

A new multilocus phylogeny reveals overlooked diversity in African freshwater crabs (Brachyura: Potamoidea): a major revision with new higher taxa and genera

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The taxonomy of 185 species of Afrotropical freshwater crabs is revised to conform to the updated phylogenetic relationships within this large assemblage, based on the largest taxonomic sampling to date (that includes almost all genera and 57% of the species). Four DNA loci were sequenced including three mitochondrial loci (*COI*, 12S rRNA, 16S rRNA) and one nuclear locus (histone 3), and evolutionary relationships were estimated using maximum likelihood and Bayesian approaches. The divergence times of the major clades were estimated with a Yule tree prior and an uncorrelated lognormal relaxed molecular clock. The taxonomic acts proposed here include the recognition of two Afrotropical families of freshwater crabs (Potamonautidae and Deckeniidae) each with two subfamilies. In the revised Potamonautidae, three new tribes and three new genera (*Maritimonautes* **gen. nov.**, *Nesonautes* **gen. nov.**, *Occidensonautes* **gen. nov.**), are established, three previously published genera are revised and four subgenera are raised to genus (*Arcopotamonautes*, *Lirrangopotamonautes*, *Longipotamonautes*, *Rotundopotamonautes*). An updated species list and identification keys for the new taxa, revised distribution maps, digital images and illustrations of diagnostic characters are provided.

ADDITIONAL KEYWORDS: 12S rRNA – 16S rDNA – Africa – Bayesian analysis – *COI* mtDNA – Eocene – maximum likelihood – molecular phylogeny – taxonomic revision.

INTRODUCTION

Freshwater crabs of the family Potamonautidae [Bott, 1970](#) are distributed throughout the Afrotropical region in continental sub-Saharan Africa, Madagascar and the Seychelles Archipelago. These decapods are found in all freshwater habitats from mountain streams to major rivers, lakes, wetlands and phytotelmic water pools. Despite the importance of this fauna, Afrotropical freshwater crabs were poorly known and largely overlooked until the middle of the 20th century when interest was kindled by the continent-wide monograph by [Bott \(1955\)](#). The numerous contributions since then have increased

the known diversity from 44 species in four genera ([Bott, 1955](#)) to currently 185 species in 28 genera; however, the taxonomy of this group still requires revision. For example, [Bott \(1955\)](#) placed all African freshwater crabs in Potamonidae [Ortmann, 1896](#) consisting of *Deckenia* [Hilgendorf, 1869](#) (two species), *Potamonautes* [MacLeay, 1838](#) (with 15 subgenera, 38 species and 13 subspecies), *Sudanonautes* [Bott, 1955](#) (three species and five subspecies) and *Liberonautes* [Bott, 1955](#) (one species). Later, [Bott \(1970\)](#) updated his classification and recognized two families of African freshwater crabs: Potamonautidae and Parathelphusidae [Alcock, 1910](#). Both classifications ([Bott, 1955, 1970](#)) were based mainly on shared morphological characters of the first gonopod of adult males, but despite forming the historical monographic reference for the continental freshwater crab fauna, it did not provide a stable taxonomy for subsequent workers.

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Cumberlidge *et al.* (2008) and Cumberlidge & Ng (2009) radically revised the higher classification of the African freshwater crabs based on the first molecular phylogeny of a large taxonomic sample that included crabs from continental Africa, Madagascar and the Seychelles (Daniels *et al.*, 2006). The latter study found the entire Afrotropical freshwater crab fauna to be a monophyletic assemblage with no representatives outside of the region. Furthermore, Daniels *et al.* (2006) and Cumberlidge *et al.* (2008) recognized Potamonautidae as a single family that diverged 30.14 Mya during the Eocene-Oligocene into two subfamilies, Potamonautinae Bott, 1970 (throughout sub-Saharan Africa) and Deckeniinae Ortmann, 1897 (from parts of Africa, the Seychelles and Madagascar). Those authors (Daniels *et al.*, 2006; Cumberlidge *et al.*, 2008) found no phylogenetic support for the inclusion of any genus from the Afrotropical region in Gecarcinucidae Rathbun, 1904 (formerly Parathelphusidae Alcock, 1910), which they treated as an exclusively Oriental-Indomalayan taxon.

Although the classification of Deckeniinae by Cumberlidge *et al.* (2008) assigned genera to tribes and subtribes that corresponded to monophyletic groups in the subfamily (Daniels *et al.*, 2006; Cumberlidge *et al.*, 2008), they did not address the numerous other relationships between the genera that were discovered within Potamonautinae. The latter subfamily is the focus of the present work. Here the most comprehensive taxon sampling of Potamonautinae to date is used, that includes all known genera and 57% of the species. This produced an updated phylogeny based on partial sequences of four genes (three mitochondrial 12S rRNA, 16S rRNA, *COI*; and one nuclear, histone 3). Currently, Potamonautinae includes the largest assemblage of Afrotropical region freshwater crabs, with 157 species in eight continental genera namely *Buea* Cumberlidge *et al.*, 2019, *Erimetopus* Rathbun, 1894, *Liberonautes*, *Louisea* Cumberlidge, 1994, *Platythelphusa* A. Milne-Edwards, 1887, *Potamonautes*, *Potamonemus* Cumberlidge & Clark, 1992 and *Sudanonautes*.

Interest in Afrotropical freshwater crabs has increased in recent years, and there have been a number of works that have greatly expanded our knowledge of the diversity of this fauna. Some have focused on the entire Afrotropical region (Cumberlidge & Ng, 2009; Cumberlidge, 2011a, b, 2014; Wood *et al.*, 2019), while others have focused on regional faunas such as West Africa (Cumberlidge, 1999, 2006, 2009c; Duris & Koch, 2010; Cumberlidge & Naskrecki, 2011), Central Africa (Cumberlidge & Boyko, 2000; Cumberlidge *et al.*, 2002, 2018, 2019; Cumberlidge & Reed, 2004; Cumberlidge & Meyer, 2011; Meyer & Cumberlidge, 2011, 2015, 2017a, b; Daniels, 2017; Cumberlidge, 2017a, b; Mvogo Ndongo *et al.*, 2017a, b, c, 2019, 2020; Cumberlidge & Clark,

2018; Cumberlidge & Daniels, 2018), north-east Africa (Cumberlidge, 2009a, b; Cumberlidge & Meyer, 2010; Cumberlidge & Clark, 2012), East Africa (Cumberlidge, 1999, 2005, 2009a, b, 2018; Cumberlidge *et al.*, 1999; Cumberlidge & Vannini, 2004; Marijnissen *et al.*, 2004; Reed & Cumberlidge, 2004, 2006a; Cumberlidge & Dobson, 2008; Cumberlidge & Clark, 2010a, b, 2016, 2017, 2018; Meyer & Cumberlidge, 2011) and southern Africa (Daniels *et al.*, 1998, 2001, 2002, 2006, 2014, 2015, 2019; Gouws *et al.*, 2000; Gouws & Stewart, 2001; Cumberlidge & Tavares, 2006; Cumberlidge & Daniels, 2007, 2009; Daniels, 2011, 2017; Daniels & Bayliss, 2012; Phiri & Daniels, 2013, 2014, 2016; Peer *et al.*, 2015, 2017; Cumberlidge *et al.*, 2016, 2019; Wood & Daniels, 2016).

The currently available classification (Cumberlidge *et al.*, 2008; Cumberlidge & Ng, 2009) does not recognize any diversification within Potamonautinae, despite the considerable morphological diversity known to occur within *Potamonautes s.l.*, the largest African genus, and the fact that this genus shows extensive evolutionary patterning dating back to the Eocene (Daniels *et al.*, 2006, 2015; Daniels & Klaus, 2018; Wood *et al.*, 2019). For example, Daniels *et al.* (2006, 2015), Daniels & Klaus (2018), Wood *et al.* (2019) and the present study (Fig. 1) demonstrated the existence of two genera (*Erimetopus* and *Platythelphusa*) nested in *Potamonautes s.l.* (Fig. 1B2, 1B3). Furthermore, these phylogenetic studies did not support monophyly for most of the 15 subgenera of *Potamonautes s.l.* established by Bott (1955). The ongoing problem of taxonomic inconsistencies associated with the subgenera of *Potamonautes s.l.* of Bott (1955) has been recognized by a number of authors (Cumberlidge, 1999, 2011; Cumberlidge *et al.*, 2008; Ng *et al.*, 2008) which, although recognizing *Potamonautes s.l.*, have not accepted the subgenera of Bott (1955) based on morphological grounds. This lack of support was because Bott (1955) established subgenera without evolutionary considerations, and grouped taxa by similar characters, despite in some cases uniting taxa from geographically disjunct regions of Africa (Ng *et al.*, 2008; Cumberlidge *et al.*, 2009). Therefore, the subgenera of *Potamonautes s.l.* (Bott, 1955) are re-examined with reference to the new morphological and molecular evidence presented here.

The revised classification of the Afrotropical freshwater crab fauna in this study (Tables 1–3) is congruent with morphological, phylogenetic and biogeographical data. The new taxonomic groups reflect shared common ancestry, that is, common membership of a well-supported monophyletic group or clade. Furthermore, the taxonomic acts proposed here include the recognition of two Afrotropical families of

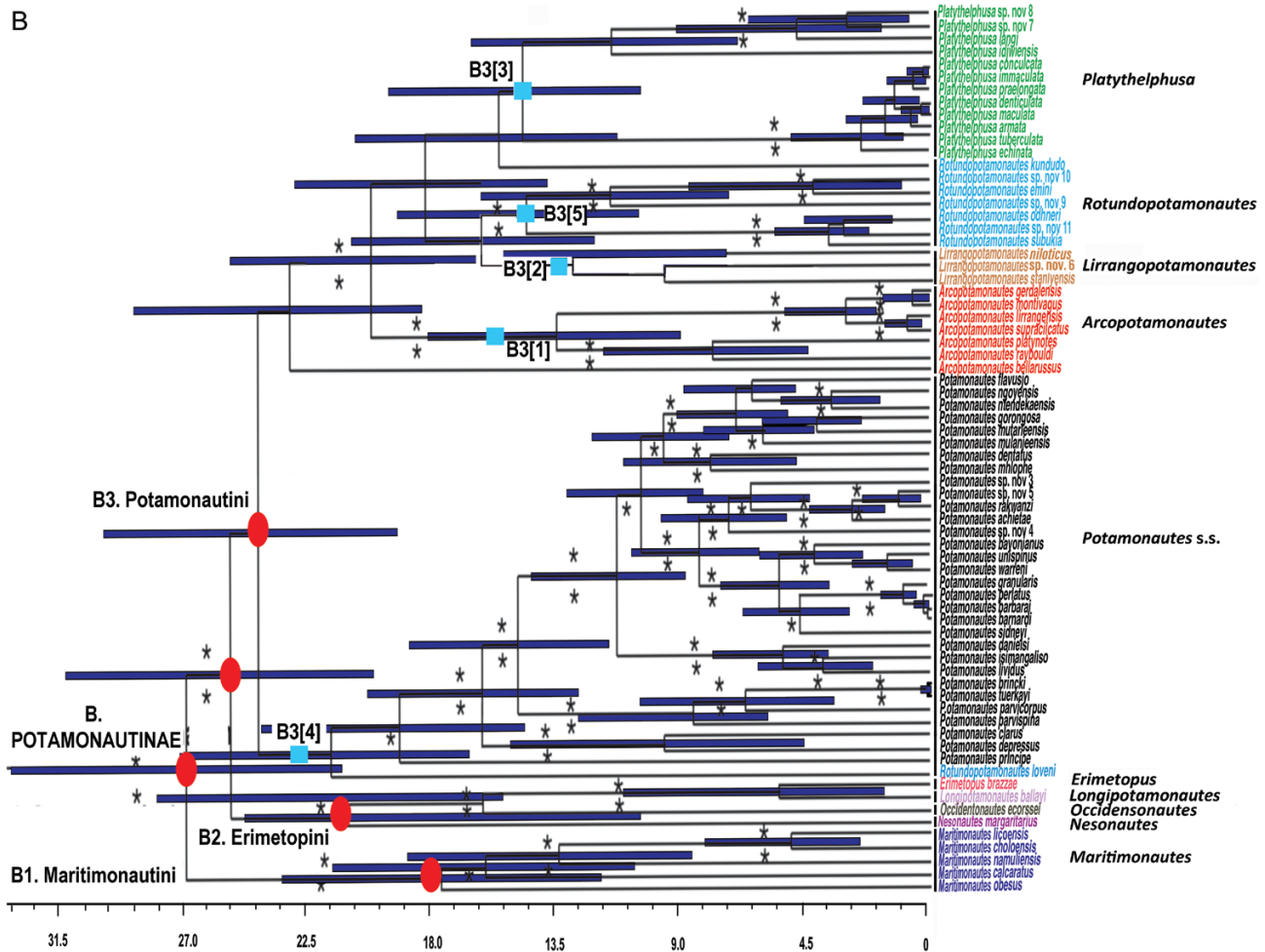


Figure 1. Continued.

morphological analysis of the Afrotropical fauna is completely comprehensive and includes all described taxa listed in Table 3. The authorities for all taxa cited in this work are provided in Table 3, which includes a species list based on the updated classification of the entire Afrotropical freshwater crab fauna currently recognized.

DNA EXTRACTION, PCR AND SEQUENCING

Muscle tissue was extracted from the walking legs of crabs and DNA was extracted using a Nucleospin kit (Macherey-Nagel, Duren, Germany) following the manufacturers protocol. Extracted DNA was stored at -20°C until required for PCR. A $1\mu\text{L}$ DNA in $19\mu\text{L}$ water dilution was performed prior to use. Three partial mtDNA gene fragments (*COI*, 12S rRNA, 16S rRNA) and one nuDNA locus (histone 3) were selected for the present study. Each of these four loci has a different mutation rate and each has

been successfully used in the past for reconstructing evolutionary relationships among freshwater crabs (Daniels *et al.*, 2002, 2006, 2015, 2019, 2020; Phiri & Daniels, 2013, 2014, 2016; Gouws *et al.*, 2015; Wood & Daniels, 2016; Daniels & Klaus, 2018; Wood *et al.*, 2019; Mvogo Ndongo *et al.*, 2019, 2020). Primer pairs for these four loci are outlined in Daniels *et al.* (2015). Standard PCR conditions for amplification and DNA sequencing protocols were followed (Daniels *et al.*, 2015). The outgroup taxa were selected from two other freshwater crab families: Potamidae (*Geothelphusa* sp., *Johora tiomanensis* and *Socotra pseudocardisoma*) and Gecarcinucidae (*Parathelphusa* sp., *Rouxana* sp. 1 and *Rouxana* sp. 2) (Daniels *et al.*, 2015).

PHYLOGENETIC ANALYSES

Sequence Navigator (Applied Biosystems) was used to compute a consensus sequence from forward and reverse strands for each of the four gene fragments.

Table 1. List of new and revised higher taxa and genera of Afrotropical freshwater crabs (Potamoidea [Ortmann, 1896](#))

Potamoidea [Ortmann, 1896](#)

Potamonautidae [Bott, 1970](#)
 Liberonautinae subfam. nov.
 Potamonautinae [Bott, 1970](#)
 Erimetopini trib. nov.
 Potamonautini ([Bott, 1970](#)) trib. nov.
 Maritimonautini trib. nov.
Occidensonautes gen. nov.
Nesonautes gen. nov.
Maritimonautes gen. nov.
Longipotamonautes ([Bott, 1955](#)) stat. nov.
Erimetopus [Rathbun, 1894](#)
Arcopotamonautes ([Bott, 1955](#)) stat. nov.
Lirrangopotamonautes ([Rathbun, 1904](#)) stat. nov.
Platythelphusa [A. Milne-Edwards, 1887](#)
Potamonautes [Macleay, 1838 s.s.](#)
Rotundopotamonautes ([Bott, 1955](#)) stat. nov.
 Deckeniidae [Ortmann, 1897](#)
 Hydrothelphusinae [Bott, 1955](#)

No insertions or deletions were evident for the protein-coding genes *COI* and histone 3, and these sequences were aligned manually. The two rRNA loci (12S rRNA and 16S rRNA) were aligned using ClustalX v.2.1 ([Thompson et al., 2003](#)). The DNA sequence data were combined into a single data matrix and all analyses conducted on the concatenated data set. Maximum likelihood (ML) and Bayesian approaches were used to estimate evolutionary relationships, and jModelTest ([Posada, 2008](#)) was used to obtain the best-fit substitution model for each of the four loci (results not shown). Missing DNA sequence data for any of the four genes were coded as absent. The DNA substitution models were used in the partitioned Bayesian analyses. Best-fit substitution models were chosen using the Akaike Information Criteria (AIC) ([Akaike, 1973](#)), because this reduces the number of parameters that contribute little to describing the data by penalizing more complex models ([Posada & Buckley, 2004](#); [Nylander et al., 2004](#)). Maximum likelihood analysis was conducted on the concatenated data set in RAxML v.7.2.7 ([Stamatakis, 2006](#)). The robustness of branches of the best ML tree was assessed with 1000 bootstrap replicates using the CAT algorithm for fast bootstrapping, whereas the final tree search was conducted under the GTR+ Γ model for all four partitions because less complicated models are not implemented in RAxML. Bootstrap values > 75% were regarded as well supported. Bayesian inferences were used to investigate optimal tree space using the

Table 2. Updated classification of the freshwater crab superfamily Potamoidea with a list of families, subfamilies, tribes and genera that occur in the Afrotropical biogeographical region with their taxonomic authorities. Letters correspond to clades in [Figure 1](#)

Superfamily Potamoidea [Ortmann, 1896](#)

Family Potamonautidae [Bott, 1970](#)
 A. Subfamily Liberonautinae subfam. nov.
Buea [Cumberlidge et al., 2019](#)
Louisea [Cumberlidge, 1994](#)
Liberonautes [Bott, 1955](#)
Potamonemus [Cumberlidge & Clark, 1992](#)
Sudanonautes [Bott, 1955](#)
 B. Subfamily Potamonautinae [Bott, 1970](#)
 B1. Tribe Maritimonautini trib. nov.
Maritimonautes gen. nov.
 B2. Tribe Erimetopini trib. nov.
Erimetopus [Rathbun, 1894](#)
Longipotamonautes ([Bott, 1955](#)) stat. nov.
Occidensonautes gen. nov.
Nesonautes gen. nov.
 B3. Tribe Potamonautini ([Bott, 1970](#)) trib. nov.
Arcopotamonautes ([Bott, 1955](#)) stat. nov.
Lirrangopotamonautes ([Bott, 1955](#)) stat. nov.
Platythelphusa [A. Milne-Edwards, 1887](#)
Potamonautes [MacLeay, 1838 s.s.](#)
Rotundopotamonautes ([Bott, 1955](#)) stat. nov.
 Family Deckeniidae [Ortmann, 1897](#)
 Subfamily Deckeniinae [Ortmann, 1897](#)
Deckenia [Hilgendorf, 1869](#)
Afrithelphusa [Bott, 1969](#)
Globonautes [Bott, 1959](#)
Seychellum [Ng et al., 1995](#)
 Subfamily Hydrothelphusinae [Bott, 1955](#)
Agora [Cumberlidge et al., 2020](#)
Boreathelphusa ([Cumberlidge & von Sternberg, 2002](#))
Foza [Reed & Cumberlidge, 2006b](#)
Glabrithelphusa [Meyer, Cumberlidge & Koppin, 2014](#)
Hydrothelphusa [A. Milne-Edwards, 1872](#)
Madagapotamon [Bott, 1965](#)
Malagasya [Cumberlidge & von Sternberg, 2002](#)
Marojejy [Cumberlidge et al., 2002](#)
Skelosophusa [Ng & Takeda, 1994](#)

program MRBAYES v.3.2.6 ([Ronquist et al., 2012](#)). For each analysis, four Markov chains were run, with each chain starting from a random tree and run for 20 million generations, sampling each chain every 10 000th tree. This process was repeated four times to ensure that trees converged on the same topology using MRBAYES v.3.2.6. A 50% majority rule consensus tree was generated from the trees retained (after the burn-in trees were discarded using likelihood plots) with

Table 3. List of all the species of Afrotropical freshwater crabs of the families Potamonautidae and Deckeniidae together with the countries where they have been recorded in the specialized literature from the mid-19th century to March 2021. The list comprises a total of two families, four subfamilies, three tribes, 28 genera and 185 species

Superfamily Potamoidea [Ortmann, 1896](#)

Family Potamonautidae [Bott, 1970](#)

Subfamily Liberonautinae subfam. nov.

1. Genus *Liberonautes* [Bott, 1955](#) (eight species—Liberia, Sierra Leone, Senegal, Mali, Cote d'Ivoire, Ghana)
 1. *Li. chaperi* ([A. Milne-Edwards, 1887](#))
 2. *Li. grandbassa* [Cumberlidge, 1999](#)
 3. *Li. latidactylus* ([De Man, 1903](#))
 4. *Li. lugbe* [Cumberlidge, 1999](#)
 5. *Li. nanooides* [Cumberlidge & Sachs, 1989](#)
 6. *Li. nimba* [Cumberlidge, 1999](#)
 7. *Li. paludicolis* [Cumberlidge & Sachs, 1989](#)
 8. *Li. rubigimanus* [Cumberlidge & Sachs, 1989](#)
2. Genus *Buea* [Cumberlidge et al., 2019](#) (four species—Cameroon)
 9. *B. asylos* [Cumberlidge, 1993](#)
 10. *B. bangem* [Mvogo Ndongo et al., 2020](#)
 11. *B. mundemba* [Mvogo Ndongo et al., 2020](#)
 12. *B. nlonako* [Mvogo Ndongo et al., 2020](#)
3. Genus *Louisea* [Cumberlidge, 1994](#) (four species—Cameroon)
 13. *L. balssi* ([Bott, 1959](#))
 14. *L. edaensis* ([Bott, 1969](#))
 15. *L. nkongsamba* [Mvogo Ndongo et al., 2019](#)
 16. *L. yabassi* [Mvogo Ndongo et al., 2019](#)
4. Genus *Potamonemus* [Cumberlidge & Clark, 1992](#) (three species—Cameroon, Nigeria)
 17. *P. mambilorum* [Cumberlidge & Clark, 1992](#)
 18. *P. man* [Mvogo Ndongo et al., 2021](#)
 19. *P. sachsi* [Cumberlidge, 1993](#)
5. Genus *Sudanonautes* [Bott, 1955](#) {14 species—Ghana, Cote d'Ivoire, Togo, Benin, Cameroon, Nigeria, Chad, Central African Republic, Republic of the Congo, South Sudan, Uganda, D.R. Congo, Cabinda (Angola)}
 20. *S. africanus* ([A. Milne-Edwards, 1869](#))
 21. *S. aubryi* ([H. Milne Edwards, 1853](#))
 22. *S. chavanesii* ([A. Milne-Edwards, 1886](#))
 23. *S. faradjensis* ([Rathbun, 1921](#))
 24. *S. floweri* ([De Man, 1901](#))
 25. *S. granulatus* s.s. ([Balss, 1929](#))
 26. *S. kagoroensis* [Cumberlidge, 1991](#)
 27. *S. koudougou* [Cumberlidge et al., 2021](#)
 28. *S. monodi* ([Balss, 1929](#))
 29. *S. nigeria* [Cumberlidge, 1999](#)
 30. *S. orthostylis* [Bott, 1955](#)
 31. *S. sanaga* [Cumberlidge & Boyko, 2000](#)
 32. *S. tiko* [Mvogo Ndongo et al., 2017a](#)
 33. *S. umaji* [Cumberlidge et al., 2021](#)

Subfamily Potamonautinae [Bott, 1970](#)

Tribe Maritimonautini trib. nov.

