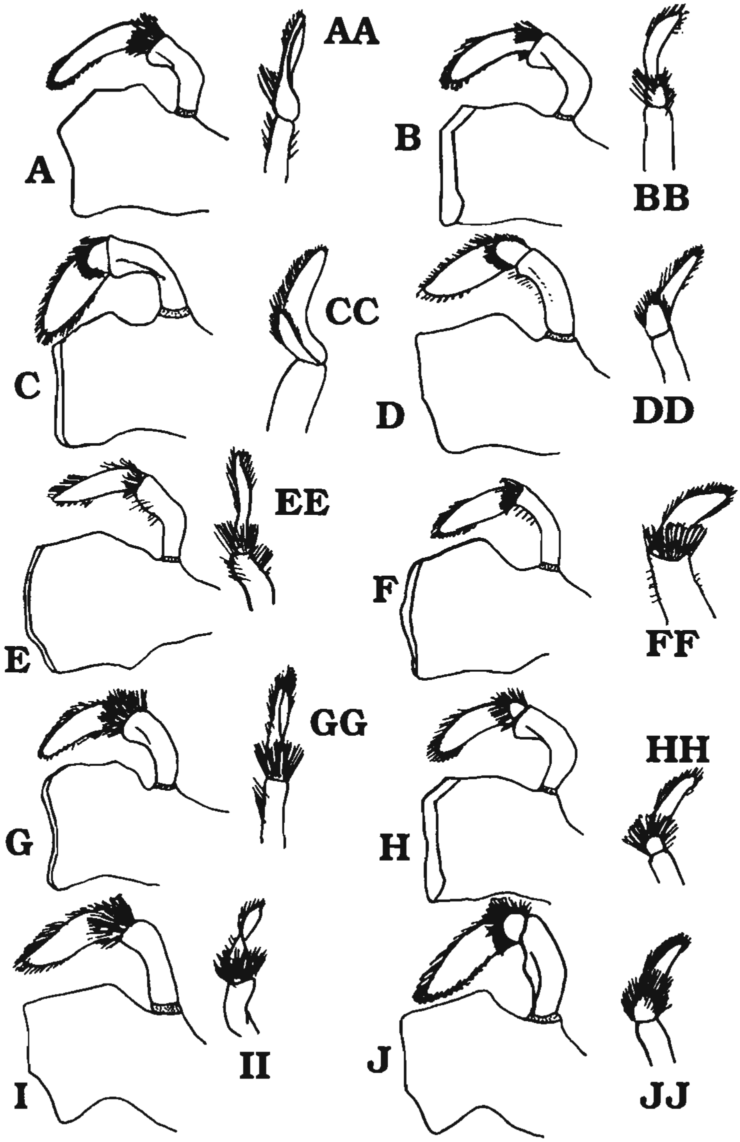


FIG. 33. Frontal view (**A-J**) and superior view (**AA-JJ**) of the left mandible of **A**, *Sudanonautes aubryi*, **B**, *S. africanus*, **C**, *S. chavanesii*, **D**, *S. floweri*, **E**, *S. faradjensis*, **F**, *S. monodi*, **G**, *S. granulatus*, **H**, *S. orthostylis*, **I**, *S. kagoroensis* and **J**, *S. nigeria*. Specimen details same as fig. 30, 31.

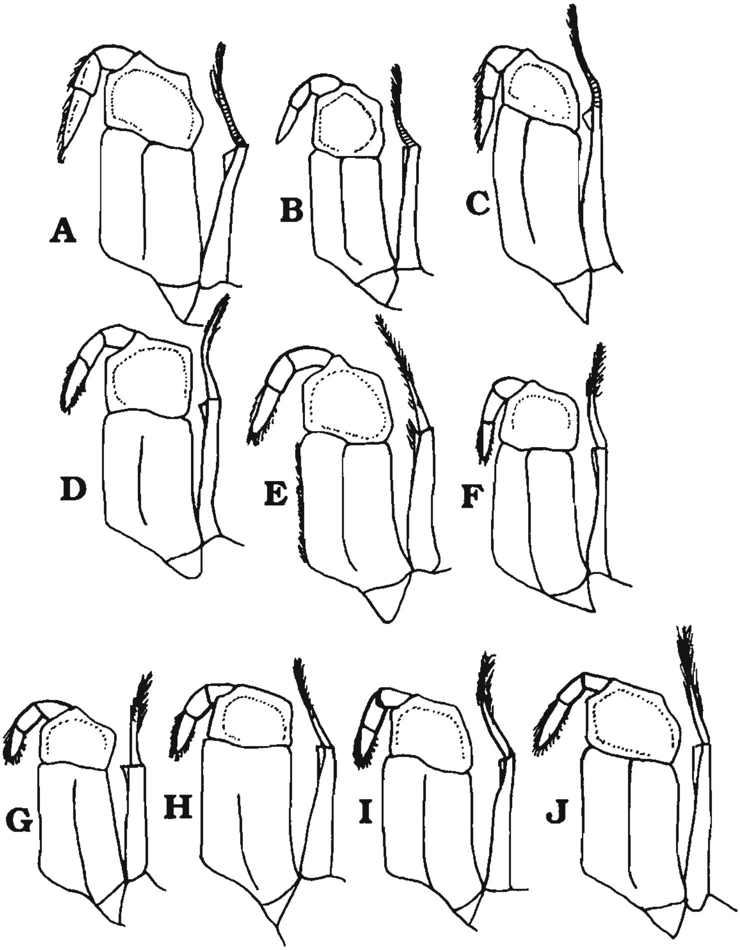


FIG. 34. Frontal view of the left third maxilliped of **A**, *Sudanonautes aubryi*, **B**, *S. africanus*, **C**, *S. chavanesii*, **D**, *S. floweri*, **E**, *S. faradjensis*, **F**, *S. monodi*, **G**, *S. granulatus*, **H**, *S. orthostylis*, **I**, *S. kagoroensis* and **J**, *S. nigeria*. Specimen details same as fig. 30, 31.

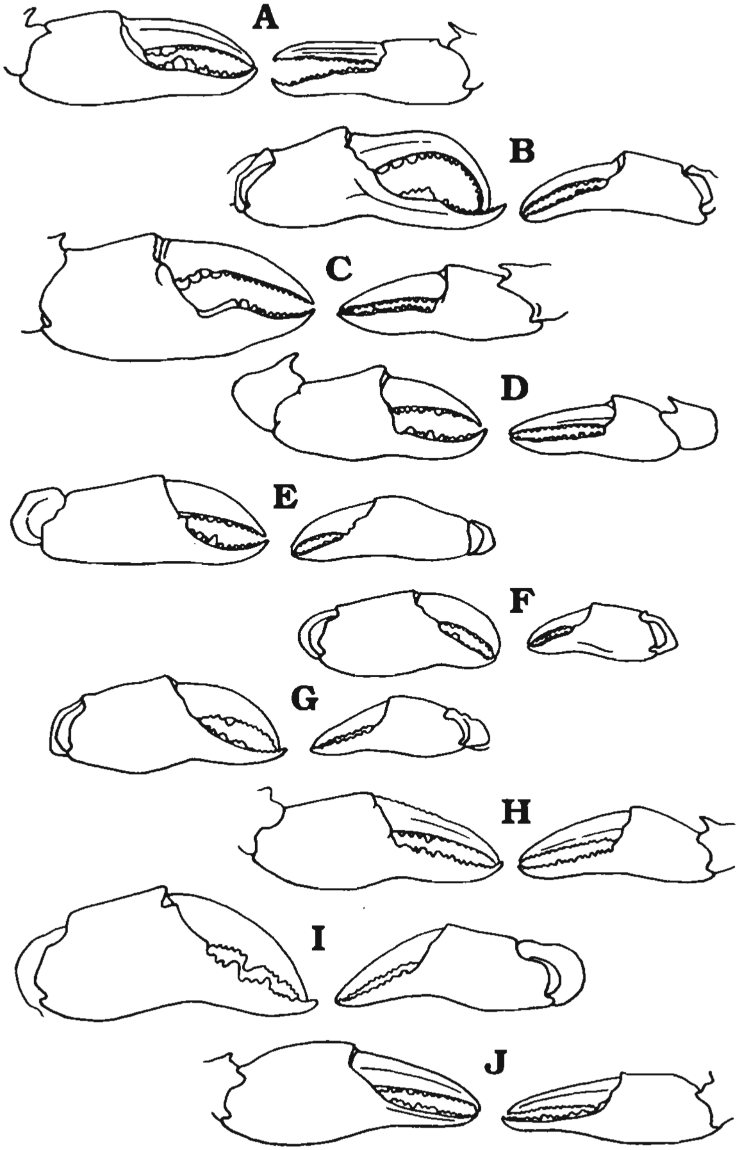


FIG. 35. Frontal view of the right and left chelipeds of **A**, *Sudanonautes faradjensis*, **B**, *S. chavanesii*, **C**, *S. africanus*, **D**, *S. aubryi*, **E**, *S. kagoroensis*, **F**, *S. orthostylis*, **G**, *S. granulatus*, **H**, *S. floweri*, **I**, *S. monodi* and **J**, *S. nigeria*. Specimen details same as fig. 30, 31.

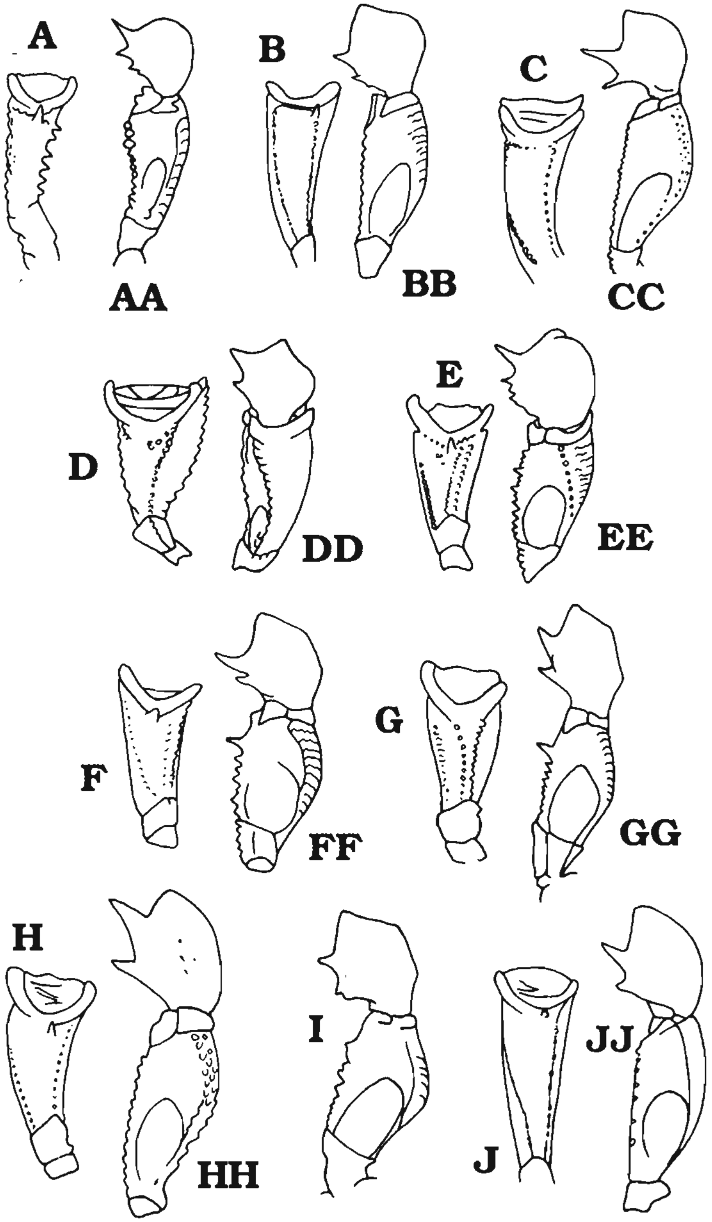


FIG. 36. Inferior view (**A-J**) and superior view (**AA-HH, JJ**) of the right carpus and merus of the cheliped of **A**, *Sudanonautes floweri*, **B**, *S. kagoroensis*, **C**, *S. monodi*, **D**, *S. nigeria*, **E**, *S. africanus*, **F**, *S. faradjensis*, **G**, *S. chavanesii*, **H**, *S. aubryi*, **I**, *S. orthostylis* and **J**, *S. granulatus*. Specimen details same as fig. 30, 31.

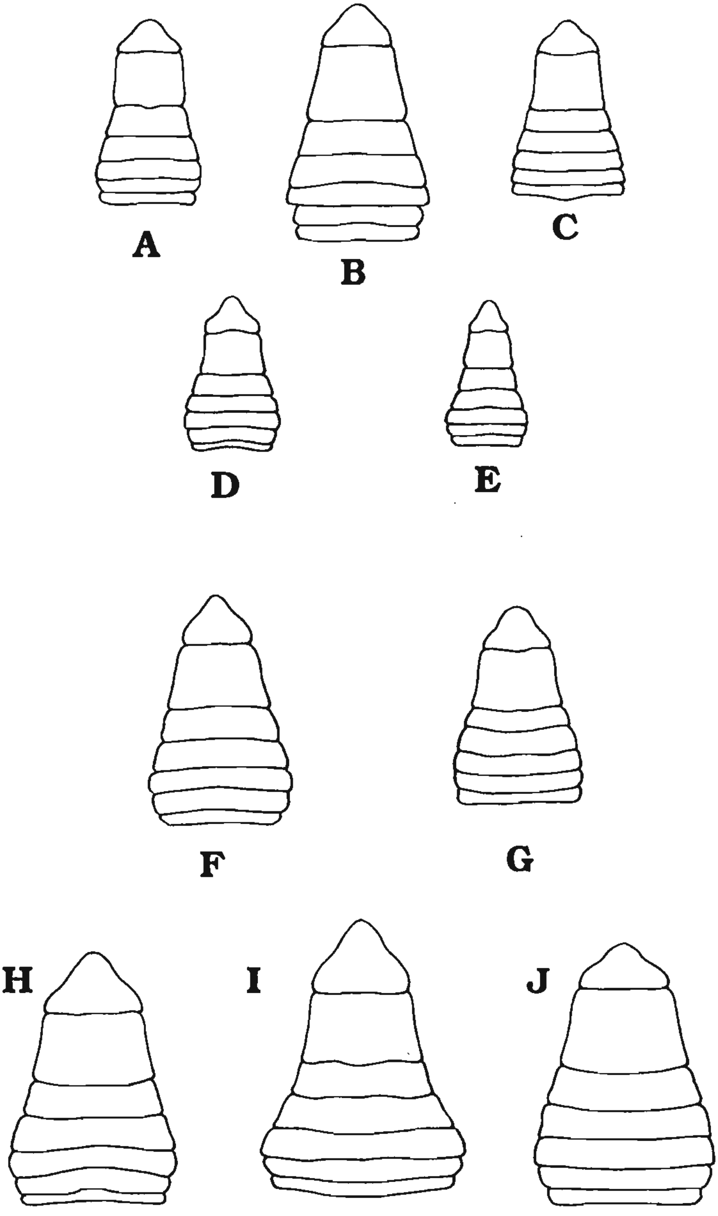


FIG. 37. Inferior view of the male abdomen of **A**, *Sudanonautes faradjensis*, **B**, *S. chavanesii*, **C**, *S. africanus*, **D**, *S. aubryi*, **E**, *S. orthostylis*, **F**, *S. monodi*, **G**, *S. granulatus*, **H**, *S. floweri*, **I**, *S. nigeria* and **J**, *S. kagoroensis*. Specimen details same as fig. 30, 31.

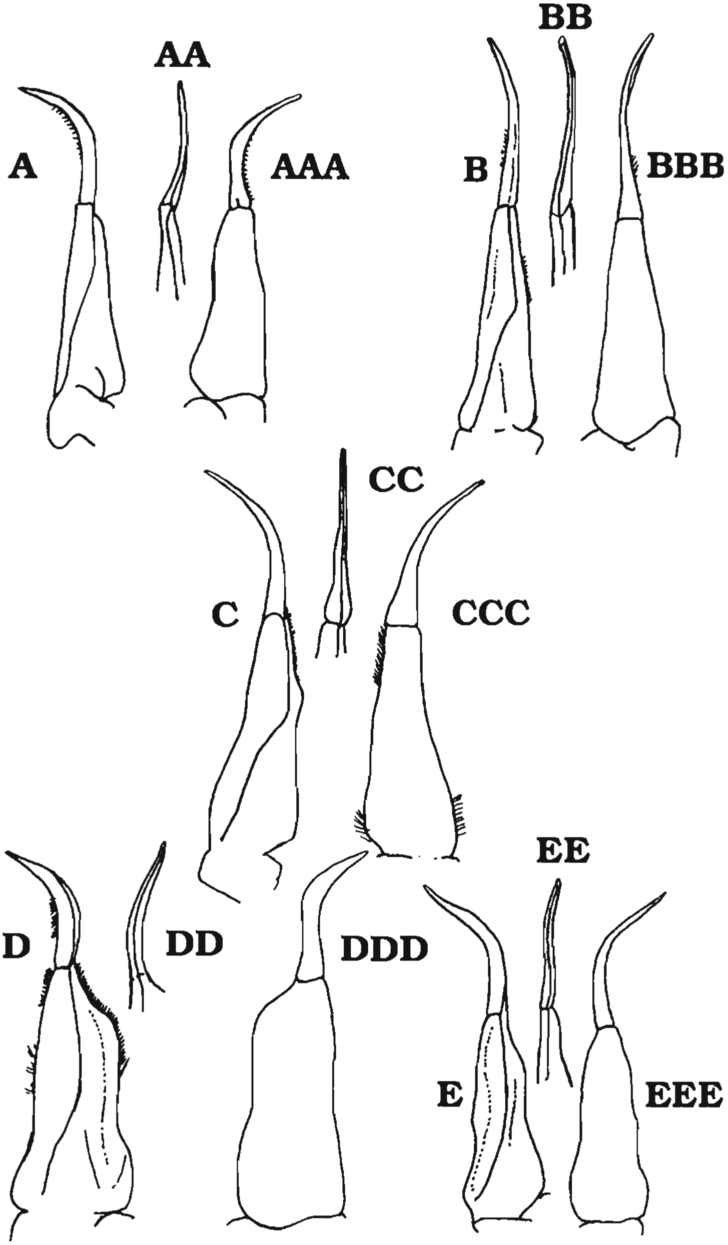


FIG. 38. Ventral view (**A-E**), superior view (**AA-EE**), and dorsal view (**AAA-EEE**) of the right gonopod 1 of **A**, *Sudanonautes aubryi*, **B**, *S. africanus*, **C**, *S. chavanesii*, **D**, *S. floweri* and **E**, *S. faradjensis*. Specimen details same as fig. 30, 31.

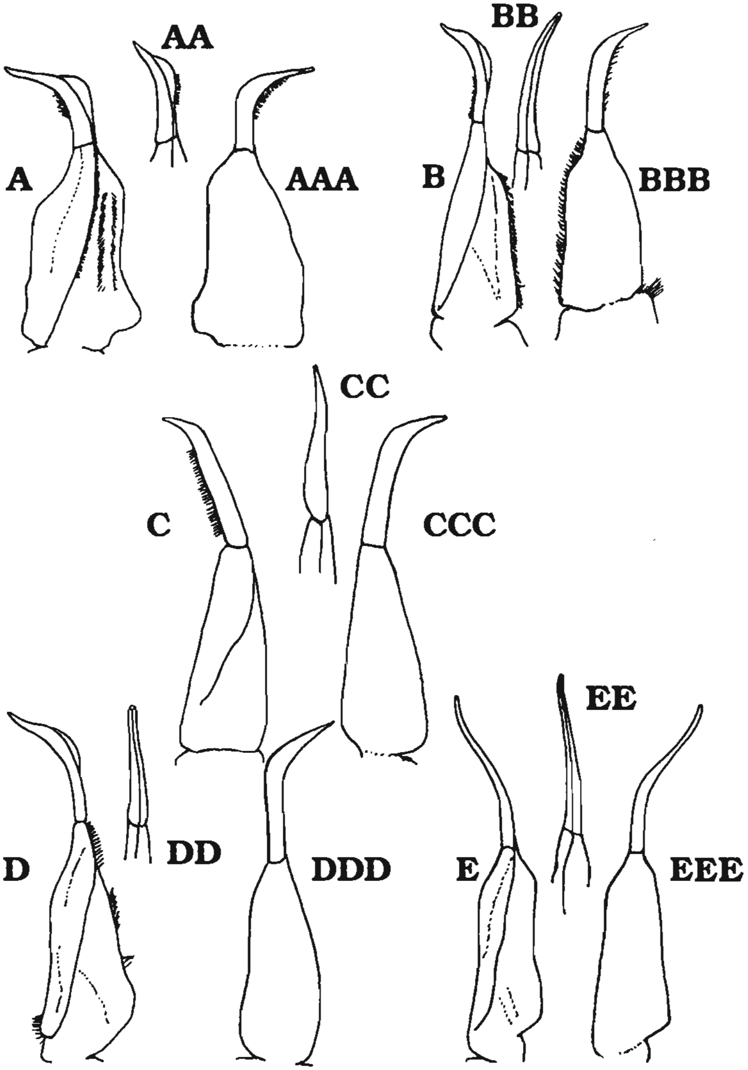


FIG. 39. Ventral view (**A-E**), superior view (**AA-EE**), and dorsal view (**AAA-EEE**) of the right gonopod 1 of **A**, *Sudanonautes monodi*, **B**, *S. granulatus*, **C**, *S. orthostylis*, **D**, *S. kagoroensis* and **E**, *S. nigeria*. Specimen details same as fig. 30, 31.

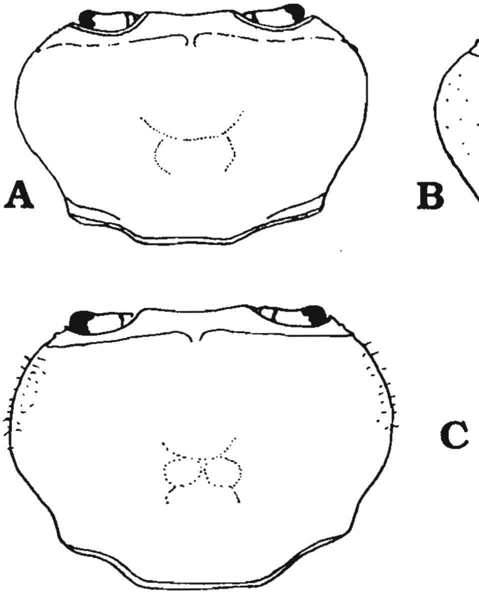


FIG. 40. Dorsal view of the carapace of **A**, *Potamonemus mambilorum* CUMBERLIDGE & CLARK, 1992, adult male holotype (cw 34.5 mm) from Somié, Cameroon (NHML 1991.183). **B**, *P. sachsi* CUMBERLIDGE, 1993a, adult male holotype (cw 33.1 mm) from Bamenda, Cameroon (ZIM K30395). **C**, *P. asylos* CUMBERLIDGE, 1993a, adult male holotype (cw 27.7 mm) from Buea, Cameroon (NHML 1994.587).

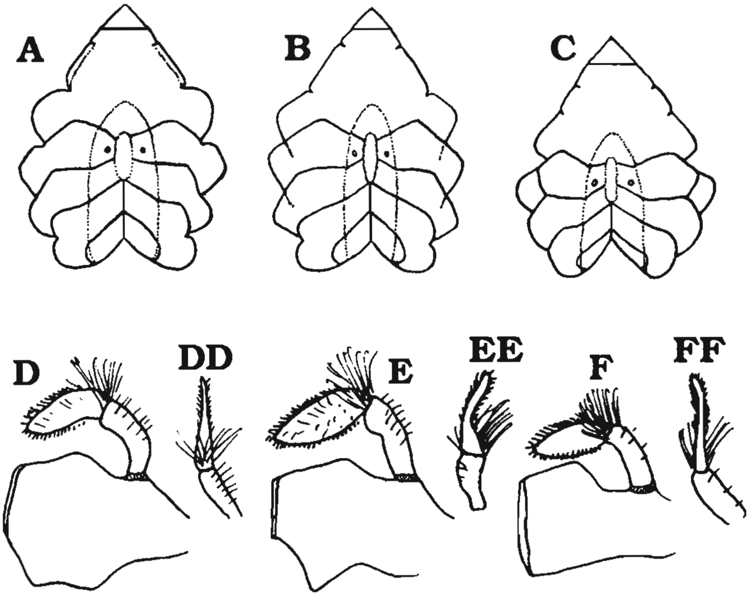


FIG. 41. Inferior view of the sternum (plastron) of **A**, *Potamonemus mambilorum*, **B**, *P. sachsi* and **C**, *P. asylos*. Frontal view (**D-F**) and superior view of terminal segment (**DD-FF**) of the left mandible of **D**, *Potamonemus mambilorum*, **E**, *P. sachsi* and **F**, *P. asylos*. Specimen details same as fig. 40.

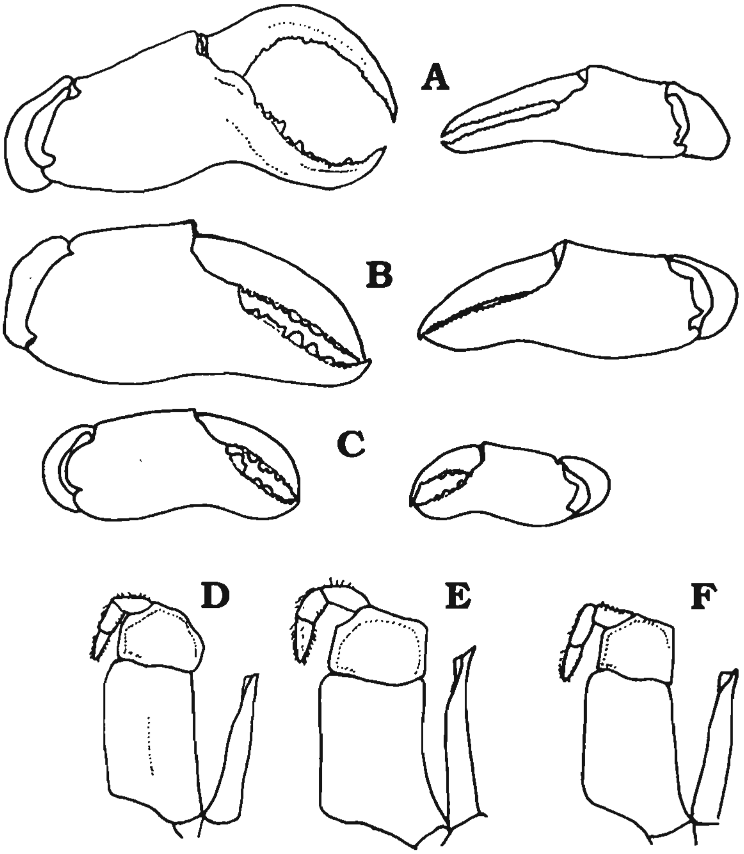


FIG. 42 Frontal view of the right and left chelipeds of **A**, *Potamonemus mambilorum*, **B**, *P. sachsi* and **C**, *P. asylos*. Frontal view of the left third maxilliped of **D**, *Potamonemus mambilorum* **E**, *P. sachsi* and **F**, P. *asylos*. Specimen details same as fig. 40.

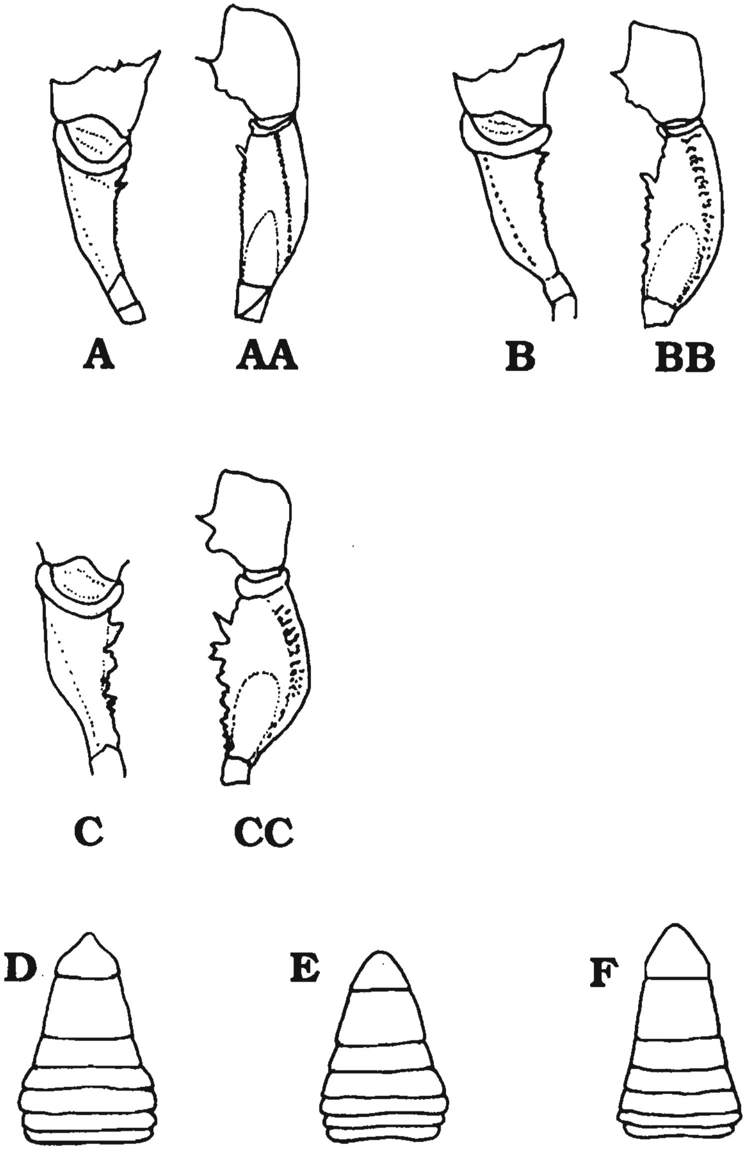


FIG. 43. Inferior view (**A-C**) and superior view (**AA-CC**) of the right carpus and merus of the cheliped of **A**, *Potamonemus mambilorum*, **B**, *P. sachsi* and **C**, *P. asylos*. Inferior view of the male abdomen of **D**, *Potamonemus mambilorum* **E**, *P. sachsi* and **F**, *P. asylos*. Specimen details same as fig. 40.

