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Erimetopus vandenbrandeni (Balss, 1936) n. comb., with notes on the taxonomy of the genus *Erimetopus* Rathbun, 1894 (Brachyura: Potamoidea: Potamonautidae) from Central Africa

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Abstract

The Central African freshwater crab genus *Erimetopus* (family Potamonautidae) is revived to accommodate two species, *E. brazzae* (A. Milne-Edwards, 1886) and *E. vandenbrandeni* (Balss, 1936) n. comb. The genus *Erimetopus* Rathbun, 1894, and the two species assigned to it here, are redescribed from type material, and lectotypes for each species are selected. *Erimetopus spinosus* Rathbun, 1894 is judged here to be a junior synonym of *E. brazzae*, and *P. (E.) b. frontospinulosa* is treated as a subspecies of *E. brazzae*. Illustrations and photographs of the type specimens of these taxa are provided, and new gonopod evidence based on *E. vandenbrandeni* is evaluated. The distributions of the species of *Erimetopus* are described and discussed, and keys to the genera of African freshwater crabs and to the species of *Erimetopus* are provided.

Key words: Crustacea, Brachyura, Potamoidea, Potamonautidae, *Erimetopus*, freshwater crab, taxonomy, Central Africa, natural history, Congo River, rainforest

Introduction

This work aims to stabilize the taxonomy of the little-known Central African freshwater crab genus *Erimetopus* Rathbun, 1894, which is endemic to the lower Congo River and its tributaries. *Erimetopus* has long attracted the interest of carcinologists because its subhexagonal/rounded carapace outline and distinctive arrangement of spines on the carapace margins and pereopods not only distinguish it from other genera of potamonautid freshwater crabs found in Africa (Cumberlidge 1999), but also impart a superficial resemblance to some species of South American trichodactylid freshwater crabs (see below).

The type species of *Erimetopus brazzae* (*Thelphusa brazzae* A. Milne-Edwards, 1886) was first described from an adult female specimen from Ngancin (= Ngabé), Republic of

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the Congo in Central Africa. One year later, A. Milne-Edwards reassigned this specimen to *Parathelphusa brazzae* (A. Milne-Edwards, 1887). Seven years after that Rathbun (1894) described a new genus and species of spiny freshwater crab from Malebo Pool (formerly Stanley Pool) in the Democratic Republic of Congo (formerly Zaire), which she named *Erimetopus spinosus* Rathbun, 1894. Although Rathbun's (1894) genus *Erimetopus* has been widely accepted by the vast majority of subsequent workers (Rathbun 1900; Ortmann 1903; Rathbun 1905, 1921; Lenz 1912; Colosi 1920; Balss 1936; Chace 1942; Cumberlidge 1999), Rathbun's (1894) species (*E. spinosus*) was treated by all later authors (including Rathbun 1905, 1921) as a junior synonym of *E. brazzae*.

Bott (1955) was alone in not recognizing *Erimetopus* as a genus, and he is still the only author to treat this taxon as a subgenus of *Potamonautes* MacLeay, 1838. Bott (1955) placed *T. brazzae* in the subgenus *Erimetopus* Rathbun, 1894 (type species *Erimetopus spinosus* Rathbun, 1894 (= *Parathelphsua brazzae* A. Milne-Edwards, 1886)), with two subspecies, *P. (E.) b. brazzae*, and *P. (E.) b. frontospinulosa* Bott, 1955. Unfortunately, Bott's (1955) taxonomic opinion of the generic status of *E. brazzae* was not based on the direct examination of the types of *T. brazzae* and *E. spinosus*, and he depended on previously-unidentified specimens from the D. R. Congo housed in the Museum Royale d'Afrique Centrale, Tervuren, Belgium (MRAC). Furthermore, Bott (1955) offered little taxonomic rationale as to why *Erimetopus* should be transferred to the genus *Potamonautes*, and did not discuss the putative congeneric relationships between *Erimetopus* and *Potamonautes*.

In the present work we have carefully reviewed the available evidence for the genus *Erimetopus* as a whole by referring to name-bearing type specimens of *E. spinosus*, *E. brazzae*, and *E. vandenbrandeni* loaned from the collections of the Museum of Comparative Zoology, Cambridge, Massachusetts, USA (MCZ), the Muséum National d'Histoire Naturelle, Paris, France (MNHN), the Museum Royale d'Afrique Centrale, Tervuren, Belgium (MRAC), and the United States National Museum of Natural History, Smithsonian Institution, Washington D.C., USA (USNM). Our findings lead us to support the traditional view that *Erimetopus* is a valid genus, to recognize two species in this genus, *E. brazzae* and *E. vandenbrandeni* (Balss, 1936), to treat *E. spinosus* as a junior synonym of *E. brazzae*, and to treat *P. (E.) b. frontospinulosa* as a subspecies of *E. brazzae*.