6. Genus *Maritimonautes* gen. nov. (five species—South Africa, Mozambique, Tanzania, Kenya, Somalia)
 34. *M. calcaratus* ([Gordon, 1929](#)) comb. nov.
 35. *M. choloensis* ([Chace, 1953](#)) comb. nov.
 36. *M. licoensis* ([Daniels et al., 2020](#)) comb. nov.
 37. *M. namuliensis* ([Daniels & Bayliss, 2012](#)) comb. nov.
 38. *M. obesus* ([A. Milne-Edwards, 1868](#)) comb. nov.

Tribe Erimetopini trib. nov.

7. Genus *Erimetopus* [Rathbun, 1894](#) (two species—Republic of the Congo, D.R. Congo)
 39. *E. brazzae* ([A. Milne-Edwards, 1886](#)) comb. nov.
 40. *E. vandenbrandeni* ([Balss, 1936](#)) comb. nov.

Table 3. Continued

8. Genus *Longipotamonautes* (Bott, 1955) stat. nov. (nine species—Republic of the Congo, D.R. Congo, Nigeria, Cameroon, Senegal to Nigeria)
41. *Lo. acristatus* (Bott, 1955) comb. nov.
 42. *Lo. adentatus* (Bott, 1955) comb. nov.
 43. *Lo. ballayi* (A. Milne-Edwards, 1886) comb. nov.
 44. *Lo. nheena* (Cumberlidge, 2017a) comb. nov.
 45. *Lo. paecilei* (A. Milne-Edwards, 1886) comb. nov.
 46. *Lo. punctatus* (Bott, 1955) comb. nov.
 47. *Lo. reidi* (Cumberlidge, 1999) comb. nov.
 48. *Lo. schubotzi* (Balss, 1936) comb. nov.
 49. *Lo. semilunaris* (Bott, 1955) comb. nov.
9. Genus *Occidensonautes* gen. nov. (four species—Burkina Faso, Cote d'Ivoire, Ghana, Mali, Mauritania, Niger, Nigeria, Senegal, Togo)
50. *O. ecorse* (Marchand, 1902) comb. nov.
 51. *O. lipjke* (Duris & Koch, 2010) comb. nov.
 52. *O. senegalensis* (Bott, 1970) comb. nov.
 53. *O. triangulus* (Bott, 1959) comb. nov.
10. Genus *Nesonautes* gen. nov. (two species—São Tomé)
54. *N. margaritarius* (A. Milne-Edwards, 1869) comb. nov.
 55. *N. saotome* (Cumberlidge & Daniels, 2018) comb. nov.
- Tribe Potamonautini (Bott, 1970) stat. nov.
11. Genus *Arcopotamonautes* (Bott, 1955) stat. nov. (15 species—D.R. Congo, Kenya, Malawi, Rwanda, Tanzania, Zambia)
56. *A. amosae* (Cumberlidge, Johnson, Clark & Genner, 2021) comb. nov.
 57. *A. bellarussus* (Daniels *et al.*, 2014) comb. nov.
 58. *A. caputanatis* Cumberlidge, Clark & Fastiggi, 2019) comb. nov.
 59. *A. gerdalensis* (Bott, 1955) comb. nov.
 60. *A. infravallatus* (Hilgendorf, 1898) comb. nov.
 61. *A. johnstoni* (Miers, 1885) comb. nov.
 62. *A. loveridgei* (Rathbun, 1933) comb. nov.
 63. *A. montivagus* (Chace, 1953) comb. nov.
 64. *A. orbitospinus* (Cunnington, 1907) comb. nov.
 65. *A. platycentron* (Hilgendorf, 1897) comb. nov.
 66. *A. platynotus* (Cunnington, 1907) comb. nov.
 67. *A. raybouldi* (Cumberlidge & Vannini, 2004) comb. nov.
 68. *A. suprasulcatus* (Hilgendorf, 1898) comb. nov.
 69. *A. unisulcatus* (Rathbun, 1921) comb. nov.
 70. *A. xiphoidus* (Reed & Cumberlidge, 2006) comb. nov.
12. Genus *Lirrangopotamonautes* (Bott, 1955) stat. nov. (nine species—Republic of the Congo, Central African Republic, D.R. Congo)
71. *Lr. congoensis* (Rathbun, 1921) comb. nov.
 72. *Lr. didieri* (Rathbun, 1904) comb. nov.
 73. *Lr. dybowski* (Rathbun, 1905) comb. nov.
 74. *Lr. kisangani* (Cumberlidge, Johnson, Clark & Genner, 2021) comb. nov.
 75. *Lr. lirrangensis* s.s. (Rathbun, 1904) comb. nov.
 76. *Lr. lueboensis* (Rathbun, 1904) comb. nov.
 77. *Lr. niloticus* (H. Milne Edwards, 1837) comb. nov.
 78. *Lr. stanleyensis* (Rathbun, 1921) comb. nov.
 79. *Lr. walderi* (Colosi, 1924) comb. nov.
13. Genus *Platythelphusa* A. Milne-Edwards, 1887 (11 species—Burundi, D.R. Congo, Tanzania, Zambia)
80. *Pl. armata* A. Milne-Edwards, 1887
 81. *Pl. conculcata* (Cunnington, 1907)
 82. *Pl. denticulata* Capart, 1952
 83. *Pl. echinata* Capart, 1952
 84. *Pl. idjiwiensis* (Chace, 1942) comb. nov.

Table 3. Continued

85. *Pl. immaculata* Marijnissen, Schram, Cumberlidge & Michel, 2004
 86. *Pl. langi* (Rathbun, 1921) comb. nov.
 87. *Pl. maculata* (Cunnington, 1902)
 88. *Pl. polita* Capart, 1952
 89. *Pl. praelongata* Marijnissen, Schram, Cumberlidge & Michel, 2004
 90. *Pl. tuberculata* Capart, 1952
14. Genus *Potamonautes* MacLeay, 1838 s.s. (32 species—Angola, Namibia, Botswana, Malawi, South Africa, Mozambique, D.R. Congo, Príncipe)
 91. *Po. adeleae* Bott, 1968
 92. *Po. anchietae* (Brito-Capello, 1871)
 93. *Po. barbarai* Phiri & Daniels, 2014
 94. *Po. barnardi* Phiri & Daniels, 2014
 95. *Po. bayonianus* (Brito-Capello, 1864)
 96. *Po. biballensis* Bott, 1951
 97. *Po. brincki* (Bott, 1960)
 98. *Po. clarus* Gouws, Stewart & Coke, 2000
 99. *Po. danielsi* Peer, Gouws, Lazo-Wasem, Perissinotto & Miranda, 2017
 100. *Po. dentatus* Stewart, Coke & Cook, 1995
 101. *Po. depressus* (Krauss, 1843)
 102. *Po. dubius* (Brito-Capello, 1873)
 103. *Po. flavusjo* Daniels *et al.*, 2014
 104. *Po. gorongosa* Cumberlidge *et al.*, 2016
 105. *Po. granularis* Daniels *et al.*, 1998
 106. *Po. isimangaliso* Peer, Perissinotto, Gouws, Miranda, 2015
 107. *Po. kensleyi* Cumberlidge & Tavares, 2006
 108. *Po. lividus* Gouws *et al.*, 2001
 109. *Po. macrobrachii* Bott, 1953
 110. *Po. mhlophe* Daniels, 2017
 111. *Po. mulanjeensis* Daniels & Bayliss, 2012
 112. *Po. mutareensis* Phiri & Daniels, 2013
 113. *Po. ngoyensis* Daniels *et al.*, 2019
 114. *Po. ntendekaensis* Daniels *et al.*, 2019
 115. *Po. parvicorpus* Daniels *et al.*, 2001
 116. *Po. parvispina* Stewart, 1997
 117. *Po. perlatus* (H. Milne Edwards, 1837)
 118. *Po. principe* Cumberlidge *et al.*, 2002
 119. *Po. sidneyi* (Rathbun, 1904)
 120. *Po. tuerkayi* Wood & Daniels, 2016
 121. *Po. unispinus* Stewart & Cook, 1998
 122. *Po. warreni* (Calman, 1918)
15. Genus *Rotundopotamonautes* (Bott, 1955) stat. nov. (35 species—D.R. Congo, Egypt, Ethiopia, Kenya, Malawi, Rwanda, Sudan, Tanzania, Uganda)
 123. *R. alluaudi* (Bouvier, 1921) comb. nov.
 124. *R. aloysiisabaudiae* (Nobili, 1906) comb. nov.
 125. *R. amalerensis* (Rathbun, 1935) comb. nov.
 126. *R. antheus* (Colosi, 1920) comb. nov.
 127. *R. berardi* (Audouin, 1826) comb. nov.
 128. *R. bipartitus* (Hilgendorf, 1898) comb. nov.
 129. *R. bourgaultae* (Cumberlidge & Meyer, 2009) comb. nov.
 130. *R. busingwe* (Cumberlidge & Clark, 2017) comb. nov.
 131. *R. bwindii* (Cumberlidge & Clark, 2018) comb. nov.
 132. *R. elgonensis* (Cumberlidge & Clark, 2010a) comb. nov.
 133. *R. emini* (Hilgendorf, 1892) comb. nov.
 134. *R. entebbe* (Cumberlidge & Clark, 2017) comb. nov.
 135. *R. gonocristatus* (Bott, 1955) comb. nov.

Table 3. Continued

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136. *R. holthuisi* (Cumberlidge & Meyer, 2009) comb. nov.
 137. *R. ignestii* (Parisi, 1923) comb. nov.
 138. *R. imatongensis* (Cumberlidge & Clark, 2016) comb. nov.
 139. *R. jeanneli* (Bouvier, 1921) comb. nov.
 140. *R. kantsyore* (Cumberlidge & Clark, 2017) comb. nov.
 141. *R. kivu* (Cumberlidge & Clark, 2018) comb. nov.
 142. *R. kundudo* (Cumberlidge & Clark, 2012) comb. nov.
 143. *R. loashiensis* (Bott, 1955) comb. nov.
 144. *R. loveni* (Colosi, 1924) comb. nov.
 145. *R. minor* (Bott, 1955) comb. nov.
 146. *R. morotoensis* (Cumberlidge & Clark, 2016) comb. nov.
 147. *R. mutandensis* (Chace, 1942) comb. nov.
 148. *R. neumanni* (Hilgendorf, 1898) comb. nov.
 149. *R. odhneri* (Colosi, 1924) comb. nov.
 150. *R. perparvus* (Rathbun, 1921) comb. nov.
 151. *R. pilosus* (Hilgendorf, 1898) comb. nov.
 152. *R. rodolphianus* (Rathbun, 1909) comb. nov.
 153. *R. rothschildi* (Rathbun, 1909) comb. nov.
 154. *R. rukwanzi* (Corace *et al.*, 2001) comb. nov.
 155. *R. ruenzori* (Cumberlidge & Clark, 2018) comb. nov.
 156. *R. subukia* (Cumberlidge & Dobson, 2008) comb. nov.
 157. *R. williamsi* (Cumberlidge & Clark, 2010a) comb. nov.
- Family Deckeniidae Ortman, 1897
 Subfamily Deckeniinae Ortman, 1897
16. Genus *Deckenia* Hilgendorf, 1869 (two species—Somalia, Kenya, Tanzania).
 158. *D. imitatrix* Hilgendorf, 1869
 159. *D. mitis* Hilgendorf, 1869
17. Genus *Seychellum* Ng *et al.*, 1995 (three species—granitic Seychelles).
 160. *Sy. alluaudi* (A. Milne-Edwards & Bouvier, 1893)
 161. *Sy. mahefregate* Cumberlidge & Daniels, 2014
 162. *Sy. silouette* Cumberlidge & Daniels, 2014
- Genus *Afrithelphusa* Bott, 1969 (four species—Guinea, Sierra Leone).
 163. *Af. afzelii* (Colosi, 1924)
 164. *Af. gerhildae* Bott, 1969
 165. *Af. leonensis* (Cumberlidge, 1987)
 166. *Af. monodosa* (Bott, 1959)
19. Genus *Globonantes* Bott, 1959 (one species—Guinea, Liberia)
 167. *G. macropus* (Rathbun, 1898)
- Subfamily Hydrothelphusinae Bott, 1955
20. Genus *Agora* Cumberlidge, Soma, Leever & Daniels, 2020 (one species—Madagascar)
 168. *Ag. goudoti* (H. Milne Edwards, 1853)
21. Genus *Boreathelphusa* (Cumberlidge & von Sternberg, 2002) (one species—Madagascar)
 169. *B. uglowi* (Cumberlidge & von Sternberg, 2002)
22. Genus *Foza* Reed & Cumberlidge, 2006b (three species—Madagascar)
 170. *F. raimundi* Reed & Cumberlidge, 2006b
 171. *F. ambohitra* Cumberlidge & Meyer, 2009
 172. *F. manonae* Cumberlidge *et al.*, 2015)
23. Genus *Glabrithelphusa* Meyer *et al.*, 2014 (one species—Madagascar)
 173. *G. angene* Meyer *et al.*, 2014
24. Genus *Hydrothelphusa* A. Milne-Edwards, 1872 (four species—Madagascar)
 174. *H. agilis* A. Milne-Edwards, 1872
 175. *H. madagsgarensis* A. Milne-Edwards, 1872
 176. *H. bombetokensis* (Rathbun, 1904)
 177. *H. vencesi* Cumberlidge *et al.*, 2007
-

Table 3. Continued

25. Genus *Madagapotamon* Bott, 1965 (one species—Madagascar)
 178. *Ma. humberti* Bott, 1965
26. Genus *Malagasya* Cumberlidge & von Sternberg, 2002 (three species—Madagascar)
 179. *Ml. antongilensis* (Rathbun, 1904)
 180. *Ml. goodmani* (Cumberlidge, Boyko & Harvey, 2002)
 181. *Ml. elvisi* Cumberlidge, Soma, Leever & Daniels, 2020
27. Genus *Marojejy* Cumberlidge, Boyko & Harvey, 2002 (one species—Madagascar)
 182. *Mr. longimerus* Cumberlidge, Boyko & Harvey, 2002
28. Genus *Skelosophusa* Ng & Takeda, 1994 (three species—Madagascar)
 183. *Sk. gollardi* (Bott, 1965)
 184. *Sk. eumeces* Ng & Takeda, 1994
 185. *Sk. prolixa* Ng & Takeda, 1994

posterior probabilities (pP) for each node estimated by the percentage of time the node was recovered. Posterior probabilities values < 0.95 were regarded as poorly resolved (Daniels *et al.*, 2019). When stationarity was reached, the average standard deviation of split frequencies = 0.003926 and the maximum standard deviation of split frequencies = 0.032051.

DIVERGENCE TIME ESTIMATION

The divergence times for the African potamonautid crabs were estimated with a Yule tree prior and an uncorrelated lognormal relaxed molecular clock after initial test runs (investigating if the standard deviation of the uncorrelated lognormal clock approaches zero). Potamonautid substitution rates (and their standard deviations) were used as priors that originated from a fossil calibrated phylogeny of the family Potamonautidae (Daniels *et al.*, 2015): 0.81% per Myr for the rRNA loci (SD = 0.0013; linked clock models) and 2.85% per Myr (SD = 0.005) for the *COI* locus. The maximum clade credibility tree was determined and annotated in TREEANNOTATOR v.2.4.1 (part of the BEAST package) after removal of 10% of the trees as burn-in.

MORPHOLOGICAL COMPARISONS

Taxonomically important characters of gonopods 1 and 2 (G1 and G2) of representatives of newly-recognized taxa were examined in detail and photographed with a digital camera and a Keyence VHX 5000 digital microscope. Post-processing was undertaken using Adobe Photoshop CC5. Measurements of the subterminal articles (SA) of G1 and G2 were made along a straight line beginning at the midpoint of the basal margin and ending at the midpoint of the distal margin (at the junction between the two parts).

Measurements of the terminal articles (TAs) of G1 and G2 were made on the ventral face along the midline beginning at the midpoint of the basal margin that forms the SA-TA junction and ending at the TA tip. The length of the TA of G1 and G2 relative to the length of the SA of each of these structures is presented as the ratio of the terminal article/subterminal article (TA/SA). The terminology used follows Cumberlidge (1999) and Davie *et al.* (2015). The following abbreviations are used: CW, carapace width measured at widest point; CL, carapace length measured along median line from anterior to posterior margin; CH, carapace height measured at maximum height of cephalothorax; FW, front width measured along anterior frontal margin between inner angles of orbits; G1, first gonopod; G2, second gonopod; TA, terminal article of G1 or G2; TS, terminal article of mandibular palp; S, thoracic sternal article; S1/2, sulcus between S1 and S2; SA, subterminal article of G1 or G2.

NOMENCLATURE

Ideally, nomenclatural protocols require that species should be given binominal names comprising a generic name and specific epithet. This protocol has not always been followed in freshwater crab taxonomy (e.g. Bott, 1955, 1970; Pretzmann, 1971), especially in the years before objective phylogenies showing evolutionary relationships became available. For example, the literature for African freshwater crabs includes numerous trinomial and quadrinomial names (genera, subgenera, species and subspecies). It is the view of this study that the earlier taxonomies that introduced such names reflected uncertainties in recognizing species and genus boundaries when dealing with variable characters and convergence, made in the absence of any knowledge of the evolutionary relationships of the group (Ng *et al.*, 2008; Cumberlidge *et al.*, 2009).

The current revision of the Afrotropical freshwater crabs is based on their evolutionary relationships (Fig. 1) coupled with new morphological evidence. The classification proposed here (Tables 2, 3) follows a strict binomial nomenclature, and consideration is given to the validation of existing subgeneric and subspecific names, by either recognizing them as valid but requiring a new rank, or by rejecting them following due consideration.

RESULTS

The combined DNA sequence data set comprised 1720 base pairs. A monophyletic continental Afrotropical clade was recovered, with the revised family Potamonautidae sister to the revised family Deckeniidae Ortmann, 1897 (Daniels *et al.*, 2015; Tables 1–3). The revised taxonomic designations within the Deckeniidae include a monophyletic Hydrothelphusinae Bott, 1955, for the Malagasy species (now with nine genera and 21 species) sister to the monophyletic Deckeniinae (with four genera and nine species). A comprehensive taxonomic revision of the Malagasy freshwater crab fauna is currently being undertaken by the authors (Cumberlidge *et al.*, 2020).

The continental African Potamonautidae is revised here with two subfamilies: the new Liberonautinae (Fig. 1A) and Potamonautinae (Fig. 1B) that diverged 30.14 Mya [95% HPD 23.77–36.86 Mya] during the Eocene-Oligocene. Liberonautinae (Fig. 1A) includes five genera (*Buea*, *Liberonautes*, *Louisea*, *Potamonemus* and *Sudanonautes*) that diverged 27.65 Mya [95% Highest Posterior Density (HPD) interval 23.73–37.02 Mya] during the Eocene-Oligocene. *Louisea* diverged from *Sudanonautes*, *Potamonemus* and *Buea* 25.14 Mya [95% HPD interval 18.79–32.38 Mya] during the Oligocene-Miocene, while *Sudanonautes* diverged from *Potamonemus* and *Buea* 19.12 Mya [95% HPD interval 13.78–25.08 Mya] during the Miocene and *Potamonemus* diverged from *Buea* 17.09 Mya [95% HPD interval 11.90–22.85 Mya] during the Miocene.

The revised Potamonautinae (Fig. 1B) recognized here comprises a well-supported clade (Fig. 1B) that is a highly diversified assemblage of ten genera and 124 species that exhibits extensive phylogenetic structuring within it at the genus level and above. Potamonautinae (Fig. 1B) has three major divisions: the new tribe Maritimonautini (Fig. 1B1, endemic to coastal eastern and southern Africa, Fig. 8B), the new tribe Congowestini (Fig. 1B2, endemic to Central Africa, Fig. 8C) and Potamonautini (Bott, 1970) stat. nov. (Fig. 1B3, found throughout northern, eastern, central and southern Africa, Fig. 8D). Maritimonautini (Fig. 1B1) diverged from the common

ancestor of Potamonautinae 23.41 Mya (95% HPD interval 18.42–28.88 Mya), Erimetopini (Fig. 1B2) diverged 22.03 Mya (95% HPD interval 17.54–27.21 Mya) and Potamonautini (Fig. 1B3) diverged 21.10 Mya (95% HPD interval 16.83–26.05 Mya).

Of particular note in the revised Potamonautinae (Fig. 1B) is the extensive taxonomic reorganization necessary, where the 124 species formerly assigned to three genera (*Erimetopus*, *Platythelphusa* and *Potamonautes s.l.*) are here included in one of the ten genera and three tribes recognized here. For example, Maritimonautini (Fig. 1B1) includes species found between the Rift Valley and the coast of eastern and southern Africa (Fig. 8B) that are transferred from *Potamonautes s.l.* to the new genus *Maritimonautes*. Erimetopini (Fig. 1B2) includes eight species from Central and West Africa (Fig. 8C) that were formerly assigned to *Potamonautes s.l.* that are transferred to three new genera [*Longipotamonautes* (Bott, 1955), *Nesonautes* and *Occidensonautes* and two species of *Erimetopus* for which generic assignment remains unchanged. Finally, Potamonautini (Fig. 1B3) includes 101 species formerly assigned to *Potamonautes s.l.* that are assigned to one of five genera recognized here (Table 2).