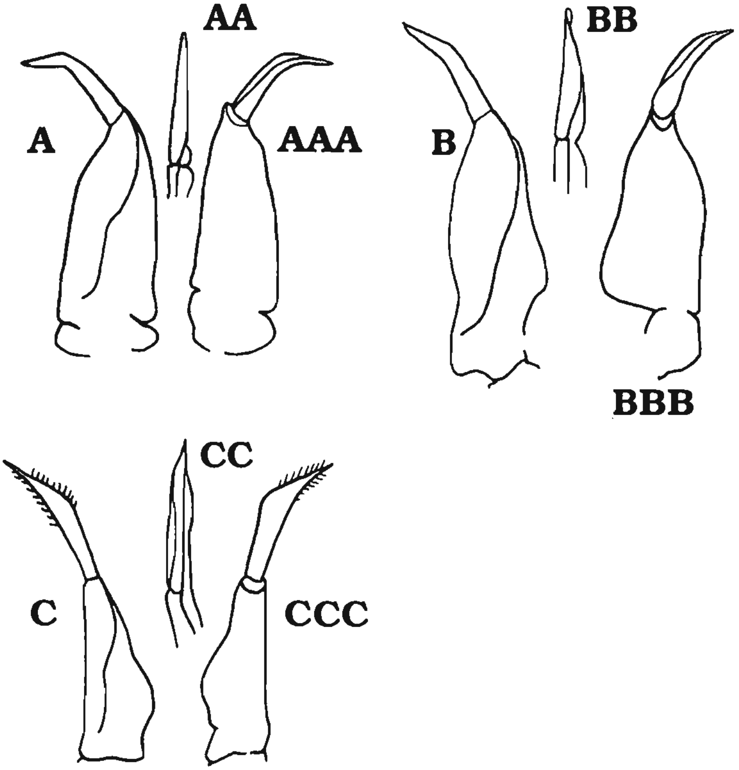


FIG. 44. Ventral view (**A-C**), superior view (**AA-CC**) and dorsal view (**AAA-CCC**) of the right gonopod 1 of **A**, *Potamonemus mambilorum*, **B**, *P. sachsi* and **C**, P. *asylos*. Specimen details same as fig. 40.

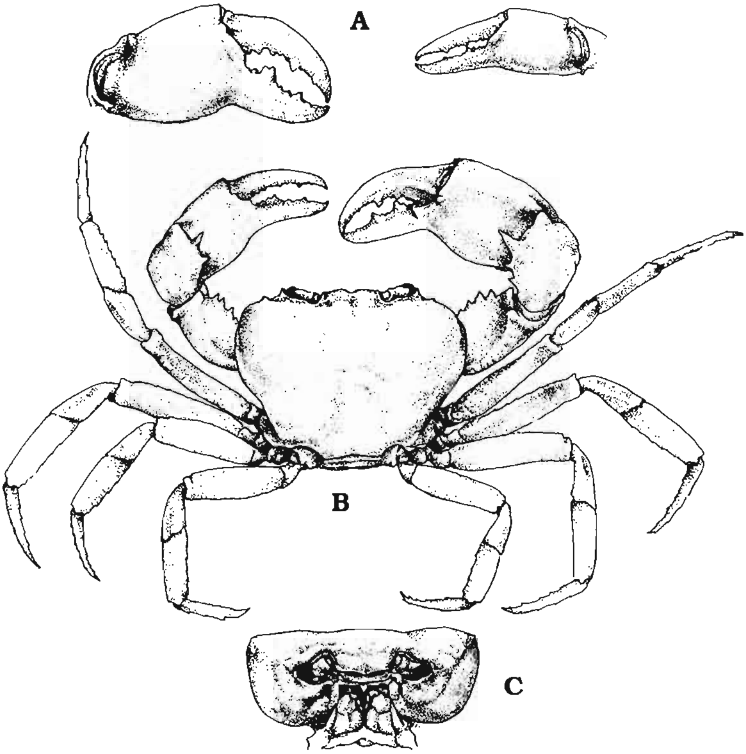


FIG. 45. *Globonautes macropus* (RATHBUN, 1898), adult male (cw 33.5 mm) from Cape Mount County, Liberia (NMU 18.VIII.1988). **A**, frontal view of the chelipeds, **B**, dorsal view of the whole animal and **C**, frontal view of the carapace.

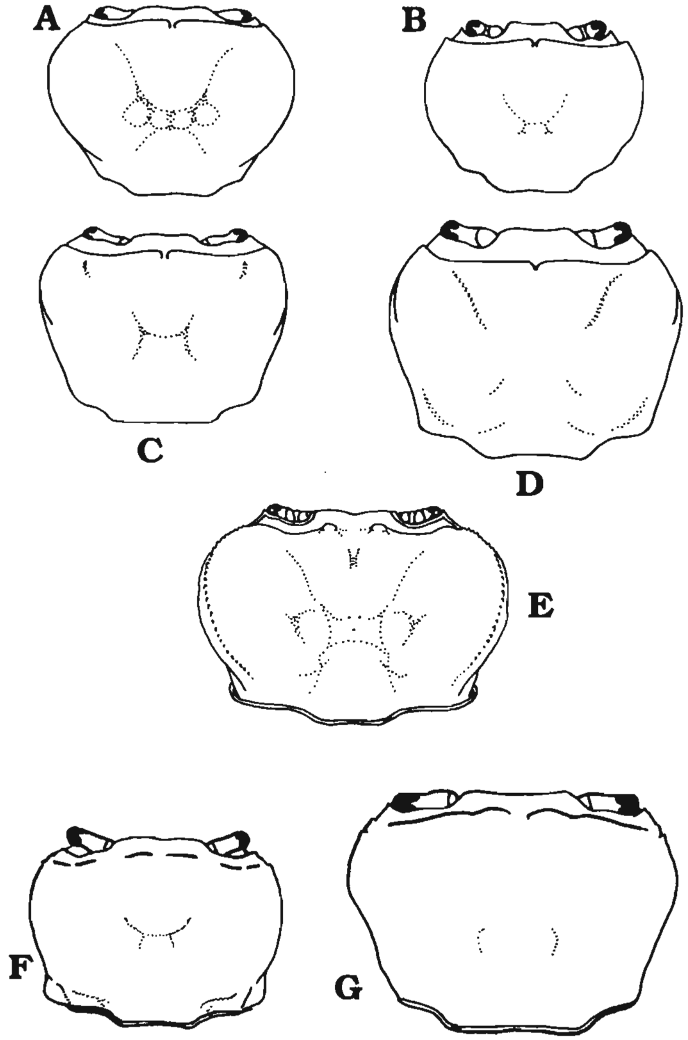


FIG. 46. Dorsal view of the carapace of **A**, *Afrithelphusa gerhildae* Bott, 1969, adult male holotype (cw 21 mm) from Kindia, Guinea (SMF 2619a). **B**, *A. afzelii* (Colosi, 1924), adult male lectotype (cw 29.5 mm) from Sierra Leone (SSN 168). **C**, *A. monodosus* Bott, 1959, adult male holotype (cw 21.5 mm) from Boké, Guinea (MNHN-B 5302). **D**, *A. leonensis* (Cumberlidge, 1987), adult male lectotype (cw 26.4 mm) from Sugar Loaf Mountain, Sierra Leone (NHML 1955.10.7.42-43). **E**, *Globonautes macropus* (Rathbun, 1898), adult male (cw 33.5 mm) from Cape Mount County, Liberia (NMU 18.VIII.1988). **F**, *Louisea edeaensis* (Bott, 1969), adult male holotype (cw 22.5 mm) from Edea, Cameroon (ZSM 1118/1). **G**, *L. balssi* (Bott, 1959), adult male (cw 18.1 mm) from Yabassi, Cameroon (ZMB 21575).

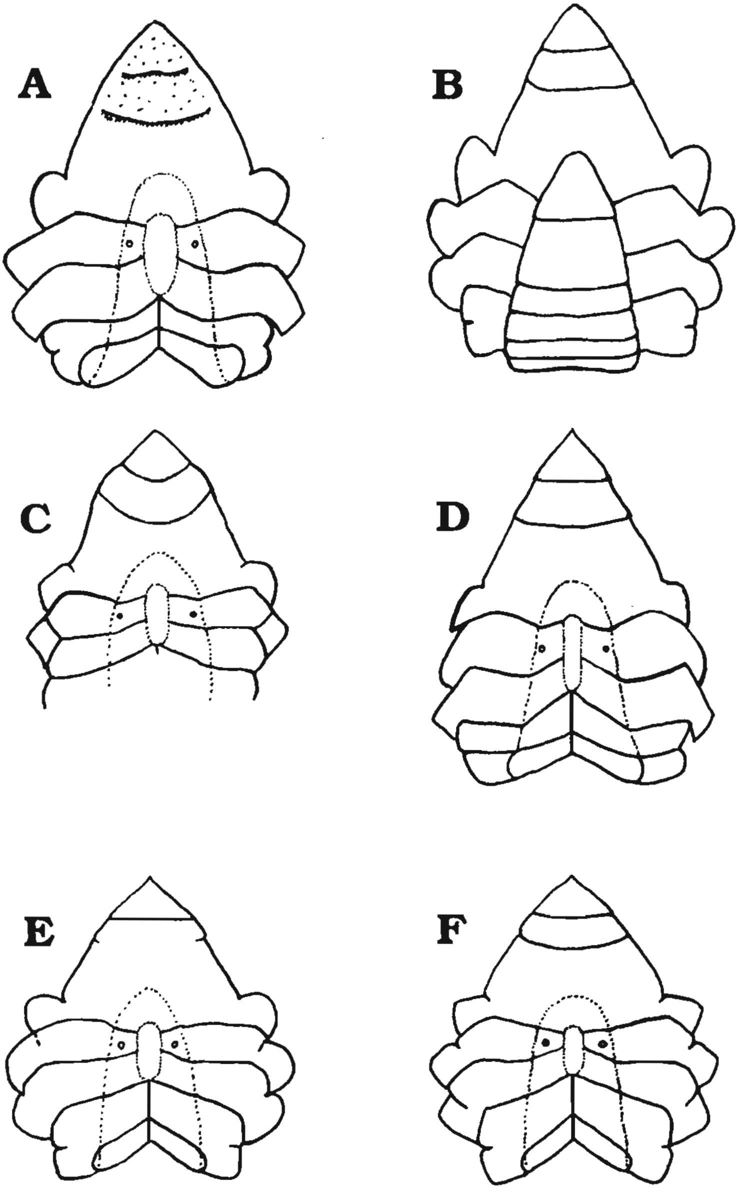


FIG. 47. Inferior view of the sternum (plastron) of **A**, *Afrithelphusa gerhildae*, ***B***, *A. afzelii*, **C**, *A. monodosus*, **D**, *A. leonensis*, **E**, *Globonautes macropus* and **F**, *Louisea edeaensis*. Specimen details as in fig 46.

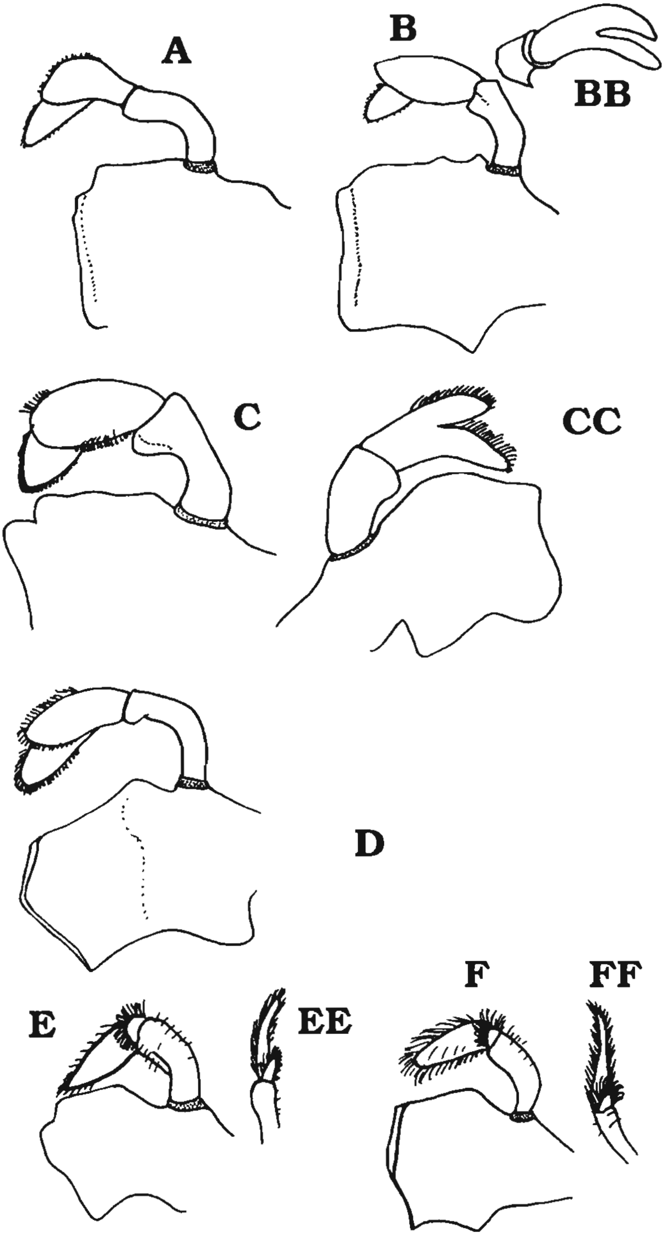


FIG. 48. Frontal view (**A-F**), superior view (**BB**, **EE-FF**) and posterior view (**CC**) of the left mandible of **A**, *Afrithelphusa gerhildae*, **B**, *A. monodosus*, **C**, *A. leonensis*, **D**, **E**, *Louisea edeaensis* and **F**, *L. balssi*. Specimen details as in fig 46.

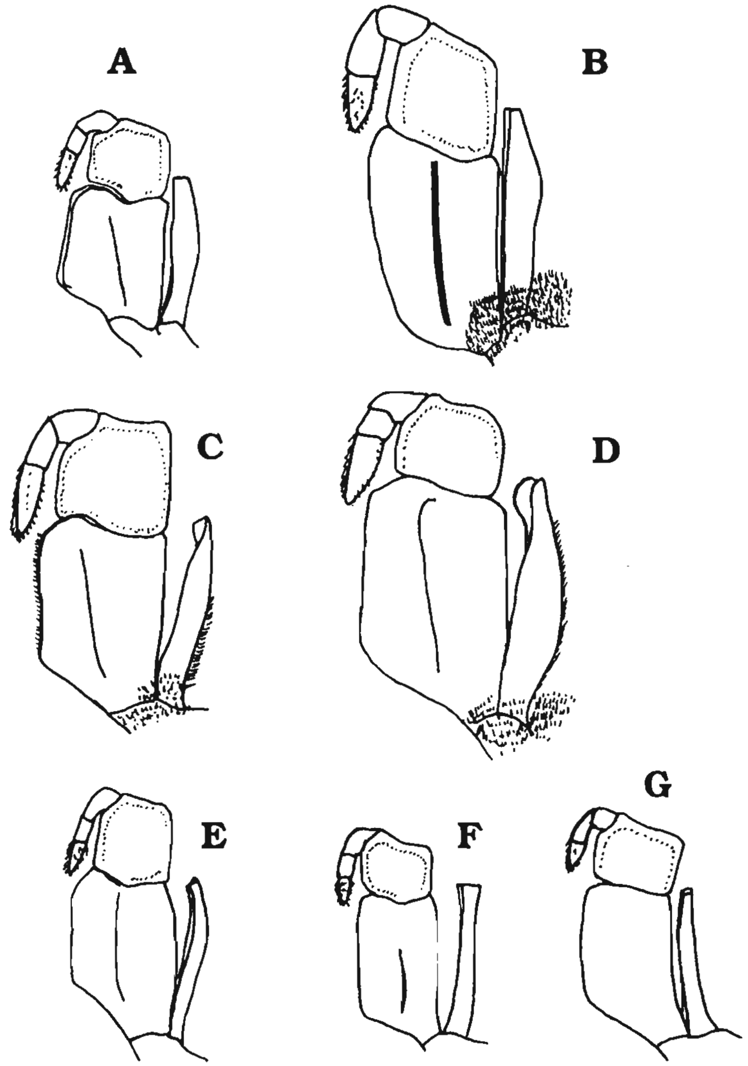


FIG. 49. Frontal view of the left third maxilliped of **A**, *Afrithelphusa gerhildae*, **B**, *A. afzelii*, **C**, *A. monodosus*, **D**, *A. leonensis*, **E**, *Globonautes macropus* and **F**, *Louisea edeaensis* and **G**, *L. balssi*. Specimen details as in fig 46.

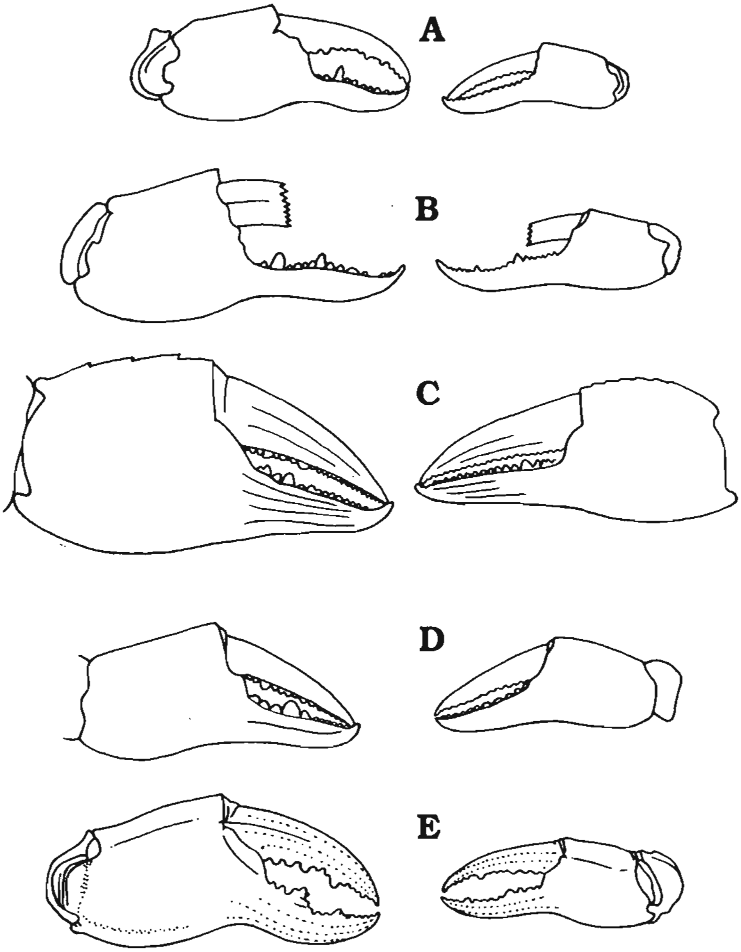


FIG. 50. Frontal view of the right and left chelipeds of **A**, *Afrithelphusa gerhildae*, **B**, *A. afzelii*, **C**, *A. monodosus*, **D**, *A. leonensis* and **E**, *Globonautes macropus*. Specimen details as in fig 46.

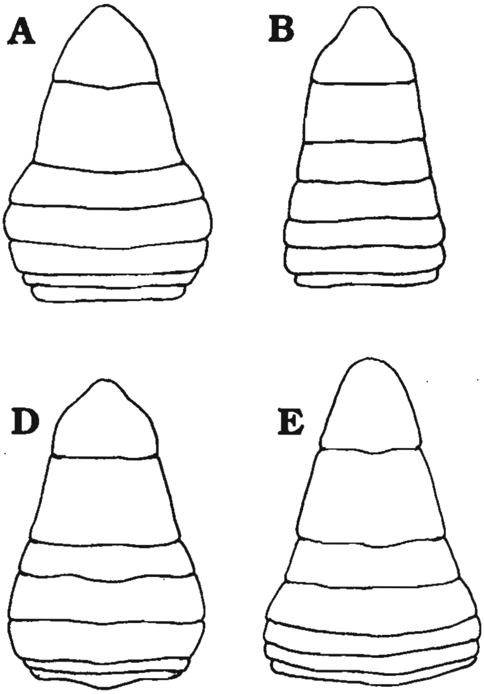


FIG. 51. Inferior view of the male abdomen of **A**, *Afrithelphusa gerhildae*, **B**, *A. afzelii*, **C**, *A. monodosus*, **D**, *A. leonensis*, **E**, *Globonautes macropus* and **F**, *Louisea edeaensis*. Specimen details as in fig 46.

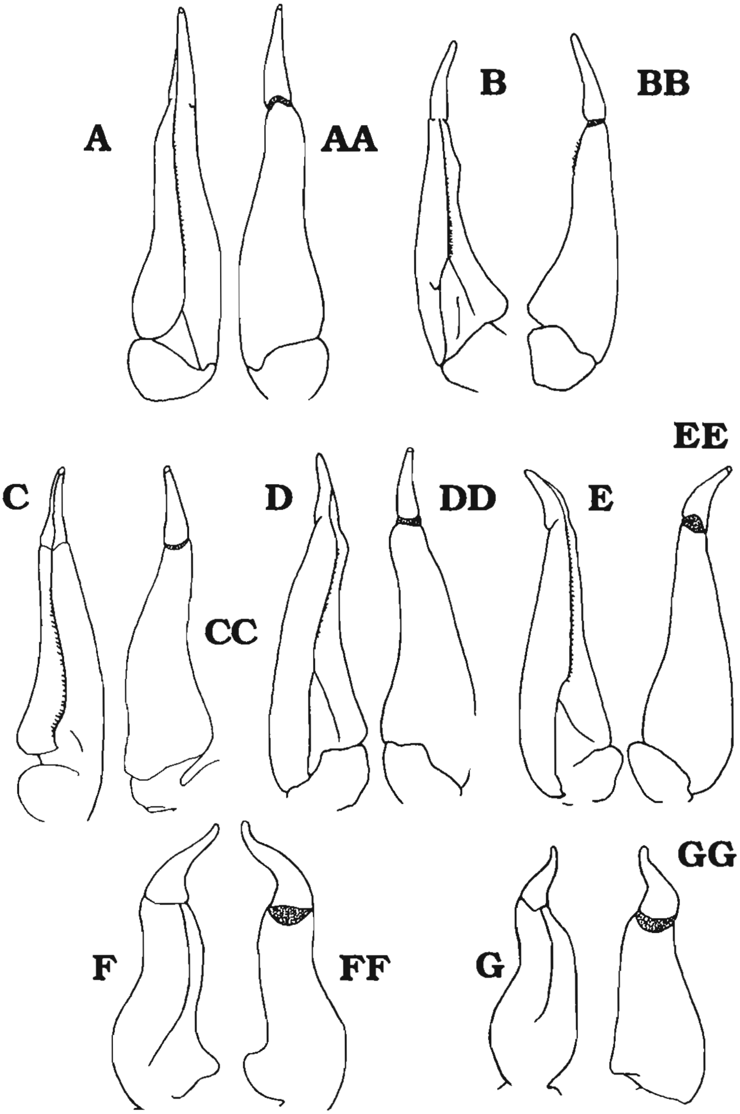


FIG. 52. Ventral view (**A-G**) and dorsal view (**AA-GG**) of the right gonopod 1 of **A**, *Globonautes macropus*, **B**, *Afrithelphusa gerhildae*, **C**, *A. leonensis*, **D**, *A. afzelii*, **E**, *A. monodosus*, **F**, *Louisea edeaensis* and **G**, *L. balssi*. Specimen details as in fig. 46.

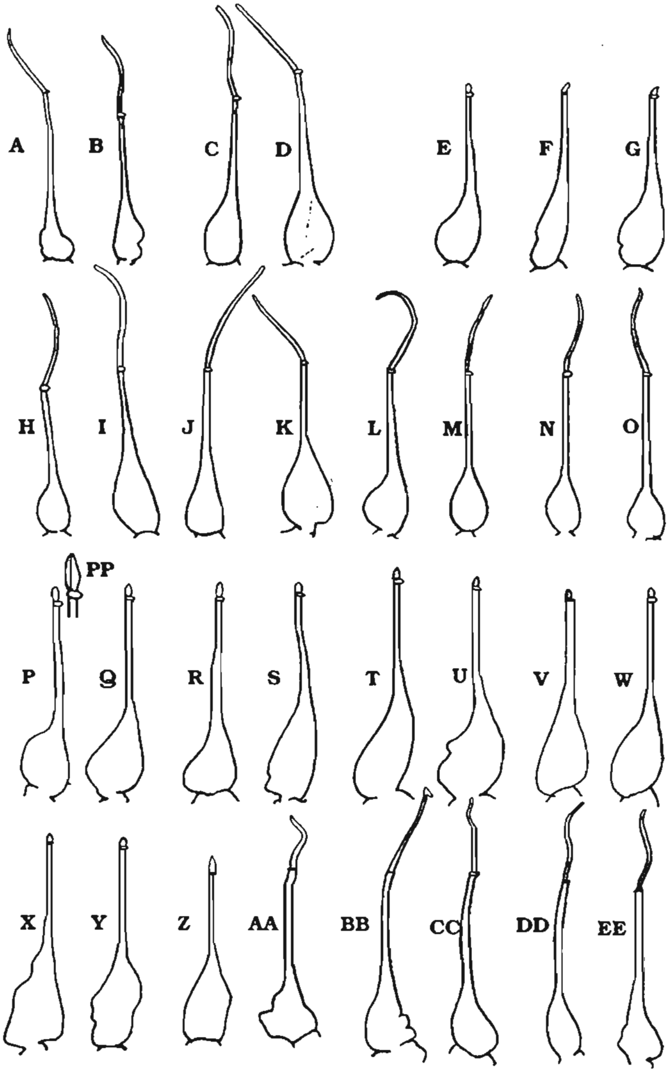


FIG. 53. Ventral view of the right gonopod 2. First row: **A**, *Potamonautes ecorssei*, **B**, *P. triangulus*, **C**, *P. senegalensis*, **D**, *P. reidi*, **E**, *Potamonemus mambilorum*, **F**, *P. sachsi* and **G**, *P. asylos*. Second row: **H**, *Liberonautes latidactylus*, **I**, *L. paludicolis*, **J**, *L. chaperi*, **K**, *L. nanoides*, **L**, *L. rubigimanus*, **M**, *L. nimba*, **N**, *L. lugbe* and **O**, *L. grandbassa*. Third row: **P**, *Sudanonautes africanus*, **Q**, *S. aubryi*, **R**, *S. chavanesii*, **S**, *S. faradjensis*, **T**, *S. floweri*, **U**, *S. monodi*, **V**, *S. orthostylis* and **W**, *S. granulatus*. Fourth row: **X**, *S. kagoroensis*, **Y**, *S. nigeria*, **Z**, *Globonautes macropus*, **AA**, *Afrithelphusa gerhildae*, **BB**, *A. monodosus*, **CC**, *A. leonensis*, **DD**, *Louisea edeaensis* and **EE**, *L. balssi*. Specimen details given in above figures showing gonopod 1.

Morphometric Relationships

fig. 54-62, table IX

Measurements of cw, cl, ch, and fw were made with digital vernier callipers, and most are given correct to at least 0.1 mm. Carapace proportions were calculated according to fw or cl. The ratios of carapace width, carapace length and carapace height to front width (cw/fw, cl/fw and ch/fw) and front width relative to carapace length (fw/cl) were each found to provide a useful index for making interspecific comparisons.