Despite the relatively large numbers of specimens of *E. brazzae* available, all are females (either adults or subadults). Adult male specimens of *E. brazzae* are still unknown, and the gonopods of this species have yet to be described. The second species of *Erimetopus* was first described by Balss (1936) as *Potamon (Potamonautes) vandenbrandeni* Balss, 1936, based on specimens from Kinshasa (formerly Leopoldville) in the D. R. Congo. This taxon was subsequently treated by Bott (1955) as *Potamonautes (Longipotamonautes) vandenbrandeni*. Although the majority of specimens of *E. vandenbrandeni* are adult ovigerous females, a single subadult male specimen of this taxon is available, and gonopods 1 and 2 of this animal are illustrated here.

In the present work, *E. brazzae* and *E. vandenbrandeni* are redescribed based on the examination of all available type material, plus other specimens of *E. brazzae* and *E. vandenbrandeni* housed in the MRAC and several other museums (including the MCZ, the MNHN, the USNM, and The Natural History Museum, London, U.K. (NHML)). Important taxonomic characters of *E. brazzae* and *E. vandenbrandeni* are illustrated, gonopod evidence is evaluated for the first time, photographs of the type specimens are provided, distributions of the two taxa are described, and keys to the genera of African freshwater crabs and to the species of *Erimetopus* are provided.

Abbreviations. cw, distance across the carapace at the widest point; cl, carapace length measured along the median line, from the anterior to the posterior margin; ch, carapace height, the maximum height of the cephalothorax; fw, front width measured along the anterior margin; s4/s5, s5/s6, s6/s7, s7/s8, sternal sulci between adjacent thoracic sternites; s4/e4, s5/e5, s6/e6, s7/e7, episternal sulci between adjacent thoracic sternites and episternites; P1, pereiopod 1, cheliped; P2–P5, pereopods 2–5, walking legs.

Potamonautidae Bott, 1970

Erimetopus Rathbun, 1894 (Figs. 1–45)

Erimetopus Rathbun, 1894:26; 1900: 285; 1905: 270; 1921: 433; Ortmann, 1903: 300; Lenz, 1912: 9; Colosi, 1920: 27; Balss, 1936: 195; Chace, 1942: 225; Cumberlidge, 1999: 45.

Type species. *Erimetopus spinosus* Rathbun, 1894.

Diagnosis. Carapace outline subhexagonal/rounded; epibranchial tooth large, sharp, pointing forward, positioned well behind postfrontal crest; mandibular palp two-segmented, terminal segment simple; orbit narrow (1/7 cw), upper orbital margin semi-circular; anterolateral margin between exorbital and epibranchial teeth very long, curving slightly outward, with several small pointed teeth, lacking identifiable intermediate tooth; exopod of third maxilliped with long flagellum, ischium smooth lacking vertical sulcus; first carpal tooth on inner margin of carpus of cheliped large, slender, pointed, curving forward; series of pointed teeth on outer margin of carpus of P1; superior margins of meri of P2–P5 with two large, pointed distal teeth; carpi of P2–P4 with spines on anterior margins, posterior margins smooth; propodi of P2–P4 with spines on anterior margins, posterior margins smooth; propodus of P5 with spines on anterior and posterior margins.

Discussion. The absence of gonopod characters for some of the taxa included in this study is unfortunate, but it does not in itself discount the validity of utilizing other morphological characters to characterize the genus and to distinguish between its species. For example, our assignment of *Erimetopus* to the Potamonautidae is based on characters of the mandibular palp (2-segmented) (Bott 1955; Cumberlidge 1999), and of the second antennal segment (broad enough to fill the lateral margin of the antennular fossa). These

characters are shared with the other genera of potamonautid freshwater crabs, including *Potamonautes*. Additional family-level characters found in *Erimetopus* (which have still to be confirmed for *E. brazzae*) include a first gonopod that is in 4 parts, with a terminal article that is about one-third as long as the subterminal segment (Figs. 31–33, 42–44), and a second gonopod with a flagellum-like terminal article (Figs. 34–35).