SYSTEMATIC ACCOUNT

This phylogenetic analysis included 83/117 species and 8/8 genera of described Potamonautinae and 21/27 species and 8/9 genera of described Deckeniinae (Table 3). The phylogeny presented here (Fig. 1) shows significant new relationships in Afrotropical freshwater crabs that are recognized in our revised classification. This classification is based on our molecular phylogeny plus our morphological studies of the entire Afrotropical freshwater crab fauna (which includes the 34 species of Potamonautinae not included in our molecular phylogeny). Diagnoses of the families Potamoidea, Potamonautidae and Deckeniidae and subfamilies Potamonautinae, Liberonautinae, Deckeniinae and Hydrothelphusinae are presented, together with diagnoses of the new or revised genera. The morphological traits of the gonopods of a representative of each major taxon are illustrated in Figures 2–6. The updated distribution of each taxon is shown in Figures 7–11. A complete list of taxonomic authorities is provided in Table 3.

SUPERFAMILY POTAMOIDEA ORTMANN, 1896

Diagnosis: One diagnostic apomorphy for Potamoidea is a G1 with a broad dorsal membrane between the TA and the SA on the dorsal side only, a character which distinguishes this superfamily from Gecarcinucoidea



Figure 2. Liberonautinae. Gonopods 1 and 2 of *Liberonautes latidactylus*, NMU9.V.2005B (CW 72, CL 47.2, CH 20.5, FW 19.3 mm) Guinea, West Africa. A, left G1 ventral view; (B) left G1 dorsal view; (C) left G2 ventral view. Scale bar: A, B = 2.8 mm, C = 1.8 mm.

that have a G1 which is either lacking a dorsal membrane between the TA and the SA on the dorsal side, or is only rudimentary.

Families included: Deckeniidae [Ortmann, 1897](#), Potamidae [Ortmann, 1896](#) and Potamonautidae [Bott, 1970](#).

Remarks: Potamoidea of [Ng et al. \(2008\)](#) and [De Grave et al. \(2009\)](#) included only two families: Potamidae and Potamonautidae. Potamidae of those authors included two genera and three species from the Afrotropical region, nine genera and 86 species from the Palaearctic region and 72 genera and 432 species from the Oriental region. Potamonautidae of [Ng et al. \(2008\)](#) and [De Grave et al. \(2009\)](#) included 12 genera with 115 species all from Africa and Madagascar.

The phylogenetic studies of [Daniels et al. \(2006, 2015; Fig. 1\)](#) indicated that Potamonautidae and Deckeniidae diverged c. 30.14 Mya during the Eocene-Oligocene. Accordingly, both groups ([Cumberlidge et al., 2008](#)) are here afforded family status ([Table 1](#)) and the present work revises Potamoidea to include these families. While Potamidae remain unchanged from [Ng et al. \(2008\)](#) and [De Grave et al. \(2009\)](#), Deckeniidae is established in addition to a revised Potamonautidae ([Tables 1–3](#)) ([Cumberlidge et al., 2008](#)).

Deckeniidae and Potamonautidae are proposed here for the entire Afrotropical freshwater crab fauna with each family being further divided into two subfamilies. Thirteen genera and 28 species from the Afrotropical region are assigned to Deckeniidae and 15 genera with 154 species are assigned to Potamonautidae ([Fig. 7A; Table 3](#)).

The taxonomy of Deckeniidae has been unstable for a number of years. [Bott \(1955\)](#) and [Martin and Davis \(2001\)](#) recognized the family Deckeniidae for one East African genus (*Deckenia*) with two species (*Deckenia imitatrix* [Hilgendorf, 1869](#) and *Deckenia mitis* [Hilgendorf, 1869](#)), which was included in the African Potamonautidae (Potamoidea). [Klaus et al. \(2006\)](#) expanded Deckeniidae to include six genera assigned to three Afrotropical subfamilies: Deckeniinae (*Deckenia*, *Seychellum* [Ng et al., 1995](#)), Globonautinae (*Afrithelphusa* [Bott, 1969](#), *Globonautes* [Bott, 1959](#)) and Hydrothelphusinae (*Hydrothelphusa* [A. Milne-Edwards, 1872](#), *Madagapotamon* [Bott, 1965](#)), which they assigned to the Asian superfamily Gecarcinucoidea. [Cumberlidge et al. \(2008\)](#) did not recognize Deckeniidae and included *Afrithelphusa*, *Deckenia*, *Globonautes*, *Seychellum* and all Malagasy genera in the subfamily Deckeniinae, while [Ng et al. \(2008\)](#) included all of these same genera (plus *Louisea*) in Hydrothelphusinae of Potamonautidae. In the present work we recognize the family Deckeniidae with two subfamilies: Deckeniinae (for *Afrithelphusa*, *Deckenia*, *Globonautes*, *Seychellum*) and Hydrothelphusinae for all Malagasy genera ([Table 3](#)).

FAMILY POTAMONAUTIDAE [BOTT, 1970](#)

([FIGS 1–10; TABLES 1–3](#))

Rediagnosis: Potamonautidae taxa are recognized by a mandibular palp with two articles comprising either a small ledge at their junction, or a simple terminal article completely lacking a lobe.

Subfamilies included: Liberonautinae subfam. nov. and Potamonautinae.

Genera included: *Arcopotamonautes* ([Bott, 1955](#)) stat. nov., *Buea* [Cumberlidge, Mvogo Ndongo, Clark & Daniels, 2019](#), *Erimetopus* [Rathbun, 1894](#), *Liberonautes* [Bott, 1955](#), *Lirrangopotamonautes* ([Bott, 1955](#)) stat. nov., *Longipotamonautes* ([Bott, 1955](#)) stat. nov., *Louisea* [Cumberlidge, 1994](#), *Maritimonautes* gen. nov., *Nesonautes* gen. nov., *Occidensonautes* gen. nov., *Platythelphusa* [A. Milne-Edwards, 1887](#), *Potamonautes* [MacLeay, 1838 s.s.](#), *Potamonemus* [Cumberlidge & Clark, 1992](#), *Rotundopotamonautes* ([Bott, 1955](#)) stat. nov. and *Sudanonautes* [Bott, 1955](#).

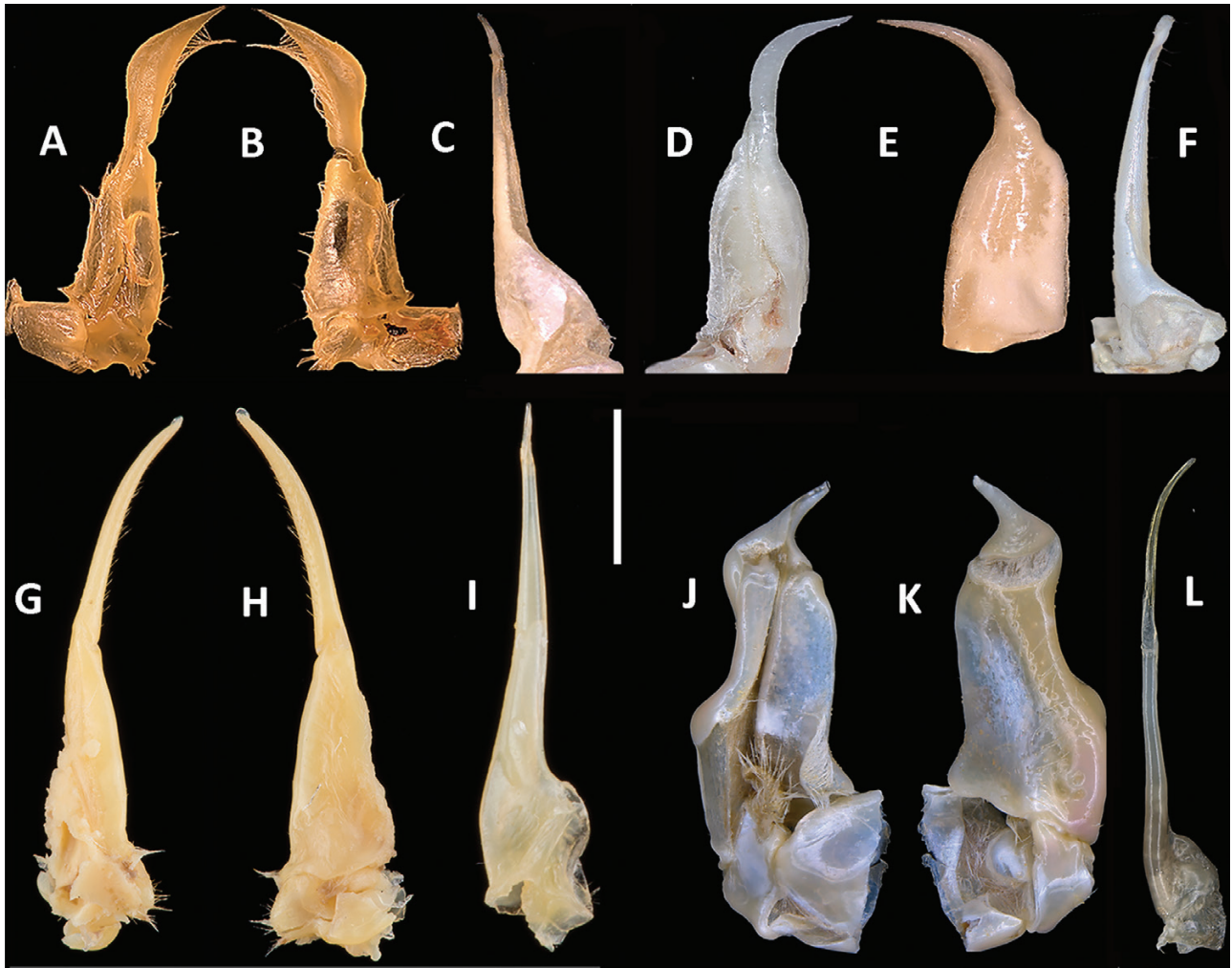


Figure 3. Gonopods 1 and 2 of four genera in Liberonautinae. A–C, *Buea asylos* (Cumberlidge *et al.*, 2019: fig. 7a, d; 8a); D–F, *Potamonemus mambilorum* (Cumberlidge *et al.*, 2019: fig. 7b, e; 8b); G–I, *Sudanonautes floweri*; J–L, *Louisea balssi* (Mvogo Ndongo *et al.*, 2018: fig. 5a–c, © Magnolia Press, reproduced with permission from the copyright holder). A, D, G, J, left G1 ventral view; B, E, H, K, left G1 dorsal view; C, F, I, L, left G2 ventral view. Scale bar: A, B, D, E, G, H, J, K = 2.0 mm, C, F, I, L = 1.8 mm.

Distribution: Taxa of this family are found throughout sub-Saharan Africa (Cumberlidge, 1999; Fig. 6B).

Remarks: The revised Potamonautidae includes the majority of species found on the African continent except for seven species in three genera of Deckeniidae and a species of *Potamon* (Potamidae) found in North Africa. Potamonautidae is divided here (Tables 2–3; Figs 7A–C) into Liberonautinae and Potamonautinae. The differences between these two subfamilies reflect phylogenetic divergence within the clade for Potamonautidae c. 30.14 Mya during the Eocene-Oligocene that gave rise to two lineages, each of which includes groups of morphologically distinct genera (Daniels *et al.*, 2006, 2015; Fig. 1).

LIBERONAUTINAE SUBFAM. NOV.

(FIGS 1A, 2, 3, 7B; TABLES 1–3)

Zoobank registration: urn:lsid:zoobank.org:act:89F59361-7EE0-4D1D-9795-8CC0D9EEB5C7

Diagnosis: Taxa of Liberonautinae are recognized by the presence of an intermediate tooth on the anterolateral margin in between the exorbital and epibranchial teeth.

Type genus: *Liberonautes* Bott, 1955, gender masculine.

Etymology: Liberonautinae is derived from the genus name *Liberonautes*.

KEY TO THE GENERA OF POTAMONAUTIDAE

1	No intermediate tooth on anterolateral margin between exorbital and epibranchial teeth	6
1'	Intermediate tooth on anterolateral margin between exorbital and epibranchial teeth	2
2	G1 TA directed inwards	<i>Liberonautes</i>
2'	G1 TA either straight or directed outwards	3
3	Third maxilliped exopod with long flagellum	<i>Sudanonautes</i>
3'	Third maxilliped exopod lacking flagellum	4
4	G2 TA long and flagellum-like	<i>Louisea</i>
4'	G2 TA short stub, lacking flagellum	5
5	G1 TA elongate (TA/SA 0.86)	<i>Buea</i>
5'	G1TA medium length (TA/SA 0.63)	<i>Potamonemus</i>
6	G1 TA short or medium length (0.25–0.30 × as long as G1 SA)	7
6'	G1 TA long (0.40–0.45 × as long as G1 SA)	<i>Nesonautes</i>
7	G1 TA slim, tapering to pointed tip	8
7'	G1 TA hose-like, ending in broad tip	<i>Longipotamonates</i>
8	Endemic to West Africa	<i>Occidensonautes</i>
8'	Not found in West Africa	9
9	Outer margins of S4 raised and thickened	<i>Maritimonautes</i>
9'	Outer margins of S4 low, not raised	10
10	Cheliped carpus outer margin with two or three small teeth	<i>Erimetopus</i>
10'	Cheliped carpus outer margin smooth, lacking teeth	11
11	Third maxilliped ischium with vertical sulcus	12
11'	Third maxilliped ischium smooth, lacking vertical sulcus	13
12	G1 TA with only slightly raised dorsal fold	<i>Potamonates s.s.</i>
12'	G1 TA with distinctly raised dorsal fold	<i>Arcopotamonates</i>
13	Thoracic sternal sulcus S3/4 completely traversing sternum	14
13'	Thoracic sternal sulcus S3/4 completely traversing sternum	<i>Rotundopotamonates</i>
14	G1 SA slim (SA base 0.25 × SA length)	<i>Lirrangopotamonates</i>
14'	G1 SA broad (SA base 0.5 × SA length)	<i>Platythelphusa</i>

Genera included: *Buea* [Cumberlidge, Mvogo Ndongo, Clark & Daniels, 2019](#), *Liberonautes* [Bott, 1955](#), *Louisea* [Cumberlidge, 1994](#), *Potamonemus* [Cumberlidge & Clark, 1992](#) and *Sudanonautes* [Bott, 1955](#).

Distribution: Liberonautinae is recorded from West and Central Africa ([Cumberlidge, 1999](#); [Fig. 7B](#)). The eight *Liberonautes* species are found in West Africa west of Ghana, in Senegal, Mali, Guinea, Guinea Bissau, Burkina Faso, Sierra Leone, Liberia and Cote d'Ivoire ([Cumberlidge, 1999](#); [Daniels et al., 2016](#)). The 14 *Sudanonautes* species ([Cumberlidge, 1999](#); [Cumberlidge & Boyko, 2000](#); [Mvogo Ndongo et al., 2017a](#); [Cumberlidge et al., 2021](#)) are found in West Africa, from Cote d'Ivoire to Nigeria, in Central Africa (Cameroon, D.R. Congo, Gabon, Equatorial Guinea, Central African Republic, Republic of the Congo and Cabinda) and in East Africa (South Sudan and northern Uganda). The distributional ranges of *Liberonautes* and *Sudanonautes* overlap in Ghana and Cote d'Ivoire, whereas the four *Buea* species ([Cumberlidge et al., 2019](#); [Mvogo Ndongo et al., 2020](#))

and *Louisea* ([Cumberlidge, 1994](#); [Mvogo Ndongo et al., 2017c, 2019](#)) are all endemic to Cameroon and the three *Potamonemus* species ([Cumberlidge & Clark, 1992](#); [Cumberlidge, 1993](#); [Mvogo Ndongo et al., 2021](#)) are endemic to Nigeria and Cameroon.

Remarks: Liberonautinae diverged from Potamonautinae c. 30.14 Mya during the Eocene-Oligocene ([Fig. 1](#)). Within Liberonautinae, *Liberonautes* forms a well-supported clade ([Fig. 1A](#)) which split from the clade that includes *Sudanonautes*, *Potamonemus*, *Buea* and *Louisea* ([Fig. 1A](#)) c. 27.65 Mya during the Eocene-Oligocene. *Liberonautes* is endemic to West Africa west of Ghana and is morphologically and geographically distinct from the other Liberonautinae genera ([Cumberlidge, 1999](#)). *Liberonautes* can be distinguished from the other four genera by a G1 TA that is directed inwards ([Fig. 2A, B](#)), vs. a G1 TA that is directed outward in the other four genera ([Fig. 3A–L](#)). In addition, the G1 TA of *Buea*, *Potamonemus* and *Sudanonautes* is long (0.4 to 0.5 × the G1 SA length), curved and tapers to a pointed tip ([Fig. 3A–B](#),

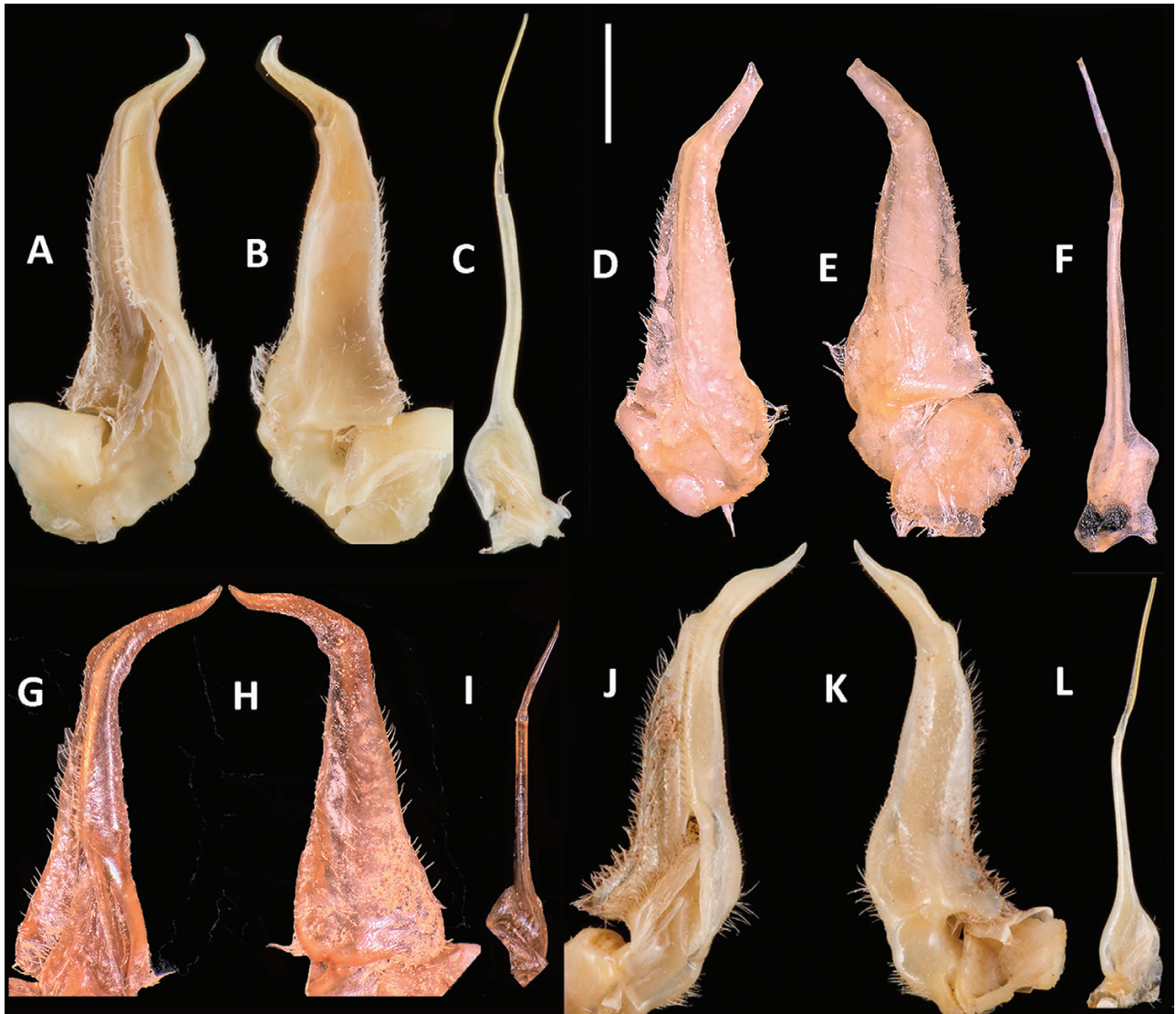


Figure 4. Gonopods 1 and 2 of the four genera in Erimetopini. A–C, *Erimetopus vandenbrandeni*; D–F, *Longipotamonautes ballayi*; G–I, *Nesonautes margaritarius*; J–L, *Occidensonautes ecorsssei*. Scale bar: A–L = 2.0 mm.

D–E, G–H), vs. a G1 TA in *Louisea* that is of medium length ($0.3 \times$ the G1 SA length, Fig. 3J–K), weakly S-shaped and tube-like with a rounded tip. Moreover, the G2 TA of *Buea*, *Potamonemus* and *Sudanonautes* is noticeably shortened and reduced to a short stub ($0.1 \times$ the G2 SA length, Fig. 3C, F, I), vs. a G2 TA in *Louisea*, which is elongated and flagellum-like, TA/SA 0.64 (Fig. 3K). Finally, the third maxilliped exopod of *Buea*, *Louisea* and *Potamonemus* lacks a flagellum, vs. a third maxilliped exopod with a long flagellum in *Sudanonautes* (Cumberlidge, 1993, 1994, 1999; Mvogo Ndongo *et al.*, 2017b, c).

The molecular phylogeny presented here (Fig. 1) agrees with the phylogeny of Wood *et al.* (2019), which recovered a well-supported clade shared by

Buea, *Liberonautes*, *Louisea*, *Potamonemus* and *Sudanonautes* (Fig. 1A). *Liberonautes* (Fig. 1A) diverged from the other four genera (Fig. 1A) *c.* 27.65 Mya during the Eocene-Oligocene. *Louisea* split from the *Buea*, *Potamonemus* and *Sudanonautes* clade *c.* 25.14 Mya during the Oligocene-Miocene (Fig. 1A), while *Sudanonautes* diverged from *Buea* and *Potamonemus* *c.* 19.12 Mya (during the Miocene), and *Potamonemus* diverged from *Buea* *c.* 17.09 Mya (also during the Miocene). Two of the endemic Cameroonian genera, *Buea* and *Potamonemus*, have a sister-group relationship represented by a lineage that split from *Sudanonautes* *c.* 17 Mya. *Louisea*, also endemic to Cameroon, represents the earliest lineage in this clade that evolved in long isolation from the other genera in



Figure 5. Gonopods 1 and 2 of one genus in Maritimonautini and three genera in Potamonautini. A–C, *Maritimonautes obesus*; D–F, *Arcopotamonautes suprasulcatus*; G–I, *Lirrangopotamonautes dybowskii*; J–L, *Platythelphusa armata*. Scale bar: A, B, G–L = 2.0 mm, C, F = 1.8 mm; D, E = 5.0 mm; L = 6.7 mm.

this tribe for 25 Myr, and as a result it is distinguished by a cluster of distinct synapomorphies not observed in any other African taxa (Cumberlidge, 1999).