Carapace width.- The cw/fw value for *Menippe* is 3.94, for *Goniopsis* is 2.04, for *Potamon* is 3.03 and for *Platythelphusa* is 2.89. Thus *Menippe* has a wide carapace (about 3.9 x the fw) and a relatively narrow front resulting in a transversely oval outline, which is the plesiomorphic state. *Gecarcinucus* has a very wide carapace with a transversely oval outline. The extremely high value for the cw/fw of *Gecarcinucus* (in the range cl/fw 4.1-6.3) is the result of the unusually narrow front in this species. *Potamon* has a wider front than *Menippe* and *Gecarcinucus* and has a carapace of medium width (cw/fw 3.1-3.5) which also produces a transversely oval outline, while *Goniopsis* and *Platythelphusa* each have a very wide front and a relatively narrow carapace (cw/fw 2.0-3.0) which produces an almost square carapace outline, an apomorphic state. Both of these types of carapace outline are found in African freshwater crabs: transversely oval (e.g., *Sudanonautes*) and subhexagonal or almost square (e.g., *Platythelphusa*). All of the West African species have a carapace with a transversely oval outline, about 1.5 times wide as long. In most genera of West African freshwater crabs there is a trend towards an increase in cw reflecting the lateral expansion of the branchial chambers. The cw/fw values for the entire series of species of West African freshwater crabs are continuous data that fall into three main groups: species with a relatively wide carapace (cw/fw 3.6-4.2, plesiomorphic), species with a carapace of medium width (cw/fw 3.1-3.5) and species with a relatively narrow carapace (cw/fw 2.0-3.0).

Species with a very wide carapace include *Globonautes macropus*, all four species of *Afrithelphusa*, *Potamonautes senegalensis*, *L. rubigimanus*, and eight species of *Sudanonautes*. The widest carapace is that of *Sudanonautes floweri*, which is over four times the front width (cw/fw 4.18). The cw/cl ratio for crabs with the widest carapace is 1.56, that is the carapace is more than 1.5 times wider than long. The relatively wide carapace is associated with a trend towards a more terrestrial lifestyle. A widened carapace is common in air-breathing species, and has arisen independently in a number of genera from West Africa. A similarly widened carapace shared by two species belonging to different genera may be the result of independent, parallel adaptation to the same environmental conditions. Crabs with a carapace of medium width include all three species of *Potamonemus* (cw/fw 3.15 - 3.35), *Potamonautes triangulus* (cw/fw 3.08), two out of ten species of *Sudanonautes* (*S. granulatus* and *S. orthostylis*), and five species of *Liberonautes*. The cw/cl ratio for crabs with a medium wide carapace is around 1.5, that is, the carapace is about 1.5 times wider than long. A moderately widened carapace is common in stream-living species. Completely aquatic groups such as the marine *Goniopsis* and the lake-living *Platythelphusa* have a relatively narrow carapace (cw/fw 2.0 - 2.95), with an outline approaching a subhexagon or even a square. The least wide carapace is found in the two species of *Louisea edeaensis* and *L. balssi* (cw/fw 2.89 and 2.90 respectively), and in *Potamonautes reidi* and *P. ecorssei* (cw/fw 2.60 and 2.83 respectively). The cw/cl ratio for freshwater crabs with the narrowest carapace is around 1.3.

Carapace length.- The cl/fw value for *Menippe* is 2.9, for *Goniopsis* is 1.71, for *Potamon* is 2.57 and for *Platythelphusa* is 2.49. Thus *Menippe*, *Potamon* and *Platythelphusa* each have a carapace of medium length (in the range cl/fw 2.5 - 3.0) which is the plesiomorphic state, and *Goniopsis* has a relatively short carapace (in the range cl/fw 1.7 - 2.4) which is an apomorphic state. *Gecarcinucus* has a relatively long carapace but the extremely high value of the cl/fw of *Gecarcinucus* (in the range cl/fw 3.1-4.5) is the result of the unusually narrow front in this species.

Most genera of West African freshwater crabs include species with a carapace of medium length and species with a relatively short carapace. The cl/fw value for the entire series of species of West African freshwater crabs are continuous data that fall into two main groups: species with a carapace of medium length (cl/fw range 2.5 - 3.0, the plesiomorphic state), and species with a relatively short carapace (cl/fw range 1.7 - 2.4, an apomorphic state). Species with a carapace of medium length (or a little longer) include *Globonautes macropus* (cl/fw 3.04), all four species of *Afrithelphusa* (cl/fw 2.66 - 2.88), and seven out of ten species of *Sudanonautes* (cl/fw 2.57 - 2.79). A carapace of medium length, or a little longer, is common in West African freshwater crabs, especially in the air-breathing species, and may be a symplesiomorphy. In contrast, species of completely aquatic forms such as the lake-living *Platythelphusa* have a short carapace (cl/fw 2.03-2.49). A relatively short carapace is also found in *Louisea* (cl/fw 2.16 - 2.19), *Sudanonautes orthostylis* (ch/fw 2.15), four species of *Potamonautes* (cl/fw 2.02 - 2.24), *Potamonemus* (cl/fw 2.23 - 2.32), five species of *Liberonautes* (cl/fw 2.14 - 2.38), *Potamonautes senegalensis* (cl/fw 2.4), *Sudanonautes granulatus* and *S. kagoroensis* (cl/fw 2.37 and 2.49), and *Liberonautes rubigimanus* (cl/fw 1.49).

Carapace height.- Most genera of West African freshwater crabs include species with a flat carapace and species with a highly arched carapace. A carapace of medium height is the plesiomorphic condition, and is associated with aquatic respiration and an aquatic habitat. A highly arched carapace reflects the dorsal expansion of the lateral branchial regions of the carapace associated with increased air breathing. The increased volume of the branchial chambers above the gills created by this expansion provides an air store for gaseous exchange between air and the blood (via the vascularized branchiostegal lining).

The ch/fw value for *Menippe* is 1.38, for *Goniopsis* is 0.8, for *Potamon* is 1.16 and for *Platythelphusa* is 1.0. Thus *Menippe* and *Potamon* each have a carapace of medium height (ch/fw 1.1-1.4) which is the plesiomorphic state, while *Goniopsis* and *Platythelphusa armata* each have a very flat carapace, which is an apomorphic state. While the carapace of *Gecarcinucus* is highly arched, the extremely high value for ch/fw of this species (cl/fw 2.5) is the result of the unusually narrow front in this species. The ch/fw values for the entire series of species of West African freshwater crabs (table IX) are continuous data that fall into three main groups: species with a carapace of medium height (ch/fw 1.1 - 1.4, the plesiomorphic state), species with a flat carapace (ch/fw 0.8 - 1.0, an apomorphic state), and species with a high, arched carapace (cw/fw 1.41 - 2.5, an apomorphic state). Crabs with a carapace of medium height include all three species of *Potamonemus* (ch/fw 1.06 - 1.1), both species of *Louisea* (ch/fw 1.17 - 1.2), *Potamonautes triangulus* and *P. ecorssei* (ch/fw 1.01 and 1.01 respectively), together with seven out of ten species of *Sudanonautes* (ch/fw 1.06 - 1.29), and four species of *Liberonautes* (ch/fw 1.0 - 1.11). In this latter genus the ch/fw ratio is around 1.0, that is, the ch is approximately equal to the fw. Species of completely aquatic forms such as the lake-living genus *Platythelphusa* have either a carapace of medium height (*P. armata, P. polita* and *P. tuberculata*, ch/fw 1.0, 1.1 and 1.1 respectively, the plesiomorphic state), or a relatively flat carapace (*P. conculata, P. echinata* and *P. maculata*, ch/fw 0.77, 0.76, 0.86 respectively, an apomorphic condition). In the West African freshwater crabs the flattest carapace is found in *Liberonautes chaperi* and *L. nanoides* (ch/fw 0.87 and 0.99 respectively), both of which are completely aquatic river crabs. Species with a high, arched carapace include *Globonautes macropus* and all four species of *Afrithelphusa*, as well as *Sudanonautes nigeria*, *S. monodi* and *Potamonautes senegalensis* (ch/fw 1.46, 1.46 and 1.56 respectively). Among these, the highest carapaces are seen in the semi-terrestrial species such as *Sudanonautes floweri* (ch/fw 1.68), *Globonautes macropus* (ch/fw 1.69), and *Afrithelphusa monodosus* (ch/fw 1.86).

The trend towards an increase in ch within a genus is associated with a trend towards a more terrestrial lifestyle. A high, arched carapace is common in air-breathing species, and has arisen independently in a number of genera from West Africa. A similarly high carapace shared by two species belonging to different genera may be the result of independent, parallel adaptation to the same environmental conditions. The high, arched carapace is evidently an apomorphy related to increased air-breathing, while the decrease from a medium to a flat carapace seen in some species of completely aquatic crabs such as species of the lake-living *Platythelphusa* may be an apomorphy related to adaptations favouring concealment from predators under rocks and ledges.

Front width.- The width of the lower margin of the front is also a measurement of the interantennular distance in most species, because the basal joint of the antenna arises at the lateral margin of the front. A decrease in the fw/cw may reflect the reorganisation of internal organs of the cephalothorax to accommodate the modification of the mouthparts and the expansion of the branchial chambers associated with the adaptation of the respiratory system to aerial respiration and an amphibious life style. The fw/cl value for *Menippe* is 0.34, for *Goniopsis* is 0.58, for *Potamon* is 0.39 and for *Platythelphusa* is 0.41 - 0.51. Thus *Menippe* and *Potamon* each have a front of medium width (fw/cl 0.35 - 0.39) which is the plesiomorphic state, while *Goniopsis* and *Platythelphusa* each have a very wide front (fw/cl 0.4 - 0.6) which is an apomorphic state. *Gecarcinucus* has an unusually narrow front and the lowest fw/cl value (fw/cl 0.25) for all taxa compared here. The fw/cl value for the entire series of species of West African freshwater crabs are continuous data that fall into two main groups: species with a front of medium width (fw/cl 0.35 - 0.39, the plesiomorphic state) and species with a relatively wide front (fw/cl 0.4 - 0.5). Typically the frontal margin tends to be wide in aquatic freshwater crabs (*Platythelphusa* fw/cl 0.41 - 0.51) and of medium width or relatively narrow in semi-terrestrial forms. A relatively wide front is found in *S. orthostylis* and *S. granulatus* (fw/cl 0.41, 0.45 respectively), and in all species of *Potamonautes* (fw/cl 0.46 - 0.5), *Potamonemus* (fw/cl 0.43-0.46), and *Liberonautes* (fw/cl 0.41- 0.44). For example, the front of *Afrithelphusa* (fw/cl 0.35-0.37) and the majority of species of *Sudanonautes* (fw/cl 0.35 - 0.39) is of medium width, while that of *Globonautes* is relatively narrow (fw/cl 0.34). A similarly proportioned frontal region shared by two species belonging to different genera may be the result of independent, parallel adaptation to the same environmental conditions.

Conclusions

Carapace proportions were calculated according to fw or cl. The ratios of carapace width, carapace length, and carapace height to front width (cw/fw, cl/fw and ch/fw) provide a useful index for making interspecific comparisons. Morphometric relationships of the dimensions and proportions of the carapace (such as carapace width, cw/fw; carapace length, cl/fw; carapace height, ch/fw and frontal margin width, fw/cl) revealed trends in changes in the width, length and height of the carapace in species within a genus. These trends can be correlated with the habitat and lifestyle of each species. For example, freshwater crabs with a flat carapace or a carapace of medium height tend to live a completely aquatic existence in lakes and/or rivers (e.g., *P. maculata*, *S. faradjensis* and *L. chaperi*). Freshwater crabs with a high to very high carapace tend to show modifications of the branchial chambers for aerial respiration which is typical of species with a semiterrestrial or terrestrial lifestyle (e.g., *S. floweri*, *S. monodi*, *G. macropus* and *A. monodosus*). Characters derived from carapace proportions can be useful secondary characters for the identification of species within a genus, but should not be used without consideration of other diagnostic characters (such as those of the gonopods and mouthparts). No significant difference was found between the carapace proportions of male and female freshwater crabs examined in this study. In some species (e.g., *P. ecorssei*, *L. chaperi*, *S. chavanesii* and *G. macropus*) the carapace proportions were found to remain unaltered as an animal grows (no significant difference was found between carapace proportions between juvenile, subadult and adult animals) and the carapace proportions of specimens of any age were used. In other species (e.g., *L. paludicolis*, *S. aubryi* and *S. monodi*) the carapace proportions of adults were found to be significantly different from those of juvenile and subadult animals and in these cases only the carapace proportions of adults were used.

Trends in the change in the carapace proportions (such as from species with a moderately high carapace to species with a flattened or highly arched carapace) were found to be expressed separately in different genera, especially in those genera with large numbers of species (e.g., *Potamonautes*, *Liberonautes* and *Sudanonautes*). This was interpreted as parallel evolution within each genus associated with radiation into, and subsequent adaptation to, different habitats. For this reason characters derived from carapace proportions were considered to be homoplasious and were not used in the cladistic analysis.

TABLE IX

Mean carapace proportions of taxa included in this study

Species	**cw/fw mean ± s.d.**		**cl/fw mean ± s.d.**		**ch/fw mean ± s.d.**	
P. ecorssei (n = 56)	2.83	0.17	2.09	0.19	1.01	0.05
P. triangulus (n = 14)	3.08	0.24	2.17	0.18	1.01	0.02
P. senegalensis (n = 1)	3.65		2.4		1.56	
P. reidi (n = 22)	2.60	0.25	2.02	0.19	0.94	0.09
L. latidactylus (n = 87)	3.36	0.14	2.33	0.10	1.00	0.02
L. paludicolis (n = 37)	3.35	0.32	2.33	0.15	1.11	0.08
L. chaperi (n = 23)	3.35	0.21	2.33	0.10	0.87	0.05
L. nanoides (n= 58)	3.46	0.2	2.38	0.16	0.99	0.05
L. rubigimanus (n = 25)	3.77	0.38	2.47	0.14	1.07	0.07
L. nimba (n = 8)	3.01	0.19	2.14	0.10	1.10	0.10
L. lugbe (n = 2)	3.39		2.19		1.05	
L. grandbassa (n = 2)	3.26		2.30		1.15	
S. aubryi (n= 99)	3.52	0.22	2.57	0.16	1.29	0.17
S. africanus (n = 88)	3.57	0.34	2.63	0.21	1.06	0.12
S. chavanesii (n = 14)	3.55	0.26	2.65	0.18	1.09	0.09
S. floweri (n = 106)	4.18	2.65	2.79	1.73	1.68	1.12
S. faradjensis (n = 15)	3.63	0.15	2.65	0.12	1.09	0.1
S. granulatus (n = 80)	3.27	0.27	2.37	0.17	1.18	0.12
S. monodi (n = 91)	3.82	0.21	2.60	0.13	1.46	0.09
S. kagoroensis (n = 45)	3.58	0.25	2.49	0.14	1.15	0.11
S. orthostylis (n = 12)	3.10	0.18	2.15	0.13	1.07	0.08
S. nigeria (n = 4)	4.03	0.32	2.75	0.21	1.46	0.1
P. mambilorum (n = 24)	3.15	0.15	2.23	0.10	1.07	0.08
P. sachsi (n = 54)	3.20	0.17	2.25	0.12	1.06	0.09
P. asylos (n = 10)	3.35	0.18	2.32	0.08	1.10	0.11
G. macropus (n = 33)	3.94	1.18	3.04	1.0	1.69	0.53
A. gerhildae (n = 3)	3.46	0.27	2.66	0.22	1.48	0.18
A. afzelii (n = 1)	3.69		2.88		1.44	
A. monodosus (n=1)	3.58		2.83		1.83	
A. leonensis (n = 3)	3.47	0.08	2.72	0.03	1.55	0.06
L. edeaensis (n = 6)	2.89	0.05	2.16	0.08	1.17	0.10
L. balssi (n = 4)	2.90	0.20	2.19	0.11	1.20	0.16
P. armata (n = 131)	2.47	0.18	2.13	0.15	1.00	0.08
P. fluviatilis (n = 1)	3.03		2.57		1.16	
G. jacquemonti (n = 2)	6.30		4.33		2.51	
G. pulchra (n = 1)	2.04		1.71		0.80	
M. mercenaria (n = 1)	3.94		2.90		1.38	

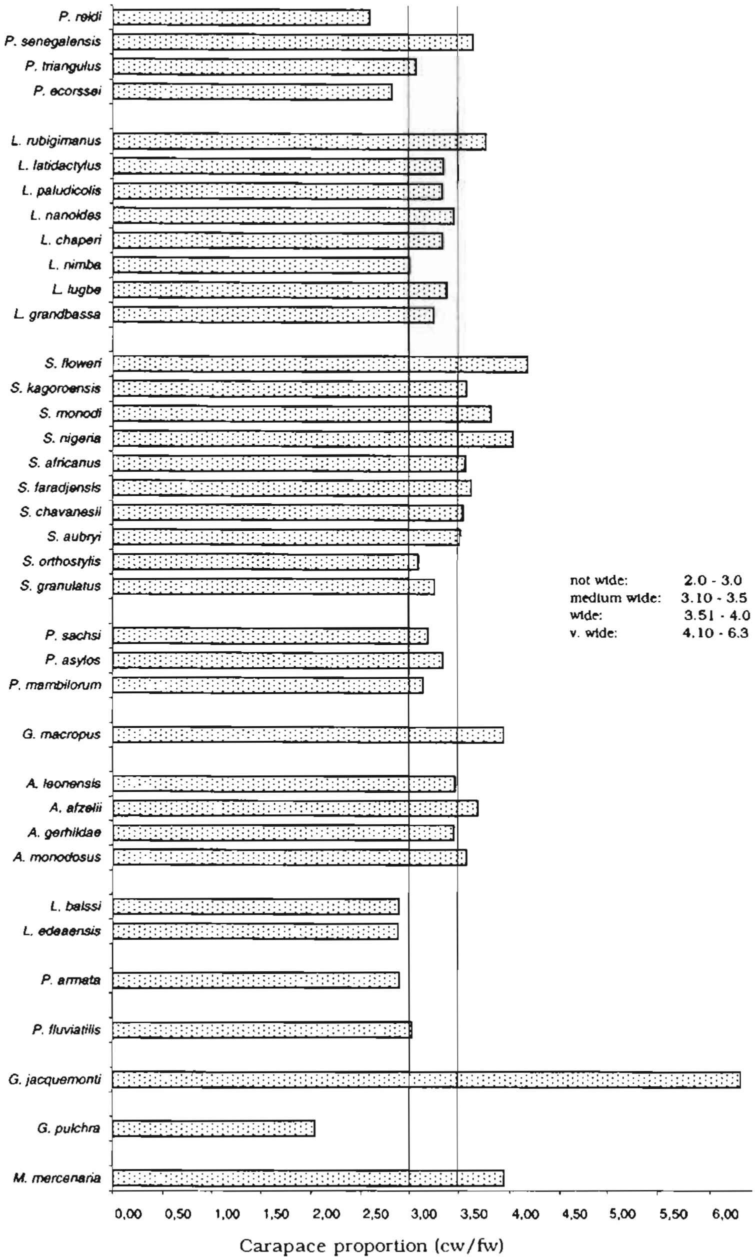


FIG. 54. The freshwater crabs of West Africa and outgroup taxa. Comparison of the relative width of the carapace (cw/fw).

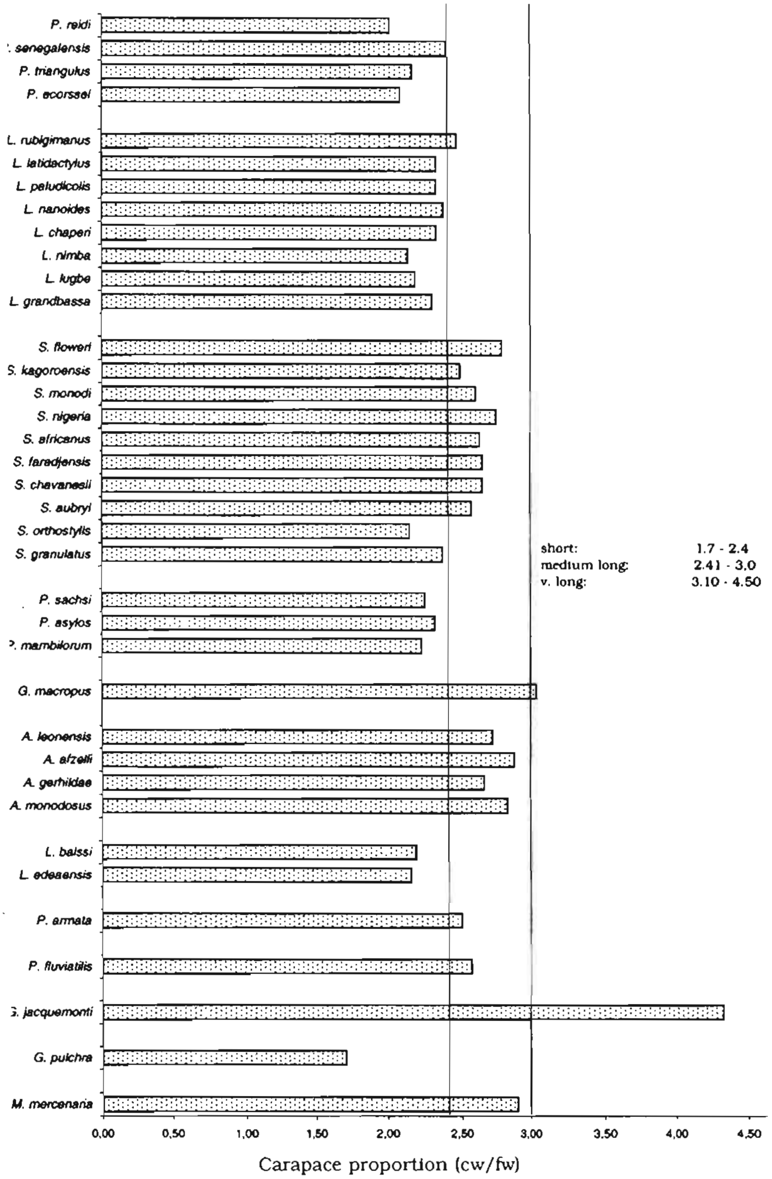


FIG. 55. The freshwater crabs of West Africa and outgroup taxa. Comparison of the relative length of the carapace (cl/fw).

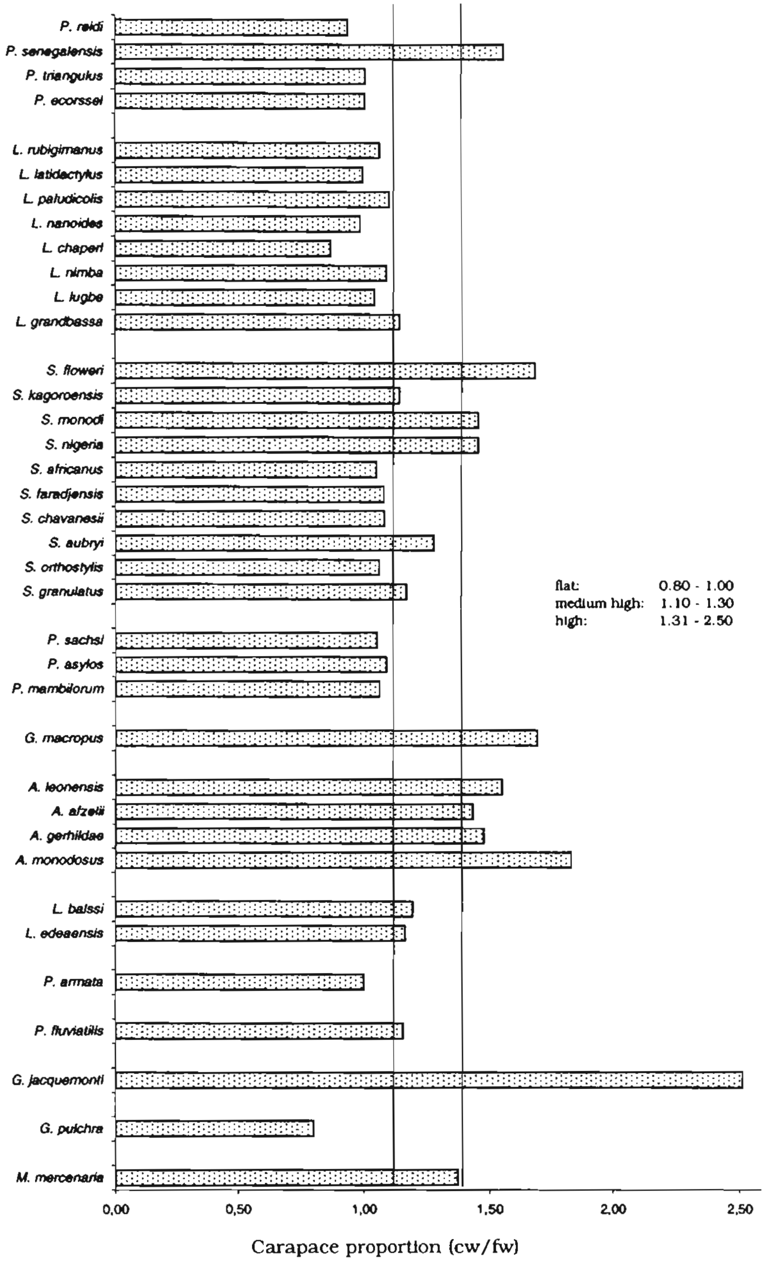


FIG. 56. The freshwater crabs of West Africa and outgroup taxa. Comparison of the relative height of the carapace (ch/fw).

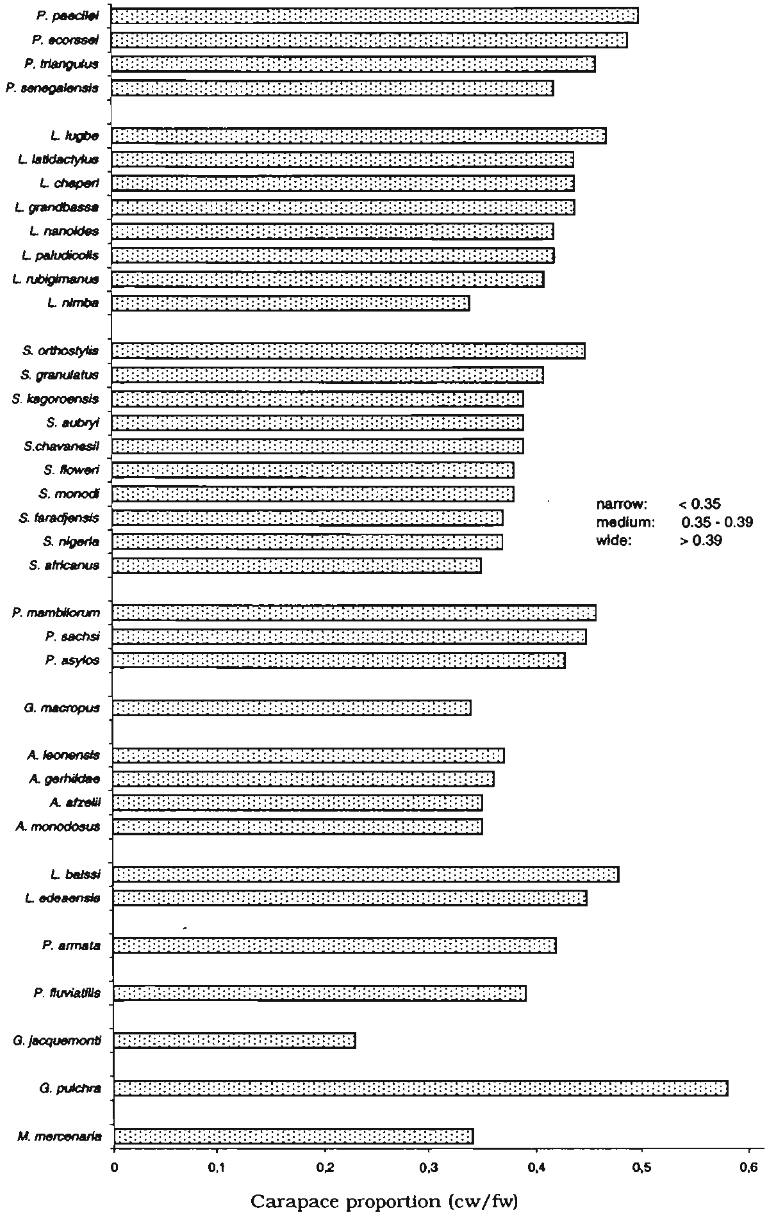


FIG. 57. The freshwater crabs of West Africa and outgroup taxa. Comparison of the relative width of the front (fw/cl).