Fortunately, even without gonopod evidence, *Erimetopus* is clearly distinct in many respects from other potamonautid genera in Africa. Characters that unequivocally characterize this genus when considered in combination include a carapace outline that is subhexagonal/rounded; a series of pointed teeth on the outer margin of the carpus of the cheliped; two large, pointed distal teeth on the superior margins of the meri of pereopods P2–P5; spines on the anterior margins of the carpi of pereopods P2–P4; spines on the anterior margins of the propodi of pereopods P2–P4; and spines on the anterior and posterior margins of the propodus of P5. Similarly, other characters of the carapace, eyes, and pereopods easily distinguish between the two species of *Erimetopus*.

The absence of gonopod evidence in this case presents a challenge to taxonomists who are continually seeking new characters (whether gonopod or not) to distinguish between taxa. In this regard, it should be remembered that gonopod characters (although informative) restrict the use of identification keys to males, whereas diagnostic characters of the carapace, eyes, anterior sternum, and pereopods offer the advantage that they permit the identification of all specimens, including females and juveniles.

The lack of gonopod evidence for *E. brazzae* prompted Bott (1955) to admit to uncertainty about the proper taxonomic placement of *Erimetopus*. Despite this uncertainty, that author took the radical taxonomic step of assigning *Erimetopus* to the genus *Potamonautes*. Bott (1955) assigned *E. brazzae* to the genus *Potamonautes* because both taxa share a 2-segmented mandibular palp, and because both lack an intermediate tooth on the anterolateral margin of the carapace between the exorbital and epibranchial teeth. However, neither of these characters is exclusive to *Potamonautes* or to *Erimetopus*. For example, a 2-segmented mandibular palp is shared by all African potamonautid genera, and an intermediate tooth is also lacking in *Potamonemus* (Cumberlidge 1999). Unfortunately, the characters used by Bott (1955) to distinguish *E. brazzae* from his subgenera of *Potamonautes* (such as differences in the cornea length and carapace anterolateral margin tooth patterns) are not shared by all species of *Erimetopus*, and are therefore interpreted here as characters suitable for species separation within the genus *Erimetopus*. In the present work, characters that are shared by both species of *Erimetopus*, and which distinguish this genus from *Potamonautes* include a subhexagonal carapace outline, the presence of a row of small teeth on the anterolateral margin between the exorbital and epibranchial teeth, 2 or 3 teeth on the outer margin of the carpus of the cheliped, and spines on the margins of the carpi and propodi of pereopods P2–P5.

In the present study we have made a cautious use of the newly available gonopod characters of *E. vandenbrandeni*, because of the absence of male specimens of *E. brazzae*, *E.*

spinosus and *P. (E.) b. frontospinulosa*. As a general rule, certain gonopod characters tend to be invariant at different taxonomic levels. For example, a four-part first gonopod (consisting of three segments plus a well-developed terminal article) is typical of that found in all families of Old World freshwater crabs (Bott 1970; Ng 1988; Cumberlidge 1999). Gonopod characters that tend to be invariant among congeners include the overall length and shape of the subterminal segments and terminal articles of gonopods 1 and 2. We consider it likely that these characters in *E. vandenbrandeni* will likely prove to be similar to those of *E. brazzae* (Bott 1955; Cumberlidge 1999) when the appropriate specimens become available.

Relationships. A number of characters seen in *Erimetopus* are also found in species of platythelphusid African freshwater crabs such as *Platythelphusa armata* (A. Milne-Edwards, 1887) from Lake Tanganyika in East Africa (Cumberlidge *et al*. 1999). These characters include a subhexagonal carapace outline, a row of small teeth on the anterolateral margin of the carapace between the exorbital and epibranchial teeth, a cheliped whose carpus has 2 or 3 teeth on the outer margin, and a front whose anterior margin projects straight out or is only slightly deflexed. However, *Erimetopus* can be easily distinguished from *Platythelphusa* as follows. The number of segments of the mandibular palp is normally used as a family-level character for the freshwater crabs (Bott 1970; Ng 1988; Cumberlidge 1999). In this case, the mandibular palp of *Platythelphusa* is 3-segmented, whereas that of *Erimetopus* is 2-segmented. In addition, the following characters in *Platythelphusa* are different from those in *Erimetopus*: the external angles of the front are either marked by sharp spines or by small granules, there is a stout triangular process (which may be produced into a small tooth) beneath the external angles of the front that descends into the orbital hiatus, and the medial end of the suborbital margin is marked by a distinct spine or small tooth (Cumberlidge *et al*. 1999). In addition, the first gonopod of *Platythelphusa* tapers to a pointed tip, whereas that of *Erimetopus* is tubular (although this character has yet to be confirmed for *E. brazzae*).