SUBFAMILY POTAMONAUTINAE **BOTT, 1970**
(FIGS 1B, 4, 6, 8A; TABLES 1–3)

Diagnosis: Potamonautinae are recognized by the lack of an intermediate tooth between the exorbital and epibranchial teeth on the anterolateral margin of the carapace, by the elongated G2 TA, $0.9 \times$ the G2 SA

length (Fig. 4C, F, I) and by the exopod of the third maxilliped that has a flagellum that is subequal in length to the exopod (Figs 4A–I, 5A–E).

Type genus: *Potamonautes* **MacLeay, 1838**, by monotypy, gender masculine.

Etymology: Potamonautinae is derived from the family level name Potamonautidae **Bott, 1970** and this subfamily is assigned here to the Potamonautidae.



Figure 6. Gonopods 1 and 2 of two genera in Potamonautini. A–C, *Potamonautes anchetiae* (CAW 450A), Angola. A, D, left G1 ventral view. D–F, *Rotundopotamonautes loveni*, Kenya, B, E, left G1 dorsal view; C, F, left G2 ventral view. Scale bar: A, B, D, E = 2.0 mm, C, F = 1.8 mm.

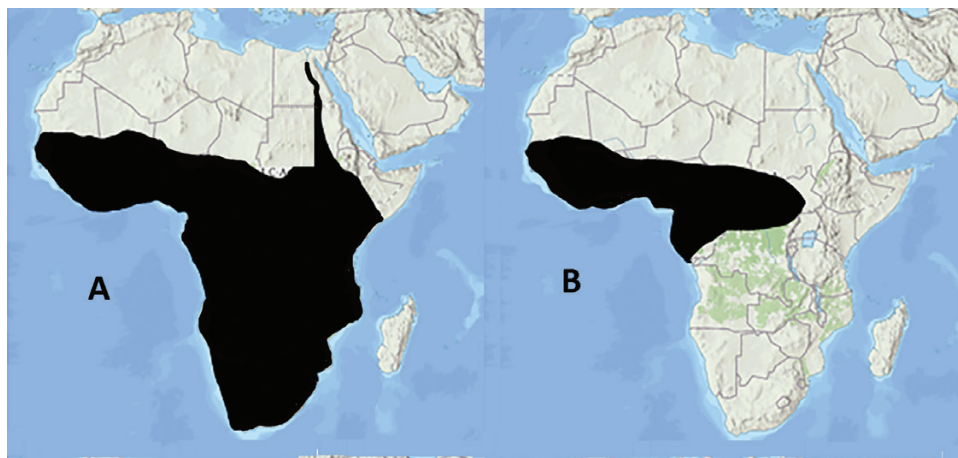


Figure 7. Maps showing the distributional range of (A) Potamonautidae, (B) Liberonautinae.

Tribes included: Erimetopini tribe nov., Maritimonautini tribe nov. and Potamonautini (Bott, 1970) stat. nov.

Genera included: *Arcopotamonautes* (Bott, 1955) stat. nov., *Erimetopus* Rathbun, 1894, *Lirangopotamonautes* (Bott, 1955) stat. nov., *Longipotamonautes* (Bott, 1955) stat. nov., *Maritimonautes* gen. nov., *Nesonautes* gen. nov., *Occidensonautes* gen. nov., *Platythelphusa* A. Milne-Edwards, 1887, *Potamonautes* MacLeay, 1838 s.s. and *Rotundopotamonautes* (Bott, 1955) stat. nov.

Distribution: Potamonautinae is found throughout sub-Saharan Africa in the following regions and

countries: West Africa (from Senegal to Nigeria), São Tomé Island, Central Africa (Cameroon, Central African Republic, Gabon, Equatorial Guinea, Republic of the Congo and the D.R. Congo), eastern and northern Africa (Tanzania, Kenya, South Sudan, Sudan, Egypt, Somalia) and southern Africa (Angola, Malawi, Mozambique, Zambia, Zimbabwe, Botswana, Namibia, South Africa, Eswatini, Lesotho) (Fig. 8A).

Remarks: Potamonautinae is a monophyletic assemblage (Fig. 1B) with three main lineages, the Maritimonautini for *Maritimonautes* (Fig. 1B1), the Congowestini (Fig. 1B2) for *Erimetopus*, *Longipotamonautes*, *Nesonautes* and

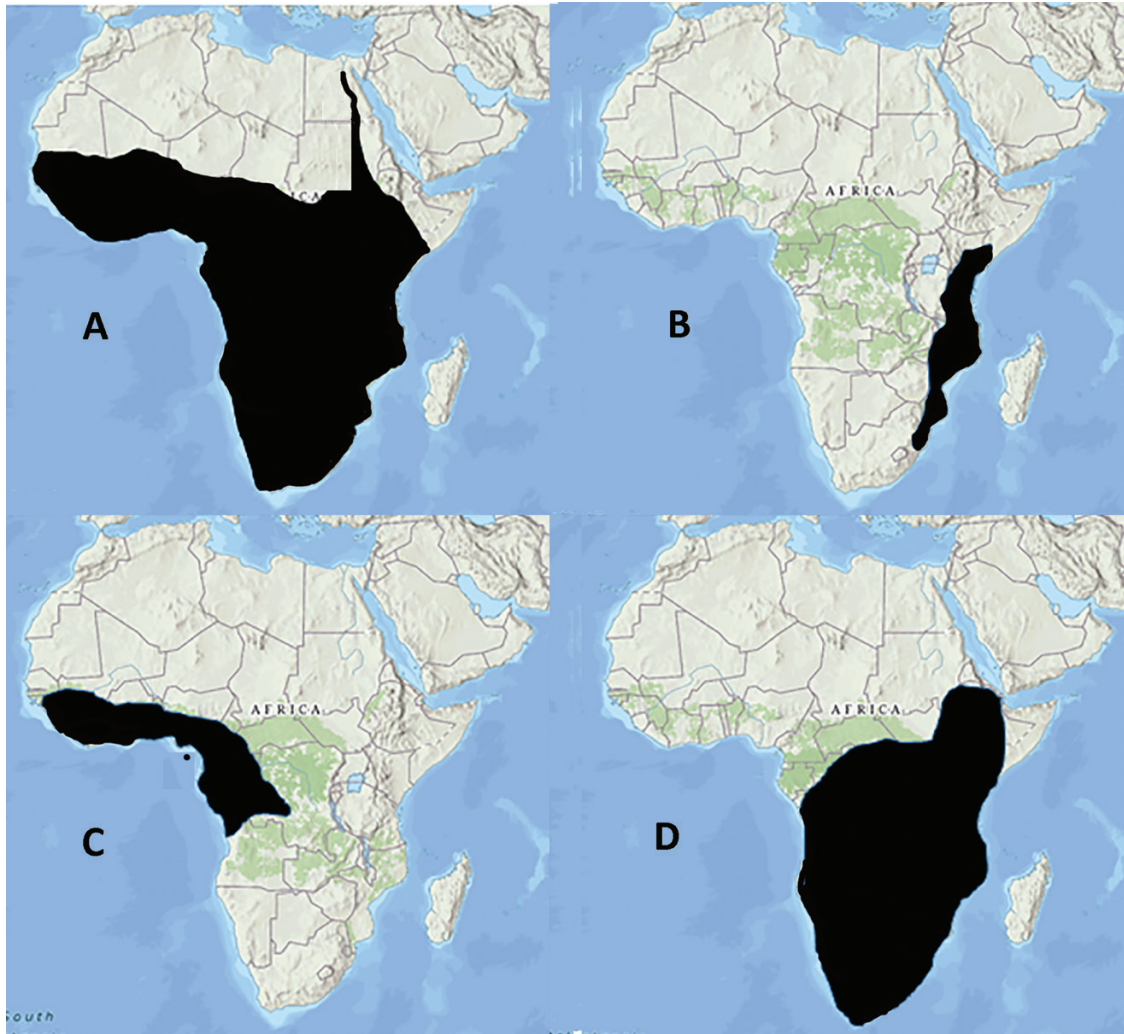


Figure 8. Maps showing the distributional ranges of (A) Potamonautinae, (B) Maritimonautini, (C) Erimetopini and (D) Potamonautini.

Occidensonautes and the Potamonautini (Fig. 1B3) for *Arcopotamonautes*, *Lirrangopotamonautes*, *Platythelphusa*, *Potamonautes* s.s. and *Rotundopotamonautes*. The relationships in the updated phylogeny (Fig. 1B) agree with those of Daniels & Klaus (2018) and Wood *et al.* (2019) each of which recovered a well-supported clade (Fig. 1B, the Potamonautinae) with the three lineages that are recognized here as three tribes (Fig. 1B1, B2, B3). Divergence within the Potamonautinae took place 23.41 Mya during the Oligocene-Miocene when the earliest clade (the Maritimonautini; Fig. 1B1) branched off. This was followed by the Erimetopini (Fig. 1B2), which diverged 22.03 Mya, and by the Potamonautini (Fig. 1B3), which diverged 21.10 Mya.

MARITIMONAUTINI TRIBE NOV.

(FIGS 1B1, 5A–C, 8B; TABLES 1–3)

Zoobank registration: urn:lsid:zoobank.org:act:C6FA3FDB-7C33-4AE0-9AB8-5C4BBDD4C19E.

Diagnosis: S3/4 deep, V-shaped, completely traversing sternum (or deep at margins, faint in the middle); outer margins of S4 raised and thickened; third maxilliped ischium lacking vertical suture (or if present, faint); anterolateral margin of carapace posterior to epibranchial tooth either smooth or granulated, but lacking teeth; G1 TA short (TA length $0.25 \times$ SA length), slim, either not widened in midsection (or dorsal fold slightly higher than ventral fold), tapering evenly to pointed tip (Fig. 5A, B).

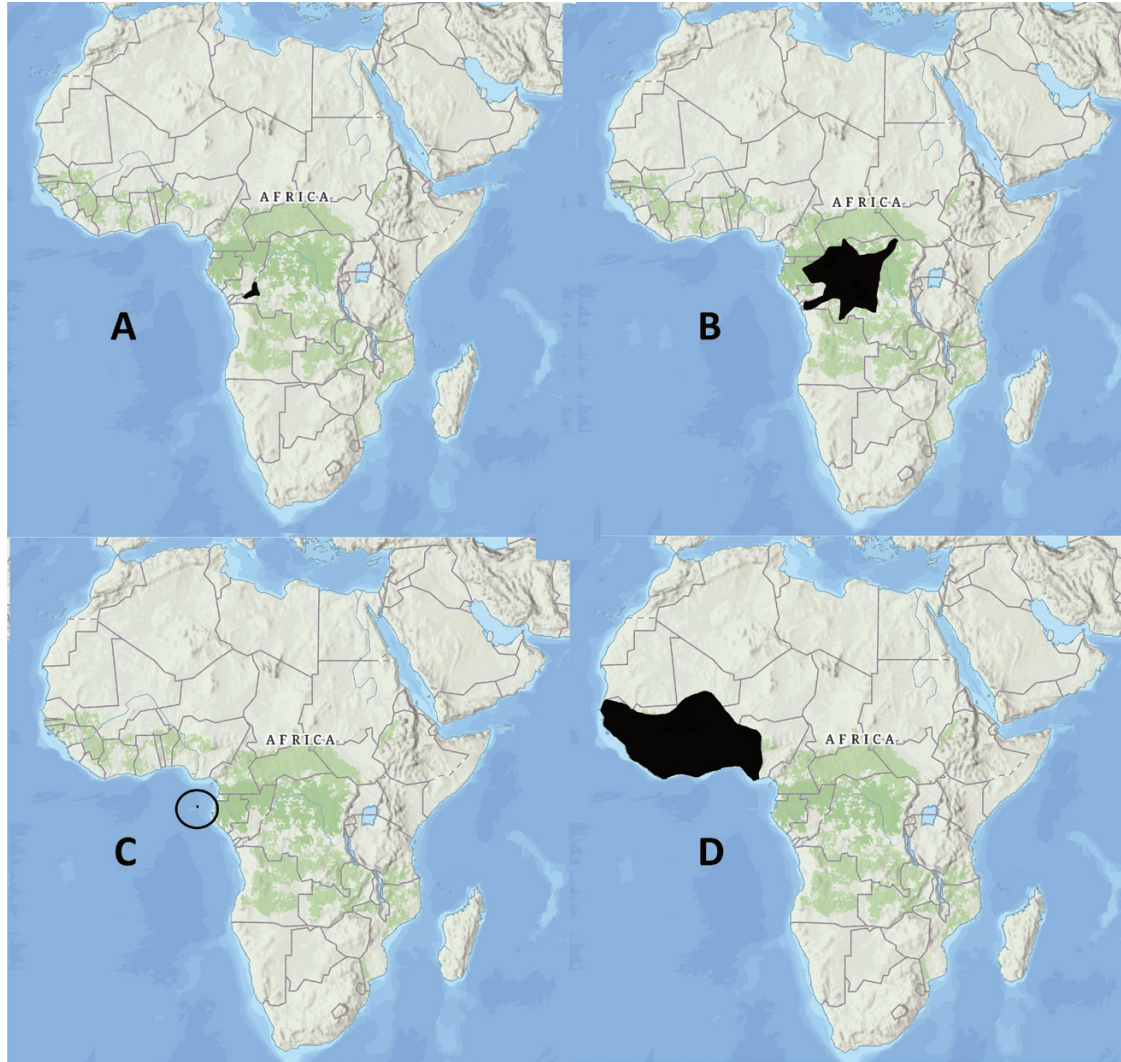


Figure 9. Maps showing the distributional ranges of the four genera of Erimetopini (A) *Erimetopus*, (B) *Longipotamonautes*, (C) *Nesonautes* and (D) *Occidensonautes*.

Etymology: Maritimonautini is derived from the genus-level name *Maritimonautes*.

Type genus: *Maritimonautes* gen. nov., gender masculine.

Genus included: *Maritimonautes*.

Distribution: *Maritimonautes* is found mainly in the low-lying eastern coastal region of Africa (an area of about 200–300 km wide inland from the coast as far as the Rift Valley) including Somalia, Kenya, Tanzania (from the east coast of Africa to the north coast of Lake Malawi, including Tanzania plus Zanzibar and Pemba Islands), Mozambique and South Africa (Fig. 8C).

Remarks: The molecular phylogeny presented here (Fig. 1) agrees with the phylogenies of Daniels & Klaus (2018) and Wood *et al.* (2019), each of which recovered the species assigned here to Mauritonautini as a well-supported clade that forms a distinct lineage (Fig. 1B1) at the base of the large and diverse clade of Potamonautinae (Fig. 1B). Mauritonautini (Fig. 1B1) split from the other lineages (Fig. 1B2, B3) in this subfamily over 27 Mya during the Oligocene-Miocene.

MARITIMONAUTES GEN. NOV.

(FIGS 1B1, 5A–C, 8B; TABLES 1–3)

Zoobank registration: urn:lsid:zoobank.org:act:29BB5EDB-5AB4-48E5-8B42-AA97939DDA7F

Thelphusa A. Milne-Edwards, 1868: 86, pl. 20, figs 1–4; 1869: 178; 1887: 146; Pfeffer, 1889: 33.

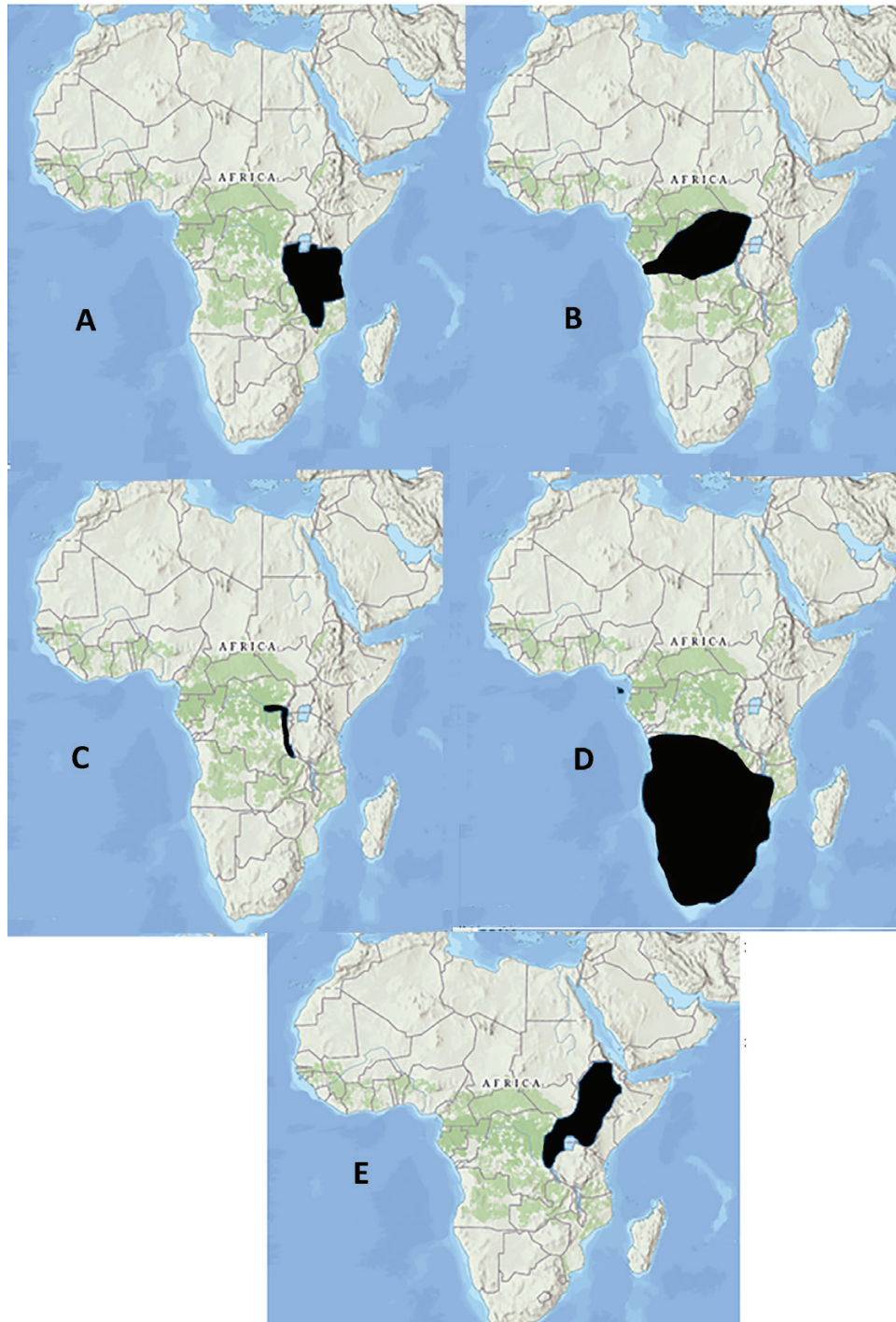


Figure 10. Maps showing the distributional ranges of the five genera of Potamonautini. (A) *Arcopotamonautes*, (B) *Lirrangopotamonautes*, (C) *Platythelphusa*, (D) *Potamonautes* s.s. and (E) *Rotundopotamonautes*.

Telphusa Hilgendorf, 1879: 801; 1891: 20; 1898: 16.

Potamon (*Potamonautes*) Ortmann, 1897: 303, 305.

Potamon De Man, 1898: 434, 437; Chace, 1942: 190.

Potamon (*Potamonautes*) De Man, 1898: 262–270, 436, fig. 3; Rathbun, 1904: pl. 15, figs 8, 9; 1905: 180, fig. 45; 1933: 258; 1935: 26; Sandler, 1912: 199; Bouvier, 1921: 49; Colosi, 1925: 2; Parisi, 1925: 98; Barnard, 1950: 192, fig. 34 f, g.

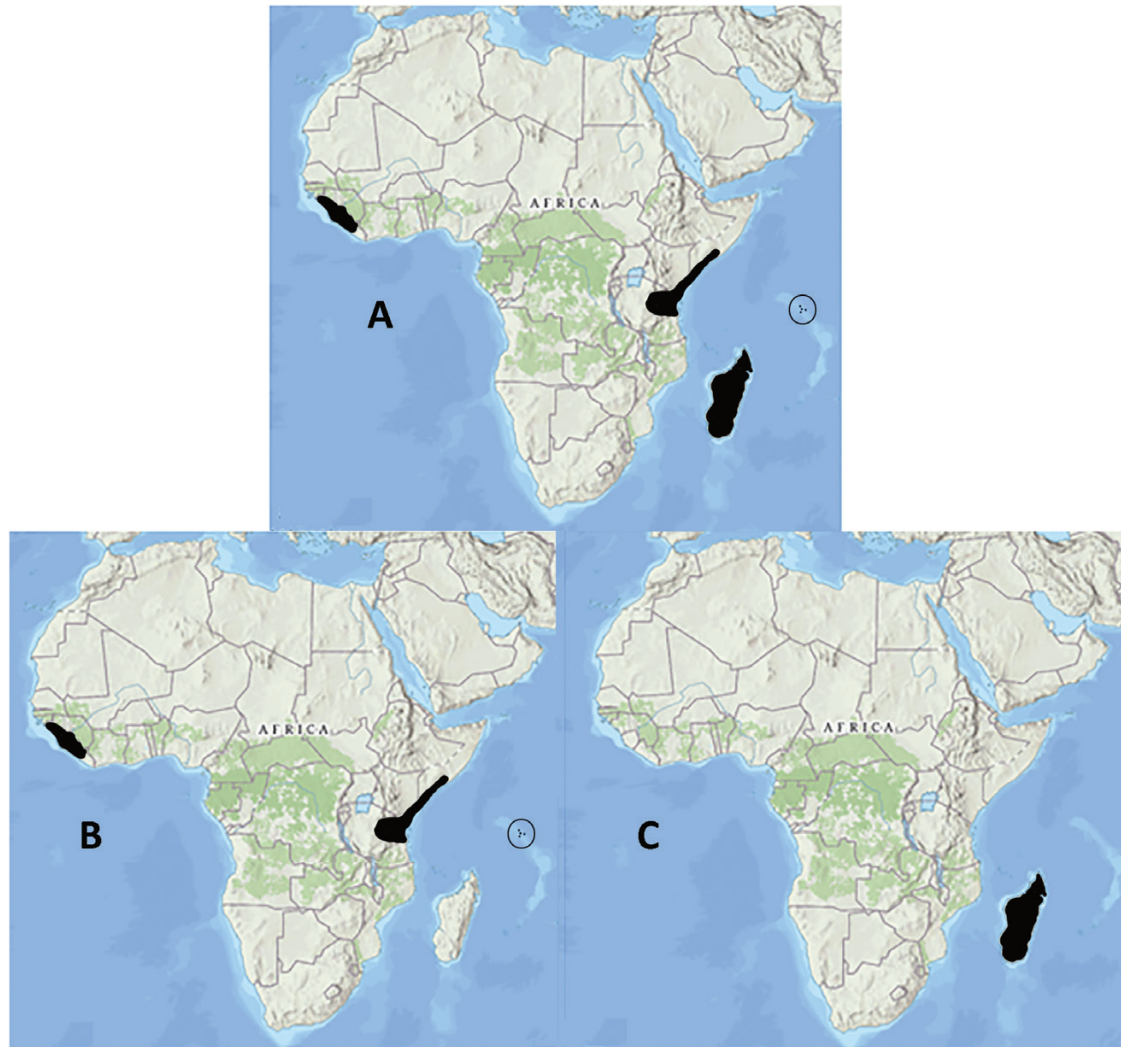


Figure 11. Maps showing the distributional ranges of (A) Deckeniidae, (B) revised Deckeniinae and (C) revised Hydrothelphusinae.