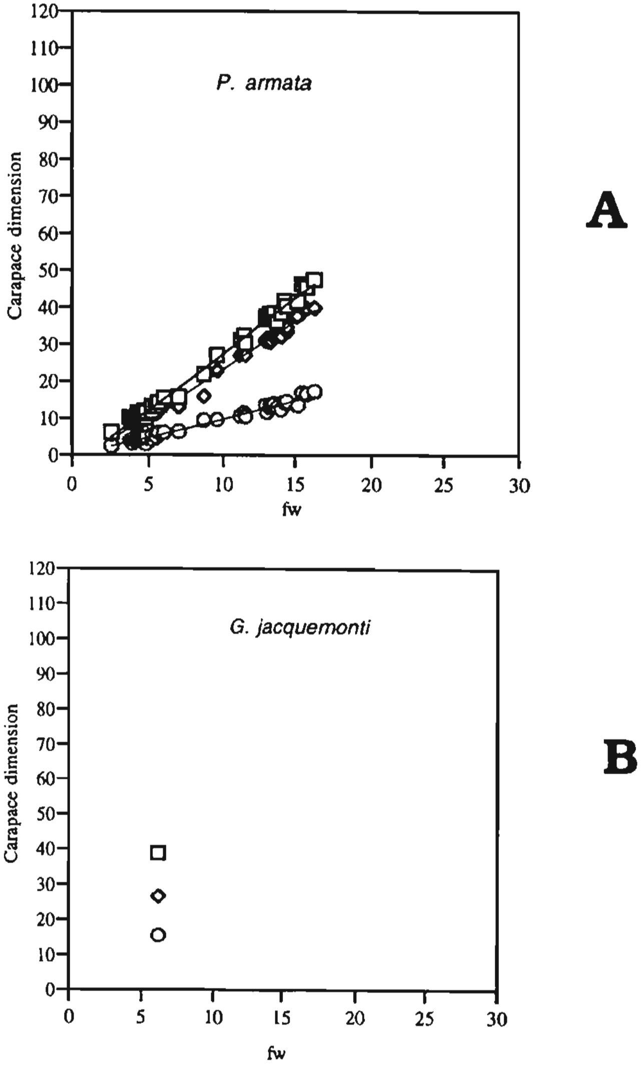
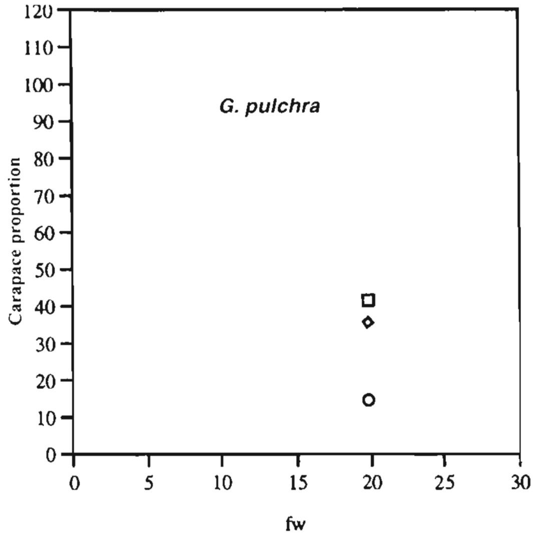
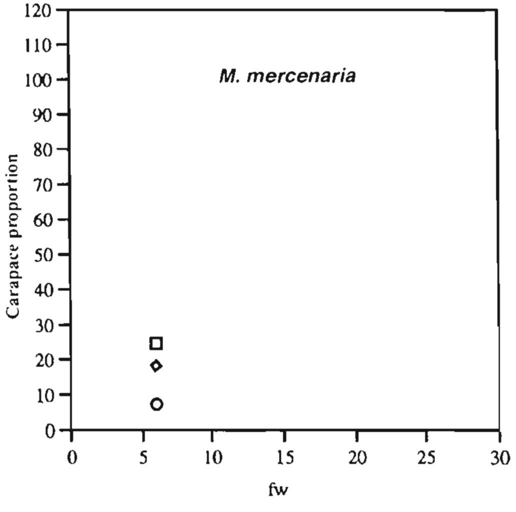


FIG. 58. Dimensions of the carapace (cw = square, ch = triangle, cl = circle) compared to front width (fw) of **A**, 21 specimens of *Platythelphusa armata* (cw 27 to 47.5 mm), relationships are described by cw = 3.15fw - 4.56, r = 0.98; cl = 2.63fw -3.13, r = 0.98; ch = 1.12fw - 1.96, r = 0.92; all r values indicate a highly significant correlation (P < 0.001) at 5 degrees of freedom. **B**, *Gecarcinucus jacquemonti* cw 38.8 mm.



C



D

FIG. 58. **C**. *Goniopsis pulchra* cw 40.2 mm. **D**. *Menippe mercenaria* cw 22.9 mm.

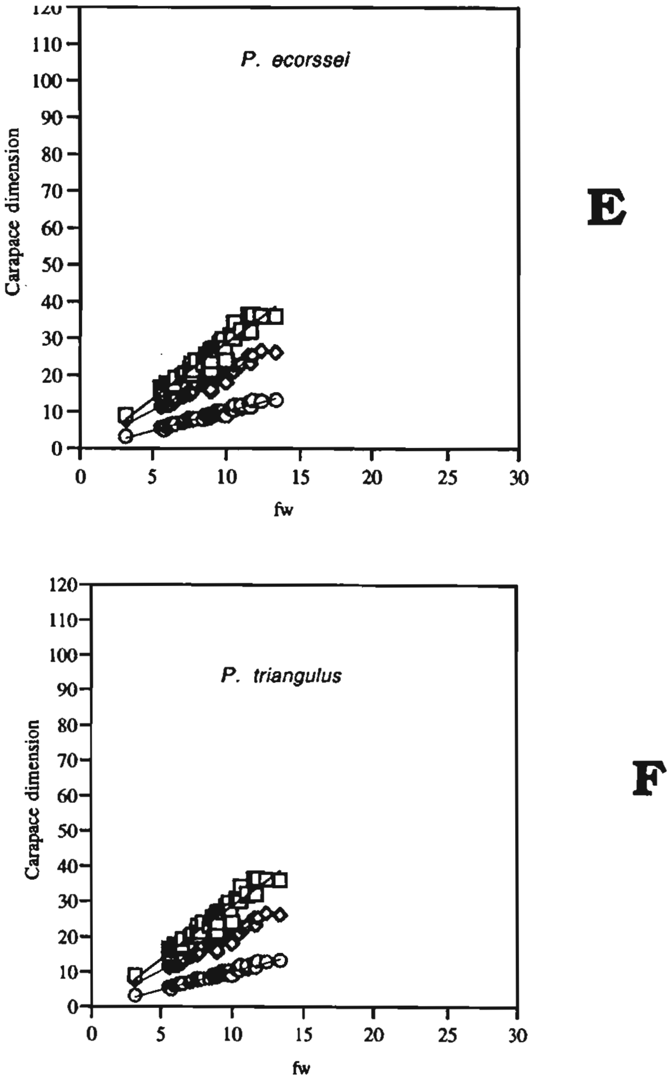


FIG. 58. **E**, 56 specimens of *Potamonautes ecorssei* (cw 9.1 to 36.1 mm), relationships are described by cw = 3.02fw - 1.55, r = 0.97; cl = 2.08fw + 0.01, r = 0.94; ch = 1.07fw - 0.47, r = 0.98, all r values indicate a highly significant correlation (P < 0.001) at 55 degrees of freedom. **F**, 14 specimens of *Potamonautes triangulus* (cw 17.7 to 24.5 mm), relationships are described by cw = 2.95fw + 0.88, r = 0.84; cl = 1.38fw + 5.08, r = 0.75; ch = 1.08fw - 0.46, r = 0.98, all r values indicate a highly significant correlation (P < 0.001) at 13 degrees of freedom.

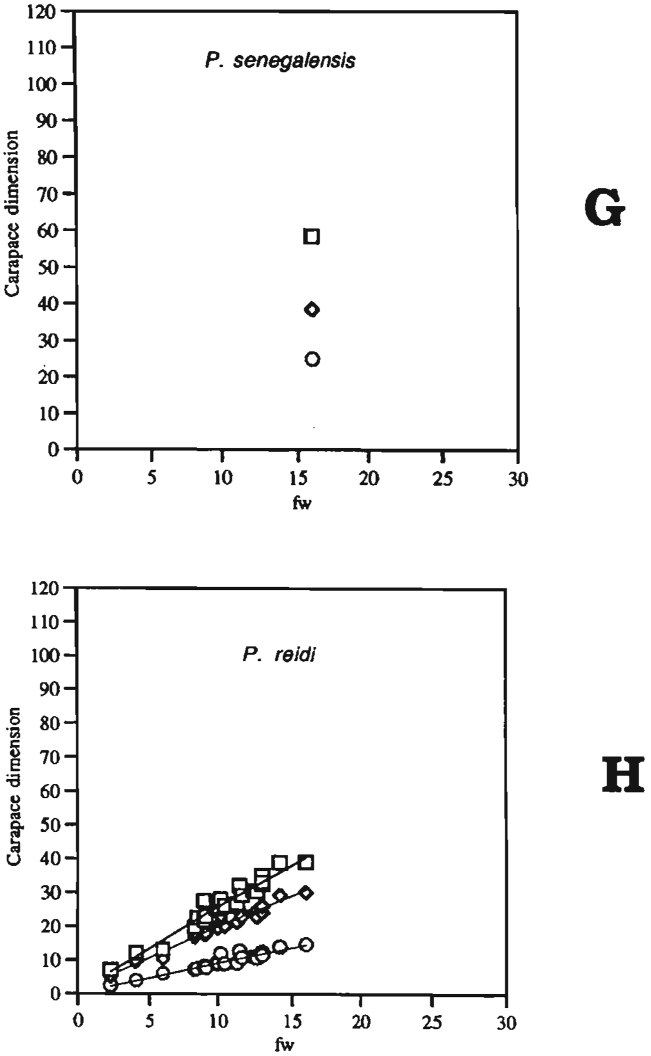


FIG. 58. **G.** *Potamonautes senegalensis* cw 58.5 mm. **H.** 16 specimens of *Potamonautes reidi* (cw 14.0 to 36.5 mm), relationships are described by cw = 2.45fw + 1.14, r = 0.98; cl = 1.83fw + 1.67, r = 0.97; ch = 0.90fw + 0.26, r = 0.97, all r values indicate a highly significant correlation ($P < 0.001$) at 15 degrees of freedom.

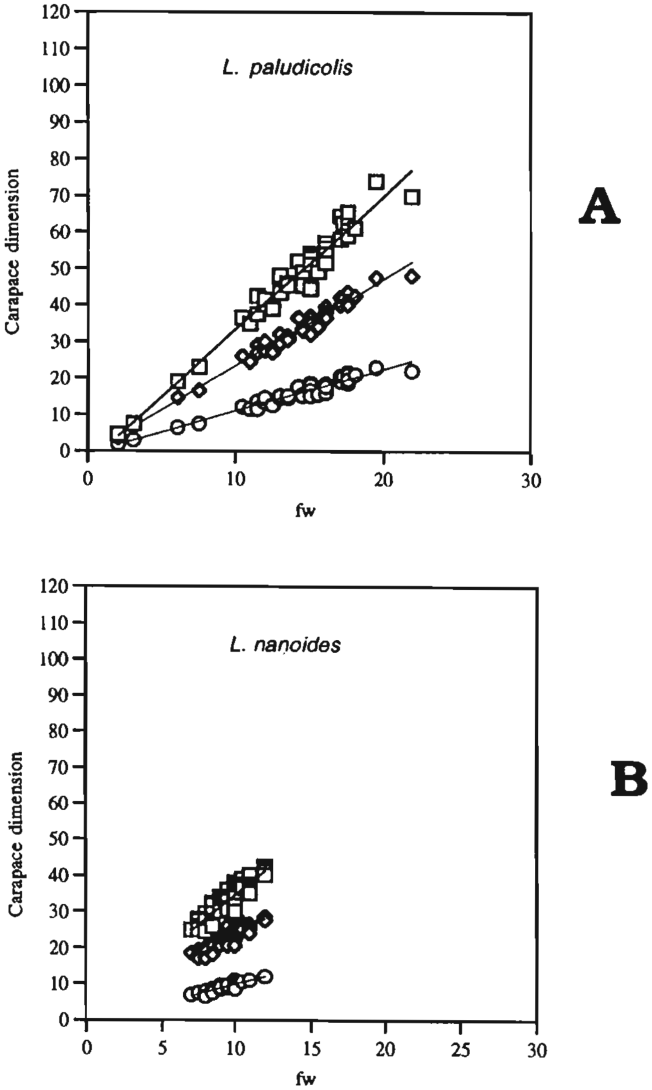


FIG. 59. Dimensions of the carapace (cw = square, ch = triangle, cl = circle) compared to front width (fw) of **A**, 37 specimens of *Liberonautes paludicolis* (cw 4.5 to 74 mm), relationships are described by cw = 3.64fw - 3.06, r = 0.98; cl = 2.37fw -0.30, r = 0.99; ch = 1.15fw - 0.43, r = 0.97, all r values indicate a highly significant correlation (P < 0.001) at 36 degrees of freedom. **B**, 16 specimens of *Liberonautes nanoides* (cw 24.5 to 42.5 mm), relationships are described by cw = 3.31fw + 1.46, r = 0.91; cl = 1.75 + 2.20fw, r = 0.89; ch = 0.06fw - 0.65, r = 0.95, all r values indicate a highly significant correlation (P < 0.001) at 15 degrees of freedom.

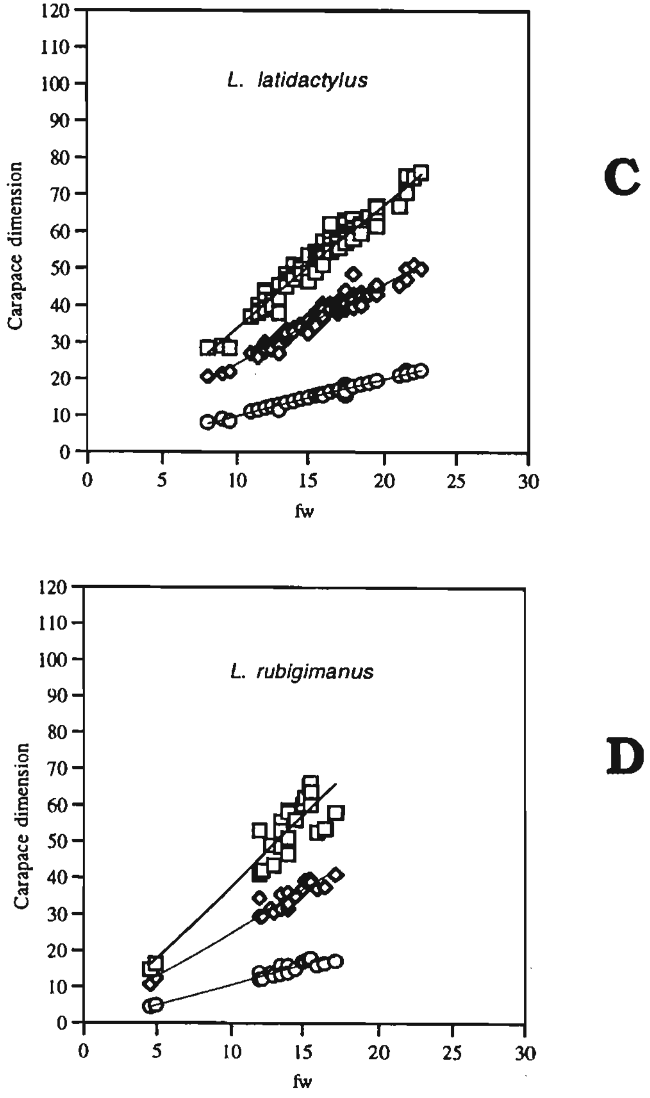
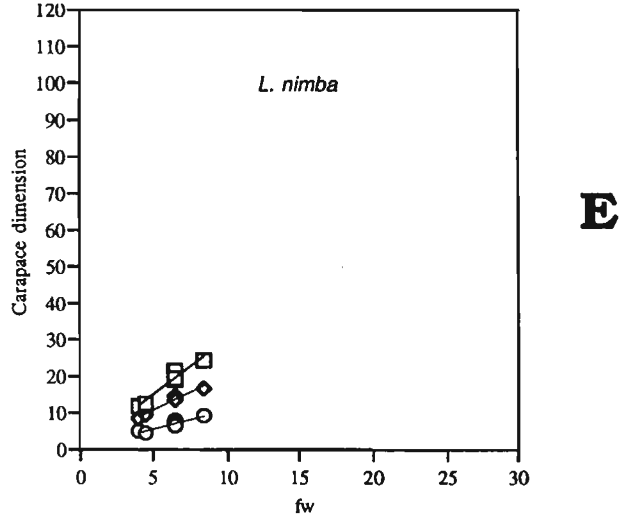


FIG. 59. **C**, 87 specimens of *Liberonautes latidactylus* (cw 28.5 to 76 mm), relationships are described by cw = 3.33fw - 0.49, r = 0.97; cl = 2.53 + 2.17fw, r = 0.97; ch = 1.02fw - 0.31, r = 0.99, all r values indicate a highly significant correlation (P < 0.001) at 86 degrees of freedom. **D**, 25 specimens of *Liberonautes rubigimanus* (cw 14.8 to 66 mm), relationships are described by cw = 3.92fw - 1.67, r = 0.91; cl = 0.94 + 2.40fw, r = 0.97; ch = 1.11fw - 0.43, r = 0.96, all r values indicate a highly significant correlation (P < 0.001) at 24 degrees of freedom.



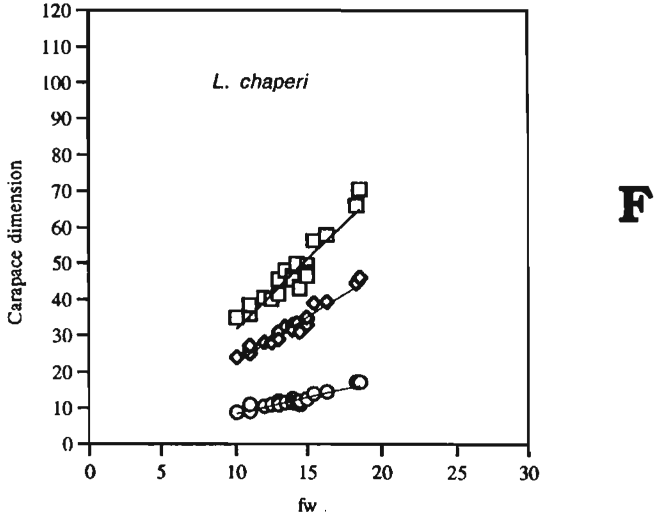


FIG. 59. **E**, 8 specimens of *Liberonautes nimba* (cw 11.8 to 24.5 mm), relationships are described by cw = 2.74fw + 1.90, r = 0.96; cl = 1.79fw + 2.19, r = 0.97; ch = 1.08fw - 0.27, r = 0.96, all r values indicate a highly significant correlation (P < 0.001) at 7 degrees of freedom. **F**, 23 specimens of *Liberonautes chaperi* (cw 35 to 70.5 mm), relationships are described by cw = 3.88fw - 7.25, r = 0.94; cl = 2.51fw - 2.50, r = 0.97; ch = 0.92fw - 0.70, r = 0.97, all r values indicate a highly significant correlation (P < 0.001) at 22 degrees of freedom.

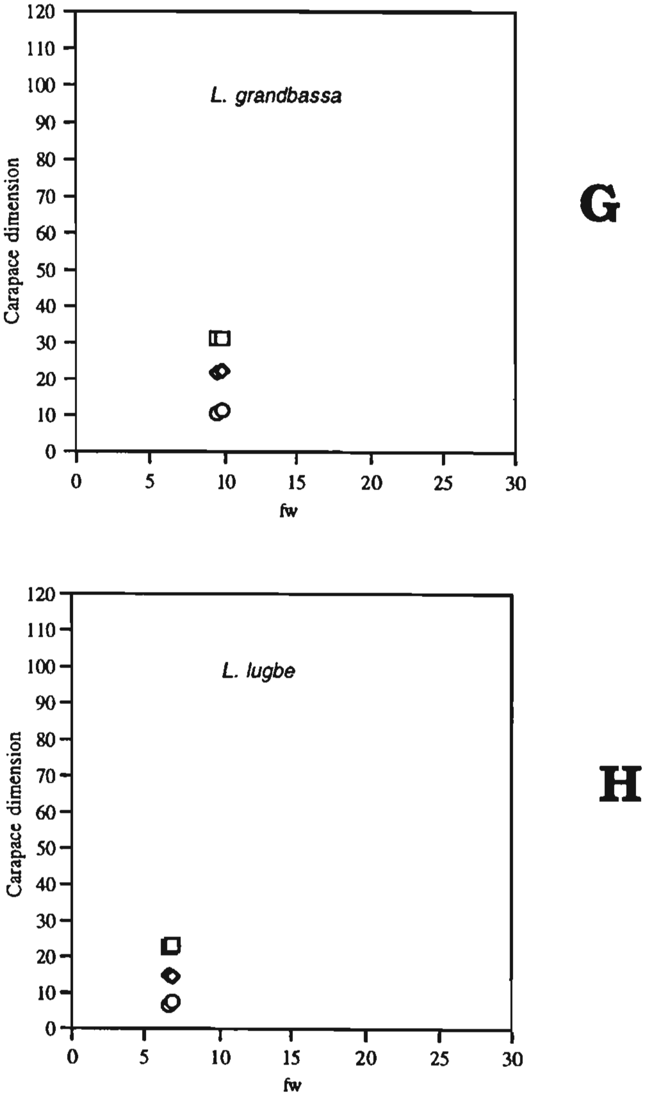
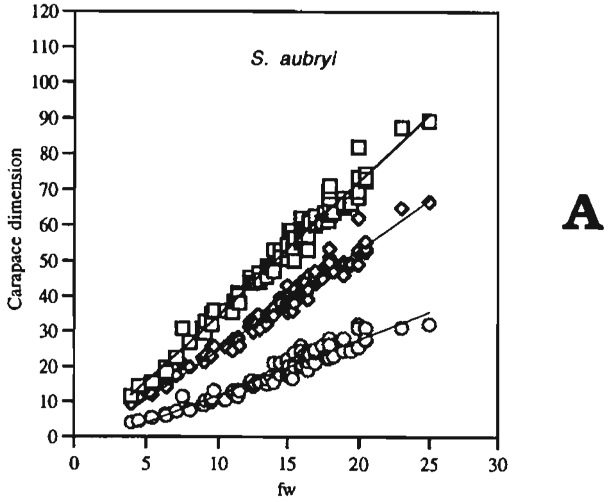


FIG. 59. **G**, two specimens of *Liberonautes grandbassa* (cw 31.3 to 31.4 mm). **H**, two specimens of *Liberonautes lugbe* (cw 22.7 to 23.2 mm).



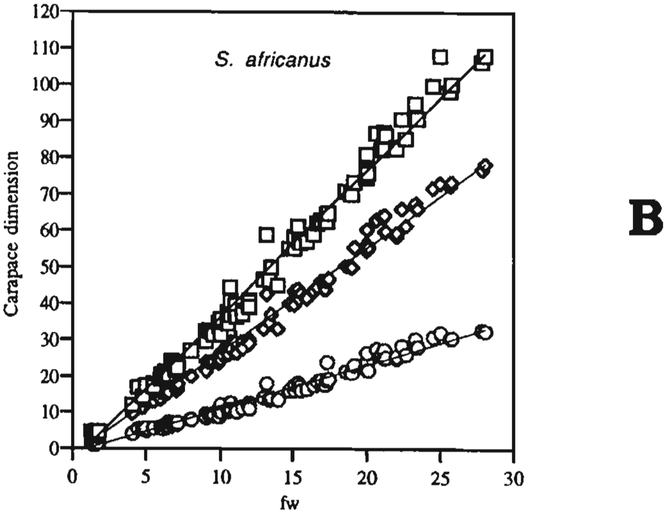


FIG. 60. Dimensions of the carapace (cw = square, ch = triangle, cl = circle) compared to front width (fw) of **A**, 100 specimens of *Sudanonautes aubryi* (cw 11.5 to 53 mm), relationships are described by cw = 3.77fw - 3.17, r = 0.99; cl = 2.83fw - 3.60, r = 0.98; ch = 1.59fw - 4.01 r = 0.96, all r values indicate a highly significant correlation (P < 0.001) at 99 degrees of freedom. **B**, 99 specimens of *Sudanonautes africanus* (cw 12 to 108.2 mm), relationships are described by cw = 3.99fw - 3.44, r = 0.99; cl = 2.85fw - 1.69, r = 0.99; ch = 1.22fw - 1.19, r = 0.99, all r values indicate a highly significant correlation (P < 0.001) at 98 degrees of freedom.

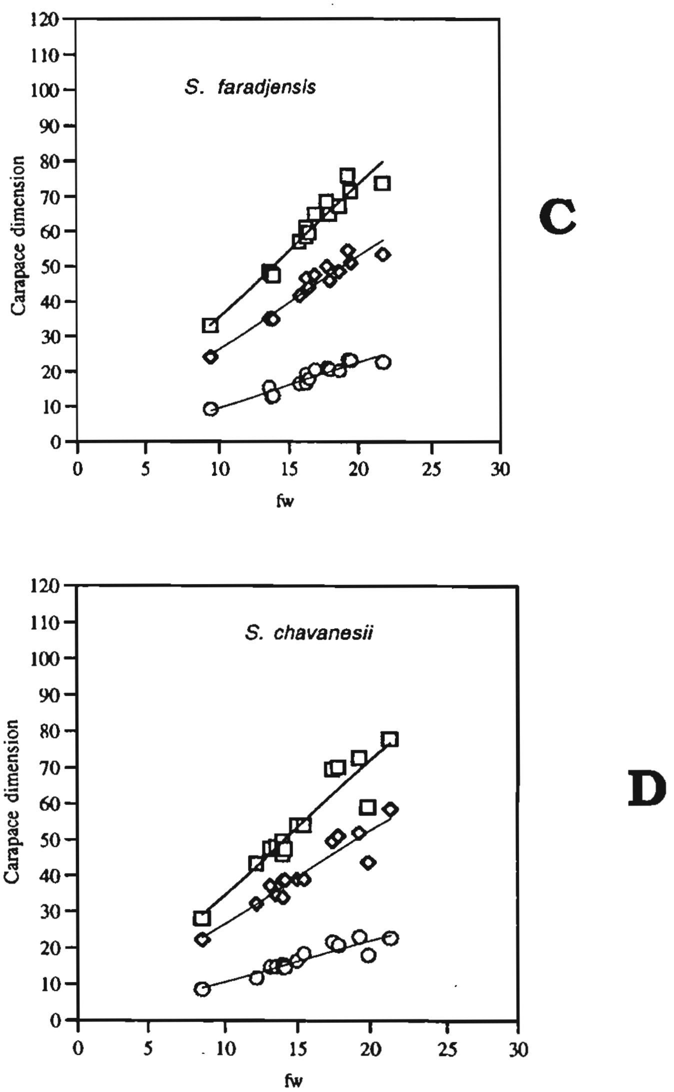
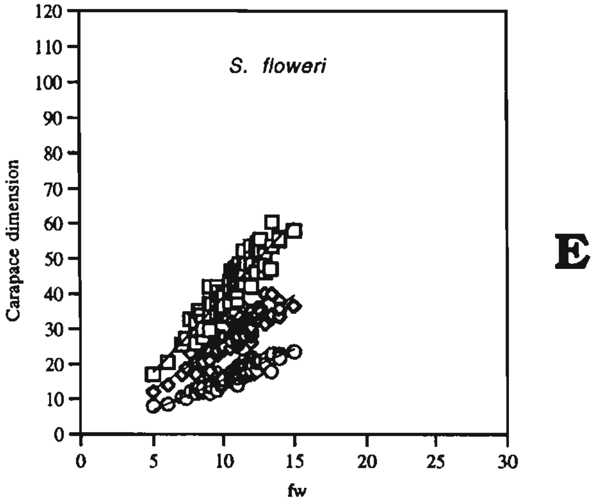


FIG. 60. **C**. 15 specimens of *Sudanonautes faradjensis* (cw 33.1 to 75.9 mm), relationships are described by cw = 3.78fw - 2.24, r = 0.97; cl = 2.66fw - 0.16, r = 0.97; ch = 1.30fw - 3.38, r = 0.95, all r values indicate a highly significant correlation (P < 0.001) at 14 degrees of freedom. **D**. 14 specimens of *Sudanonautes chavanesii* (cw 28.1 to 78 mm), relationships are described by cw = 3.75w - 2.89, r = 0.94; cl = 1.00 + 2.60fw, r = 0.94; ch = 1.14fw - 0.75, r = 0.93, all r values indicate a highly significant correlation (P < 0.001) at 13 degrees of freedom.



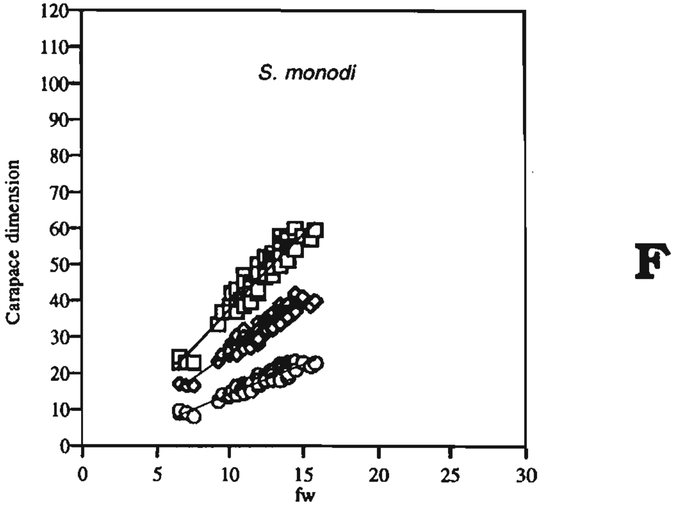


FIG. 60. **E**, 106 specimens of *Sudanonautes floweri* (cw 20.5 to 60.4 mm), relationships are described by cw = 4.26fw - 3.48, r = 0.93; cl = 2.67fw -0.41, r = 0.90; ch = 1.72fw - 1.59, r = 0.93, all r values indicate a highly significant correlation (P < 0.001) at 105 degrees of freedom. **F**, 91 specimens of *Sudanonautes monodi* (cw 23 to 60 mm), relationships are described by cw = 4.17fw - 4.16, r = 0.96; cl = 2.74fw - 1.72, r = 0.96; ch = 1.66fw - 2.34, r = 0.96, all r values indicate a highly significant correlation (P < 0.001) at 90 degrees of freedom.