Potamonautes Balss, 1929: 348; Barnard, 1935: 484; Capart, 1954: 841, fig. 36, 17; Cumberlidge, 1997: 580–582; 1998: 198, 202–203.

Potamonautes (Obesopotamonautes) Bott, 1955: 257–259, pl. XXII, figs 2a–d, 19, 80; Pretzmann, 1977: 238, figs 7–12.

Diagnosis: S3/4 deep, V-shaped, completely traversing sternum (or deep at margins, faint in the middle); outer margins of S4 raised and thickened; third maxilliped ischium lacking vertical suture (or if present faint); anterolateral margin of carapace posterior to epibranchial tooth either smooth or granulated, but lacking teeth; G1 TA short (TA length $0.25 \times$ SA length), slim, either not widened in midsection (or dorsal fold slightly higher than ventral fold), tapering evenly to pointed tip (Fig 5A, B).

Etymology: *Maritimonautes* is derived from the Latin *maritimus*, coastal, referring to the coastal plain of East Africa, east of the Rift Valley where this genus is found, and the Greek *ναύτες*, seamen, a common suffix for African freshwater crabs. Gender masculine.

Type species: *Thelphusa obesa* A. Milne-Edwards, 1868, by original designation.

Species included: *Maritimonautes calcaratus* (Gordon, 1929) comb. nov., *Maritimonautes choloensis* (Chace, 1953) comb. nov., *Maritimonautes licoensis* (Daniels, Bittencourt-Silva, Muianga, & Bayliss, 2020) comb. nov., *Maritimonautes namuliensis* (Daniels & Bayliss, 2012) comb. nov. and

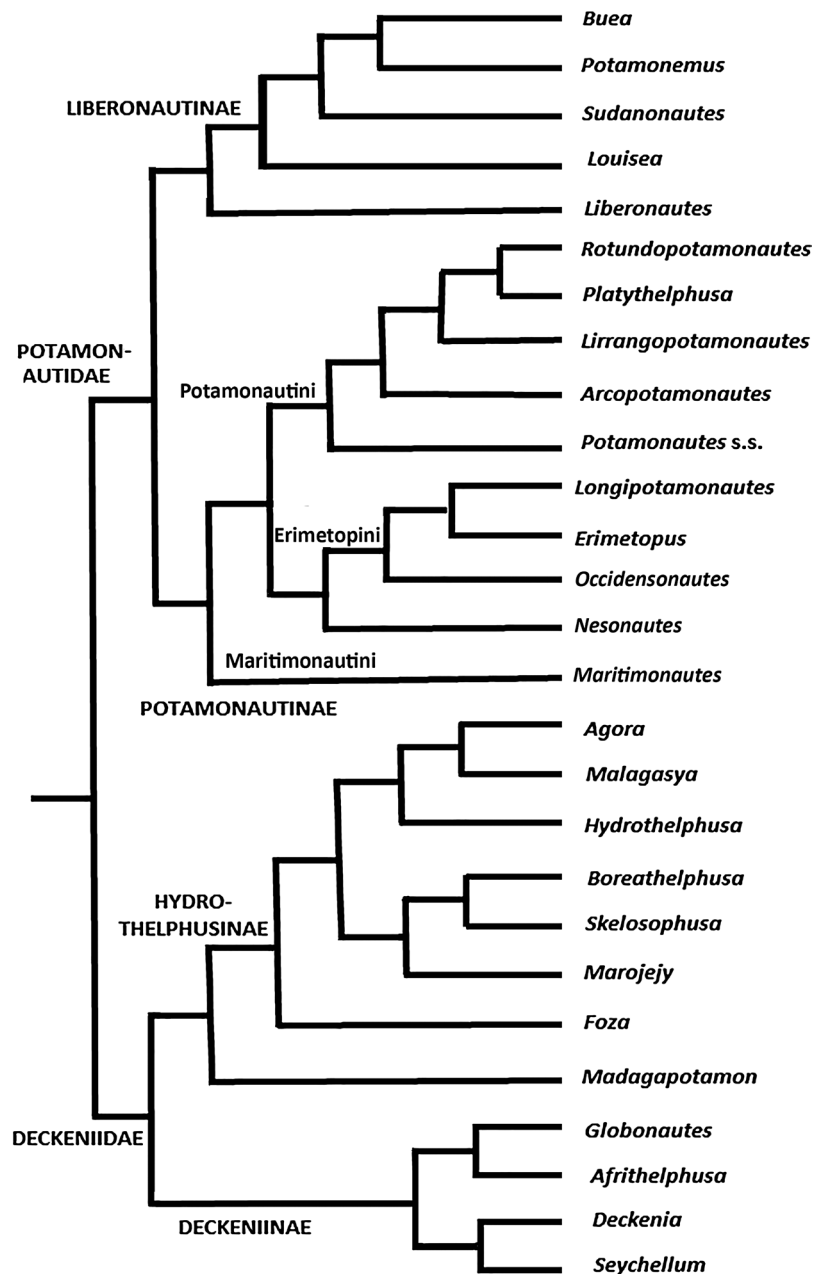


Figure 12. Diagram showing the relationships between 27 genera of Afrotropical freshwater crabs and the higher taxonomy proposed here (based on Fig. 1 and Daniels *et al.*, 2015: fig.1). *Glabrithelphusa* is not included because of the lack of sequencable DNA of this genus.

Maritimonautes obesus (A. Milne-Edwards, 1868) comb. nov.

Distribution: *Maritimonautes* is found in the low-lying coastal plains of Somalia, Kenya and Tanzania (plus Zanzibar and Pemba islands), including the north coast of Lake Malawi in Tanzania (Ruvuma, Iringa and Mbeya Provinces), Mounts Inago, Mabu, Namuli and Lico in northern Mozambique, Mount Nyangoni

(Manicaland Province) in eastern Zimbabwe and the Kruger National Park in Mpumapanga Province, South Africa (Chace, 1953; Reed & Cumberlidge, 2004; Daniels & Bayliss, 2012; Daniels *et al.*, 2014, 2020; Fig. 8B).

Remarks: *Maritimonautes* is established for five species formerly assigned to *Potamonautes s.l.* DNA data are available for five of these species

that are grouped together in a well-supported clade (Daniels *et al.*, 2015: fig. 2; Daniels & Klaus, 2018: fig. 1; Wood *et al.*, 2019: fig. 1; Fig. 1B1). The most recently-described species of this genus (*M. licoensis*) from Mozambique is included based on morphology and the phylogeny published with the description (Daniels *et al.*, 2020). Two of the species transferred here to *Maritimonautes* (*M. calcaratus* and *M. obesus*) were assigned by Bott (1955) to *Potamonautes* (*Obesopotamonautes*) Bott, 1955. The latter subgenus is not recognized here, because it is not monophyletic: two of its three taxa belong to the new genus *Maritimonautes* (Fig. 1B1), but the third species, *Platythelphusa langi*, is positioned in a separate lineage for *Platythelphusa* (Fig. 1B3[3]).

ERIMETOPINI TRIBE NOV.

(FIGS 1B2, 4A–L, 8C; TABLES 1–3)

Zoobank registration: urn:lsid:zoobank.org:act:61AF1486-7B40-4EC9-A244-6875EAD2C1CE.

Diagnosis: Third maxilliped ischium smooth, lacking vertical sulcus; epibranchial tooth small, pointed; postfrontal crest distinct, completely traversing carapace.

Etymology: Erimetopini is derived from a combination of the English words Congo and West, as a reference to the range of this tribe that includes an area that encompasses the Congo Basin and all of West Africa (Fig. 8C). The gender is masculine.

Type genus: *Erimetopus* Rathbun, 1894.

Genera included: *Erimetopus* Rathbun, 1894, *Longipotamonautes* (Bott, 1955) stat. nov., *Nesonautes* gen. nov. and *Occidensonautes* gen. nov.

Distribution: Erimetopini is found in West and Central Africa in the following countries: *Erimetopus* occurs in the Republic of the Congo and the D.R. Congo (Fig. 9A), *Longipotamonautes* occurs in Nigeria, Cameroon, the D.R. Congo, the Central African Republic, Gabon and the Republic of the Congo (Fig. 9B), *Nesonautes* is endemic to São Tomé Island (Fig. 9C) and *Occidensonautes* is found in West Africa from Senegal to Nigeria (Fig. 9D).

Remarks: Each of the four genera in this tribe has been recovered as a well-supported lineage in the clade for Erimetopini (Fig. 1B2) and these relationships are also supported by other recent molecular studies of these taxa (Daniels & Klaus, 2018: fig. 1; Wood *et al.*,

2019: fig. 1). The genera can be distinguished from each other by differences in the G1 TA (Fig. 4A–L; see key to genera above).

GENUS *ERIMETOPUS* RATHBUN, 1894

(FIGS 1B2, 4A–C, 9A; TABLES 1–3)

Erimetopus Rathbun, 1894: 26; 1900: 285; 1905: 270, pl. 19, fig. 8; 1921: 433–434, pl. 33, fig. 15; Lenz, 1912: 9; Colosi, 1920: 27; Balss, 1936: 195; 1957: 164; Chace, 1942: 225; Capart, 1954: 846, fig. 43; Cumberlidge, 1998: 196; 2008: 72, 77, tab. 1; 2011: 79, 82–83 tabs 6.1, 6.3; Ng *et al.*, 2008: 171.

Potamon (*Acanthothelphusa*) Ortman, 1903: 300.

Potamonautes (*Erimetopus*) Bott, 1955: 224–225, fig. 7a–b, pl. III, fig. 1a–c; 1955: 225–226, fig. 8a–b, pl. III, fig. 2a–c.

Diagnosis: Anterolateral margin denticulated between exorbital, epibranchial teeth. Cheliped carpus inner margin with two large subequal pointed teeth; cheliped carpus outer margin with two or three teeth; anterolateral margin of carapace behind epibranchial tooth with several small teeth; carpi, propodi of P2–5 with spines on their margins; margins of meri of P2–5 either smooth or sparsely setose; G1 TA slim tapering, not widened by raised lobes (Fig. 4A–C).

Type species: *Erimetopus brazzae* A. Milne-Edwards, 1886, by original designation.

Species included: *Erimetopus brazzae* (A. Milne-Edwards, 1886) and *Erimetopus vandenbrandeni* (Balss, 1936).

Distribution: *Erimetopus brazzae* and *E. vandenbrandeni* are endemic to the Lower and Middle Congo River Basin in the Republic of the Congo and the D.R. Congo (Cumberlidge, 1999; Cumberlidge & Reed, 2004; Fig. 9A).

Remarks: *Erimetopus* is revised and redescribed here. *Erimetopus* accommodates two species of unusual freshwater crabs from the Lower Congo Basin in Central Africa (Cumberlidge & Reed, 2004). Bott (1955) established *Potamonautes* (*Erimetopus*) with *Erimetopus spinosus* Rathbun, 1894 as the type species for two species, *Potamonautes* (*Erimetopus*) *brazzae* and *Potamonautes* (*Erimetopus*) *brazzae frontospinulosa*. Cumberlidge & Reed (2004) recognized *Erimetopus* as a valid genus with two species, *E. brazzae* and *E. vandenbrandeni*. The phylogenies of Daniels *et al.* (2015: fig. 2), Daniels & Klaus (2018: fig. 1) and Wood *et al.* (2019: Fig. 1) all recovered *E. brazzae* as a well-defined lineage sister to *Longipotamonautes ballayi*.

The lineage represented by *Longipotamonautes* (Bott, 1955) is sister to the branch for *Occidensonautes ecorseii* from West Africa (Fig. 1B2).

GENUS LONGIPOTAMONAUTES (BOTT, 1955) STAT. NOV.

(FIGS 1B2, 4D–F, 9B; TABLES 1–3)

Zoobank registration: urn:lsid:zoobank.org:act:A3AD3513-16B3-461A-82CD-C4CE7E88E8AD

Thelphusa A. Milne-Edwards, 1886: 149; 1887: 132, pl. 7: fig. 2, fig. 2a.

Potamon De Man, 1898: 436; Chace, 1942: 206.

Potamon (*Potamonautes*) Rathbun, 1900: 284.

Potamon (*Potamon*) Rathbun, 1904: 296, pl. 12, fig. 9; 1921: 419–422, pl. 27, 28, figs 1, 10.

Potamonautes (*Longipotamonautes*) Bott, 1955: 244–245, pl. 7: fig. 2a–d, figs 23, 73; Coulter, 1991: 256.

Potamonautes Balss, 1936: 174–177, figs 9, 12, 13; Ng *et al.*, 2008: 171; Cumberlidge, 2008: 72, 77, tab. 1; 2011: 79, 82–83, tabs 6.1, 6.3.

Diagnosis: Epibranchial tooth large, pointed, directed forward; third maxilliped ischium smooth, lacking vertical sulcus; S3/4 incomplete, missing except for deep notches on lateral ends; G1 TA medium long (TA length 0.33 × SA length), tubular, with parallel sides, medial and lateral folds low (Fig. 4A–B); telson bell-shaped with lateral margins indented; pleon broadly triangular, sides, base subequal. Major chela propodus lower margin longer than carapace width; dactylus slim, highly arched; G1 TA tip broad with hook (Fig. 4D–F); anterolateral margin between exorbital tooth, epibranchial tooth with variable number of large pointed teeth.

Type species: *Thelphusa ballayi* A. Milne-Edwards, 1886, by original designation.

Species included: *Longipotamonautes acristatus* (Bott, 1955) comb. nov., *Longipotamonautes adentatus* (Bott, 1955) comb. nov., *Longipotamonautes ballayi* (A. Milne-Edwards, 1886) comb. nov., *Longipotamonautes nheenae* (Cumberlidge, 2017a) comb. nov., *L. paecilei* (A. Milne-Edwards, 1886) comb. nov., *Longipotamonautes punctatus* (Bott, 1955) comb. nov., *Longipotamonautes reidi* (Cumberlidge, 1999) comb. nov., *Longipotamonautes schubotzi* (Balss, 1936) comb. nov. and *Longipotamonautes semilunaris* (Bott, 1955) comb. nov.

Distribution: *Lo. acristatus*, *Lo. adentatus*, *Lo. ballayi*, *Lo. paecilei* and *Lo. punctatus* are all found in the D.R. Congo, *Lo. schubotzi* is found in the Central African Republic, *Lo. reidi* is found in Nigeria and Cameroon and *Lo. nheenae* is endemic to Gabon (Balss, 1936; Bott, 1955; Cumberlidge, 1999, 2017a; Cumberlidge & Boyko, 2000; Cumberlidge & Reed, 2004; Fig. 9B).

Remarks: Subgenus *Potamonautes* (*Longipotamonautes*) Bott, 1955 is given genus rank and is re-described here. Bott (1955) established *Potamonautes* (*Longipotamonautes*) with *Thelphusa ballayi* A. Milne-Edwards, 1886 as the type species and included four species and two subspecies in this subgenus. *Longipotamonautes* is established here to accommodate seven species of freshwater crabs from the Lower Congo Basin in Central Africa that were previously considered to be species of *Potamonautes s.l.* All six taxa that Bott (1955) assigned to *Po.* (*Longipotamonautes*) are transferred here to *Longipotamonautes*, with the addition of *Lo. nheenae* from Gabon and *Lo. reidi* from Nigeria and Cameroon. Unfortunately, DNA data are only available for one of these species, *Lo. ballayi*. The phylogeny presented here (Fig. 1) together with those of Daniels & Klaus (2018: fig. 1) and Wood *et al.* (2019: fig. 1) consistently recovered *Lo. ballayi* as part of a well-defined clade (Fig. 1B2) that is sister to the branch represented by *Erimetopus*, and separate from the clades of *Maritimonautini* (Fig. 1B1) and *Potamonautini* (Fig. 1B3). The other species are included in *Longipotamonautes* based on shared morphological characters that conform to the above generic diagnosis.

GENUS NESONAUTES GEN. NOV.

(FIGS 1B2, 4G–I, 9C; TABLES 1–3)

Zoobank registration: urn:lsid:zoobank.org:act:558E16D5-0F1C-45CE-A1AE-F1F2438C5758.

Thelphusa A. Milne-Edwards, 1869: 185, pl. 9, fig. 4, fig. 4a–b; Greef, 1882: 37; 1884: 54; A. Milne-Edwards, 1886: 150; 1887: 130; Ozorio, 1887: 221; 1889: 129, 132; 1892: 199; 1905: 149.

Thelphusa Brito-Capello, 1871: pl. 2, fig. 12 [not A. Milne-Edwards].

Potamon (*Potamonautes*) Ortmann, 1897: 304, 308; Rathbun, 1900: 283; 1904: pl. 14, fig. 10; 1905: 168–169; De Man, 1914: 135.

Potamon Chace, 1942: 216.

Potamonautes (*Platypotamonautes*) Bott, 1955: 229, 235, pl. XXX: figs 1a–d, 11 (only *Po.* (*Pl.*) *margaritarius* = *N. margaritarius* comb. nov.; not *Po.* (*Pl.*) *ecorseii* = *Occidensonautes ecorseii* comb. nov., *Po.* (*Pl.*) *platynotus* = *Arcopotamonautes platynotus* comb. nov., *Po.* (*Pl.*) *pilosus* = *Rotundopotamonautes pilosus* comb. nov., *Potamonautes* (*Rotundopotamonautes*) *neumanni* = *Rotundopotamonautes neumanni* comb. nov.

Potamonautes margaritarius Balss, 1914: 102; Ng *et al.*, 2008: 171; Cumberlidge, 2008: 72, 77, tab. 1; 2011: 79, 82–83, tabs 6.1, 6.3; Daniels & Klaus, 2018: 119–127, figs 1–3, tab 1; Cumberlidge & Daniels, 2018: 289–295, figs 1–3.

Diagnosis: G1 TA long (TA/SA 0.45–0.48 length of G1 SA); G1 TA angled at 45° to the longitudinal

axis of G1 SA; G1 TA widened in the middle (dorsal fold higher than ventral fold); G1 TA terminating in highly upcurved tip (Fig. 4G–I); carapace flattened (CH/FW 1.0); anterolateral margin behind epibranchial tooth either finely toothed or granular; third maxilliped ischium smooth, lacking vertical suture.

Etymology: The genus name is a combination of the Greek νῆσος, island, and ναύτες seamen, “-nautes” being a common suffix for freshwater crabs. This to recognize that this genus of freshwater crabs is endemic to São Tomé Island. The gender is masculine.

Type species: *Thelphusa margaritaria* A. Milne-Edwards, 1869, by present designation.

Species included: *Nesonautes margaritarius* (A. Milne-Edwards, 1869) comb. nov. and *Nesonautes saotome* (Cumberlidge & Daniels, 2018) comb. nov.

Distribution: *Nesonautes* species are endemic to São Tomé Island (São Tomé and Príncipe) (Daniels & Klaus, 2018; Cumberlidge & Daniels, 2018; Fig. 9C).

Remarks: *Nesonautes* is established here to accommodate two species of freshwater crabs that are endemic to São Tomé Island, which were previously considered to be species of *Potamonautes* s.l. (Bott, 1955; Cumberlidge & Daniels, 2018). A new genus is necessary because these two species form a unique genetic lineage separate from the large clade for Potamonautini (Fig. 1B3) and the clade formed by *Erimetopus*, *Longipotamonautes* and *Occidensonautes* (Daniels & Klaus, 2018). Because neither of the included species is the type species of a genus or a subgenus, a new genus name is provided here.

Bott (1955) included *N. margaritarius* (as *P. margaritarius*) as one of five species in his subgenus *Potamonautes* (*Platypotamonautes*) (together with *Potamonautes ecorseii*, *Potamonautes platynotus*, *Potamonautes pilosus* and *Potamonautes neumanni*). However, subgenus *P. (Platypotamonautes)* is not monophyletic because the species he included were found here to belong to four different phylogenetic lineages (Daniels et al., 2006, 2015; Fig. 1) and it is therefore not recognized here. *Potamonautes margaritarius* is thus assigned to *Nesonautes*, *P. ecorseii* is transferred to *Occidensonautes*. *Potamonautes platynotus* is moved here to *Arcopotamonautes* and *P. pilosus* and *P. neumanni* are now assigned to *Rotundopotamonautes*.

GENUS OCCIDENSONAUTES GEN. NOV.

(FIGS 1B2, 4J–L, 9D; TABLES 1–3)

Zoobank registration: urn:lsid:zoobank.org:act:86B558AA-36DF-464F-AEAA-266D9FFEA94A.

Potamon (Potamonautes) Marchand, 1902: 334–342, pls 1, 3, figs 2–6; Rathbun, 1905: 180; Roux, 1935: 32–34.

Potamon Chace, 1942: 210.

Potamonautes (Platypotamonautes) Bott, 1955: 229; 1959: 1002–1004, fig. 4.

Potamonautes (Isopotamonautes) Bott, 1955: 247; 1959: 1004; 1970: 340–341, pl. 1.

Potamonautes Cumberlidge, 1999: 129–130; Ng et al., 2008: 170; Duriš & Koch, 2010: 220.

Diagnosis: Exorbital tooth small, low; epibranchial tooth small but distinct; anterolateral margin between exorbital, epibranchial teeth lacking intermediate tooth; anterolateral margin posterior to epibranchial tooth raised, lacking teeth; episternal sulci S4/E4, S5/E5, S6/E6 all clearly visible; S7/E7 lacking visible groove. Posterior margin of carapace ~1/2 as wide as CW; third maxilliped ischium smooth (or with faint vertical sulcus); S3/4 deep, V-shaped, midpoint meeting anterior margin of sterno-pleonal cavity; G1 TA short (~1/3 as long as G1 SA), tip pointed (Fig. 4J–L).

Etymology: The genus name is a combination of Latin *occidens*, west and “nautes”, Ancient Greek for seamen, a common suffix for African freshwater crabs, in recognition that this genus is endemic to West Africa. The gender is masculine.

Type species: *Potamon (Potamonautes) ecorseii*, Marchand, 1902, by present designation.

Species included: *Occidensonautes ecorseii* (Marchand, 1902) comb. nov., *O. lipjkei* (Duriš & Koch, 2010) comb. nov., *O. senegalensis* (Bott, 1970) comb. nov. and *O. triangulus* (Bott, 1959) comb. nov.

Distribution: *Occidensonautes* is endemic to West Africa from Senegal to the Niger River Basin in Nigeria (Cumberlidge, 1999; Duriš & Koch, 2010). *O. ecorseii* is the species with the widest distributional range and is found from the Senegal River Basin (Senegal) to the Niger River Basin in Nigeria, *Occidensonautes lipjkei* and *Occidensonautes senegalensis* are both endemic to Senegal, while *Occidensonautes triangulus* is endemic to Ghana (Fig. 9D).

Remarks: All four of these West African species were previously assigned to *Potamonautes* s.l. DNA data are only available for *O. ecorseii*, and so the other three species are included here based on

shared morphological characters that conform to the above generic diagnosis. A new genus has been established, because the phylogeny indicates that *O. ecorseii* represents a unique genetic lineage sister to *Longipotamonautes* (Daniels *et al.*, 2015: fig. 1; Fig. 1B2), but separate from the clades for Potamonautini (Fig. 1B3) and Maritimonautini (Fig. 1B1). In addition, a new genus is necessary because no published genus-level name is available and none of the included species is the type species of either a genus or a subgenus. The earlier taxonomic assignment by Bott (1955, 1959) of *O. ecorseii* and *O. triangulus* to *Potamonautes* (*Platypotamonautes*) Bott, 1955 is not recognized here because this subgenus as configured by Bott (1955) is not monophyletic according to the phylogenetic relationships presented here (Fig. 1). For example, *Po. ecorseii* was one of five species included by Bott (1955) in *Po.* (*Platypotamonautes*) a paraphyletic assemblage that groups together species from four different phylogenetic lineages within the Potamonautinae (Daniels *et al.*, 2006, 2015; Fig. 1). For this reason, *Po. ecorseii* is moved to *Occidensonautes* (Fig. 1B2), *Po. margaritarius* is assigned to *Nesonautes* (Fig. 1B2), *Po. platynotus* is transferred to *Arcopotamonautes* (Fig. 1B3[1]) and *Po. pilosus* and *Po. neumanni* are moved to *Rotundopotamonautes* (Fig. 1B3[5]).

POTAMONAUTINI (BOTT, 1970) TRIB. NOV.

(FIGS 1B3, 5D–L, 6A–F, 8D, 10A–E; TABLES 1–3)

Zoobank registration: urn:lsid:zoobank.org:act:836CD5A5-4950-4264-9859-7D4EB9C49B2C.

Diagnosis: Outer margins of the anterior thoracic sternum S4 low.

Etymology: Potamonautini is derived from the family level name Potamonautidae Bott, 1970.

Type genus: *Potamonautes* MacLeay, 1838.

Genera included: *Arcopotamonautes* (Bott, 1955) stat. nov., *Lirrangopotamonautes* (Bott, 1955) stat. nov., *Platythelphusa* A. Milne-Edwards, 1887, *Potamonautes* MacLeay, 1838 s.s. and *Rotundopotamonautes* (Bott, 1955) stat. nov.

Distribution: Potamonautini is widely distributed in sub-Saharan Africa in eastern and northern Africa (Tanzania, Kenya, South Sudan, Sudan, Egypt, Somalia) and southern Africa (Angola, Malawi, Mozambique, Zambia, Zimbabwe, Botswana, Namibia, South Africa, Eswatini and Lesotho) (Fig. 8D). This tribe is not found in West Africa (from Senegal to Nigeria).

Remarks: Potamonautini includes five genera and 101 species that form a well-supported and highly diverse group in the present study (Fig. 1B3), as well as in the most recent molecular studies of this fauna (Daniels & Klaus, 2018: fig. 1; Wood *et al.*, 2019: fig. 1).

GENUS ARCOPOTAMONAUTES (BOTT, 1955) STAT. NOV.

(FIGS 1B3[1], 5D–F, 10A; TABLES 1–3)

Zoobank registration: urn:lsid:zoobank.org:act:187310FB-E397-49F6-A482-254C75929C62.

Telphusa Hilgendorf, 1898: 8–9, fig. 5, 5a–d.

Potamon De Man, 1898: 438; Chace, 1942: 222.

Potamon (*Potamonautes*) Rathbun, 1905: 172; 1933: 256; 1935: 26; Colosi, 1924: 4.

Potamonautes Balss, 1929: 348; Barnard, 1935: 484; Cumberlidge, 1997: 581–582; 1998: 204; 2004: 418–423, figs 1–8, 17–25, 30; 2008: 72, 77, tab. 1; 2011: 79, 82–83, tabs 6.1, 6.3; Reed & Cumberlidge, 2006a: 34–37, figs 113–123, 167–168, 184, pl. XII; Ng *et al.*, 2008: 171.

Potamonautes (*Arcopotamonautes*) Bott, 1955: 270–272, pl. XVII, figs 1a–d, 40 (for *Telphusa suprasulcata*, Hilgendorf, 1898; not *Potamon* (*Potamonautes*) *alluaudi* Bouvier, 1921, *Telphusa bipartite* Hilgendorf, 1898).

Potamonautes (*Gerdalopotamonautes*) Bott, 1955: pl. 13, figs 3a–d, 34, 82 (for *Potamonautes* (*Gerdalopotamonautes*) *gerdalensis* Bott, 1955).

Potamonautes (*Platypotamonautes*) Bott, 1955: 229, pl. IV, figs 1a–d, 12, 66 (for *Potamon* (*Potamonautes*) *platynotus* Cunningham, 1907; not *Po. margaritarius* (= *Nesonautes margaritarius*), *Po. ecorseii* (= *Occidensonautes ecorseii*), *Po. pilosus* (= *Rotundopotamonautes pilosus*) and *Po. neumanni* (= *Rotundopotamonautes neumanni*)).

Diagnosis: Postfrontal crest distinct, traversing entire carapace between epibranchial teeth; epibranchial tooth reduced to small granule; posterior carapace sulci deep, distinct; G1 TA distinctly widened in midsection (dorsal fold higher than ventral fold), tip curved upward; except for *A. suprasulcatus* whose G1 TA is a long, slim, curving and tapered and not widened in midsection.

Type species: *Telphusa suprasulcata* Hilgendorf, 1898, by original designation.

Species included: *Arcopotamonautes amosae* (Cumberlidge, Johnson, Clark & Genner, 2021) comb. nov., *Arcopotamonautes bellarussus* (Daniels *et al.*, 2014) comb. nov., *Arcopotamonautes caputanatis* (Cumberlidge, Clark & Fastiggi, 2019) comb. nov., *Arcopotamonautes gerdalensis* (Bott, 1955) comb.

nov., *Arcopotamonautes infravallatus* (Hilgendorf, 1898) comb. nov., *Arcopotamonautes johnstoni* (Miers, 1885) comb. nov., *Arcopotamonautes loveridgei* (Rathbun, 1933) comb. nov., *Arcopotamonautes montivagus* (Chace, 1953) comb. nov., *Arcopotamonautes orbitospinus* (Cunnington, 1907) comb. nov., *Arcopotamonautes platycentron* (Hilgendorf, 1897) comb. nov., *Arcopotamonautes platynotus* (Cunnington, 1907) comb. nov., *Arcopotamonautes raybouldi* (Cumberlidge & Vannini, 2004) comb. nov., *Arcopotamonautes suprasulcatus* (Hilgendorf, 1898) comb. nov., *Arcopotamonautes unisulcatus* (Rathbun, 1921) comb. nov. and *Arcopotamonautes xiphoidus* (Reed & Cumberlidge, 2006) comb. nov.

Distribution: *Arcopotamonautes* species are found in the southern and central parts of the Rift Valley around Lake Malawi and Lake Tanganyika (Malawi, Tanzania and Zambia) (Fig. 10A). Eight species, *A. unisulcatus*, *A. xiphoidus*, *A. gerdalensis*, *A. infravallatus*, *A. johnstoni*, *A. loveridgei*, *A. platycentron* and *A. raybouldi*, have a distribution in Tanzania (Reed & Cumberlidge, 2006a), with the range of *A. platycentron* and *A. raybouldi* extending just across the border into southern Kenya (Cumberlidge & Vannini, 2004; Reed & Cumberlidge, 2006a). One species, *A. amosae*, is found in the basins of rivers draining into Lake Tanganyika in Tanzania and also in Lake Kivu, in Nord-Kivu Province in the D.R. Congo (Cumberlidge *et al.*, 2021). Three species, *A. montivagus*, *A. suprasulcatus* and *A. loveridgei*, are found in southern Tanzania (Iringa, Mbeya and Ruvuma provinces) and in Malawi (Northern Region) (Chace, 1953; Reed & Cumberlidge, 2006a) and one species *A. caputanatis* is found in Zambia (Northern Province) (Cumberlidge *et al.*, 2019). Four species in this genus are found in large lakes such as *A. platycentron* (Lake Chala) (Reed & Cumberlidge, 2006a), *A. amosae* (Lake Kivu) (Cumberlidge *et al.*, 2021), *A. platynotus* (Lake Tanganyika) (Reed & Cumberlidge, 2006a) and *A. orbitospinus* (Lake Malawi) (Cumberlidge *et al.*, 2021).

Remarks: The subgenus *Potamonautes* (*Arcopotamonautes*) Bott, 1955 is given generic status and revised. *Arcopotamonautes* is recognized here to accommodate 14 species from the African Rift Valley. Bott (1955) established *P.* (*Arcopotamonautes*) for *P.* (*A.*) *suprasulcatus suprasulcatus*, *P.* (*A.*) *s. alluaudi* and *P.* (*A.*) *bipartitus*. *Arcopotamonautes* includes *Telphusa suprasulcata* Hilgendorf, 1898, the type species of *P.* (*Arcopotamonautes*) as well as *P.* (*Gerdalopotamonautes*) *gerdalensis* Bott, 1955, the type species of *P.* (*Gerdalopotamonautes*) Bott, 1955. The latter subgenus

becomes a junior synonym of *Arcopotamonautes* under the rule of priority because *Telphusa suprasulcata* Hilgendorf, 1898, is the senior name. Similarly, *Arcopotamonautes* also includes *Potamon* (*Potamonautes*) *platynotus* Cunnington, 1907, which is the type species of the subgenus *P.* (*Platyopotamonautes*) Bott, 1955. The latter subgenus becomes a junior synonym of *Arcopotamonautes* under the rule of priority because *Telphusa suprasulcata* Hilgendorf, 1898 is the senior name.

DNA data are available for six of these species: *A. gerdalensis*, *A. montivagus*, *A. orbitospinus* (as *Po. lirrangensis* in Fig. 1B3[2]), *A. platynotus*, *A. raybouldi* and *A. suprasulcatus*. These species group together in a well-supported lineage within the large clade for the Potamonautini (Daniels *et al.*, 2015, fig. 2; Daniels & Klaus, 2018: fig 1; Wood *et al.*, 2019: fig 1; Fig. 1B3). In the absence of DNA data, the other eight species assigned here to this genus (*A. amosae*, *A. caputanatis*, *A. infravallatus*, *A. johnstoni*, *A. loveridgei*, *A. platycentron*, *A. suprasulcatus* and *A. unisulcatus*) are included based on shared morphological characters that conform to the generic diagnosis.

GENUS *LIRRANGOPOTAMONAUTES* (BOTT, 1955) STAT. NOV.

(FIGS 1B3[2], 5G–I, 10B; TABLES 1–3)

Zoobank registration: urn:lsid:zoobank.org:act:D8A4F4AA-99CB-4EF3-B381-BBF9E2F182BE.

Potamon (*Potamonautes*) *lirrangensis* Rathbun, 1904: pl. 14, fig. 8; 1905: 169; 1921: 413–415, pls 25, 26, figs 3, 8; Balss, 1914: 404; 1929: 347–348 (partim, not D.R. Congo: Kituri, Upper Lualaba, Katanga Province, Russisi River, Lake Kivu); 1936: 188–189 (partim, not D.R. Congo: Banana, Lakes Kivu, Mweru).

Potamon lirrangensis Chace, 1942: 188–189; Capart, 1954: 836, fig. 28.

Potamonautes (*Lirrangopotamonautes*) *lirrangensis* Bott, 1955: 268–269 (partim, not Lake Kivu, Kindu, Lokandu, Kinshasa, Buta, Lubo, Lulua, Luzizi, Ruzizi rivers, Luvungu, Lake Tanganyika (Mpala, Uvira), Lake Malawi).

Potamonautes lirrangensis Cumberlidge, 1998: 264 (partim, not Tanzania: Tukuyu (formerly Neu-Langenburg); Malawi: Lake Malawi; Reed & Cumberlidge, 2006a (partim, not Tanzania: Kigoma area, Taveta, Mungonya River, Uvinza, Malagarasi River, Malawi: Lake Malawi); Ng *et al.*, 2008: 171 (partim).

Potamonautes (*Tripotamonautes*) Bott, 1955: 264, pl. XIV, figs 2a–d, 32, 33 [partim: for *Potamon* (*Potamonautes*) *walderi* Colosi, 1924, not *Potamon* (*Potamonautes*) *loveridgei* Rathbun, 1933].

Diagnosis: Postfrontal crest distinct, completely traversing carapace between epibranchial teeth;

exorbital tooth small, epibranchial tooth reduced to small granule; cheliped carpus with two subequal long teeth, cheliped merus with large pointed distal meral tooth; third maxilliped ischium smooth, lacking vertical sulcus (or with faint vertical sulcus); thoracic sternal sulcus S3/4 deep, completely traversing sternum (or deep only at sides, faint in middle).

Type species: *Potamon (Potamonautes) lirrangensis* Rathbun, 1904, by original designation.

Species included: *Lirrangopotamonautes congoensis* (Rathbun, 1921) comb. nov., *Lirrangopotamonautes didieri* (Rathbun, 1904) comb. nov., *Lirrangopotamonautes dybowskii* (Rathbun, 1905) comb. nov., *Lirrangopotamonautes kisangani* (Cumberlidge *et al.*, 2021) comb. nov., *Lirrangopotamonautes lirrangensis* (Rathbun, 1904) comb. nov. s.s., *Lirrangopotamonautes lueboensis* (Rathbun, 1904) comb. nov., *Lirrangopotamonautes niloticus* (H. Milne Edwards, 1837) comb. nov., *Lirrangopotamonautes stanleyensis* (Rathbun, 1921) comb. nov., *Lirrangopotamonautes walderi* (Colosi, 1924) comb. nov.

Distribution: The range of *Lirrangopotamonautes* is centred on the Congo River in the D.R. Congo including the Middle Congo (*Lr. kisangani*, *Lr. congoensis*, *Lr. didieri* and *Lr. stanleyensis* are found in the provinces of Tshopo, Haut-Uele, Bas-Uele and Ituri, *Lr. lirrangensis* and *Lr. dybowskii* are found in the province of Equateur, *Lr. lueboensis* is found in the Lower Congo provinces of Kwango, Kwilu and Kasai and *Lr. walderi* is found in Central Province (Chace, 1942; Bott, 1955; Corace *et al.*, 2001; Cumberlidge, 2015; Cumberlidge *et al.*, 2021; Fig. 10B). *Lr. niloticus* is found in the entire Nile River drainage from its upper reaches in Rwanda and Lake Victoria to Uganda, Kenya, South Sudan, Ethiopia, Sudan and Egypt (Cumberlidge & Clark, 2010a).

Remarks: The subgenus *Potamonautes (Lirrangopotamonautes)* Bott, 1955 is given genus status and is revised to accommodate 12 species from the Middle and Upper Congo River Basin, Uganda, Tanzania and lakes Tanganyika and Kivu. Bott (1955) established *Po. (Lirrangopotamonautes)* for *Po. (Lr.) lirrangensis*, *Po. (Lr.) johnstoni johnstoni* and *Po. (Lr.) johnstoni platycentron*. Of these, only *Po. (Lr.) lirrangensis* s.s. (Cumberlidge *et al.*, 2021) is included here, while *Po. (Lr.) johnstoni* and *Po. (Lr.) platycentron* are transferred to *Arcopotamonautes*.

Lirrangopotamonautes includes the type species of the subgenus *Potamon (Potamonautes) lirrangensis*

Rathbun, 1904. In addition, *Lirrangopotamonautes* also includes *Potamon (Potamonautes) walderi* Colosi, 1924, the type species of the subgenus *Potamonautes (Tripotamonautes)* Bott, 1955. The latter subgenus becomes a junior synonym of *Po. (Lirrangopotamonautes)* under the rule of priority because *Potamon (Po.) lirrangensis* Rathbun, 1904 is the senior name. Furthermore, *Lr. niloticus* was assigned by Bott (1955) to *Po. (Acanthothelphusa)* Bott, 1955, as the type species of that subgenus (as *Thelphusa nilotica* H. Milne Edwards, 1837). This now becomes a junior synonym of *Lirrangopotamonautes*, because *Potamon (Po.) lirrangensis* was described earlier.

Although DNA data are available for only three of these species (*Lr. niloticus*, *Lr. stanleyensis* and *Lr. sp. nov.* 6) the molecular phylogenies group these species together in a well-supported clade within the Potamonautini (Fig. 1B3[2]; Daniels *et al.*, 2015: fig. 2; Daniels & Klaus, 2018: fig 1; Wood *et al.*, 2019: fig 1). The other species are included in *Lirrangopotamonautes* based on shared morphological characters that conform to the diagnosis for the genus. Notably, *Lr. niloticus*, which diverged early in this clade, differs in that it has pointed exorbital and epibranchial teeth, large spines lining the anterolateral margins, and the cheliped carpus inner margin has a long pointed distal tooth and a distinctly smaller proximal tooth.

GENUS *PLATYTHELPHUSA* A. MILNE-EDWARDS, 1887

(FIGS 1B3[3], 5J–L, 10C; TABLES 1–3)

Platythelphusa A. Milne-Edwards, 1887: 146; Hilgendorf, 1898: 21; Moore, 1903: 286; Rathbun, 1905: 268; Cunnington, 1907: 266–268; 1920: 557; Alcock, 1910: 253–261; Colosi, 1920: 9–10; Balss, 1936: 196; Chace, 1942: 224; Cumberlidge, 1999: 16, 17, 25, 36, 37, 42, 45, 66–69, 74, 76–79, 100–113, 116, 317; 2008: 72, 77, tab. 1; 2011: 79, 82–83, tabs 6.1, 6.3; Cumberlidge *et al.*, 1999: 1491–1493; Marijnissen *et al.*, 2004: 515; Ng *et al.*, 2008: 171.

Limnothelphusa Cunnington, 1899: 698; Moore, 1903: 280; Rathbun, 1905: 269.

Hydrothelphusa (Platythelphusa) Bouvier, 1917a: 615–621; 1917b: 657–659; 1921: 41.

Potamonautes (Platythelphusa) Bott, 1955: 226–229; Coulter, 1991: 253–257.

Potamonautes (Obesopotamonautes) Bott, 1955: pl. XII: figs 1a–d, 17, 18, 79a, b (partim, for *Potamon (Potamonautes) langi* Rathbun, 1921; not *Thelphusa obesa* A. Milne-Edwards, 1868 (= *Maritimonautes obesus*) or *Potamon (Potamonautes) calcaratus* Gordon, 1929 (= *Maritimonautes calcaratus*).

Diagnosis: Third maxilliped ischium smooth, lacking vertical sulcus (or with faint vertical sulcus); thoracic

sternal sulcus S3/4 deep, completely traversing sternum (or deep only at sides, faint in middle).

Distribution: *Platythelphusa* includes 11 species with a distribution centred on Lake Tanganyika and its drainage basin (in Malawi, Tanzania, D.R. Congo, Rwanda and Burundi), except for two species from the D.R. Congo: *Platythelphusa langi* from Tshopo Province and *Platythelphusa idjwiensis* from Lake Kivu in Nord-Kivu Province (Cumberlidge *et al.*, 1999; Marijnissen *et al.*, 2004; Reed & Cumberlidge, 2006a; Cumberlidge, 2015; Fig. 10C).

Type species: *Platythelphusa armata* A. Milne-Edwards, 1887, by monotypy.

Species included: *Platythelphusa armata* A. Milne-Edwards, 1887, *Platythelphusa conculcata* (Cunnington, 1907), *Platythelphusa denticulata* Capart, 1952, *Platythelphusa echinata* Capart, 1952, *Platythelphusa idjwiensis* (Chace, 1942) comb. nov., *Platythelphusa immaculata* Marijnissen, Schram, Cumberlidge & Michel, 2004, *Platythelphusa langi* (Rathbun, 1921) comb. nov., *Platythelphusa maculata* (Cunnington, 1902), *Platythelphusa polita* Capart, 1952, *Platythelphusa praelongata* Marijnissen, Schram, Cumberlidge & Michel, 2004, *Platythelphusa tuberculata* Capart, 1952.

Remarks: The subgenus *Potamonautes* (*Platythelphusa*) Bott, 1955 is reestablished, revised and given genus status here to accommodate 11 species: all nine *Platythelphusa* species from Lake Tanganyika, plus *Pl. langi* (now *Platythelphusa*) from the Upper Congo Basin in the D.R. Congo and *Pl. idjwiensis* (now *Platythelphusa*) from Lake Kivu. Daniels *et al.* (2015: fig. 1), Daniels & Klaus (2018: fig. 1) and Wood *et al.* (2019: fig. 1) and the present study (Fig. 1B3) all group these species together in a well-supported clade within the Potamonautini. *Platythelphusa* has two clear lineages within it, with one branch for the nine species endemic to Lake Tanganyika, and the other branch for species from the Upper Congo Basin in the D.R. Congo (including Lake Kivu).