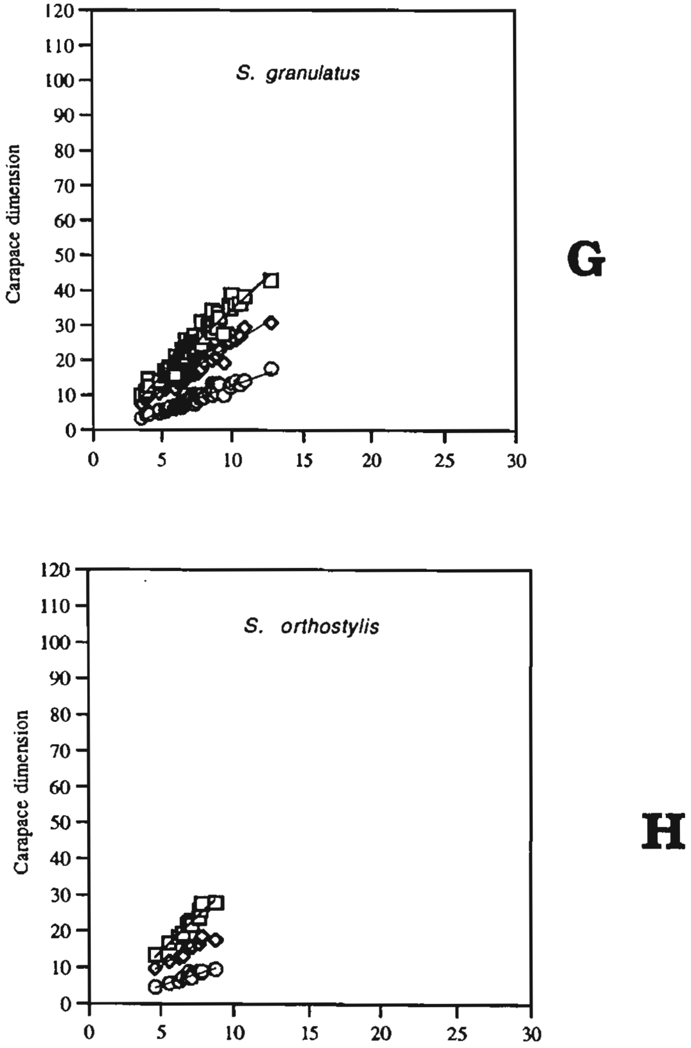


FIG. 60. **G**. 80 specimens of *Sudanonautes granulatus* (cw 9.88 to 42.9 mm), relationships are described by cw = 3.85fw - 3.95, r = 0.97; cl = 2.67fw - 2.05, r = 0.97; ch = 1.49fw - 2.16, r = 0.95, all r values indicate a highly significant correlation (P < 0.001) at 79 degrees of freedom. **H**, 12 specimens of *Sudanonautes orthostylis* (cw 13.3 to 27.8 mm), relationships are described by cw = 3.79w - 4.69, r = 0.97; cl = 2.32fw - 1.12, r = 0.94; ch = 1.28fw - 1.41, r = 0.95, all r values indicate a highly significant correlation (P < 0.001) at 11 degrees of freedom.

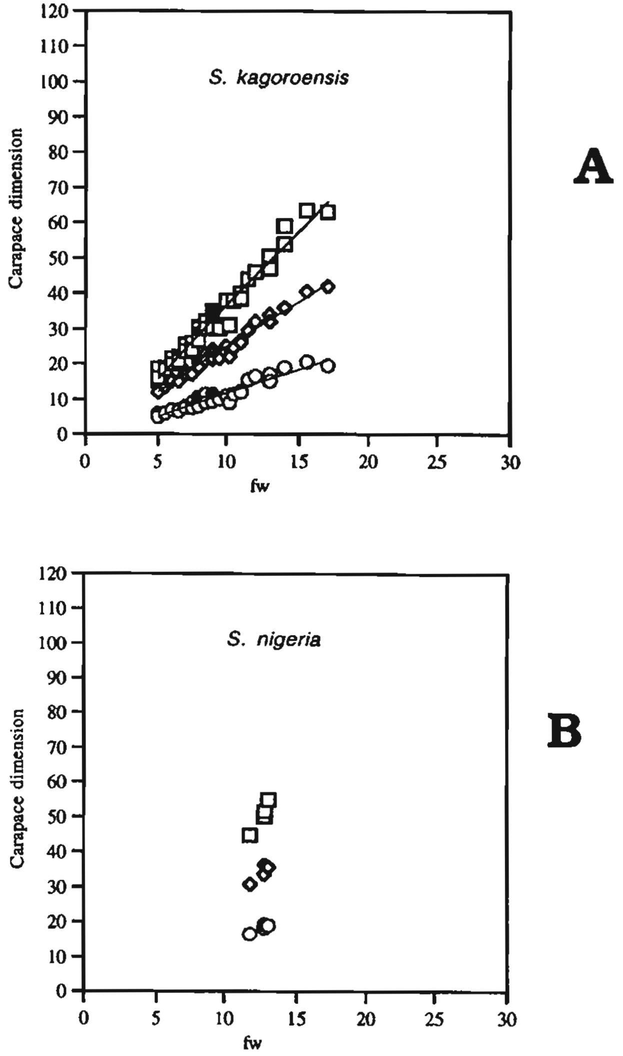


FIG. 61. Dimensions of the carapace (cw = square, ch = triangle, cl = circle) compared to front width (fw) of **A**, 46 specimens of *Sudanonautes kagoroensis* (cw 16 to 63.5 mm), relationships are described by cw = 4.16fw - 4.20, r = 0.98; cl = 2.56fw - 0.58, r = 0.98; ch = 1.33fw - 1.54, r = 0.96, all r values indicate a highly significant correlation ($P < 0.001$) at 45 degrees of freedom. **B**, 4 specimens of *Sudanonautes nigeria* (cw 44.65 to 54.74 mm).

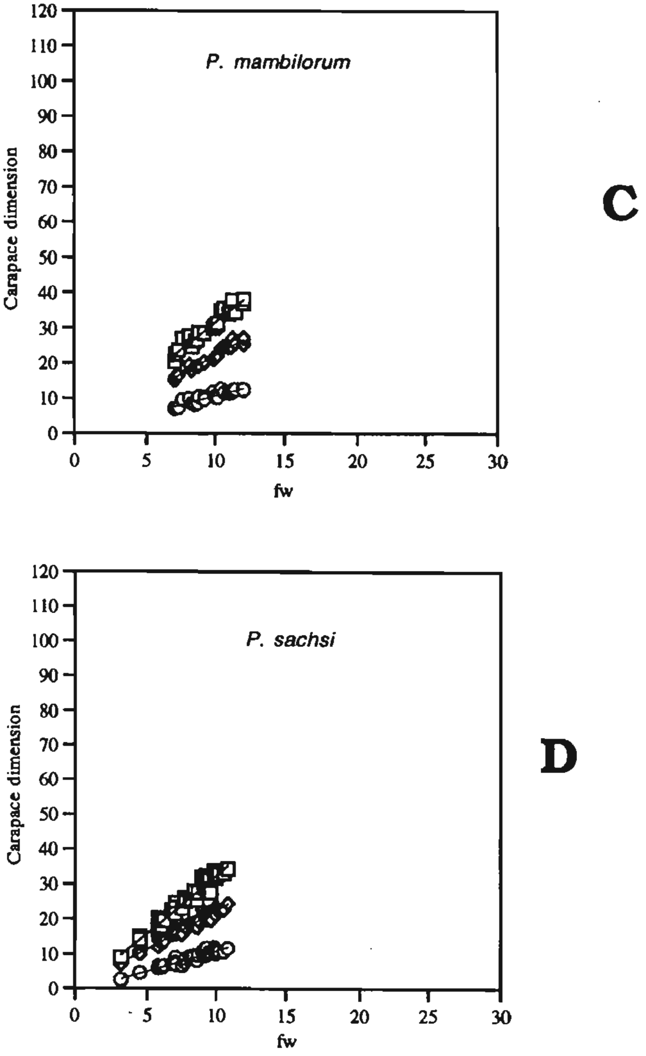


FIG. 61. **C**, 25 specimens of *Potamonemus mambilorum* (cw 24.2 to 38.1 mm), relationships are described by cw = 3.06fw - 0.87, r = 0.96; cl = 1.03 + 2.12fw, r = 0.97; ch = 1.01fw + 0.52, r = 0.91, all r values indicate a highly significant correlation (P < 0.001) at 24 degrees of freedom. **D**, 43 specimens of *Potamonemus sachsi* (cw 9 to 34.4 mm), relationships are described by cw = 3.31fw - 0.80, r = 0.98; cl = 0.46 + 2.19fw, r = 0.98; ch = 2.17fw - 0.84, r = 0.96, all r values indicate a highly significant correlation (P < 0.001) at 42 degrees of freedom.

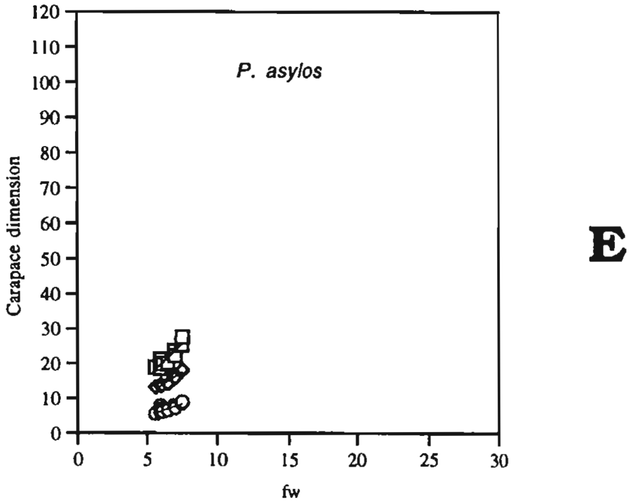


FIG. 61. **E**. 10 specimens of *Potamonemus asylos* (cw 18.9 to 22.56 mm), relationships are described by cw = 3.824w - 3.08, r = 0.92; cl = 2.61fw - 1.891, r = 0.97; ch = 1.36fw - 1.70, r = 0.83, all r values indicate a highly significant correlation (P < 0.001) at 9 degrees of freedom.

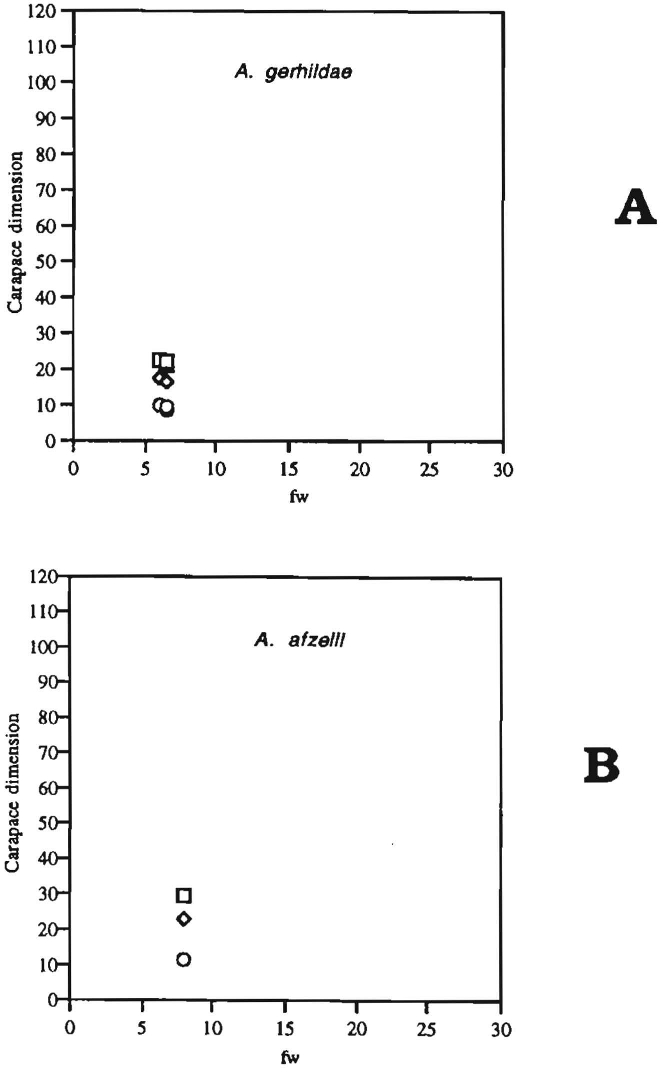


FIG. 62. Dimensions of the carapace (cw = square, ch = triangle, cl = circle) compared to front width (fw) of **A**, three specimens of *Afrithelphusa gerhildae* (cw 21.0 to 22.5 mm). **B**, *Afrithelphusa afzelii* cw 29.5 mm.

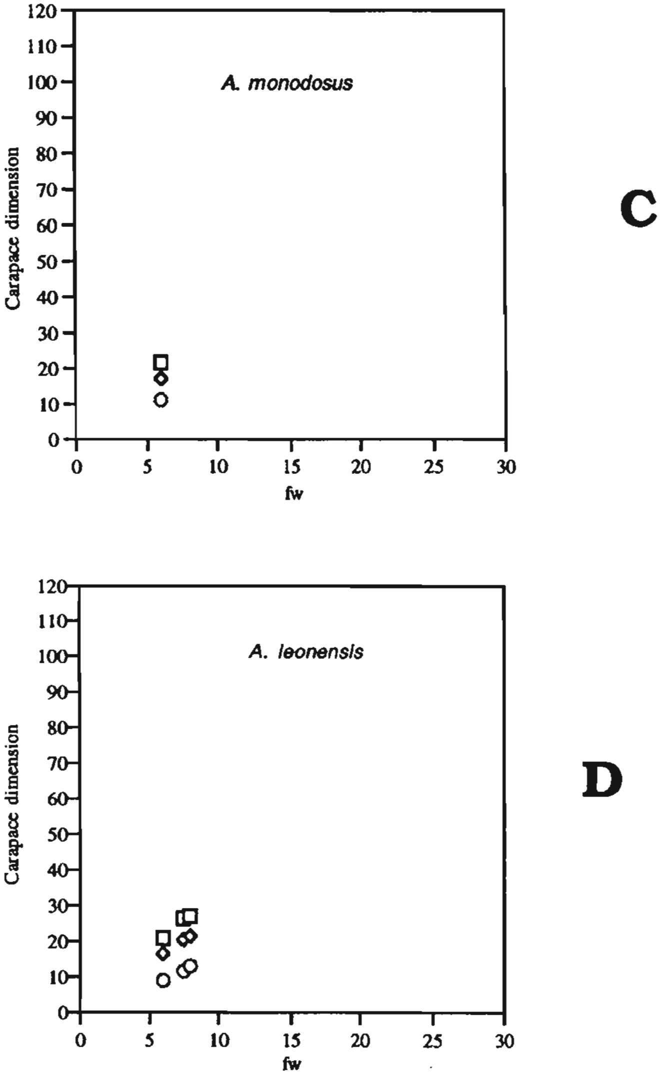
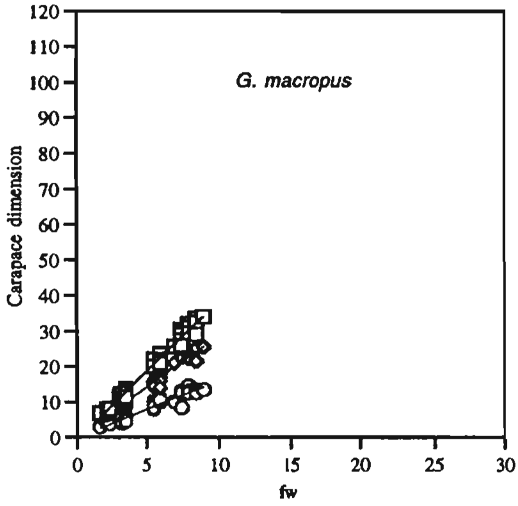


FIG. 62. **C**. *Afrithelphusa monodosus* cw 21.5 mm. **D**. three specimens of *Afrithelphusa leonensis* (cw 21 to 27 mm).



E

FIG. 62. **E**, 33 specimens of *Globonautes macropus* (cw 11 to 33 mm), relationships are described by cw = 3.84fw - 0.47, r = 0.99; cl = 0.02 + 2.85fw, r = 0.98; ch = 0.16 + 1.57fw, r = 0.96, all r values indicate a highly significant correlation (P < 0.001) at 32 degrees of freedom.

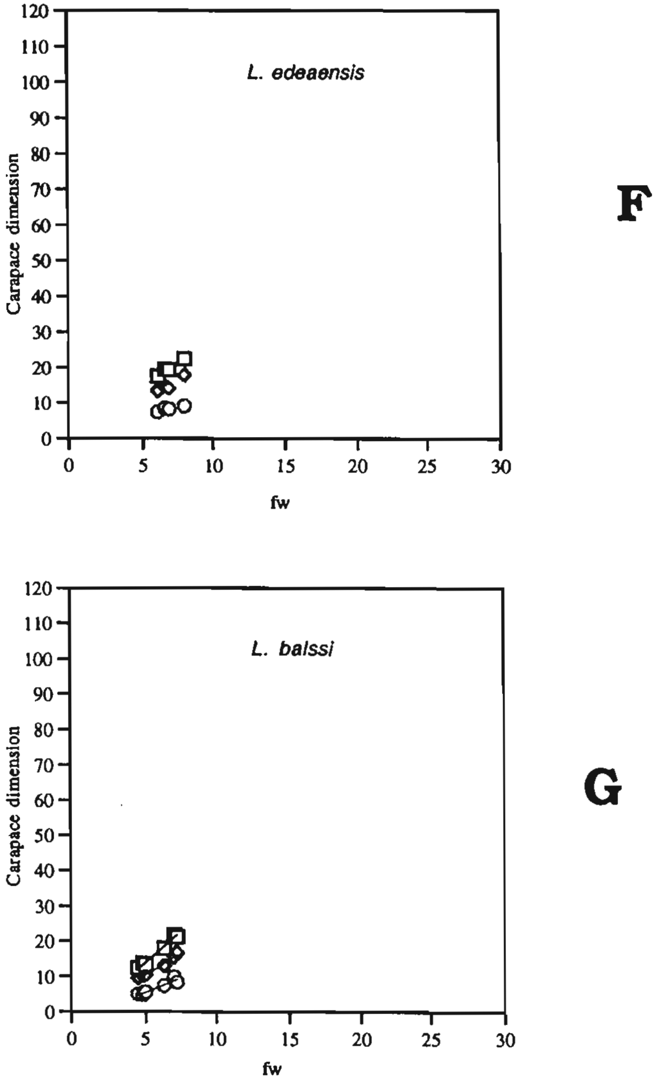


FIG. 62. **F**, four specimens of *Louisea edeaensis* (cw 17.5 to 22.5 mm). **G**, six specimens of *Louisea balssi* (cw 12.5 to 22 mm), relationships are described by cw = 3.53fw - 3.61, r = 0.99; cl = 2.56fw -2.27, r = 0.99; ch = 1.65fw - 2.73, r = 0.94, all r values indicate a highly significant correlation ($P < 0.001$) at 5 degrees of freedom.

Biogeography and Biology

Distribution of the species

fig 63-68, table X, XI

The northern boundary of the area covered by this book is formed by the division of the Ethiopian and Palaearctic zoogeographical regions which crosses the Sahara desert in north Africa (roughly south of the 18°-20°N line of latitude). The eastern boundary of the area is formed by the eastern border of Chad, the southern boundary by the southern border of Cameroon and the western and southern boundaries by the Atlantic Ocean. The land surface of West Africa is mostly flat and somewhat geographically featureless, with the exception of mountain ranges such as the Fouta Djallon mountains of Guinea, the Loma mountains of Sierra Leone, Mount Nimba of Liberia, Guinea and Côte-d'Ivoire, the Jos Plateau of Nigeria and the Cameroon highlands. Of these, the Cameroon highlands are the highest and most extensive, and consist of a chain of mountains and hills that stretch for several hundred kilometres along the border between Nigeria and Cameroon. The highest point in this range is Mount Cameroon (3962 m), while the mountainous islands of Bioko (Fernando Po), Principe, Sao Thomé and Annobon in the Gulf of Guinea are also part of the same system. The Cameroon highlands have generated a great deal of zoological interest because their high-altitude forests and grasslands support distinctive montane floral and faunal assemblages.

The most extensive ecosystems in West Africa are desert, savanna and forest while montane and wetland habitats occupy much smaller geographical areas. Although the savanna zone covers by far the largest area, the highest numbers of species of freshwater crabs in West Africa are found in the rainforest ecosystems. The major rivers in the region are the Sénégal, Gambia, Niger, St. Paul, Cavally, Sassandra, Bandama, Komoe, Tano, Black Volta, White Volta, Benue, Cross and Sanaga. The longest river in the region is the Niger, which is 4184 km long and which drains the greater part of West Africa west of Cameroon. Many of the major rivers in the region (the Niger, Benue, Tchad, Sénégal, Gambia and Volta) flow principally through savanna. The banks, islands and associated flood plains and marshes of the major rivers provide vast areas of seasonal wetland habitats in an otherwise arid ecosystem.

Climate and vegetation

fig 2

West Africa lies entirely within the tropics where the day and night temperatures are generally high (25°-30°C) except in the cooler high-altitude localities. The most important climatic element is the rainfall because this determines both the type of vegetation at a particular locality, and influences the characteristics of rivers and other wetland habitats. Most terrestrial animals are adapted to live in habitats dominated by a particular type of vegetation, while most aquatic animals live in habitats with a particular water quality and quantity. Since many of the species of freshwater crabs are amphibious or terrestrial in habit, the ecological conditions of both terrestrial and aquatic habitats need to be considered.

West Africa experiences a great deal of geographical variation in the intensity and pattern of rainfall, and most places, including the rainforests, experience a rainy season and a dry season. In West Africa the rainy season coincides with the summer months in the northern hemisphere while the dry season coincides with the winter months in the northern hemisphere. In general, the rainfall at any locality in West Africa is usually a direct function of its nearness to the equator. Local exceptions to this are due to such factors as the orientation of the coastline to rain-bearing winds, the proximity of cold ocean currents, or the presence of mountains. In the dry deserts and savannas of West Africa (from Mauritania to Chad) the rainfall is very low and infrequent, and the ground is sandy or rocky and supports only sparse vegetation. In the moist coastal regions (from Sierra Leone and Liberia to Cameroon and Gabon), the rainfall is high (often over 250 cm a year) and the vegetation takes the form of tropical rainforest. The savanna zone lies between these two climatic extremes and there is a gradual transition in rainfall and vegetation from lush moist forest to hot dry savanna. In general, savanna occurs in areas that receive the lowest amounts of rainfall and is characterised by a predominance of grassland with occasional trees and shrubs, and its appearance varies both locally and seasonally. In moist woodland and guinea savanna the grass grows tall and thick and the trees are typically soft-leafed. In dry sudan savanna and Sahel the grass is short and the trees and shrubs are thorny. Woodland savanna is found on the margins of the rainforest, Sahel and sudan savanna are found at the margins of the desert, and guinea savanna is found in between woodland and sudan savanna. The transition from one kind of savanna to another is usually gradual, but the transition from savanna to rainforest is more abrupt. The dry savanna coastland of eastern Ghana, Togo and Benin (the 250 km wide Dahomey Gap) probably owes its low rainfall and savanna vegetation to the orientation of the coastline (parallel to the prevailing winds), and to the presence of cold waters along the coast between July to October that are brought to the surface by seasonal upwelling. Rainforest occurs in areas of high rainfall and is characterised by evergreen trees and an absence of grass, and the appearance of the forest does not change dramatically with the change in the seasons. Coastal Sierra Leone, Liberia and the Nimba mountains probably owe their high rainfall and forest vegetation to the orientation of the coastline across the path of the rain-bearing winds.

The Lower Guinea forest is the most species rich of the entire West African region and has representatives of *Sudanonautes*, *Potamonautes* and *Potamonemus* and the endemic genus *Louisea*. The freshwater crab fauna of the Lower Guinea forest is distinct from that of the Upper Guinea forest, and completely lacks representatives of *Liberonautes*, *Globonautes* and *Afrithelphusa*. The freshwater crab fauna of the western Lower Guinea forest in Nigeria consists of seven species in three genera (*Sudanonautes*, *Potamonautes* and *Potamonemus*) and includes two endemic species (*Sudanonautes nigeria* and *Potamonautes reidi*). The freshwater crab fauna of the eastern Lower Guinea forest in Cameroon consists of twelve species in three genera and includes five endemic species (*Sudanonautes orthostylis*, *Potamonemus asylos*, *P. mambilorum*, *Louisea edeaensis* and *L. balssi*) and one endemic genus (*Louisea*).

Rainforest.

The tropical rainforest zone in the West African region consists of two main parts, the Upper Guinea forest block (in Guinea, Sierra Leone, Liberia, Côte-d'Ivoire, Ghana and Togo) and the Lower Guinea forest (a much larger forest block in south east Nigeria, south Cameroon, Gabon, Congo, Central African Republic and Zaire). Each forest block supports a distinct freshwater crab fauna. These two forests are separated by the Dahomey Gap, a stretch of coastal savanna in Ghana, Togo and Benin.

Upper Guinea forest.

The Upper Guinea rainforest is the largest forest in West Africa, and extends along the coast from Guinea to southern Togo. The distribution of the flora and fauna of the Upper Guinea forest is not entirely uniform, and there is a notable division between the western Upper Guinea forest (the 'Liberian' zone, from western Côte-d'Ivoire to Guinea) and the eastern Upper Guinea forest (the 'Ghanaian' zone, from eastern Côte-d'Ivoire to Togo). This division of the freshwater crab fauna coincides with a V-shaped incursion of savanna into the forest (the Baoulé-V), which is centred on the Bandama river in central Côte-d'Ivoire. It is thought that the Baoulé-V marks the place where there was a complete break in the forest cover in the recent past. This past separation of the forest forms on either side of the savanna incursion caused them to evolve in isolation from one another, and may explain some of the floral and faunal differences seen today between these two apparently similar areas of forest. Indeed, the freshwater crab fauna of the western Upper Guinea forest is different from that of the eastern Upper Guinea forest.

The freshwater crab fauna of the western part of the Upper Guinea forest (in Guinea, Sierra Leone and Liberia) consists of thirteen species in three genera (*Liberonautes*, *Globonautes* and *Afrithelphusa*); eleven species and two genera (*Globonautes* and *Afrithelphusa*) are endemic. This forest is dominated by species of *Liberonautes* but also includes representatives of the rare and threatened species that belong to *Globonautes* and *Afrithelphusa*; *Potamonautes* and *Sudanonautes* are absent from this part of the forest. Two species (*Liberonautes latidactylus* and *L. chaperi*) range east of this area, but only as far as southwest Ghana in the eastern Upper Guinea forest. Here, freshwater crabs are found in lowland forest streams, large rivers, swampy regions of the forest floor and mountain streams. In Liberia and Guinea *Globonautes macropus* lives in holes in forest trees.

The freshwater crab fauna of the eastern part of the Upper Guinea forest (in Côte-d'Ivoire, Ghana and Togo) consists of six species in three genera (*Liberonautes*, *Potamonautes* and *Sudanonautes*); only one species, *Potamonautes triangulus*, is endemic. This part of the forest supports two species in each of these three genera, while *Globonautes* and *Afrithelphusa* are absent. The fauna of the eastern Upper Guinea forest includes elements of both the western Upper Guinea forest and of the Lower Guinea forest, and its species diversity is a function of its being an area of faunal overlap.

Lower Guinea forest

The Lower Guinea forest includes the lowland forest of the coastal region (from eastern Nigeria to Gabon) and the montane forest of the Cameroon highlands in Cameroon and eastern Nigeria and is continuous with the large equatorial forest of Central Africa. The Lower Guinea forest is the most species rich of the entire West African region and has representatives of *Sudanonautes*, *Potamonautes* and *Potamonemus* and the endemic genus *Louisea*. The freshwater crab fauna of the Lower

Guinea forest is distinct from that of the Upper Guinea forest, and completely lacks representatives of *Liberonautes*, *Globonautes* and *Afrithelphusa*. Representatives of this Lower Guinea fauna are also found in the savanna to the north and west of the river Niger, and two species (*Sudanonautes aubryi* and *S. granulatus*) reach as far west as the eastern Upper Guinea forest in Côte-d'Ivoire. The western part of the Lower Guinea forest in Nigeria is home to seven species in three genera (*Sudanonautes*, *Potamonautes* and *Potamonemus*) and includes two endemic species (*Sudanonautes nigeria* and *Potamonautes reidi*). The eastern part of the Lower Guinea forest in southern Cameroon consists of twelve species in four genera (*Sudanonautes*, *Potamonautes*, *Potamonemus* and *Louisea*) and includes five endemic species (*Sudanonautes orthostylis*, *Potamonemus asylos*, *P. mambilorum*, *Louisea edeaensis* and *L. balssi*) and one endemic genus (*Louisea*).