Bott (1955) established the subgenus *Po.* (*Platythelphusa*) for *Po. (Pl.) armata armata* and *Po. (Pl.) a. conculcata*. The genus as revised here retains the name *Platythelphusa* because it includes the type species *Platythelphusa armata* A. Milne-Edwards, 1887. DNA data are available for ten of these species (Daniels *et al.*, 2015: fig. 1; Daniels & Klaus, 2018: fig. 1; Wood *et al.*, 2019: fig. 1; Fig. 1B3). The remaining species, *Pl. denticulata*, is included here based on shared morphological characters that conform to the generic diagnosis (Cumberlidge *et al.*, 1999). One of the species included here in *Platythelphusa*

[*Potamon (Potamonautes) langi* Rathbun, 1921] was assigned by Bott (1955) as the type species of the subgenus *Potamonautes (Obesopotamonautes)* Bott, 1955. Despite this, the genus name for these species remains as *Platythelphusa* by priority because the type species of the latter genus (*Platythelphusa armata* A. Milne-Edwards, 1887) was described before *Potamon (Potamonautes) langi* Rathbun, 1921.

All but one species assigned to *Platythelphusa* share the following characters: a distinct postfrontal crest that completely traverses the carapace between the epibranchial teeth, a small exorbital tooth, an epibranchial tooth reduced to a small granule, one or more long, sharp teeth lining the anterolateral margin of carapace, and a cheliped carpus with two subequal long, sharp teeth. *Pl. idjwiensis* is included because of phylogenetic evidence that positions it in the same clade as the other congeners (Fig. 1B3[3]) despite the fact that *Pl. idjwiensis* lacks a postfrontal crest, has a completely smooth anterolateral margin that lacks teeth, and has a small reduced proximal tooth on the cheliped carpus inner margin.

GENUS POTAMONAUTES MACLEAY, 1838 s.s.

(FIGS 1B3[4], 6A–C, 10D; TABLES 1–3)

Thelphusa A. Milne-Edwards, 1886: 149; 1887: 132, pl. 7: fig. 2, fig. 2a.

Potamon De Man, 1898: 436; Chace, 1942: 206.

Potamon (Potamonautes) Rathbun, 1900: 284.

Potamon (Potamon) Rathbun, 1904: 296, pl. 12: fig. 9; 1921: 419–422, pls 27, 28: fig. 1, fig. 10.

Potamonautes (Longipotamonautes) Bott, 1955: 244–245, pl. VII: fig. 2a–d; figs 23, 73.

Potamonautes Balss, 1936: 174–177, pls 9, 12, 13; Ng *et al.*, 2008: 171; Cumberlidge, 2008: 72, 77, tab. 1; 2011: 79, 82–83 tabs 6.1, 6.3.

Potamonautes (Isopotamonautes) Bott, 1955: not *Potamonautes (Isopotamonautes) senegalensis* = *Occidensonautes senegalensis*.

Potamonautes (Lirrangopotamonautes) Bott, 1955, not *Potamonautes (Lirrangopotamonautes) adeleae* = *Potamonautes adeleae*.

Potamonautes (Orthopotamonautes) Bott, 1955 for *Potamonautes (Orthopotamonautes) depressus* and *Potamonautes (Orthopotamonautes) sidneyi* [not *Potamonautes (Orthopotamonautes) depressus dybowskii* = *Lirrangopotamonautes dybowskii*].

Diagnosis: Cheliped carpus with two subequal large teeth. Third maxilliped ischium with vertical sulcus; thoracic sternal sulcus S3/4 deep, completely traversing

sternum (or deep only at sides, faint in middle). G1 TA short (~1/4 to 1/3 as long as G1 SA; Fig. 6A–C).

Type species: *Thelphusa perlata* H. Milne Edwards, 1837, by original designation.

Species included: *Potamonautes adeleae* Bott, 1968, *Potamonautes anchietae* (Brito-Capello, 1871), *Potamonautes barbarai* Phiri & Daniels, 2014, *Potamonautes barnardi* Phiri & Daniels, 2014, *Potamonautes bayonianus* (Brito-Capello, 1864), *Potamonautes biballensis* Bott, 1951, *Potamonautes brincki* (Bott, 1960), *Potamonautes clarus* Gouws *et al.*, 2000, *Potamonautes danielsi* Peer *et al.*, 2017, *Potamonautes dentatus* Stewart *et al.*, 1995, *Potamonautes depressus* (Krauss, 1843), *Potamonautes dubius* (Brito-Capello, 1873), *Potamonautes flavusjo* Daniels *et al.*, 2014, *Potamonautes gorongosa* Cumberlidge *et al.*, 2016, *Potamonautes granulatus* Daniels *et al.*, 1998, *Potamonautes isimangaliso* Peer *et al.*, 2015, *Potamonautes kensleyi* Cumberlidge & Tavares, 2006, *Potamonautes lividus* Gouws *et al.*, 2001, *Potamonautes macrobrachii* Bott, 1953, *Potamonautes mphlope* Daniels, 2017, *Potamonautes mulanjeensis* Daniels & Bayliss, 2012, *Potamonautes mutareensis* Phiri & Daniels, 2013, *Potamonautes ngoyensis* Daniels *et al.*, 2019, *Potamonautes ntendekaensis* Daniels *et al.*, 2019, *Potamonautes parvicorpus* Daniels *et al.*, 2001, *Potamonautes parvispina* Stewart, 1997, *Potamonautes perlatus* (H. Milne Edwards, 1837), *Potamonautes principe* Cumberlidge *et al.*, 2002, *Potamonautes sidneyi* (Rathbun, 1904), *Potamonautes tuerkayi* Wood & Daniels, 2016, *Potamonautes unispinus* Stewart & Cook, 1998, *Potamonautes warreni* (Calman, 1918).

Distribution: This large genus is distributed throughout southern Africa, with the northern boundary in southern Tanzania (Ruvuma, Iringa, Mbeya provinces) and southern D.R. Congo (Kwanga and Katanga provinces). Eighteen species are endemic to South Africa: *Po. barbarai*, *Po. barnardi*, *Po. brincki*, *Po. clarus*, *Po. danielsi*, *Po. dentatus*, *Po. flavusjo*, *Po. granularis*, *Po. isimangaliso*, *Po. lividus*, *Po. mphlope*, *Po. ngoyensis*, *Po. ntendekaensis*, *Po. parvicorpus*, *Po. parvispina*, *Po. perlatus*, *Po. tuerkayi* and *Po. warreni* (Bott, 1951; Stewart *et al.*, 1995; Stewart, 1997a, b; Stewart & Cook, 1998; Daniels *et al.*, 1998, 2001, 2002a, b, 2014, 2019, 2020; Gouws & Stewart, 2001; Gouws *et al.*, 2000, 2001, 2015; Phiri & Daniels, 2013; Peer *et al.*, 2015, 2017; Phiri & Daniels, 2013, 2014, 2016; Daniels, 2017; Wood & Daniels, 2016; Fig. 8D). Five species are endemic to Angola: *Po. adeleae*, *Po. anchietae*, *Po. biballensis*, *Po. kensleyi* and *Po. macrobrachii* (Cumberlidge & Tavares, 2006) and two species are endemic to Mozambique: *Po. gorongosa* and

Po. mulanjeensis (Daniels & Bayliss, 2012; Cumberlidge *et al.*, 2016). In addition, *Po. dubius* (Cumberlidge & Tavares, 2006) is endemic to Namibia, *Po. mutareensis* is endemic to Zimbabwe (Phiri & Daniels, 2013), and *Po. principe* is endemic to Príncipe (Cumberlidge *et al.*, 2002). Additionally, four *Potamonautes* species have a widespread distribution: *Po. bayonianus* in the D.R. Congo, Angola, Namibia, Zimbabwe and Zambia (Cumberlidge & Tavares, 2006), *Po. unispinus* in South Africa, Zimbabwe, Zambia and Botswana (Stewart & Cook, 1998), *Po. sidneyi* in South Africa and Eswatini (Gouws *et al.*, 2000, 2001, 2015) and *Po. depressus* in South Africa and Lesotho (Gouws *et al.*, 2000, 2001).

Remarks: *Potamonautes* s.s. is revised here to accommodate 32 species from southern Africa. Bott (1955) established *Po. (Potamonautes)* for *Po. perlatus*, *Po. warreni*, *Po. bayonianus bayonianus* and *Po. bayonianus dubius*. The first three of these taxa are grouped together with 24 other species from southern Africa in a well-supported lineage within the Potamonautini (Fig. 1B3[4]; Daniels *et al.*, 2006: fig 1; 2015: fig. 2; Daniels & Klaus, 2018: fig 1; Wood *et al.*, 2019: fig 1). The name *Potamonautes* has been retained for this clade because it includes *Thelphusa perlata* H. Milne Edwards, 1837, the type species of the genus. The freshwater crab fauna of southern Africa is the best studied on the continent, with DNA sequence data available for 31 species, the majority of which are from South Africa. Other parts of the region are less well represented. For example, so far there are DNA data for only one species from Angola (*Po. anchietae*; Fig. 1B 3[4]) and so the other five species from that country (*Po. adeleae*, *Po. biballensis*, *Po. dubius*, *Po. kensleyi* and *Po. macrobrachii*) are included in this revised genus based on morphological similarities (Bott, 1955; Cumberlidge, 1999; Cumberlidge & Tavares, 2006).

Potamonautes s.s. includes several species that have previously been designated as the type species of a genus or subgenus, and so their status is reviewed below. For example, four species included here in *Potamonautes* s.s. were assigned by Bott (1955, 1960) to *Po. (Isopotamonautes)* Bott, 1955 as *Po. (I.) anchietae*, *Po. (I.) macrobrachii*, *Po. (I.) senegalensis* and *Po. (I.) anchietae biballensis*. *Po. anchietae* from Angola is however, the type species of *Po. (Isopotamonautes)* as *Thelphusa anchietae* Brito Capello, 1871, which now becomes a junior synonym of *Potamonautes* s.s. by priority because *Thelphusa perlata* H. Milne Edwards, 1837, is the senior name. Furthermore, Bott's (1955) subgenus *Po. (Isopotamonautes)* is paraphyletic and is not recognized here because it includes species from two separate lineages (Fig. 1): all but one of which remain in *Potamonautes* s.s., because *Po. (I.) senegalensis* from Senegal is phylogenetically distinct and is here assigned to the new genus *Occidensonautes*.

Bott (1968) included *Po. adeleae* in the subgenus *Po. (Lirrangopotamonautes)* Bott, 1955, but this species is here transferred to *Potamonautes* s.s. based on morphological characters. In addition, Bott (1960) included *Po. brincki* from South Africa in *Gecarcinautes*, but subsequent authors (Stewart, 1997a; Cumberlidge, 1999; Cumberlidge & von Sternberg, 2002; Ng *et al.*, 2008) treated *Gecarcinautes* as a junior synonym of *Potamonautes* and recognized *Gecarcinautes brincki* as a valid species. In the present work, *Po. brincki* is included in *Potamonautes* s.s. (Fig. 1B3[4]).

Three taxa included here in *Potamonautes* s.s. were assigned by Bott (1955) to *Po. (Orthopotamonautes)* Bott, 1955 as *Po. (O.) d. depressus*, *Po. (O.) d. dybowskii* and *Po. (O.) sidneyi*. However, *Po. depressus* is the type species of *Po. (Orthopotamonautes)* as *Thelphusa depressa* Krauss, 1843, and this becomes a junior synonym of *Potamonautes* s.s. because *T. perlata* H. Milne Edwards, 1837 is the senior synonym. The subgenus *Potamonautes (Orthopotamonautes)* is therefore paraphyletic and not recognized here because the taxa assigned to it by Bott (1955) belong to two different genetic lineages: *Po. depressus* is moved to *Potamonautes* s.s. (Fig. 1B3[4]) and *Po. dybowskii* is moved to *Lirrangopotamonautes* (Fig. 1B3[2]).

All but one of the species included here in *Potamonautes* s.s. shares the following characters. A distinct postfrontal crest that completely traverses the carapace between the epibranchial teeth, a small exorbital tooth, an epibranchial tooth that is reduced to a small granule, and the anterolateral margin of carapace behind the epibranchial tooth is either granulated or smooth. The exception is *Po. warreni* which has small teeth lining the anterolateral margin.

GENUS ROTUNDOPOTAMONAUTES (BOTT, 1955)
STAT. NOV.

(FIGS 1B3[5], 6D–F, 10E; TABLES 1–3)

Zoobank registration: urn:lsid:zoobank.org:act:3E8357A3-511E-47C4-AC50-29671ADE964D.

Thelphusa Audouin, 1826: 82, pl. 2, fig. 6; H. Milne Edwards, 1837: 14; 1853: 212–213; White, 1847: 30; Heller, 1861: 19; Herklots, 1861: 13; A. Milne-Edwards, 1869: 177; 1869: 176, pl. 9 Fig. 1; 1887: 137; Kingsley, 1880: 35; Bell, 1894: 166; Ortmann, 1897: 312.

Cancer (Thelphusa) De Haan, 1833: 23.

Geothelphusa Stimpson, 1861: 373; Hilgendorf, 1898: 20.

Telphusa Pfeffer, 1888: 33; Henderson, 1893: 284.

Potamon (Potamonautes) Ortmann, 1897: 310, 312.

Potamon De Man, 1898: 436; Flower, 1931: 732; Chace, 1942: 207; Capart, 1954: 827, figs 4, 31.

Potamon (Geothelphusa) Rathbun, 1904: pl. 18, figs 3, 10; Rathbun, 1905: 203–204; Lenz, 1910b: 124 (4); De

Man, 1914: 126, 127, pl. 2: fig. 3, fig. 3a; Colosi, 1919: 50; Colosi, 1920: 34; Balss, 1929b: 350; Rathbun, 1935: 25.

Potamonautes (Rotundopotamonautes) Bott, 1955: 288–289, pl. 23, fig. 5, pl. 23, fig. 1a–d; Monod, 1980: 382–383, pl. V, fig. 28 (not *Potamonautes (Rotundopotamonautes) infravallatus* = *Arcopotamonautes infravallatus*).

Potamonautes (Lobopotamonautes) Bott, 1955: pl. XVIII, figs 2a, 3a; pl. XX, fig. 2a–d, figs 1, 2, 48, 50, 87, 88, 89 [partim: for *Potamon (Potamonautes) aloysiisabaudiae* Nobili, 1906, not *Potamon (Potamonautes) stanleyensis* Rathbun, 1921, *Potamon (Geothelphusa) perparvus* Rathbun, 1921, *Po. perparvus gonocristatus* Bott, 1955, *Po. perparvus minor* Bott, 1955].

Potamonautes Cumberlidge, 1997: 579; Cumberlidge, 1998: 197–198; Ng *et al.*, 2008: 171; Cumberlidge *et al.*, 2009: appendix 1, 19; Cumberlidge, 2009b: 548, 551–557, tab. 1; Cumberlidge & Meyer, 2010: 180, 184, 187, tab. 1.

Diagnosis: Third maxilliped ischium smooth, lacking vertical sulcus; thoracic sternal sulcus S3/4 incomplete, deep only at sides, interrupted in middle; cheliped carpus inner margin proximal tooth reduced to small granule; G1 TA distinctly widened in midsection (dorsal fold higher than ventral fold), tip curved upward.

Type species: *Thelphusa berardi* Audouin, 1826, by original designation.

Species included: *Rotundopotamonautes alluaudi* (Bouvier, 1921) comb. nov., *Rotundopotamonautes aloysiisabaudiae* (Nobili, 1906) comb. nov., *Rotundopotamonautes amalerensis* (Rathbun, 1935) comb. nov., *Rotundopotamonautes antheus* (Colosi, 1920) comb. nov., *Rotundopotamonautes berardi* (Audouin, 1826) comb. nov., *Rotundopotamonautes bipartitus* (Hilgendorf, 1898) comb. nov., *Rotundopotamonautes bourgaultae* (Cumberlidge & Meyer, 2009) comb. nov., *Rotundopotamonautes busingwe* (Cumberlidge & Clark, 2017) comb. nov., *Rotundopotamonautes bwindii* (Cumberlidge & Clark, 2018) comb. nov., *Rotundopotamonautes elgonensis* (Cumberlidge & Clark, 2010a) comb. nov., *Rotundopotamonautes emini* (Hilgendorf, 1892) comb. nov., *Rotundopotamonautes entebbe* (Cumberlidge & Clark, 2017) comb. nov., *Rotundopotamonautes gonocristatus* (Bott, 1955) comb. nov., *Rotundopotamonautes holthuisi* (Cumberlidge & Meyer, 2009) comb. nov., *Rotundopotamonautes ignestii* (Parisi, 1923) comb. nov., *Rotundopotamonautes imatongensis* (Cumberlidge & Clark, 2016) comb. nov., *Rotundopotamonautes jeanneli* (Bouvier, 1921) comb. nov., *Rotundopotamonautes kantsyore* (Cumberlidge & Clark, 2017) comb. nov., *Rotundopotamonautes kivu* (Cumberlidge & Clark, 2018) comb. nov.,

Rotundopotamonautes kundudo (Cumberlidge & Clark, 2012) comb. nov., *Rotundopotamonautes loashiensis* (Bott, 1955) comb. nov., *Rotundopotamonautes loveni* (Colosi, 1924) comb. nov., *Rotundopotamonautes minor* (Bott, 1955) comb. nov., *Rotundopotamonautes morotoensis* (Cumberlidge & Clark, 2016) comb. nov., *Rotundopotamonautes mutandensis* (Chace, 1942) comb. nov., *Rotundopotamonautes neumanni* (Hilgendorf, 1898) comb. nov., *Rotundopotamonautes odhneri* (Colosi, 1924) comb. nov., *Rotundopotamonautes perparvus* (Rathbun, 1921) comb. nov., *Rotundopotamonautes pilosus* (Hilgendorf, 1898) comb. nov., *Rotundopotamonautes rodolphianus* (Rathbun, 1909) comb. nov., *Rotundopotamonautes rothschildi* (Rathbun, 1909) comb. nov., *Rotundopotamonautes rukwanzi* (Corace, Cumberlidge & Garms, 2001) comb. nov., *Rotundopotamonautes rwenzori* (Cumberlidge & Clark, 2018) comb. nov., *Rotundopotamonautes subukia* (Cumberlidge & Dobson, 2008) comb. nov. and *Rotundopotamonautes williamsi* (Cumberlidge & Clark, 2010a) comb. nov.

Distribution: The range of *Rotundopotamonautes* centres on Uganda, Kenya and Ethiopia, with the border between Kenya and Tanzania serving as the south-eastern boundary line and Sudan and Egypt the northern boundary (Fig. 10E). The distribution also includes the central and northern parts of the Rift Valley around Lakes Tanganyika, Kivu and Victoria and their drainages [D.R. Congo (Nord-Kivu and Ituri provinces), Rwanda, Burundi, Tanzania (Kagoro Province)] and South Sudan (Chace, 1942; Corace *et al.*, 2001; Cumberlidge, 2004, 2009b; Cumberlidge & Dobson 2008; Cumberlidge & Clark, 2010a, b, 2012, 2016, 2017, 2018; Cumberlidge & Meyer, 2010, 2011).

Remarks: The subgenus *Rotundopotamonautes* of Bott (1955) is raised here to genus rank. This genus is established to accommodate 36 species of *Potamonautes* from the Nile River Basin, Lake Kivu, Uganda, Kenya, Ethiopia, South Sudan, Sudan and Egypt. Bott (1955) established *Po.* (*Rotundopotamonautes*) for seven taxa: *Po. loveni* (as *Po. granviki*), *Po. infravallatus*, *Po. semilunaris*, *Po. emini*, *Po. loashiensis*, *Po. berardi* and *Po. ignestii*. Six of these (including *Po. berardi*) are assigned to this revised genus, with the exception of *Po. infravallatus*, which is here transferred to *Arcopotamonautes*. The name *Rotundopotamonautes* is retained because it includes the type species of the subgenus *Po.* (*Rotundopotamonautes*), *Thelphusa berardi* Audouin, 1826. One of the species included here in *Rotundopotamonautes* is *Potamon* (*Potamonautes*) *aloyisabaudiae* Nobili, 1906, from Uganda, the type species of *Potamonautes* (*Lobopotamonautes*) Bott,

1955. This latter subgenus is treated here as a junior synonym of *Rotundopotamonautes* under the rule of priority because *Potamon* (*Potamonautes*) *lirrangensis* Rathbun, 1904, is the senior name. DNA data are available for only six of these species: *R. kundudo*, *R. loveni*, *R. rukwanzi*, *R. alluaudi*, *R. odhneri* and *R. subukia*. The molecular phylogenies group these species together in a well-supported clade within the larger clade for *Potamonautes* *s.s.* (Fig. 1B3; Daniels *et al.*, 2015: fig. 1; Daniels & Klaus, 2018: fig 1; Wood *et al.*, 2019: fig. 1). The other 29 species are included here based on shared morphological characters that conform to the genus diagnosis. For example, all of the species in this distinctive genus have a faint, incomplete postfrontal crest that does not traverse the carapace, reduced or absent exorbital and epibranchial teeth, and a smooth anterolateral margin of the carapace behind the epibranchial tooth.

FAMILY DECKENIIDAE ORTMANN, 1897 (FIGS 1, 11A–C; TABLES 1–3)

Diagnosis: Deckeniidae taxa are recognized by characters of the second gonopod (G2). When the G2 is viewed in cross section the dorsal side of the SA-TA junction has a setose spoon-like structure. When the G2 TA is viewed in cross section the dorsal margin is either lacking or it is extremely reduced. The G2 TA is long and flagellum-like, with a ventral margin that is folded to create a tube, but the degree of folding varies from completely open (*Afrithelphusa*), to partly closed (*Seychellum*), to almost closed (*Hydrothelphusa*, *Malagasya* and *Madagapotamon*). For Deckeniidae taxa the G2 TA flagellum is never a completely closed tube as in *Potamon* (Klaus *et al.*, 2006).

Type genus: *Deckenia* Hilgendorf, 1869, by original designation.