Savanna

The moist savanna zone in West Africa bounded by the river Niger in Nigeria and the Volta river in Ghana represents an area of species paucity as far as the freshwater crabs are concerned, as does the drier more northern sudan savanna which stretches from Burkina Faso to southern Sudan. Forest and savanna ecosystems in West Africa support different freshwater crab faunas, and there is little overlap between the two. The highest numbers of species of freshwater crabs in West Africa are found in rainforest ecosystems despite the fact that the savanna zone covers by far the largest area in the region, The western part of the savanna zone from northern Côte-d'Ivoire, Guinea, Mali, to Sénégal and The Gambia, is home to only three species of freshwater crab (*Liberonautes latidactylus*, *Potamonautes ecorssei* and *P. senegalensis*); the former two species are widespread, the latter species is endemic to Sénégal.

Rivers

The rivers of West Africa and the northern part of Central Africa are home to a distinct fauna that includes species of *Potamonautes*, *Sudanonautes* or *Liberonautes*. The Niger and the Volta that flow through savanna regions of West Africa support two species of river crab: *Potamonautes ecorssei* and *P. triangulus*. The latter species is endemic to the rivers of Ghana.

Islands

Freshwater crabs are found on the Atlantic Islands of Sao Thomé and Bioko (Fernando Po). Sao Thomé has one endemic species (*Potamonautes margaritarius*) which is considered here to be part of the Central African faunal region, while Bioko has two species (*Sudanonautes floweri* and *S. granulatus*) which are also found on the nearby mainland.

Comparisons

The freshwater crab fauna of the Upper Guinea forest (fifteen species in five genera) is completely different from that of the Lower Guinea forest (eighteen species in five genera), and only two species (*Sudanonautes aubryi* and *S. granulatus*) occur in both areas. Ecological parallels can be drawn between the different communities of crabs found in the two forest blocks, whereby different species belonging to different genera occupy similar habitats. The large, stream-living species that browses on the forest floor in Liberia is *Liberonautes latidactylus*, while *Sudanonautes africanus* occupies the same niche in the Lower Guinea forest in Nigeria and Cameroon. Similarly, the large, swamp-living semi-terrestrial forest crab in Liberia is *Liberonautes paludicolis*, while *Sudanonautes aubryi* occupies the same niche in the Lower Guinea forest in Nigeria and Cameroon. Finally, the small river-dwelling species in Liberia is *Liberonautes nanoides*, while *Potamonautes ecorssei* occupies the same niche in Nigeria.

Patterns of distribution, species diversity and endemism

fig 63-68

Very little has been written on the distribution of the freshwater crabs of West Africa. This can be attributed mainly to the lack of a sufficiently large database, rather than to a lack of interest. Many species from the region are represented by only a handful of individuals, while those species that are more plentiful have often proved problematic to identify. Uncertain identifications of even the common species have compromised the usefulness of the large amounts of museum material in distributional studies, because distributional data are only as good as the taxonomy upon which they rest. The most recent description of the distribution of West African freshwater crabs was provided by BOTT (1955). Unfortunately, BOTT's data were sparse and vague, and relied in many cases on incorrect identifications of material. Furthermore, BOTT (1955) provided no maps summarising the distribution of any species or higher taxonomic group from Africa. BOTT's (1955, 1959, 1964, 1969a,b, 1970a,b) conclusions regarding the distribution of the freshwater crab genera in Africa were eventually summarised by MONOD (1977, 1980) who added new localities for some of the species, and by BANARESCU (1991). BOTT's (1970b) conclusions regarding the distribution of the freshwater crab genera in Asia and in the neotropics were summarised by BANARESCU (1991). That work was critically reviewed by NG & RODRIGUEZ (1996) who raised problems with BANARESCU's methods and rationale.

In the present work distribution data have been derived from specimen records, from museum collection records, and from literature records. Distributions for each species have been compiled from a large series of available specimens, but are still likely to be incomplete. Other species are either known only from the type locality or from only a few localities, and further collections are necessary to ascertain their actual distribution. Records for the distribution of a species in the present work have been restricted here to include only those individuals that have been identified by direct examination. Limited and cautious use has been made of literature records due to the uncertain taxonomy of the group, and these have been included only if the species has been illustrated clearly enough to allow identification. The new distribution data, identification keys, and classification presented here allow a discussion of the patterns of distribution and the diversity of the freshwater crabs of West Africa for the first time. A list of species in West Africa is provided to summarise the freshwater crab faunal records of each country in the region.

Distribution patterns

The thirty two species of freshwater crabs found in the West African region represent about one-third of the species and subspecies presently known from the entire continent (BOTT, 1955, 1959, 1960, 1964, 1969a, 1970a,b; MONOD, 1977, 1980; CUMBERLIDGE, 1985a-1997, table X, XI). Most of the species dealt with in the present study occur exclusively in West Africa (from Sénégal to Nigeria), while the range of several species of *Sudanonautes* extends into Central Africa. This latter area includes Cameroon, Chad, southern Sudan, the Central African Republic, the Democratic Republic of the Congo (formerly Zaire) north of the river Congo/Zaire, the Republic of the Congo, Gabon and Equatorial Guinea (the island of Bioko). The taxonomic diversity of the West African region at the genus level (seven genera) is higher than that of the whole of the rest of Africa (four genera). Species diversity within the West African region clearly depends on vegetation cover, where the highest numbers of species occur in rainforest ecosystems, and the fewest in savanna ecosystems. One species (*Potamonautes ecorssei*) is even found in the desert zone in Mali, but only where the river Niger flows through Timbuktu. Eight of the thirty two species of West African freshwater crabs have a wide distribution over an extensive area, while most (twenty one out of thirty two species) have a restricted distribution. Three species (*Suda-*

nonautes aubryi, *S. granulatus* and *Potamonemus sachsi*) have a disjunct distribution pattern, occurring in two geographically separated areas, but not in the interval between them.

Potamonautes

This genus includes by far the largest number of species in Africa: according to the literature (Bott, 1955, 1959, 1964, 1968, 1970a; Stewart, Coke & Cook, 1995; Stewart, 1997; present work) there are some forty three species and sixteen subspecies. *Potamonautes* is found throughout sub-Saharan Africa from the Cape to Cairo and from Sénégal to the Horn of Africa, and has the widest distribution of any freshwater crab genus in Africa. The only region where *Potamonautes* does not occur is in the Sahara desert and in the coastal fringe of northwest Africa (the Maghreb) which is the part of Africa that lies in the Palaearctic zoogeographical region. The largest number of species and subspecies of *Potamonautes* occur in the forested Zaire river basin, which represents the centre of diversity of the genus. The total number of species of *Potamonautes* decreases with increasing distance from this centre. Although well represented in the rest of the continent, there are only four species of *Potamonautes* in West Africa. All four species are endemic to the region, and none occur elsewhere in Africa. Some West African species (*Potamonautes ecorssei*) are widespread and are found in the rivers flowing through the savanna region from Sénégal to Nigeria, as well as in the rivers of the rainforest zone (Cumberlidge, 1985b). One species of river crab (*Potamonautes senegalensis*) is associated exclusively with the Sénégal river in Sénégal and has adopted a semi-terrestrial air-breathing habit. Another species (*Potamonautes reidi*) is endemic to southeast Nigeria and *Potamonautes triangulus* is endemic to a small region of Ghana.

Sudanonautes

This genus includes ten species distributed in West and Central Africa (Cumberlidge, 1989, 1991, 1993b,c, 1994b, 1995,a,b,c,d, present work). The largest number of species of *Sudanonautes* are found in the forested region of southeast Nigeria and southwest Cameroon. This area represents the centre of diversity of this genus and the number of species decreases with increasing distance from this centre. The western limit of the range of *Sudanonautes* is Côte-d'Ivoire, the eastern limit is southwest Sudan and the southern limit is northern Angola. On the island of Bioko, the genus is also represented by two species (*Sudanonautes floweri* and *S. granulatus*) neither of which is endemic to the island. Two species of *Sudanonautes* are endemic to Nigeria (*S. nigeria* and *S. kagoroensis*) and one species (*S. orthostylis*) is endemic to southwest Cameroon. Species of *Sudanonautes* occur in most of the major ecosystems of West Africa (tropical rainforest, guinea and sudan savanna) except for desert, and are found in aquatic habitats (standing water, streams and major rivers) and on land. *Sudanonautes africanus*, *S. nigeria*, *S. granulatus*, *S. orthostylis*, *S. chavanesii* and *S. faradjensis* occur exclusively in rainforest habitats, while *S. aubryi* and *S. floweri* are found in both rainforest and woodland savanna. *Sudanonautes kagoroensis* occurs only in guinea savanna, while the semi-terrestrial air-breathing *S. monodi* is the only species found in both guinea and in dry sudan savanna.

Liberonautes

This genus includes eight species which are restricted to the western part of West Africa, to the west of Ghana (Cumberlidge, 1985, 1999; Cumberlidge & Sachs, 1989a,b. The centre of diversity of the genus is located in the forested region of Liberia where the largest number of species occur. The total number of species of *Liberonautes* decreases with increasing distance from this centre. The western limit of the distribution of *Liberonautes* is Sénégal, the eastern limit is Ghana, and the northern limit is Mali. One species (*L. latidactylus*) is widespread over the entire range of the genus, while the remaining seven species each have a limited distribution centring on Liberia. Species of *Liberonautes* are found mostly in rainforest, although *L. latidactylus* is also found in both guinea and sudan savanna zones. Most species are found in aquatic habitats (streams or major rivers) while *Liberonautes paludicolis* is more terrestrial and *L. rubigimanus* and *L. nimba* are found at high altitudes. *Liberonautes chaperi* and *L. nanoides* are found exclusively in the major rivers.

Potamonemus.

Three species of *Potamonemus* occur in the forested highlands of southeast Nigeria and southwest Cameroon, in the nearby forested lowlands of southwest Cameroon and in the forested highlands of western Togo. *Potamonemus mambilorum* occurs in the highlands of southwest Cameroon (Bamenda, Bambulae, Nfom Grasslands), and the lowlands of south Cameroon (Douala, Yaounde). *Potamonemus asylos* occurs in southwest Cameroon from Kumba to Victoria, while *P. sachsi* is found in the Bamenda highlands in southwest Cameroon, on the Obudu plateau in southeast Nigeria and in Togo. These species occur in small streams and probably leave the water at night to feed (Cumberlidge & Clark, 1992; Cumberlidge, 1993a).

Globonautes

Globonautes macropus the tree hole crab, occurs only in the western part of the Upper Guinea forest in Liberia and in Guinea. This species lives in the small water reservoirs that collect in holes in trees growing in parts of the forest that are well away from creeks, rivers and swamps (CUMBERLIDGE & SACHS, 1991; CUMBERLIDGE, 1991a, 1996a,b).

Afrithelphusa

This genus of rare freshwater crabs includes four species, *Afrithelphusa gerhildae*, *A. afzelii*, *A. monodosus* and *A. leonensis*. All occur only in the western part of the Upper Guinea forest of West Africa from Guinea to Sierra Leone. *Afrithelphusa gerhildae* and *A. monodosus* are both found only in Guinea, while *A. afzelii* and *A. leonensis* are both known only from Sierra Leone (CUMBERLIDGE, 1987, 1991a; 1996a,b).

Louisea

Two species of the endemic genus *Louisea* are found only in southwest Cameroon. One species (*L. balssi*) occurs in the forested highlands of southwest Cameroon, while *L. edeaensis* is found in the moist lowland rainforests of the Littoral Province of southwest Cameroon (CUMBERLIDGE, 1994a).

Interpretation of distribution patterns

fig 69

One important pattern shown by the distribution of plants and animals in African forests is the presence of centres of high biotic diversity (core areas) surrounded by apparently identical forest areas which have a gradient of declining species numbers. The core areas are rich in species and typically include a high proportion of endemic species. Core areas of forest that fit this description are found in both the Lower Guinea and Upper Guinea forest blocks of West Africa. It is difficult to explain the patterns of distribution shown by the freshwater crabs in West and Central Africa entirely in terms of presently-existing environmental conditions because these forest habitats do not appear to be dramatically different from each other. One way to interpret the distribution of freshwater crabs in West and Central Africa is to regard present-day distribution as the result of an interplay between current ecological conditions and past climatic conditions.

During the Pleistocene epoch the climate in Africa consisted of a series of changing climatic periods (each lasting several thousand years) that alternated between cool dry conditions and warm wet conditions. These climatic cycles coincided with the glacial and interglacial cycles in the northern latitudes. Northern ice ages caused the climate in Africa to become drier, while northern interglacial periods caused the climate in Africa to become wetter. Rainforest could not survive during the prolonged arid periods in West Africa and most of the vegetation of the region converted to some form of savanna. However, the forest cover did not completely disappear during these ice age dry periods. Small areas of forest persisted in parts where the local conditions (such as orientation across the path of rain-bearing winds combined with high mountain ranges or a closeness to favourable ocean currents) ensured a continued high rainfall. Thus the vegetation in West Africa during the arid northern ice ages was predominantly savanna and desert interspersed with a few small 'islands' of forest. During the interglacials in West Africa the return to a moist climate caused the forest to spread out and the savanna and desert to retreat.

Three relatively small areas of the African rainforest stand out as having an unusually high number of species and a higher than normal number of endemic species. These areas are in the Upper Guinea forest in West Africa, in the Lower Guinea forest in Nigeria and Cameroon, and in the forests of eastern Zaire. The Pleistocene forest refuge hypothesis (see HAMILTON, 1976 for a review) postulates that these species-rich areas of forest represent the oldest parts of the forest. It is suggested that throughout the Pleistocene epoch these areas of forest continued to receive sufficient rainfall while elsewhere in Africa the alternating moist and arid climatic periods associated with the northern ice ages and interglacials caused major shifts in the vegetation cover. The idea that there were small areas of stable, undisturbed areas of forest in Africa during the Pleistocene is supported by distributional data from independent studies of other groups (trees, mammals, butterflies, amphibia and birds) which also identify (among others) these same three centres of species richness and endemism in the African forests (CARCASSON, 1964; HAMILTON, 1976; DIAMOND & HAMILTON, 1980; MAYR & O'HARA, 1986).

Today, as in the past, the species rich forest refuges of West and Central Africa offer relatively stable environments for freshwater crabs. The number of species present in each core area today is undoubtedly a function in part of the environmental conditions which prevail today, and in part of the age, size and stability of the area during past periods of maximum forest contraction. Furthermore, the Pleistocene forest refuge hypothesis may also provide an explanation for the observed gradients of species richness seen in the African forests surrounding these core areas. The Earth is presently experiencing an interglacial period and mean global temperatures and rainfall are relatively high (in comparison with values during glacial periods). The last glacial period ended about 12,000 BP and since then the climate in West Africa has become wetter and warmer, and the forests have expanded so that the old species-rich refuge areas are now part of a much larger expanse of younger forest. The expansion of the forests has allowed species of freshwater crabs from the refuge areas to disperse out of the refuges into the adjacent new growth forests. This may have been responsible for the observed gradients of increasing species poverty with increasing distance from the refuge areas.

The above interpretation deals only with events in the geologically recent past and does not address questions about the phylogeny and historical biogeography of the African freshwater crabs. The answer to those kinds of questions awaits a detailed phylogenetic study of the origins and relationships of the freshwater crabs of the world.

Biology

Respiratory system

African freshwater crabs usually have nine pairs of gills, but a reduction in this number is seen in some air-breathing species such as *Globonautes macropus*. The gills lie in the two branchial chambers formed by the branchiostegites of the carapace. The right and left sets of gills lie directly beneath the epibranchial, mesobranchial and metabranchial regions of the carapace. There are three types of gills in freshwater crabs recognised by differences in the site of attachment of the gill to the animal. Those attached to the body wall above the base of the thoracic limbs are pleurobranch (podobranch) gills, those attached to the membrane beneath the coxa and body wall are arthrobranch gills, while those that arise from the coxal segment of the limb are phyllobranch gills. The anterior gills associated with the maxillipeds and chelipeds are always the smallest, and are always pleurobranch gills. The posterior gills are always the largest of the gills and are usually phyllobranch gills.

Respiratory water enters the branchial chamber ventrally through the inhalant openings (the Milne-Edwards openings) situated between the basal joints of the chelipeds and the neighbouring margin of the carapace. Exhalent water leaves the branchial chambers via the two efferent branchial canals at the lateral corners of the epistome on either side of the buccal cavity. The respiratory stream is maintained by the beating action of the scaphognathites of the second maxillae. Some terrestrial species of African freshwater crabs (e.g., *Globonautes macropus*) regularly carry out aerial respiration by means of a "lung" (called a "pseudolung" by DIAZ & RODRIGUEZ, 1977) that consists of a fleshy vascularized branchiostegal membrane in the branchial chamber, although this species has also retained fully functional gills (CUMBERLIDGE, 1991b).

A number of groups of African freshwater crabs have evolved the air-breathing semi-terrestrial habit and these are well represented in West Africa. Many species that occur in the region spend part of their lives out of water, and several are capable of breathing air as well as water (for a discussion see CUMBERLIDGE, 1986). Species of freshwater crabs in African forests are found in habitats ranging from deep rivers to land. In moist rainforest the high rainfall, high humidity, and deep shade of the forest provide favourable conditions for crabs to feed on vegetation and other organic matter on the forest floor. In dry savanna the disappearance of the surface waters in the dry season and the very low humidities have favoured the evolution of burrow-living, air-breathing, semi-terrestrial species of crabs such as *Sudanonautes monodi*. The general evolutionary trend in freshwater crabs is from an aquatic life in rivers towards an amphibious life in streams and on land, and from breathing water to breathing air as well as water. These changes have resulted in a number of modifications of the respiratory system. The majority of characters associated with the respiratory system of fully aquatic freshwater crabs (e.g., river-living species of *Sudanonautes*, *Liberonautes* and *Potamonautes* and lake-living species of *Platythelphusa*) tend to be in the plesiomorphic state, since the habitat of these groups most closely resembles that of the presumed marine and early freshwater crab ancestors. The medium-high carapace of aquatic crabs means that the volume of each gill chamber is completely filled by the nine pairs of large gills. The wide high carapace of amphibious and semi-terrestrial species of African freshwater crabs forms an enlarged gill chamber that houses nine (or fewer) pairs of smaller gills that occupy only the ventral part of the chamber. The rest of the gill chamber becomes an air store that is surrounded by a thickened and highly vascularized branchiostegal lining membrane with respiratory function (sometimes called the 'lung' or 'pseudolung', DIAZ & RODRIGUEZ, 1977). In the more terrestrial species of West African freshwater crabs there is a trend toward a reduction in both the size and the number of the gills (CUMBERLIDGE, 1986), and toward an increase in the size and complexity of the tissues that breathe air (which form a fleshy 'lung' in *Globonautes*; CUMBERLIDGE, 1991b). The gills are never completely lost in any species of air-breathing freshwater crab. The mouthparts of terrestrial air breathing freshwater crabs such as *Globonautes* and *Louisea* also become modified. These crabs generally show a tendency toward a loss or reduction of the flagellum on the exopod of the first, second and third maxillipeds, since these flagellae no longer have to direct an aquatic respiratory stream.

Reproductive system

Male

The male reproductive system consists of the paired testes, vas deferens, penes and the two gonopods. The development of male sexual characters up to and beyond the moult of puberty is promoted by secretions from the pair of androgenic glands (in the coxae of P5), which act by inhibiting the eyestalk hormone responsible for the development of female characters. The testes of male African freshwater crabs lie in the cephalothorax on top of the hepatopancreas, unite in the mid-line and extend laterally into the angles of the carapace. Their products (spermatozoa) are carried away in paired ducts (the vasa deferentia) which open ventrally. The distal region of each vas deferens is glandular and is modified to produce spermatophores. The paired reproductive tracts open through the right and left penises, which are soft, flexible membranous tubes located at the terminal ends of the vasa deferens. The penises are sited on the medial margin of the coxae of P5 (the last pair of thoracic legs) close to the posterolateral margins of s8 and they do not perforate the sternum in any species of freshwater crab from West Africa. Each penis is relatively long and projects into the basal part of the gonopod chamber between the broad bases of the subterminal segments of gonopods 1 and 2 and is supported by the wide part of segment three of gonopod 1.

Copulation

Gonopods 1 and 2 are modified as copulatory organs to transfer the spermatophores from the male penes to the female sexual openings. Each gonopod 1 is basically a four-part tapering hollow tubular organ with an apical opening in the terminal article and two basal openings in the subterminal segment. The long thin, broad-based gonopod 2 fits tightly into the subterminal segment of gonopod 1 and leaves a lateral basal opening into which the penis extends. Male and female freshwater crabs copulate in the normal brachyuran way, by laying head-to-head and sternum-to-sternum, with their abdomens relaxed so that the abdomen of the female overlaps that of the male. This brings the female openings into contact with the gonopods which swing out away from the sternum when the male abdomen is relaxed. The terminal articles of gonopods 1 connect with, and are inserted into, the paired vulvae of the female sited on s6. The spermatozoa (in spermatophores), together with the secretions of the vas deferens, are ejected through the penis into the subterminal gonopod chamber between the bases of the subterminal segments of the two gonopods. According to GUINOT *et al.*, (1997) there is only a single spermatozoa in each spermatophore (i.e., freshwater crabs exhibit cleistospermy). From there the pumping action of gonopod 2 forces the spermatophores up the gonopod chamber inside the two gonopods. The spermatophores are pumped out of the apical opening of the terminal article of gonopod 1 into the spermathecae that lie just deep to the female sexual openings, where they are stored until the eggs are laid. After copulation the spermathecae of the female contain a mass of spermatozoa (normally no longer in spermatophores). The presence of spermatozoa in a female crab's spermatheca is evidence that copulation has taken place.

Female

The female reproductive system consists of the paired ovaries, ovarian ducts, spermathecae, vaginas and vulvae. The development of the sexual characters in maturing female crabs is due to the secretion of eyestalk hormones that cause the gonads to develop as ovaries. The ovaries of female African freshwater crabs lie in the cephalothorax on top of the hepatopancreas, unite in the mid-line and extend laterally. The eggs are carried away in paired ovarian ducts that open ventrally through the pair of female openings (vulvae) on s5. The vulvae are elongated sideways to receive the terminal articles of the first gonopods, and the distal parts of the oviducts just deep near to the openings have spermathecae to receive and store the spermatophores. Female freshwater crabs mate when their carapace is hard, and do not have to wait until they have just moulted (as is the case for many species of marine crabs). Mating when the carapace is hard is a strategy that is commonly found in the more terrestrial species of crabs. Female crabs store the spermatophores for long periods, and the eggs do not have to be laid immediately after mating. Sperm in the spermatophores fertilises the eggs as they are laid. The fertilised eggs are attached to the setose pleopods by long sticky threads secreted by the female.

Development

True freshwater crabs spend their entire lives in freshwater and it is a shared defining characteristic to be able to complete their entire life cycle independently of seawater. All true freshwater crabs lay their eggs and rear their young in a freshwater environment, rather than in a brackish or marine habitat. The adaptation of true freshwater crabs to freshwater environments has involved a number of modifications of their reproductive system and behaviour. These modifications include the production of relatively few eggs, each of a relatively large diameter, a complete reduction of the larval stages ("direct development") whereby the eggs hatch directly into juvenile crabs ("hatchlings"), and the protection of the hatchlings for several weeks after egg hatching (GURNEY, 1942; BOTT, 1969b). The number of eggs laid by species of marine crabs varies with the size of the species, and large-bodied species can lay from several thousand to more than a million eggs (WARNER, 1977; ANGER, 1995). In contrast, female freshwater crabs produce far fewer eggs: by the hundreds, rather than by the thousands or tens of thousands. The newly laid eggs of marine crabs are very small (0.25-0.35 mm in diameter), and double in size as they develop. In contrast, the newly laid eggs of freshwater crabs are much larger (about 1 mm in diameter), increase to between 3 and 5 mm in diameter as they develop, and remain attached to the pleopods of the female until hatching. The newly laid eggs of African freshwater crabs are bright orange and change colour slowly to dull brown, dirty grey, and then to black before they finally hatch into small crabs. Young freshwater crabs leave the eggs as small (juvende) versions of adult crabs rather than as larvae. The hatchlings are retained on the female's pleopods in the female's abdominal brood pouch for several weeks after hatching and female freshwater crabs show a degree of maternal care.

Breeding season

Very little direct information is available on the breeding season of African freshwater crabs; the following are the preliminary results of field studies carried out by the author. Population statistics (such as age, gender and the presence of eggs and hatchlings) were recorded year round for *Liberonautes latidactylus* and *Globonautes macropus* from the rainforest zone of Liberia, and for *Sudanonautes monodi* from the savanna zone of northern Nigeria. These species show a distinct breeding season that begins in the dry season (January and February) and extends into the early rainy season (June and July). Eggs are laid between February and April (which is the only time of the year when egg-bearing females were caught) and hatchlings appear on female pleopods between March and June. Significantly, eggs or hatchlings are not found on females of these species collected between July and December. This means that each year's recruits are added to the free-living population some time between March and June.

Other crabs in fresh water

Not all crabs found in freshwater are true freshwater crabs. CUMBERLIDGE & SACHS (1989a) reported on the presence of *Sesarma angolense* (Grapsidae, Sesarminae) in Liberian rivers. In fact, world-wide, some 30 species of non-freshwater crabs (mostly belonging to the Sesarminae) breed in freshwater and show an abbreviated larval development (but not direct development). One exception may be *Geosesarma notophorum* NG & TAN, 1995, a terrestrial sesarmine from Sumatra which has been reported to exhibit direct development. Included in this group are 23 species of *Geosesarma* from the Indo-Pacific region (NG, 1988) and *Metopaulias depressus* plus 6 species of *Sesarma* from Jamaica (ANGER, 1995). Three species of this latter group (*Sesarma bidentatum*, *S. windsor* and *S. verleyi*) are the only non-freshwater crabs to pass their entire life cycle in a freshwater habitat (HARTNOLL, 1964; TÜRKAY & DIESEL, 1994; ANGER, 1995). All of these freshwater species of Sesarminae have retained free-swimming larval stages: their eggs hatch into first zoea larvae which rapidly moult to second zoea larvae. Unlike the larvae of marine crabs, neither of the zoeal stages of *Sesarma* and *Metopaulias* can swim freely, and neither one can feed. The next larval stage in these species is the megalopa; this feeds actively and it is this stage that subsequently metamorphoses into a juvenile crab (HARTNOLL, 1963; LITTLE, 1990; SCHUH & DIESEL, 1995). This reproductive strategy (known as abbreviated development) is distinct from that of both marine crabs and of true freshwater crabs (ANGER, 1995). It should be noted that some gecarcinids (e.g., species of *Cardisoma*) and some grapsids (e.g., species of *Varuna* and *Neosarmatium*) spend extended periods of time in freshwater habitats but these crabs lay small eggs and exhibit a marine zoeal development.

Size

Species of African freshwater crabs show a great deal of variation in the age at which they reach maturity (i.e., the size when the moult of puberty occurs, table XII). The pubertal moult is the lower limit of the adult size range for the species; the upper limit is estimated to be close to the size of the largest known specimen of abundant species. Three distinct size categories can be recognised in African freshwater crabs (small, medium and large), which show differences in the body size at which sexual maturity is reached. Since this varies according to species, this character can be helpful in the initial stages of identification. Large species have a delayed maturity and a moult of puberty at a relatively large body size, small species show early maturity, and a moult of puberty at a relatively small body size, and medium sized species fall in between these categories.

The timing of the age at maturity of freshwater crabs (signified by the pubertal moult) is strongly correlated with the final adult body size range of a species. Smaller species of freshwater crabs (such as *Sudanonautes granulatus* and *Liberonautes chaperi*) are mature at cw 35 mm, while the smallest species (*S. orthostylis* and *L. nimba*) are mature at cw 19.5-25 mm. These species exhibit early maturity (i.e., specimens with a very small body size are adults). The benefits of early maturity are a shorter generation time (the eggs and hatchlings are produced earlier and themselves start reproducing sooner), and a higher survival to maturity (because of a shorter period as vulnerable juveniles). Early maturity therefore improves the chances of survival to adulthood and makes it more likely that the investment in growth will be paid back.