Genera included: *Afrithelphusa* Bott, 1969, *Agora* Cumberlidge, Soma, Leever & Daniels, 2020, *Boreathelphusa* (Cumberlidge & von Sternberg, 2002), *Deckenia* Hilgendorf, 1869, *Foza* Reed & Cumberlidge, 2006b, *Glabrithelphusa* Meyer *et al.*, 2014, *Globonautes* Bott, 1959, *Hydrothelphusa* A. Milne-Edwards, 1872, *Madagapotamon* Bott, 1965, *Malagasya* Cumberlidge & von Sternberg, 2002, *Marojejy* Cumberlidge, Boyko & Harvey, 2002, *Seychellum* Ng *et al.*, 1995 and *Skelosophusa* Ng & Takeda, 1994.

Distribution: Deckeniidae taxa are found in West Africa (Liberia, Guinea, Sierra Leone), East Africa (Tanzania, Kenya, Somalia), the granitic Seychelles and Madagascar (Cumberlidge, 1999; Cumberlidge

et al., 2004; Reed & Cumberlidge, 2006a, b; Fig. 11A–C).

Remarks: The Afrotropical freshwater crabs form a well-supported monophyletic group with two distinct lineages (Daniels *et al.*, 2006, 2015) that are here recognized as two families, namely Potamonautidae and Deckeniidae (Tables 1–3), rather than two subfamilies (Cumberlidge *et al.*, 2008). The revised Potamonautidae has two phylogenetic divisions (subfamilies): Potamonautinae (Tables 2, 3) from sub-Saharan Africa, except West Africa (Fig. 8A) and the new subfamily Liberonautinae (Fig. 7B) from West and Central Africa. The revised Deckeniidae has two lineages (subfamilies): Deckeniinae (type genus: *Deckenia*) (Tables 2, 3) from West Africa, East Africa and the Seychelles, formerly Deckeniini (Cumberlidge *et al.*, 2008; Fig. 11B), and Hydrothelphusinae (type genus: *Hydrothelphusa* A. Milne-Edwards, 1872) from Madagascar, formerly Hydrothelphusini (Cumberlidge & von Sternberg, 2002; Cumberlidge *et al.*, 2008; Cumberlidge, 2021; Fig. 11C).

Earlier authors (Bott, 1955; Martin & Davis, 2001) recognized the family Deckeniidae for one genus (*Deckenia*) with two species (*Deckenia imitatrix* and *Deckenia mitis*), which was included in the African Potamonautidae. Later, Klaus *et al.* (2006) expanded Deckeniidae to include six genera assigned to three subfamilies: Deckeniinae (*Deckenia*, *Seychellum*), Globonautinae (*Afrithelphusa*, *Globonautes*) and Hydrothelphusinae (*Hydrothelphusa*, *Madagapotamon*), which they assigned to the Asian superfamily Gecarcinucoidea.

DISCUSSION

The present study is the most comprehensive integrative taxonomic review of the Afrotropical freshwater crab fauna undertaken since Bott (1955) and Cumberlidge *et al.* (2008). These results are based on a molecular phylogeny using mt and nuDNA sequence data from the largest taxonomic sample yet assembled that serves as the evolutionary framework for morphological analyses based on the entire fauna. Most notably, and where possible, the historical template of genera and subgenera defined by Bott (1955) were integrated, sometimes using new combinations, to construct a modern and stable taxonomic system based on monophyletic groups discovered by the molecular phylogeny (Fig. 1). This complete generic sampling of African Potamonautidae is a first for a molecular study of any freshwater crab family, and allows a fine-scale delineation of operational taxonomic units and a reclassification of the family.

The updated phylogenetic framework of Potamonautidae (Figs 1, 12) provides support for the recognition of all 28 freshwater crab genera that are currently known from the Afrotropical region. The revision resulted in the elevation of Potamonautinae to family status, with two subfamilies, Liberonautinae (with five genera) and Potamonautinae (with ten genera), and the elevation of Deckeniinae to family status with two subfamilies: Deckeniinae (with four genera) and Hydrothelphusinae (with nine genera; Table 3). Within Potamonautinae three new tribes are established (Fig. 1B1, 1B2, 1B3) and ten new genera are recognized (Tables 2, 3; Figs 1B, 12).

The results of this study suggest that taxonomic revisions of freshwater crab families in other undersurveyed biogeographic regions of the world are likely to yield additional taxonomic diversity. For example, a recent revision of Neotropical Pseudothelphusidae based on a molecular phylogeny resulted in the recognition of a new family and three new subfamilies (Alvarez *et al.*, 2020). Given that the latter study included only 78% of the genera and 19% of the species in the Neotropics, the species richness could prove to be even more diverse with more complete sampling. Similarly, the molecular study by Shih *et al.* (2009) of the Asian Potamidae based on 49 out of 134 genera (36.6%) revealed a complex and previously unrecognized underlying evolutionary pattern and recognized three novel genera. In addition, the molecular phylogenetic study of Asian and Australasian Gecarcinucidae by Klaus *et al.* (2010) supported the recognition of three subfamilies and revealed two paraphyletic genera, *Barytelphusa* Alcock, 1909 and *Sundathelphusa* Bott, 1969, while Klaus *et al.* (2013) discovered deep divergences between species assigned to *Parathelphusa* H. Milne Edwards, 1853 (Gecarcinucidae) suggesting paraphyly and additional undescribed taxonomic diversity. When the relationships within freshwater crab families from other parts of the world (e.g. the Trichodactylidae) are subjected to molecular analyses, the results may be expected to produce a similar taxonomic reorganization.

In the present study, the species-level coverage of the African freshwater crab fauna using DNA data has a strong bias toward southern African species because this is where most of the recent molecular systematic work has been conducted (Daniels *et al.*, 2012, 2014, 2019; Phiri & Daniels, 2013; Cumberlidge *et al.*, 2016). The largest omissions in taxonomic sampling for the present study are in Central and East Africa, especially in the forested areas of the D.R. Congo, Cameroon, Gabon, Equatorial Guinea and the East African Rift Valley. Moreover, there are still large areas of Angola, Tanzania and Mozambique that are essentially unexplored and likely to harbour

high alpha taxonomic diversity, especially in remote highland habitats. In addition, molecular studies can help future systematic studies document alpha taxonomic diversity by revealing the existence of cryptic diversity among Afrotropical freshwater crabs (Daniels *et al.*, 2012, 2014, 2019; Daniels, 2015; Cumberlidge & Daniels, 2016), particularly among species with a wide geographic distributional range. Therefore, new biogeographic surveys are encouraged to adopt protocols that preserve all freshwater crab specimens in ethanol so as to allow for future molecular analyses.

MORPHOLOGICAL CONSIDERATIONS

This phylogenetic analysis revealed distinct molecular lineages that are considered to represent subfamilies within the Potamonautidae and the Deckeniidae (Fig. 12) that can be defined by shared morphological characters. For example, characters associated with G1 and G2 were identified for these two families and subfamilies (Figs 2–6), as was reported to be the case for the Pseudothelphusidae (Alvarez *et al.*, 2020). Although mandibular palp characters are constant and shared without exception within the Pseudothelphusidae and Epiloboceridae (Alvarez *et al.*, 2020), these characters were found to be of limited use to distinguish the Potamonautidae from the Deckeniidae. This is because the mandibular palp morphology varies greatly between genera in both of the latter two families and this precludes its use as a family-level character (Cumberlidge *et al.*, 2008; table 3).

Although the 15 genera of the Potamonautidae (Fig. 12) can be distinguished by consistent phylogenetic grouping and morphological characters (see Figs 2–6 and the identification key to the genera of the Potamonautidae above), it is not easy to find characters that separate the ten genera in the large and widely distributed Potamonautinae. Although the distribution of each of the ten genera generally conforms to a distinct African region (with only minor overlaps at the borders of ranges in a few cases; Figs 8–10), there is a more distinct correlation between phylogeny and geography (Figs 8–10). Overall, there is enough evidence to allow the division of this subfamily into distinct taxonomic units.

The difficulties in observing strong patterns of phenotypic traits within and between the ten genera of the Potamonautinae may be attributed to convergent evolution, where similar-looking morphological characters have evolved independently in different genera. An illustration of this phenomenon is the presence of large sharp spines lining the anterolateral margins of the carapace seen in species belonging to different potamonautid genera. It would appear that this same character has evolved independently several

times in separate phylogenetic lineages within the Potamonautidae from different regions of Africa. For example, spines lining the anterolateral margins of the carapace are found in *Liberonantes chaperi* (West Africa), *Sudanonantes faradjensis* (Central Africa), *Erimetopus brazzae* (Lower Congo), *Platythelphusa langi* (Middle Congo), *Pl. armata* (Lake Tanganyika), *Lr. niloticus* (Nile River drainage) and *Potamonantes warreni* (South Africa). In each of these genera, large sharp spines lining the anterolateral margins of the carapace are typically found in just one species, and are lacking in all other congeners, implying that this character is an adaptation to similar ecological conditions (e.g. deep water environments) that occur in different parts of the continent.

Although the fossil record for Afrotropical freshwater crabs is not extensive (which potentially hampers accurate divergence time estimations), it does allow some preliminary statements about the origins of this group in the region. For example, there are no known fossil freshwater crabs from Madagascar or the Seychelles, and only a few are known from continental Africa (all in the East African Rift Valley) dating from Miocene and Pliocene deposits (Morris, 1976; Carriol & Secrétan, 1992; Martin & Trautwein, 2003) as far back as the Oligocene (34–23 Mya) (Feldmann *et al.*, 2007).

BIOGEOGRAPHICAL IMPLICATIONS

The present day distribution of the families, subfamilies, tribes and genera from the Afrotropical region (Figs 7–11) is interpreted here in the context of the estimated times of divergence of the major clades in Figure 1 that are broadly congruent with the multilocus estimations of phylogenetic relationships, divergence times and ancestral area estimates of Daniels *et al.* (2015). The most recent common ancestor of both families of Afrotropical freshwater crabs first entered African inland waters somewhere in West Africa during the Upper Cretaceous about 78 Mya (Daniels *et al.*, 2006, 2015; Fig. 1). From there, these crabs radiated and dispersed throughout West and Central Africa, diverging early on into two distinct evolutionary lineages: the Potamonautidae and the Deckeniidae (Figs 1, 12).

The subsequent dispersal of the ancestral freshwater crab populations in Africa took place during the Miocene (Daniels *et al.*, 2006, 2015; Fig. 1) at a time when there were large changes in the climate, geology and ecosystems in Africa, greatly influencing the evolution of freshwater crabs and their present-day distribution patterns. At this time orogeny, volcanism and climatic fluctuations between mesic and xeric conditions expanded and retracted the rainforests, modified the river courses and promoted isolation and diversification in aquatic organisms (Parrish *et al.*,

1982; Zachos *et al.*, 2001; Huber & Caballero, 2011). The continent-wide fragmentation events associated with mountain uplift and rifting (particularly in East Africa) resulted in changes to the direction of river drainage patterns and to the size of palaeolakes, and played a critical role in forest fragmentation. The drier conditions during the Middle Miocene restricted the rainforests to the equatorial region and expanded the grassland biomes so that C_4 grasses became a dominant part of the landscape (Daniels *et al.*, 2015). The increased aridification impacted freshwater habitats and established barriers to dispersal that isolated populations of widespread potamonautid freshwater crabs, resulting in the division of the West and Central African Liberonautinae from the North, East, Central and southern African Potamonautinae.

High divergences within the Liberonautinae correspond to the cladogenic events occurring in West and Central Africa during the Late Oligocene–Early Miocene. One lineage (*Liberonautes*) remained in western West Africa, while the other lineage dispersed eastward into Cameroon and other neighbouring parts of Central Africa. Today, Liberonautinae range from Senegal to South Sudan and northern Uganda, inhabiting the rainforest and savanna ecosystems throughout West Africa and Central Africa north of the Congo River. The boundaries of this subfamily are formed by the southern limits of the Sahara Desert to the north, the Rift Valley to the east and the Congo River to the south (Fig. 7B). Liberonautinae is not found anywhere in north-eastern, southern or eastern Africa (Fig. 7B).

Potamonautinae originated in Central Africa during the Eocene and expanded into the Lower Congo Basin from where branches eventually reached southern and eastern Africa (Daniels *et al.*, 2015: fig. 3). This subfamily diverged into three lineages that represent the three tribes, each of which has a discrete distributional range (Fig. 8B–D). Erimetopini remained in the Lower Congo River Basin, while Maritimonautini occupied the coastal lowlands along the east coast of Africa east of the Rift Valley. Potamonautini likely originated south of the Congo Basin from where it underwent extensive diversification and patterning within the clade resulting in the five genera recognized here.

Arcopotamonautes originated in East Africa (Daniels *et al.*, 2015: fig. 3) probably in the area of northern Zambia, Malawi, northern Mozambique and southern Tanzania and spread north into the rest of Tanzania and along the Rift Valley, but did not reach far enough north to cross the Equator. The only part of the Congo Basin included in the range of this genus is along the Rift Valley drainages associated with lakes Tanganyika and Kivu. The clade for *Arcopotamonautes* has two distinct lineages (Fig. 1B3[1]), one represented by two highly apomorphic species, the lake specialist

Arcopotamonautes platynotus found exclusively in Lake Tanganyika (Coulter, 1991; Cumberlidge *et al.*, 1999) and the phytotelmic specialist *Arcopotamonautes raybouldi* from north-eastern Tanzania and south-eastern Kenya (Cumberlidge & Vannini, 2004). The other lineage in this clade comprises four large species from Tanzania and Malawi (Fig. 10A).

Lirrangopotamonautes originated in East Africa in the region associated with the Western Rift Valley (Daniels *et al.*, 2015: fig. 3) around Lake Kivu in the D.R. Congo (Nord-Kivu Province) and dispersed west into the Middle Congo River Basin (Tshopo, Haut-Uele, Bas-Uele and Ituri provinces), along the Congo River (Equateur Province) and reached the Lower Congo River Basin in western D.R. Congo (Kwango, Kwilu, Kasai and Congo Central provinces) and the Republic of the Congo (Fig. 10B). Unfortunately, taxonomic sampling is poor from this region and our study was only able to include DNA sequences for two species in the clade for this genus (Fig. 1B3[2]), although it undoubtedly consists of more species.

Platythelphusa originated in East Africa in the region associated with the Western Rift Valley (Daniels *et al.*, 2015: fig. 3) and dispersed south along the Upper Congo River and the Lukuga River to reach Lake Tanganyika (Fig. 10C) where it speciated extensively, producing nine endemic species. The clade for *Platythelphusa* has two distinct lineages, one that entered Lake Tanganyika and one lineage represented by *Pl. langi* in the Middle Congo Basin and by *Pl. idjwiensis* in Lake Kivu in Nord-Kivu Province in the D.R. Congo (Fig. 1B3[3]). Two other as-yet-identified species of this clade (“*Platythelphusa* sp. 8” and “*Platythelphusa* sp. 7”) were sequenced in this study and are also found in the Middle Congo and are closely related to *Pl. langi*.

Potamonautes s.s. originated in East Africa (Daniels *et al.*, 2015: fig. 3) and dispersed to South Africa, Eswatini, Lesotho, Angola, Zambia, Zimbabwe, Mozambique, Namibia, Botswana and the southern D.R. Congo (Katanga and Kwanga provinces; Fig. 10D). One species of this genus (*Po. princeps*) is found outside of the southern African region on the island of Príncipe in the Gulf of Guinea. This disjunct geographical outlier represents an early lineage at the base of this clade that likely rafted overseas from the Lower Congo to colonize the island of Príncipe early in the diversification of this lineage. Subregional diversification within *Potamonautes* is evident. For example, species from Mozambique (*Po. gorongosa* and *Po. mulanjensis*) and Zimbabwe (*Po. mutarensis*) group together, as do species from Angola such as *Po. anchietae* that group with unidentified taxa from Angola sequenced in this study (Fig. 1B3[4]) “*Potamonautes* sp. 3”, “*Potamonautes* sp. 5”, “*Potamonautes* sp. 4”).

Rotundopotamonautes originated in East Africa in the region associated with the Western Rift Valley (Daniels *et al.*, 2015: fig. 3) in the area around Lake Kivu in the D.R. Congo (Nord-Kivu and Sud-Kivu provinces), Rwanda and southern Uganda. From there this genus dispersed north and east along the Nile River Basin to occupy Uganda, South Sudan, Ethiopia and Kenya as far east as the Eastern Rift Valley (but did not reach the coast of Kenya and did not spread south into Tanzania) (Fig. 10E). The clade for this genus has two distinct lineages (Fig. 1B3[5]). *Lr. niloticus* is a highly apomorphic species that colonized the entire Nile River Basin from Rwanda to Egypt, including Lake Victoria. Three other as-yet-unidentified species included in this clade (“*Rotundopotamonautes* sp. 10” from the Upper Congo, “*P. Uganda*” from Uganda and “*Rotundopotamonautes* sp. 11” from Kenya) were sequenced in this study (Fig. 1B3[5]). The first two of these are found in the Upper Congo and Uganda and are closely related to *R. emini* from north-western Tanzania, while the third species from Kenya is closely related to *R. subukia* and *R. odhneri*, also from Kenya.

The Congo River Basin: This part of Africa has overlapping elements from a number of taxonomic groups in Potamonautidae that are found in different parts of this vast and ancient river basin (Figs 7A, 8C, D, 9C, D, 10A–E). The phylogeny (Fig. 1) indicates that these lineages entered the Congo Basin separately at different times in the past. For example, only one of the five genera of Liberonautinae (*Sudanonautes*) is found in the Congo River Basin (Fig. 7B). That genus has a wide distribution in rainforest and savanna ecosystems in the D.R. Congo (in Haut Uele, Bas-Uele, Tshopo, Mongala, Equateur, Tshuapa, Mai-Ndombe, Kwilu, Kwango, Kasai, Kinshasa, Kongo-Central provinces) and the Republic of the Congo, the Central African Republic, Gabon, Cameroon and Chad (Cumberlidge, 1999: fig. 64B). Only two of the four genera of Erimetopini are found in the Congo River Basin. *Erimetopus* is restricted to the Lower Congo Basin in the D.R. Congo (Tshupa, Mai-Ndombe and Kasai provinces) and in the Republic of the Congo (Pool Province; Fig. 9A). *Longipotamonautes* has a much wider distribution in the D.R. Congo (Fig. 9B) centred along the Congo River (in Haut Uele, Bas-Uele, Tshopo, Mongala, Equateur, Tshuapa, Mai-Ndombe, Kwilu, Kwango, Kasai, Kinshasa, Kongo-Central provinces), but it is also found in the Republic of the Congo (Likouala, Pool provinces), the Central African Republic (Ombelia-Mpoko and Sangha-Mbaéré prefectures), Gabon (Ogooué-Ivindo Province), Cameroon (south-west region) and Nigeria (Cross River State).

Although all five genera of Potamonautini are present in the Congo River Basin in the D.R. Congo (Fig. 10A–E) only one, *Lirrangopotamonautes*, has a distribution that centres mainly on the Congo River

(in the D.R. Congo and part of the Republic of the Congo; Fig. 10B). Only a minor part of the range of the other four genera includes one or more provinces of the D.R. Congo. The major centre of distribution of *Arcopotamonautes* lies in Tanzania (Fig. 10A), while *Platythelphusa* is associated with the Rift Valley (Fig. 10C), *Potamonautes* is associated with southern Africa (Fig. 10D) and *Rotundopotamonautes* is found mainly in north-east Africa, Uganda and Kenya (Fig. 10E).

Freshwater crabs found on African islands: Three out of the four Gulf of Guinea islands support species of freshwater crabs and only Annobon, the oldest and the furthest from the mainland, lacks these crustaceans (Cumberlidge, 2008; Cumberlidge & Daniels, 2018). It is noteworthy that different islands host different species that belong to three genera and two subfamilies. For example, Bioko supports two species of *Sudanonautes* (Liberonautinae) (Fig. 8C) that are also found on continental Africa, São Tomé supports two endemic species of *Nesonautes* (Potamonautinae) (Fig. 9C), while Príncipe supports one endemic species of *Potamonautes* s.s. (Potamonautinae) (Cumberlidge & Daniels, 2018; Fig. 10D). The three independent phylogenetic lineages found on these three volcanic islands support separate overseas colonization, at least in the case of São Tomé and Príncipe (Cumberlidge & Daniels, 2018; Daniels & Klaus, 2018). Bioko may have supported populations of *Sudanonautes* that became separated from the mainland by sea level rises during the Pleistocene (Cumberlidge, 2008). The Indian Ocean islands of Madagascar and the Seychelles Archipelago support endemic genera and species of Deckeniidae (Fig. 11A) and there are no members of Potamonautidae found on any of these islands.

Freshwater crabs in African Rift Valley lakes: The major ancient lakes of the African Rift Valley have each been colonized by a different lineage of Potamonautini. For example, Lake Kivu supports three species of freshwater crabs that belong to three genera: *A. kisangani*, *Pl. idjwiensis* and *R. bourgaultae*. Lake Victoria supports one *Lirrangopotamonautes* species and one *Rotundopotamonautes* species: *Lr. niloticus* and *R. busingwe* and Lake Tanganyika supports nine species of *Platythelphusa* and one *Arcopotamonautes* (*A. platynotus*). Lake Malawi supports just one species: *Arcopotamonautes orbitospinus*. None of the other seven genera of African Potamonautinae, or any Deckeniidae, are represented in any of the major Rift Valley lakes.

Deckeniidae originated in the Eocene rainforests of West and Central Africa (Daniels *et al.*, 2015: fig. 3) and separated into two lineages: Deckeniinae (*Globonautes*, *Afrithelphusa*, *Deckenia* and *Seychellum*) and Hydrothelphusinae (all Malagasy genera). Only a few

Deckeniinae species survive in disjunct pockets in the Upper Guinea forests of West Africa (Liberia, Guinea, Sierra Leone), the marshy freshwater wetlands of the arid coastal part of East Africa (Tanzania, Kenya, Somalia) and the small rivers of the Seychelles Archipelago (including Mahé, Praslin, Silhouette, La Digue and Frégate) in the Indian Ocean. Deckeniidae in West and East Africa live alongside the more widely distributed and abundant species that belong to Potamonautidae. Both morphological and molecular studies arrange the genera of Malagasy freshwater crabs in a well-supported clade, indicating that these taxa form a monophyletic group (Cumberlidge & von Sternberg, 2002; Daniels *et al.*, 2006, 2015; Klaus *et al.*, 2006; Cumberlidge *et al.*, 2020). The available evidence indicates that the common ancestor of the Malagasy freshwater crabs most likely lived in Africa, belonged to Deckeniidae rather than Potamonautidae and reached Madagascar from Africa rather than the Seychelles.

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