The largest species of freshwater crab in Africa is *Sudanonautes africanus* which has a moult of puberty at cw 70-75 mm, after which it continues to grow to cw 108 mm or more. Specimens of other species of freshwater crabs from West and Central Africa reach maturity at cw 65 mm or above, but specimens of *Sudanonautes africanus* of this size are not adult animals. Medium-sized species mature at cw 45-50 mm (*Sudanonautes aubryi*, *S. floweri*, *S. chavanesii*, *S. faradjensis*, *S. kagoroensis*, *S. monodi*, *Liberonautes latidactylus*, *L. paludicolis* and *L. rubigimanus*), and continue to grow up to cw of 70-80 mm. Large species such as *Sudanonautes africanus* and *Liberonautes latidactylus* show delayed maturity, that is, they live longer, grow larger and have more time for more reproductive events. The benefits of later maturity include a higher fecundity through the longer period of growth (because the number of eggs laid increases with size), and a lower juvenile death rate (because of better parental care of the offspring). The disadvantages include a higher juvenile mortality rate due to the longer generation time which means that fewer individuals are likely to survive to maturity. The result of this strategy is that adults of large species are the rarest cohort in natural populations of freshwater crabs in Africa.

Maturity

The moult of puberty is more prominently developed in females than in males, and involves changes in features of the abdomen, pleopods and sternum. In males, external morphological characters usually affecting the chelae signal the onset of maturity. The body size at which the transition to adult occurs (the moult of puberty) can best be determined by examining a series of subadult and adult females. The moult of puberty marks the point at which male and female crabs change from non-breeding subadults into sexually mature adults capable of reproduction. The upper and lower limits of the boundary between adolescence and maturity (which is crossed at the moult of puberty) can be determined by examining the abdomen in subadult and adult females. The lower limit of the range for the moult of puberty is the cw of the largest non-adult, and the upper limit is the cw of the smallest adult.

Natural populations of a species of freshwater crab can be subdivided into three main groups: large sexually mature crabs (adults); medium-sized, not yet sexually mature crabs (subadults), and small immature crabs (juveniles) (CUMBERLIDGE & SACHS, 1989a). Juveniles and adults are the easiest to recognise, but subadults present problems, especially in the smaller species, where a seemingly subadult specimen could actually be a sexually mature breeding adult. Differences between the abdomen of male and female crabs are obvious in adults but are obscured in juveniles because the outline of the abdomen of juvenile females looks very similar to the slim triangle of juvenile and adult males.

Juveniles

This group includes small crabs ranging from hatchlings (cw 3-5 mm) still living on the maternal pleopods to small free-living specimens (cw more than 10 mm). Juvenile crabs of both sexes are characterised by their small size and general lack of differentiation of the abdomen, chelipeds and gonopods or pleopods. Abdominal segments a3-a7 of juveniles form a triangle with tapered sides and a rounded telson that is similar in both males and females. This makes it difficult to identify the gender of a juvenile specimen without lifting the abdomen and counting the number of pleopods, or looking for the presence of vulvae on s5 (females). Gonopods 1 and 2 of juvenile males are short, undeveloped and do not reach s5, and are found only on a1 and a2. The pleopods of juvenile females (four pairs) are short, narrow and non-feathery, and are found only on a2-a5, and never on a1. The abdomen of juvenile males and females is a narrow triangle, shaped like a spearhead with a rounded tip (the telson). The left and right chelipeds of both male and female juveniles are equal sized, and lack any enlargement of either side.

Subadults

Subadult freshwater crabs are characterised by partial development towards the adult form: they are clearly not juveniles, yet they are also not quite sexually mature. The abdomen of male subadults is the same slim triangular shape seen in juveniles of both sexes and adult males and is intermediate in size between the juvenile and adult form. On the other hand, the abdomen of subadult females is distinctly different from that of subadult males. Female subadults have a broad, round abdomen still more triangular than oval in outline, that neither completely covers the sternum nor reaches the coxae of the walking legs. The four pairs of pleopods of female subadults are enlarged and broad with the beginnings of hair-fringed margins, but have not reached the final form seen in adult females. The chelipeds of both male and female subadults show the beginnings of heterochely, whereby one (the major cheliped) grows noticeably longer and higher than the other (the minor cheliped). Gonopods 1 and 2 of subadult males are intermediate in length and form: they are longer than those of juveniles, shorter than those of adults, and the gonopods have not reached the final topology seen in adult crabs.

Recognition of adults

All female crabs bearing egg masses or hatchlings under the abdomen are, by definition, adult animals. Adult females without eggs or hatchlings can be recognised by a broad abdomen with an oval outline that completely covers all the sternum, and whose sides reach to the base of the coxa of each pereiopod, and by long, broad, setose pleopods. The moult of puberty is judged to occur at the size range defined by the largest subadult and the smallest adult specimen. Adult males can be recognised by long, fully formed gonopods, greatly unequal chelipeds and a characteristic species-specific major cheliped. To confirm that a male specimen is an adult, the moult of puberty and the size range of adult specimens for the species must first be established by examining a series of subadult and adult females. Abdominal segments a3-a7 of adult males form a triangle with tapered sides and a rounded telson. The chelipeds of adult male crabs are conspicuously unequal in size, with the palm of the propodus of the major cheliped being distinctly higher, wider and rounder than that of the minor cheliped. In some species the chelipeds of adult females are also unequal. The first and second gonopods of adult males are long, and the terminal articles of gonopods 1 and 2 have attained the final shape for the species. Gonopods 1 and 2 of adults are long enough to reach at least as far as the sternal condyles on s5. The details of the morphology of the two gonopods of adult males are different for each species, and can be used to distinguish between species and genera of African freshwater crabs.

Age

Very little is known about the relationship between body size and age in West African freshwater crabs. Estimates on this relationship are available only for *Sudanonautes aubryi* from Nigeria (EJIKE, 1972) and for *Liberonautes latidactylus* from Liberia (CUMBERLIDGE & SACHS, 1989a). [Voucher specimens of

"*Sudanonautes* (*S.*) *a. africanus*" deposited by EJIKE in the NHML, London (NHML 1966.10.17.5.6) belong to *Sudanonautes aubryi*, and are clearly not *S. africanus*]. Eggs of *Liberonautes latidactylus* in Liberia are laid between February and April, and the hatchlings appear between April and July. Hatchlings of *L. latidactylus* still attached to the maternal pleopods range in size from cw 3-5 mm and so the larger ones must have moulted at least once while still in the abdominal brood pouch. The smallest free-living *Liberonautes latidactylus* caught in Liberia was a juvenile cw 7.5 mm (collected in July) which must have undergone at least one moult to increase from cw 5 mm (the release size) to 7.5 mm four to six weeks later. Other small juveniles (cws 11 and 14 mm) of this species were caught in December. If these young crabs had been released from the maternal pleopods in July, it would have taken about six months to grow from cw 5 mm to cw 14 mm, an average growth rate of about 1.5 mm per month. From this it is estimated that individuals of *Liberonautes latidactylus* of cw 30 mm are about one year old. This estimate agrees with data relating carapace width to age for *Sudanonautes aubryi* from Nigeria (EJIKE, 1972) where specimens measuring 30 mm across the carapace were estimated to be about one year old. Extrapolating from this, subadults of *S. aubryi* and *L. latidactylus* (cw 31-54 mm) would be approximately two to three years old, while sexually mature adults (cw 55-80 mm) would be approximately three to six years old.

Patterns of growth

Male and female African freshwater crabs of the same species become sexually mature at a similar body size. The growth rate of juveniles of both sexes changes during ontogeny, and there are additional differences in the growth of the same character between adult males and females. After reaching maturity adult crabs continue to grow, so that adult male and female crabs show a range of body sizes. Differences in the growth pattern of secondary sexual characters - such as the gonopods 1 and 2 of males, and the chelae and abdomen of male and female African freshwater crabs - can be correlated to the extent to which they must interact with other structures to function effectively.

Gonopods

When adult males moult, their gonopods become incrementally larger (even with isometric or slightly negative allometric growth) but still retain the adult shape. For example, gonopod 1 in *Aratus* and *Eriochier* exhibits slight positive allometry before puberty, a small size increase at puberty, and a slight negative allometry in adults (HARTNOLL, 1974). Similar data are available for the growth of the gonopods of African freshwater crabs. When adult females moult the sternal sexual openings become repositioned slightly. These changes might be expected to present difficulties during copulation if the precision of fit between the size and shape of the gonopods and the position of the female openings was critical. The fact that different sized adult freshwater crabs are able to mate successfully indicates that the gonopods of small adult males are still able to reach the sexual openings of larger sized adult females, and vice versa. These small adjustments are no doubt due to the ability of the gonopods (and of the abdomen to which they are attached) to move slightly so that they can become aligned exactly with the female openings, thereby compensating for any size changes due to the moult. It is concluded here that in most cases it is unlikely that the exact overall length of gonopod 1 is a critical factor in successful mating. What may be more critical is the precise topology of the subterminal and terminal articles of gonopod 1. While gonopods 1 and 2 of one species may be long enough to reach the female openings of another species, subtle differences in the topology of the terminal article of gonopod 1 may cause the gonopod to fail to reach the female openings and so prevent successful copulation.

Abdomen and gonopods / pleopods

Differences in the shape of the outline of the abdomen of adult male and female freshwater crabs are related to the difference in function of the male gonopods and female pleopods. The growth pattern of the male abdomen follows that of the two gonopods: both organs show a slow, progressive increase in size during the subadult phase, and both increase only slightly in size at the moult of puberty. This growth pattern is related to the fact that the gonopods only function in adult animals, since they serve exclusively as intromittant organs during copulation. The abdomen in turn functions to cover and support the gonopods, and so its growth pattern is linked to that of the gonopods. In adult animals gonopod 1 has a functional relationship with other structures of the male (the abdomen, the sternum and gonopod 2), as well as with the copulatory structures of the female (the vulvae). The positive allometry shown by gonopod 1 on subadult animals and the small increase at puberty brings gonopod 1 to an operative size at adulthood (Hartnoll 1974). Any further rise in relative size would be disadvantageous so the growth rate of gonopod 1 falls, becoming negatively allometric. The negative allometry of the gonopods reduces the size variation of gonopod 1 between large and small adult males, thereby conferring on each male the possibility of mating with a wide size range of the female population.

The female abdomen (together with the female pleopods) exhibits high positive allometry in the subadult stages followed by a considerable size increase at the moult of puberty. This is because the abdomen and pleopods are linked by their joint function: the abdomen forms an incubatory chamber for the developing eggs, while the pleopods secure the eggs in the chamber. This growth strategy brings the abdomen to a functional size at maturity, and minimises the waste of resources that would have resulted had it been disproportionately enlarged in the subadult stages. After puberty the relative growth of the female abdomen decreases to a small positive allometry. This slowdown is no doubt due to the function of the abdomen in providing an incubatory chamber in conjunction with the sternum. Having once attained a sufficient relative size at puberty to accomplish this, any disproportionate increase thereafter would decrease the efficiency of the mechanism. Hence the reduction in the level of allometry following the moult of puberty.

Chelipeds

African freshwater crabs show a weak sexual dimorphism of the chelipeds with heterochely being expressed in both sexes (but with adult males possessing a dramatically enlarged major cheliped that is not usually seen in adult females in most species). The chelipeds of females also grow with a small positive allometry, but do not reach the proportions of the male chelipeds. The male chelipeds begin to exhibit high positive allometry in the subadult stage and show considerable size increases at the moult of puberty and beyond. This growth strategy brings the chelipeds to a functional size at maturity, and minimises the waste of resources that would have resulted had they been disproportionately enlarged in the subadult stage (HARTNOLL, 1974). After the moult of puberty the relative growth of the male chelipeds in African freshwater crabs increases to a still higher positive allometry in some species (e.g., *S. africanus*, *L. chaperi* and *P. mambilorum*). This is presumably because the chelipeds are basically independent characters and their function does not depend on a congruence of form with other parts of the body. In some species the propodus of the major cheliped grows to be even longer than the carapace width. The upper limit to the growth of the chelipeds seems to be influenced more by mechanical considerations and by the availability of resources for growth than by other functional limitations.

Ecology

Freshwater crabs were originally known in the vernacular as river crabs, and were given family names such as Thelphusidae and Potamonidae, the latter name being derived from the Greek word root 'Potamon' meaning 'river'. While the river-living habit is an accurate description of the lifestyle of some species of freshwater crabs it by no means applies to all species. In Africa, as in other parts of the tropics, there has also been a tendency for some species of freshwater crab to move out of rivers, streams and lakes and to colonise nearby land (table XIII). In forest and savanna ecosystems, the move on to land favoured (among other things) the development of the ability to breathe air as well as water.

Savanna

The major rivers in West Africa flow through the savanna zone at some point, and each river supports at least one species of river crab. During the rainy season in West Africa (April to September) the rivers swell and often overflow their banks, inundating the surrounding flood plains, and creating temporary pools and swamps. At the onset of the dry season (October) the rivers carry less water, and the flood plain water sources begin to dry out, stranding many river animals, including the freshwater crabs. In the savanna, freshwater crabs respond to the dry season conditions by digging into the mud and tunnelling down to reach the water table (rather than wandering over land in search of water). Savanna species living in flood plain swamps and temporary pools of West Africa (such as *S. monodi*) have developed a sedentary lifestyle centred around burrow-living and air-breathing. Their burrows collect water seepage and remain cool and wet throughout the dry season, and protect crabs from the hot sun and from predators as well as providing a damp place to hide when moulting. The meagre amount of oxygen-poor water in the burrow is unable to meet the respiratory needs of the crab for very long and the respiratory system of savanna species of freshwater crabs has become adapted for gaseous exchange from the plentiful supplies of oxygen-rich air.

TABLE X

The freshwater crabs of the West African region.
Species list by country.

Benin
Sudanonautes aubryi

Bioko
Sudanonautes aubryi
Sudanonautes granulatus

Cameroon
Louisea balssi
Louisea edeaensis
Potamonautes regnieri
Potamonemus asylos
Potamonemus mambilorum
Potamonemus sachsi
Sudanonautes africanus
Sudanonautes aubryi
Sudanonautes chavanesii
Sudanonautes faradjensis
Sudanonautes floweri
Sudanonautes granulatus
Sudanonautes monodi
Sudanonautes orthostylis

Côte-d'Ivoire
Liberonautes chaperi
Liberonautes latidactylus
Liberonautes nimba
Sudanonautes aubryi
Sudanonautes granulatus
Potamonautes ecorssei

The Gambia
Potamonautes ecorssei

Ghana
Liberonautes chaperi
Liberonautes latidactylus
Sudanonautes aubryi
Sudanonautes granulatus
Potamonautes ecorssei
Potamonautes triangulus

Guinea
Afrithelphusa monodosus
Globonautes macropus
Liberonautes latidactylus
Liberonautes nimba

Guinea Bissau
No records

Liberia
Globonautes macropus
Liberonautes chaperi
Liberonautes grandbassa
Liberonautes latidactylus
Liberonautes lugbe
Liberonautes nanoides
Liberonautes nimba
Liberonautes paludicolis
Liberonautes rubigimanus

Mali
Liberonautes latidactylus
Potamonautes ecorssei

Mauritania
Liberonautes latidactylus

Niger
Potamonautes ecorssei

Nigeria
Potamonautes ecorssei
Potamonautes reidi
Potamonemus sachsi
Sudanonautes africanus
Sudanonautes aubryi
Sudanonautes floweri
Sudanonautes granulatus
Sudanonautes kagoroensis
Sudanonautes monodi
Sudanonautes nigeria

Sénégal
Liberonautes latidactylus
Potamonautes senegalensis

Sierra Leone
Afrithelphusa afzelii
Afrithelphusa gerhildae
Afrithelphusa leonensis
Liberonautes latidactylus

Togo
Potamonautes ecorssei
Sudanonautes aubryi
Sudanonautes granulatus
Sudanonautes monodi
Potamonemus sachsi

TABLE XI

Alphabetical list of West African freshwater crabs with their distribution.

Afrithelphusa afzelii	Sierra Leone
Afrithelphusa gerhildae	Sierra Leone
Afrithelphusa leonensis	Sierra Leone
Afrithelphusa monodosus	Guinea
Globonautes macropus	Guinea, Liberia
Liberonautes chaperi	Liberia, Côte-d'Ivoire, Ghana
Liberonautes grandbassa	Liberia
Liberonautes latidactylus	Mauritania, Sénégal, Mali, Guinea, Sierra Leone, Liberia, Côte-d'Ivoire, Ghana.
Liberonautes lugbe	Liberia
Liberonautes nanoides	Liberia
Liberonautes nimba	Guinea, Liberia, Côte-d'Ivoire
Liberonautes paludicolis	Liberia
Liberonautes rubigimanus	Liberia
Louisea balssi	Cameroon
Louisea edeaensis	Cameroon
Potamonautes ecorssei	The Gambia, Burkina Faso, Mali, Niger, Côte-d'Ivoire, Ghana, Togo, Nigeria
Potamonautes reidi	Nigeria
Potamonautes senegalensis	Sénégal
Potamonautes triangulus	Ghana
Potamonemus asylos	Cameroon
Potamonemus mambilorum	Cameroon
Potamonemus sachsi	Togo, Nigeria, Cameroon
Sudanonautes africanus	Nigeria, Cameroon
Sudanonautes aubryi	Côte-d'Ivoire, Ghana, Togo, Benin, Nigeria, Cameroon, Bioko
Sudanonautes chavanesii	Cameroon
Sudanonautes faradjensis	Cameroon
Sudanonautes floweri	Nigeria, Cameroon
Sudanonautes granulatus	Côte-d'Ivoire, Ghana, Togo, Nigeria, Cameroon, Bioko
Sudanonautes kagoroensis	Nigeria
Sudanonautes monodi	Togo, Nigeria, Cameroon
Sudanonautes nigeria	Nigeria
Sudanonautes orthostylis	Cameroon

TABLE XII

Size range of the species of West African freshwater crabs

	Moult of Puberty (cw mm)	Largest known specimen (cw mm)
Potamonautes ecorssei	23-25.2	36.6
Potamonautes triangulus	18.0	24.3
Potamonautes senegalensis	?	58.5
Potamonautes reidi	22-26.6	38.9
Liberonautes chaperi	50-58	70.5
Liberonautes latidactylus	45-50	76.0
Liberonautes paludicolis	45-50	74.0
Liberonautes nanoides	19.5-25.1	42.5
Liberonautes rubigimanus	55-60	66.0
Liberonautes nimba	17.5-19.0	21.5
Liberonautes lugbe	?	23.2
Liberonautes grandbassa	?	31.4
Sudanonautes aubryi	45-50	89.5
Sudanonautes africanus	70-75	113.0
Sudanonautes chavanesii	55-65	72.7
Sudanonautes faradjensis	35-45	90.0
Sudanonautes floweri	37-42	60.4
Sudanonautes monodi	35-43	60.0
Sudanonautes granulatus	30-44	59.0
Sudanonautes orthostylis	21-22	27.8
Sudanonautes kagoroensis	40-45	63.5
Sudanonautes nigeria	40-45	54.7
Potamonemus mambilorum	23-26	34.7
Potamonemus sachsi	20-25	34.4
Potamonemus asylos	?	27.5
Globonautes macropus	?	34.0
Afrithelphusa gerhildae	?	22.5
Afrithelphusa afzelii	?	29.5
Afrithelphusa monodosus	?	21.5
Afrithelphusa leonensis	21.0	27.0
Louisea edeaensis	?	22.5
Louisea balssi	13.5-17.0	22.0

TABLE XIII

Habitat preferences of the species of West African freshwater crabs

Taxon	Ecosystem	Habitat	Habit
Potamonautes ecorssei	savannas	rivers	aquatic
Potamonautes triangulus	savannas	rivers	aquatic
Potamonautes senegalensis	sudan savanna	streams	semi-terrestrial
Potamonautes reidi	rainforest	streams	aquatic
Liberonautes chaperi	rainforest	rivers	aquatic
Liberonautes latidactylus	rainforest	streams	aquatic/terrestrial
Liberonautes paludicolis	rainforest	streams	aquatic/terrestrial
Liberonautes nanoides	rainforest	rivers	aquatic
Liberonautes rubigimanus	rainforest	mountain streams	aquatic/terrestrial
Liberonautes nimba	rainforest	mountain streams	aquatic/terrestrial
Liberonautes lugbe	rainforest	streams	aquatic/terrestrial
Liberonautes grandbassa	rainforest	streams	aquatic/terrestrial
Sudanonautes africanus	rainforest	streams	aquatic/terrestrial
Sudanonautes chavanesii	rainforest	rivers	aquatic
Sudanonautes faradjensis	rainforest	rivers	aquatic
Sudanonautes floweri	rainforest	streams	semiterrestrial
	woodland savanna	streams	semiterrestrial
	guinea savanna	streams	semiterrestrial
Sudanonautes kagoroensis	guinea savanna	streams	aquatic/terrestrial
Sudanonautes monodi	guinea	streams/marshes	semiterrestrial
	sudan savanna	streams/marshes	semiterrestrial
Sudanonautes orthostylis	rainforest	streams	?
Sudanonautes aubryi	rainforest	streams	aquatic/terrestrial
	woodland savanna	streams/ponds	aquatic/terrestrial
	guinea savanna	streams/ponds	aquatic/terrestrial
Sudanonautes granulatus	rainforest	streams	aquatic/terrestrial
Sudanonautes nigeria	rainforest	streams	?
Potamonemus mambilorum	rainforest	streams	?
Potamonemus sachsi	rainforest	streams	aquatic/terrestrial
Potamonemus asylos	rainforest	streams	aquatic/terrestrial
Globonautes macropus	rainforest	tree holes	semiterrestrial
Afrithelphusa gerhildae	rainforest	?	?
Afrithelphusa afzelii	rainforest	?	?
Afrithelphusa monodosus	rainforest	?	?
Afrithelphusa leonensis	rainforest	?	?
Louisea edeaensis	rainforest	?	?
Louisea balssi	rainforest	?	?

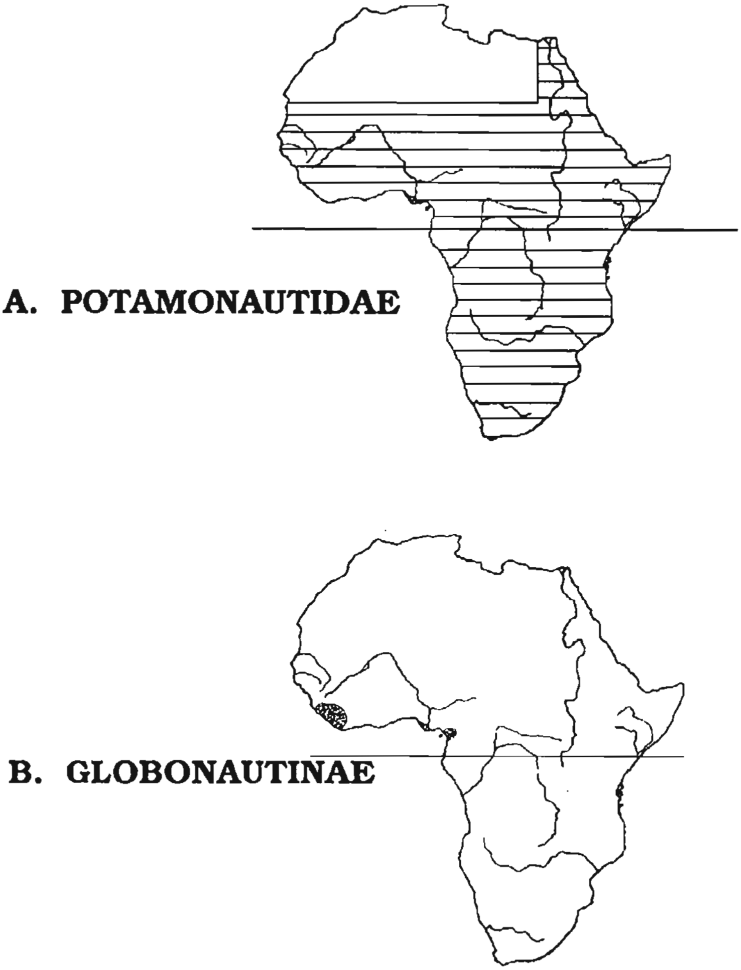


FIG. 63. Distribution (shaded area) of **A**, the Potamonautindae and **B**, Globonautinae in continental Africa.

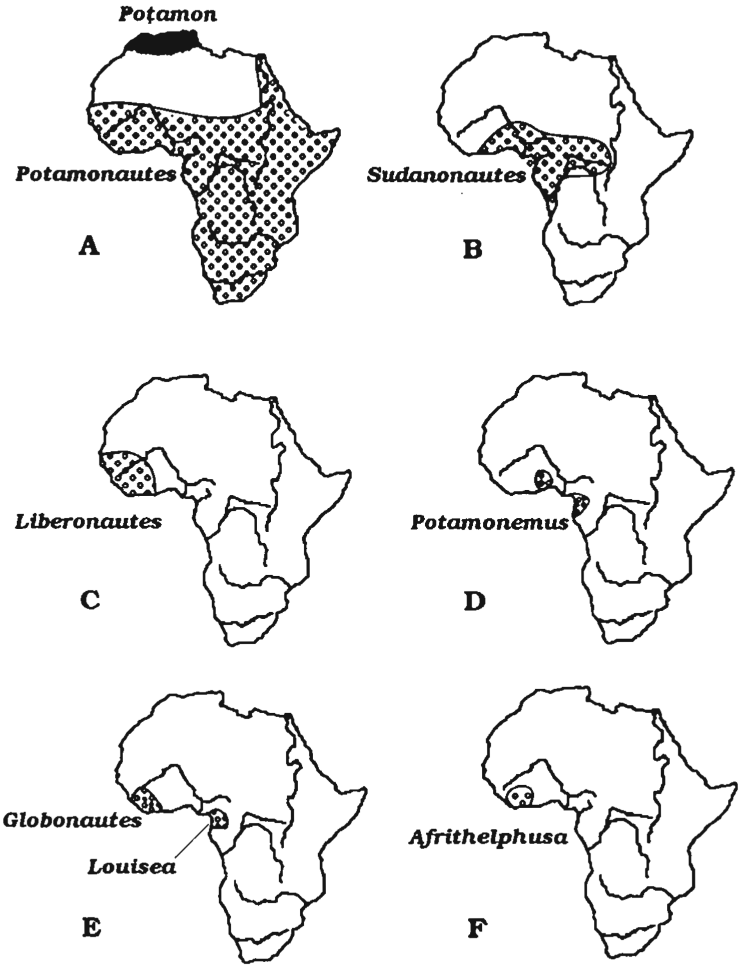


FIG. 64. Distribution (shaded area) of eight genera of freshwater crabs in Africa. **A**, Potamon and Potamonautes; **B**, Sudanonautes; **C**, Liberonautes; **D**, Potamonemus; **E**, Globonautes and Louisea; and **F**, Afrithelphusa. The maps show only the outline of the continent and the major rivers.

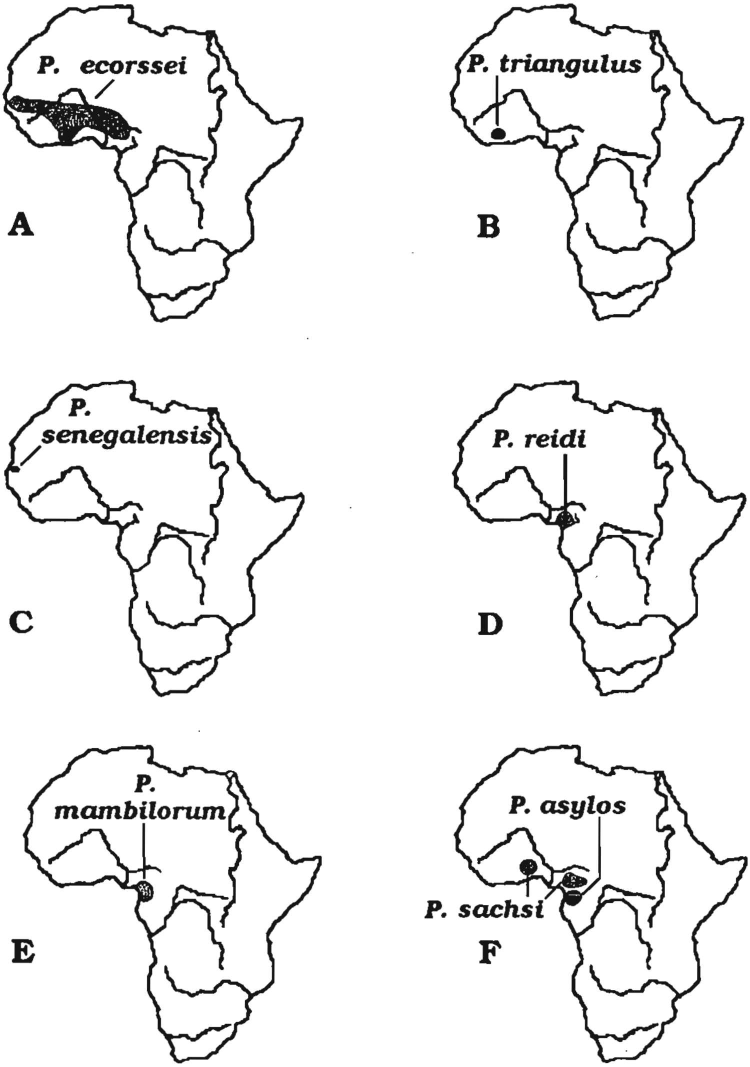


FIG. 65. Distribution (shaded area) of four species of Potamonautes and three species of Potamonemus from West Africa. **A**, *Potamonautes ecorssei*; **B**, *P. triangulus*; **C**, *P. senegalensis*; **D**, *P. reidi*; **E**, *Potamonemus mambilorum*; and **F**, *P. asylos* and **P**. *sachsi*. The maps show only the outline of the continent and the major rivers.

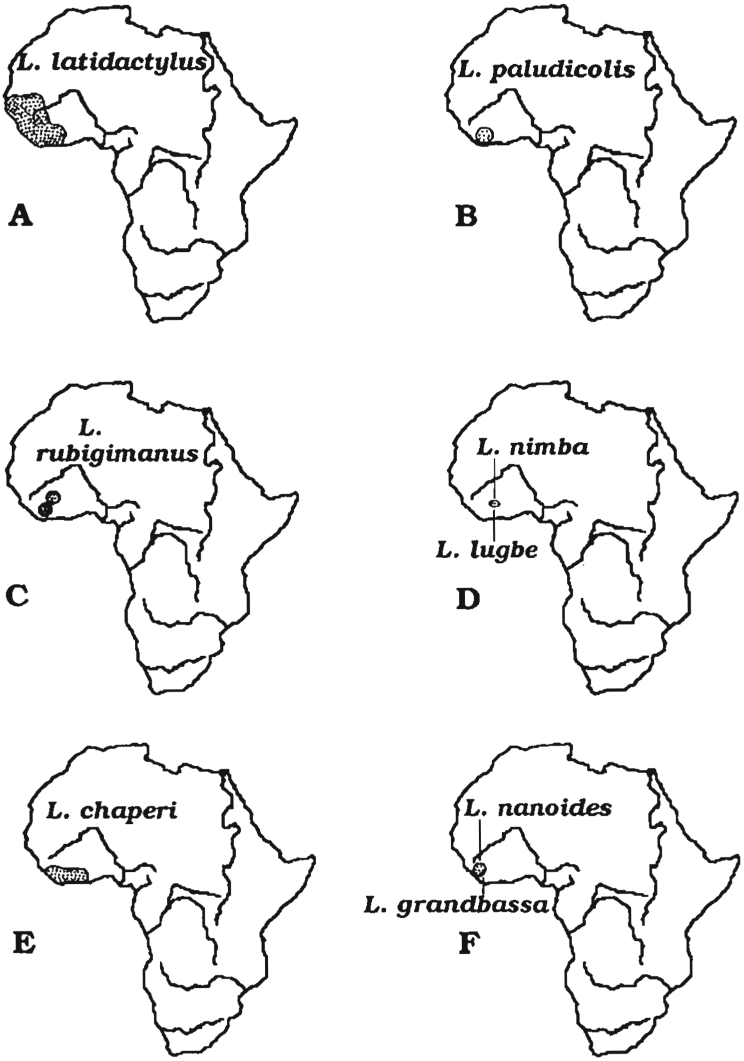


FIG. 66. Distribution (shaded area) of eight species of Liberonautes from West Africa. **A**, *Liberonautes latidactylus*; **B**, *L. paludicolis*; **C**, *L. rubigimanus*; **D**, *L. nimba* and *L. lugbe*; **E**, *L. chaperi*; and **F**, *L. nanoides* and *L. grandbassa*. The maps show only the outline of the continent and the major rivers.

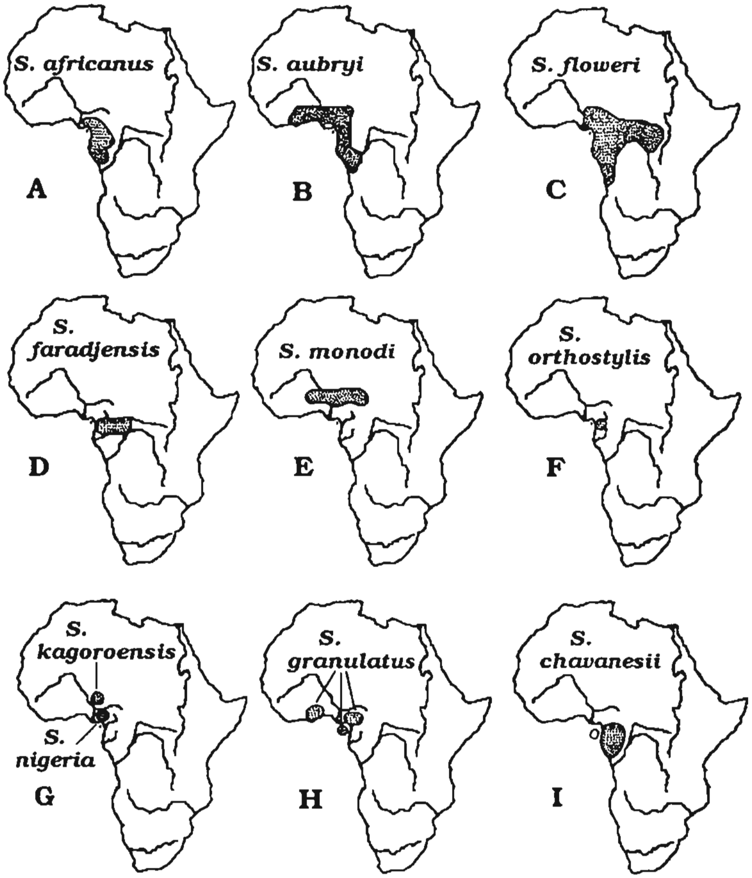


FIG. 67. Distribution (shaded area) of ten species of Sudanonautes from West and Central Africa. **A**. *Sudanonautes africanus*; **B**. *S. aubryi*; **C**. *S. floweri*; **D**. *S. faradjensis*; **E**. *S. monodi*; **F**. *S. orthostylis*. **G**. *S. kagoroensis* and *S. nigeria*; **H**. *S. granulatus* and **I**. *S. chavanesii*. The maps show only the outline of the continent and the major rivers.

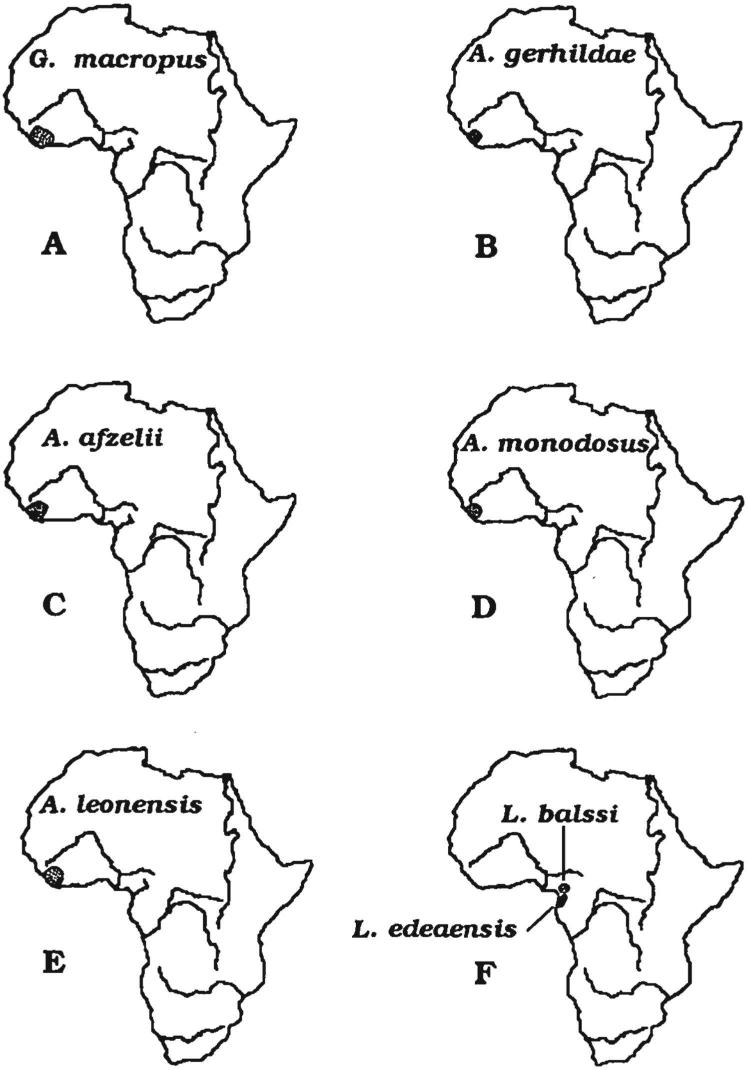


FIG. 68. Distribution (shaded area) of seven species of Globonautinae from West and Central Africa. **A**, *Globonautes macropus*; **B**, *Afrithelphusa gerhildae*; **C**, *A. afzelii*; **D**, *A. monodosus*; **E**, *A. leonensis*; and **F**, *Louisea edeaensis* and *L. balssi*. The maps show only the outline of the continent and the major rivers.

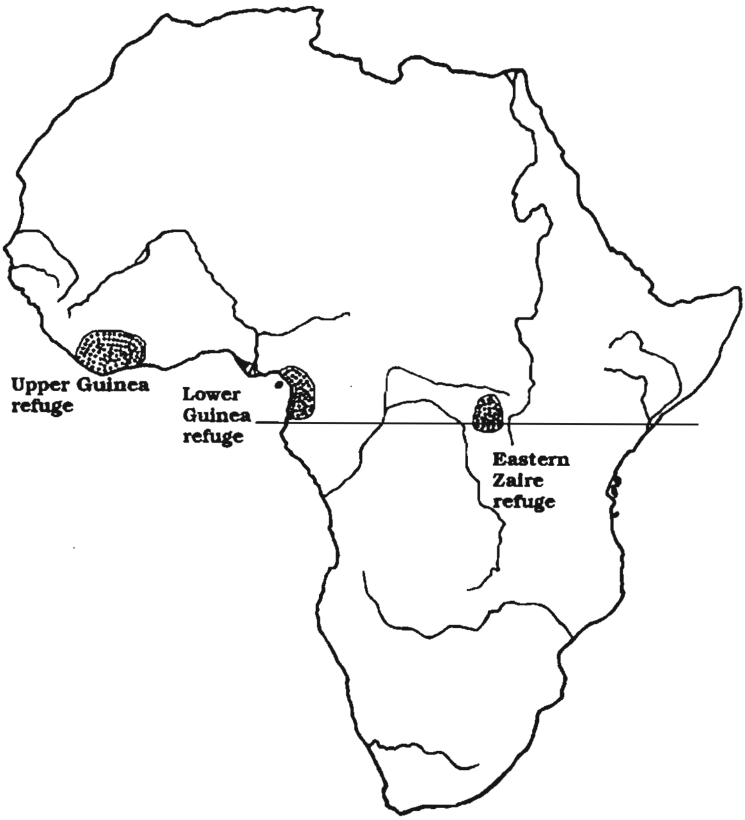


FIG. 69. Approximate forest cover in present day Africa, shaded with the positions of postulated Pleistocene forest refuges marked.

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Gazetteer

A gazetteer of collection localities

The following is a list of localities associated with the species included in the present work. The localities are taken either from the literature or from data provided with specimens. All localities are listed alphabetically by country, and the coordinates (in degrees and minutes) are provided. Spellings and coordinates are from gazetteers of the United States Board on Geographic Names. Localities listed in the species accounts that I have not been able to find are not included in this gazetteer. Other sources that have been helpful in listing West and Central African localities were The Times Gazetteer (1966) and Rathbun (1921). The numbers given in parentheses after the locality refer to the order assigned to each species in the list presented below and in the introduction.

1: *Potamonautes ecorssei*
2: *P. triangulus*
3: *P. senegalensis*
4: *P. reidi*
5: *Liberonautes chaperi*
6: *L. latidactylus*
7: *L. paludicolis*
8: *L. nanoides*
9: *L. rubigimanus*
10: *L. nimba*
11: *L. grandbassa*
12: *L. lugbe*
13: *Sudanonautes aubryi*
14: *S. africanus*
15: *S. chavanesii*
16: *S. floweri*
17: *S. faradjensis*
18: *S. monodi*
19: *S. granulatus*
20: *S. orthosylis*
21: *S. kagoroensis*
22: *S. nigeria*
23: *Potamonemus mambilorum*
24: *P. sachsi*
25: *P. asylos*
26: *Louisea balssi*
27: *L. edeaensis*
28: *Globonautes macropus*
29: *Afrithelphusa gerhildae*
30: *A. afzelii*
31: *A. monodosus*
32: *A. leonensis*

Angola

Luali river (16)	5°04'S, 12°29'E

Benin

Bassila (13)	9°01'N, 1°40'E
Cotonou (13)	6°21'N, 2°26'E

Burkina Faso

Ouagadougou (1)	12°22'N, 1°31'W

Cabinda

Landana, Côte de Loango (16)	5°15'S, 12°15'E

Cameroon

Amban (Ambain?) (14)	2°23'N, 11°17'E
Bakundu (Bakundi?) (16)	8°02'N, 10°45'E
Bambulae (23, 27)	5°55'N, 10°09'E
Bamenda (23, 24)	5°54'N, 10°13'E
Banyo (15, 17)	6°47'N, 11°50'E
Barombi lake, near Kumba (13, 14, 16)	4°43'N, 9°24'E
Batouri (14, 15, 16)	4°26'N, 14°27'E
Bibundi (14, 16)	4°16'N, 8°56'E
Bipindi (13, 14, 17, 19, 20)	3°06'N, 10°30'E
Broto (=Brutu) near Kumba (14)	5°09'N, 9°19'E
Buea (16, 24, 25)	4°09'N, 9°13'E
Douala (16, 23)	4°04'N, 9°43'E
Ebolowa (14)	2°56'N, 11°11'E
Edea (14, 27)	3°47'N, 10°15'E
Ekok, Cross River (19)	5°51'N, 10°29'E
Eséka (14)	3°40'N, 10°28'E
Foumban (15, 17)	5°17'N, 10°08'E
Garoua (18)	3°47'N, 10°15'E
Johann Albrechtshöhe see Kumba (14, 16, 19)	4°39'N, 9°26'E
Kribi(13, 14)	2°56'N, 9°56'E
Kumba (14, 16, 19, 25)	4°39'N, 9°26'E
Laro (18)	8°19'N, 12°21'E
Lolodorf (14)	3°15'N, 10°59'E
Lomie District (17)	3°09'N, 13°35'E
Longji (13)	3°04'N, 9°59'E
Mamfe (14, 16)	5°46'N, 9°18'E
Maroua (18)	10°32'N, 14°20'E
Mbabe (Mba?)	5°48'N, 10°04'E,
or (Mbabon?) (13)	5°39'N, 9°01'E
NKongsamba (14)	4°54'N, 9°53'E
Rhumsiki, Mandara Mountains (13)	10°00'N,13°28'E
Sakbayeme, near Edea (13)	3°47'N, 10°15'E
Somié (27)	6°30'N, 11°30'E
Tinta (19)	5°45'N, 7°24' E
Tiko (13)	4°02'N, 9°19'E
Victoria (13, 14, 16, 19, 25)	4°01'N, 9°12'E
Waza (18)	11°17'N, 14°41'E
Yabassi (13, 27, 28)	4°30'N, 9°59'E
Yaounde (13, 14, 23)	3°51'N, 11°31'E

Central African Republic

Bangui (16, 17)	2°30'N, 17°19'E
Douma (Douma Kaga?) (19)	7°13'N, 22°46'E
Oubangi (= Ubangi) river (19)	0 to 5°N, 18 to 23°E
Kembé (17)	4°29'N, 21°53'E
Uele river	3°30'N, 23 to 30°E

Republic of the Congo

Banana (16)	5°38'N, 12°27'E
Brazzaville	6°49'N, 1°44'E
Ganda Sundi (14, 16)	4°26'N, 14°32'E
Mayumbe District (14)	2°30'S, 27°37'E
Tshela (14)	5°43'S, 12°51'E

Congo Democratic Rep. (ex-Zaire)

Bambesa (16)	3°28'N, 25°43'E
Bangu-Bangu river (Bangu?) (14)	0°03S, 19°11'E
Banzyville (Yasanyama) (17)	4°18'N, 21°11'E
Boma (14)	5°50'S, 13°10'E
Buta(16)	2°49'N, 24°50'E
Chilongo (Shiloango) river (14)	5°S, 12° to 13°'E
Dougou (Dubgu?) river (16)	4°40'N, 28°25' to 30°40'E
Duma (16, 17)	3°54'N, 18°41'E
Epulu river (16)	1°15'N, 28°21'E
Faradje (16, 17)	3°45'N, 29°43'E
Ganza (16)	7°05'S, 29°25'E
Gamangui (16)	2°10'N, 27°20'E
Garamba Park National de la Congo (16)	4°10'N, 29°40'E
Goma (14)	5°19'S, 14°24'E
Gombari (Van Kerckhovenville) (16, 17)	3°20'N, 29°20'E
Ituri river (16)	1°30'N, 26° to 30°'E
Kibali (16)	3°37'N, 28°34'E
Kindambo (Kindamba?) (14)	4°45'S, 14°05'E
Kitobola (14)	5°22'S, 14°31'E
Kinshasa (Leopoldville) (17)	4°25'S, 15°20'E
Kisangani (Stanleyville) (16)	6°30'N, 25°15'E
Lake Albert	1°40'N, 31°00'E
Leopoldville (Kinshasa) (17)	4°25'S, 15°20'E
Lisala (17)	2°09'N, 21°31'E
Luki (16)	5°38'N, 13°04'E
Lukula (14)	5°23'S, 12°57'E
Lukunga river (14)	4°40'S, 15°38'E
Mbanza-Ngungu (Thysville) (14)	5°15'S, 14°52'E
Nepoko river (16)	2°20' to 1°35'N, 27°35' to 29°20'E
Poko (16)	3°08'N, 26°51'E
Shiloango (Chilongo) river (14)	5°S, 12° to 13°'E
Stanleypool (17)	4°15'S, 15°30'E

Stanleyville (Kisangani) (16)	6°30'N, 25°15'E
Thysville (Mbanza-Ngungu) (14)	5°15'S, 14°52'E
Tshopo river (16)	0°33'N, 25°07E
Uele river (16)	3°30' to 4°09'N, 22°26' to 30°E
Van Kerckhovenville (Gombari) (16, 17)	3°20'N, 29°20'E
Yakuluku (16)	4°20'N, 28°50'E
Yasanyama (Banzyville) (17)	4°18'N, 21°11'E

Côte d'Ivoire

Assini (5)	5°07'N, 3°17'W
Bandama river (13)	5°10'N to 7°44'N, 5°00'W to 3°48'W
Béoumi (1)	7°40'N, 5°34'W
Bouaflé (19)	7°00'N, 5°40'W
Bouaké (13)	9°37'N, 7°25'W (or 7°41'N, 5°02'W)
Lac de Kossou (1)	6°57'N, 4°58'W
Koudougou (19)	6°56'N, 5°40'W
Mt. Nimba (7)	7°35'N, 8°28'W

Equatorial Guinea

Batah (= Bata?) (13)	1°00'N, 3°00'E

Gabon

Fang forest, Ogoué river (16)	
Franceville (13, 15)	2°21'S, 12°30'E
Lac de Franceville (14, 15)	1°40'S, 9°05'E
Lambarene, Ogoué river (16)	0°41'S, 10°13'E
Libreville (16)	0°39'N, 9°25'E
Makokon (14, 17)	0°36'N, 12°15'E
N'debde (NDende?) (14)	2°49'S, 11°15'E

Ghana

Accra (2)	5°33'N, 0°15'W
Ashante region (6)	6°45'N, 0°15'W
Asiakwa (2)	5°45'N, 1°01'W (or 6°16'N, 0°30'W)
Ankobra river (19)	5°00'N, 2°14'W
Keta (1)	5°55'N, 0°59'E
Kofoudua (Koforidua?) (13)	5°26'N, 0°48'W
Ejura (13)	7°23'N, 1°22'W
Elmina (13)	5°50'N, 1°30'E
Kibi (2)	6°10'N, 0°33'W
Tafo (13)	6°44'N, 1°37'W
Volta region (13)	7°12'N, 0°30'E

Guinea

Boké (31)	10°57'N, 14°13'W
Conakry	9°31'N, 13°43'W
Fenaria (6)	9°01'N, 9°17'W

Kindia (28, 29)	10°04'N, 12°51'W
Mount Nimba (6, 9, 10)	7°35'N, 8°28'W
Ya river (9)	7°30' to 8°01'N, 8°38' to 7°57'W
Seredou (6)	9°45'N, 10°30'W

Liberia

Balloon (Balu?) creek (6, 9)	6°34' to 6°36'N, 10°23' to 10°24'W
Beyan Town (Beyanta?) (5)	6°50'N, 8°45'W
Bong Iron Mine (6)	4°49'N, 10°20'W
Farmington river (6)	6°08'N, 10°22'W
Fono (6)	7°22'N, 11°03'W
Gundeh creek (28)	6°50'N, 10°16'W
Haindi (8)	6°53'N, 10°23'W
Kendeh Town (28)	6°51'N, 10°26'W
Kuma Town (6)	5°30'N, 8°48'W
Lofa river (6)	6°36'N, 11°05'W
Lugbe (6)	7°37'N, 8°37'W
Masajah Town (28)	6°53'N, 10°18'W
Mauwa (Mawua?) (6)	6°51'N, 10°26'W
Mauwa (Mawua?) creek (6)	7°48'N, 10°23'W
Mesurado river (28)	6°30'N, 10°50'W
Millerstown (28)	6°50'N, 10°20'W
Millsburg (6)	6°29'N, 10°40'W
Mount Gibi (6, 9)	6°35'N, 10°04'W
Mount Nimba (6)	7°35'N, 8°28'W
Mount Zaweah (Za Wia?) (6)	6°04'N, 9°23'W
Putu range (6)	5°38'N, 8°12'W
Saniquellie (7)	7°22'N, 8°43'W
Toso forest (28)	6°44'N, 11°20'W
Weajaryoma forest (28)	6°59'N, 10°2'W

Mali

Goundam (1)	16°25'N, 3°40'W
Lac Télé (1)	16°26'N, 3°45'W
Manantali (1)	13°12'N, 10°28'W

Mauritania

Guidimaka (1)	15°30'N, 12°00'W

Nigeria

Abuja (21)	9°05'N, 7°30'E
Addy Arbour	5°54'N, 8°20'E
Agban river (21)	9°32'N, 8°09E
Anadaryia (18)	11°26'N, 8°25'E
Arochuku (16)	5°21'N, 7°54'E
Asaba (16)	6°11'N, 6°43'E
Awgu (13)	6°05'N, 7°26'E
Ayip-Eku Oil Palm Estate (19)	5°27'N, 8°43'E

Badeggi (18)	9°01'N, 6°10'E
Benin City (16)	6°19'N, 5°41'E
Benue river (18)	9°14'N, 12°32'E
Bida (13)	6°00'N, 9°05'E
Calabar (4, 16)	4°56'N, 8°27'E
Dabar Kwari (18)	11°48'N, 8°36'E
Ekang (14)	5°36'N, 8°49'E
Falgore (18)	10°44'N, 8°46' E
Funtua (13)	11°34'N, 7°17'E
Gadan (= Gadau) (18)	11°54'N, 10°09'E
Gwarzo (13, 18)	11°55'N, 7°57'E
Hadejia (18)	12°28'N, 10°03'E
Ibadan (13)	7°23'N, 3°56'E
Ibi, Benue river (18)	8°11'N, 9°44'E
Igbetti (13)	8°44'N, 4°08'E
Ikpan river (14)	5°27'N, 8°16'E
Ile-Ife (13)	7°33'N, 4°34'E
Ilorin (13, 21)	8°32'N, 4°34'E
Jos (13)	9°55'N, 8°52'E
Kaduna (16)	10°28'N, 7°25' E
Kafanchan (21)	9°35'N, 9°42'E
Kainje	9°51'N, 4°36'E
Kagoro (21)	9°35'N, 8°09'E
Kogar-Kasa (18)	11°46'N, 8°47'E
Kurra (21)	9°37'N, 8°50'E
Lagos (13)	6°27'N, 3°28'E
Mada river (21)	9°35'N, 8°41'E
Maigwado (18)	10°42'N, 8°42' E
Minne (=Minna) (18)	9°35'N, 6°34'E
Ningi (18)	11°15'N, 9°30'E
Njaba creek (16)	6°38'N, 6°53'E
Oban (16)	5°17'N, 8°33 E'
Oban Hills (19)	4°56'N, 8°27'E
Obubra District (13, 19)	6°05'N, 8°20'E
Obudu Plateau (24)	7°27' to 7°29'N, 9°16'E
Obudu Cattle Ranch (14, 16)	6°38'N, 9°05'E
Ogoja (14, 16)	6°40'N, 8°45'E
Ogun river, Lagos (13)	6°27'N, 3°28'E
Okigwe (13)	5°48'N, 7°20'E
Otta (16)	6°40'N, 3°20'E
Oyo (13)	7°50'N, 3°55'E
Pasakwauri (16, 21)	9°36'N, 8°25'E
Rogo (13)	11°32'N, 7°50'E
Sapele (16)	5°55'N, 5°46'E
Tiga Lake (13, 18)	11°30'N, 8°26'E
Umaji (19)	6°29'N, 9°15'E
Uzombe (22)	6°36'N, 6°53'E

Yankari Game Reserve, Wiki (16)	9°44'N, 10°35'E
Yola (18)	9°17'N, 12°28'E

Sénégal

Dakar (6)	14°40'N, 17°35'W
Niokolo-Koba (Parc National) (1)	13°00'N, 13°00'W
Sagnigui river (1)	13°02'N, 12°46'W
Sénégal river (3)	15°48'N, 16°32'W
Yoff (Yof?) (6)	14°45'N, 17°28'W

Sierra Leone

Moyamba District (6)	8°00'N, 12°30'W
Sugar Loaf Mountain (32)	8°25'N, 13°14'W

Sudan

Bahr el Gebel (16)	7°30' to 9°30'N, 30°15' to 30°40'E
Gondokoro (16)	4°54'N, 31°40'E
Juba (16)	4°50'N, 31°35'E
Lado Nipo (Mt. Lado) (16)	5°10'N, 31°32'E
Mongalla (16)	5°12'N, 31°42'E
Shamfe (Shambe?) (16)	7°08'N, 30°48'E

Togo

Agbodrafo (13)	6°07'N, 7°29'E
Aledjo (13)	9°15'N, 1°12'E
Aného (19)	6°09'N, 1°36'E
Atakpamé (13)	7°34'N, 1°14'E
Bismarksburg see Lome (13, 19)	7°06'N, 1°36'E
Blitta (13)	8°19'N, 0°59'E
Fazao (13)	8°42'N, 0°46'E
Ebéva (13)	7°31'N, 1°05'E
Klouto (=Kloto) (13, 19)	6°57'N, 0°34'E
Kpalimé or Palimé (13)	6°54'N, 0°38'E
Lac Togo (13)	6°15'N, 1°25'E
Lome (Bismarksburg) (13, 19)	7°06'N, 1°36'E
Misahöhe (=Missahohe) (13, 19)	6°56'N, 0°36'E
Niamtougou (13)	7°12'N, 1°10'E
Palimé (13, 19)	6°54'N, 0°38'E
Porto Séguro (Agbodrafo) (13)	6°07'N, 7°29'E
Sokodé (13)	8°59'N, 1°08'E
Tamboursan (18)	10°03'N, 1°07'E
Todjé river (1)	5°59'N, 0°43'E

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The taxon names used in the systematic part are printed in bold-face. Numbers in bold-face denote the pages where the main description is given; numbers in italic denote pages where an illustration is given.

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Keywords
Freshwater
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The area of West Africa covered by this book includes eighteen countries from Mauritania to Cameroon and Bioko (Equatorial Guinea). The West African freshwater crab fauna comprises at least thirty-two species in seven genera and two families. This work brings together recent contributions to the taxonomy, distribution, and ecology of the West African freshwater crabs and presents new information on phylogeny and biogeography (in 13 Tables, 69 pages of Figures, and 4 Plates). Four new species are added to the faunal list of the region and a new family, the Platythelphusidae COLOSI, 1920 is established.

The phylogenetic relationships of the freshwater crabs of West Africa were examined by means of a cladistic analysis (using PAUP 3.1) that employed thirty-three morphological characters from thirty-two ingroup taxa and five outgroup taxa. Five most parsimonious trees (all with 55 steps, a consistency index of 0.75, and a retention index of 0.79) group the West African species into two lineages, the Potamonautidae and the Globonautinae.

Morphometric relationships of the dimensions and proportions of the carapace revealed trends in changes in the width, length and height of the carapace of species within a genus that could be correlated with the habitat and lifestyle of each species.

The thirty-two species of freshwater crabs found in the West African region are arguably the most diverse in Africa and represent about one-third of the species and subspecies presently known from the continent. Species diversity within the West African region clearly depends on vegetation type, where the highest numbers of species occur in rainforest ecosystems, and the fewest in savanna ecosystems. The species composition of the freshwater crab fauna is distinctly different between the Upper Guinea forest (from Guinea to Togo) and the Lower Guinea forest (Nigeria, Cameroon and Central Africa). The Pleistocene forest refuge hypothesis, which postulates past faunal refuges in small areas of stable, undisturbed forest in West and Central Africa, is supported by distributional data presented here.

Aspects of the biology of the West African freshwater crabs, including the respiratory system, reproductive system, growth patterns, development, and ecology are also discussed.

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