Several workers (A. Milne-Edwards 1886; Balss 1936; Bott 1970; Rodriguez 1982, 1986; Ng & Rodriguez 1995) have commented on similarities (such as the subhexagonal/rounded carapace outline and the bilobed frontal margin) between *E. brazzae* and species of South American river crabs of the family Trichodactylidae (such as *Trichodactylus* and *Dilocarcinus*). However, we consider that such similarities are insufficient to argue for a relationship between *Erimetopus* and the trichodactylids. Moreover, there are a number of major differences in the diagnostic characters of *Erimetopus* and members of the Trichodactylidae (Rodriguez 1992; Magalhães & Türkay 1996a,b,c) which strongly discount a close relationship between these taxa. For example, the mandibular palp of *Erimetopus* is 2-segmented, while that of the trichodactylids is 3-segmented; the merus of the third maxilliped of *Erimetopus* is broadly rectangular, while that of the trichodactylids is slim and triangular; and the dactyli of P2–P5 of *Erimetopus* have rows of stiff corneous spines, while those of the trichodactylids lack spines and are fringed with hair-like setae. In addi-

tion, gonopod 1 of *Erimetopus* is 3-segmented with a distinct terminal article, while that of the trichodactylids is 3-segmented, and lacks the terminal article. These conclusions are supported by a number of substantial studies that indicate that the trichodactylids belong to a lineage that is independent of any of the other freshwater crab families (including the African Potamonautidae), and that the Trichodactylidae properly belongs in, or close to, the marine superfamily Portunoidea (Rodriguez 1992; Magalhães & Türkay 1996a,b,c; Sternberg 1997, 1998; Sternberg *et al*. 1999; Sternberg & Cumberlidge 2001, 2003; Martin & Davis 2001).

Key to the African genera of Potamonautidae (modified from Cumberlidge 1999)

1 Anterolateral margin with intermediate tooth between exorbital and epibranchial teeth 2
– Anterolateral margin lacking intermediate tooth between exorbital and epibranchial teeth 4
2 Terminal article of gonopod 1 directed outward (tip pointing laterally); terminal article of gonopod 2 very short (about 0.05–0.07 times as long as subterminal segment of gonopod 2); postfrontal crest complete, lateral ends meeting anterolateral margins 3
– Terminal article of gonopod 1 directed inward (tip pointing medially); terminal article of gonopod 2 a long flagellum (about 0.5Ð0.75 times as long as subterminal segment of gonopod 2); postfrontal crest incomplete, lateral ends not meeting anterolateral margins ..... ***Liberonautes***
3 Exopod of third maxilliped lacking flagellum ..... ***Potamonemus***
– Exopod of third maxilliped with long flagellum ..... ***Sudanonautes***
4 Terminal segment of mandibular palp simple, with either small ledge or no anterior process at all 5
– Terminal segment of mandibular palp distinctly bilobed, with large anterior lobe ..... ***Louisea***
5 Carapace outline transversely oval; anterolateral margin of carapace between exorbital and epibranchial teeth smooth; outer margin of carpus of cheliped lacking teeth; carpi and propodi of pereopods P2–P5 lacking spines on their margins ..... ***Potamonautes***
– Carapace outline subhexagonal; anterolateral margin between exorbital and epibranchial teeth with row of small teeth; outer margin of carpus of cheliped with 2 or 3 teeth; carpi and propodi of pereopods P2–P5 with spines on their margins ..... ***Erimetopus***

Key to the species of *Erimetopus*

1 Frontal margin deeply indented in center forming two rounded frontal lobes; eyestalk

short, tapering; cornea reduced, pigment dorsal only; margins of meri of P2–P5 either smooth or with sparse hair-like setae; second carpal tooth of P1 large (subequal to first carpal tooth); carapace medium height (ch/fw 1.4); carapace height greater than front width; anterolateral margin of carapace behind exorbital tooth lacking sinus, curving evenly to meet epibranchial tooth ..... *E. brazzae* (A Milne-Edwards, 1886)

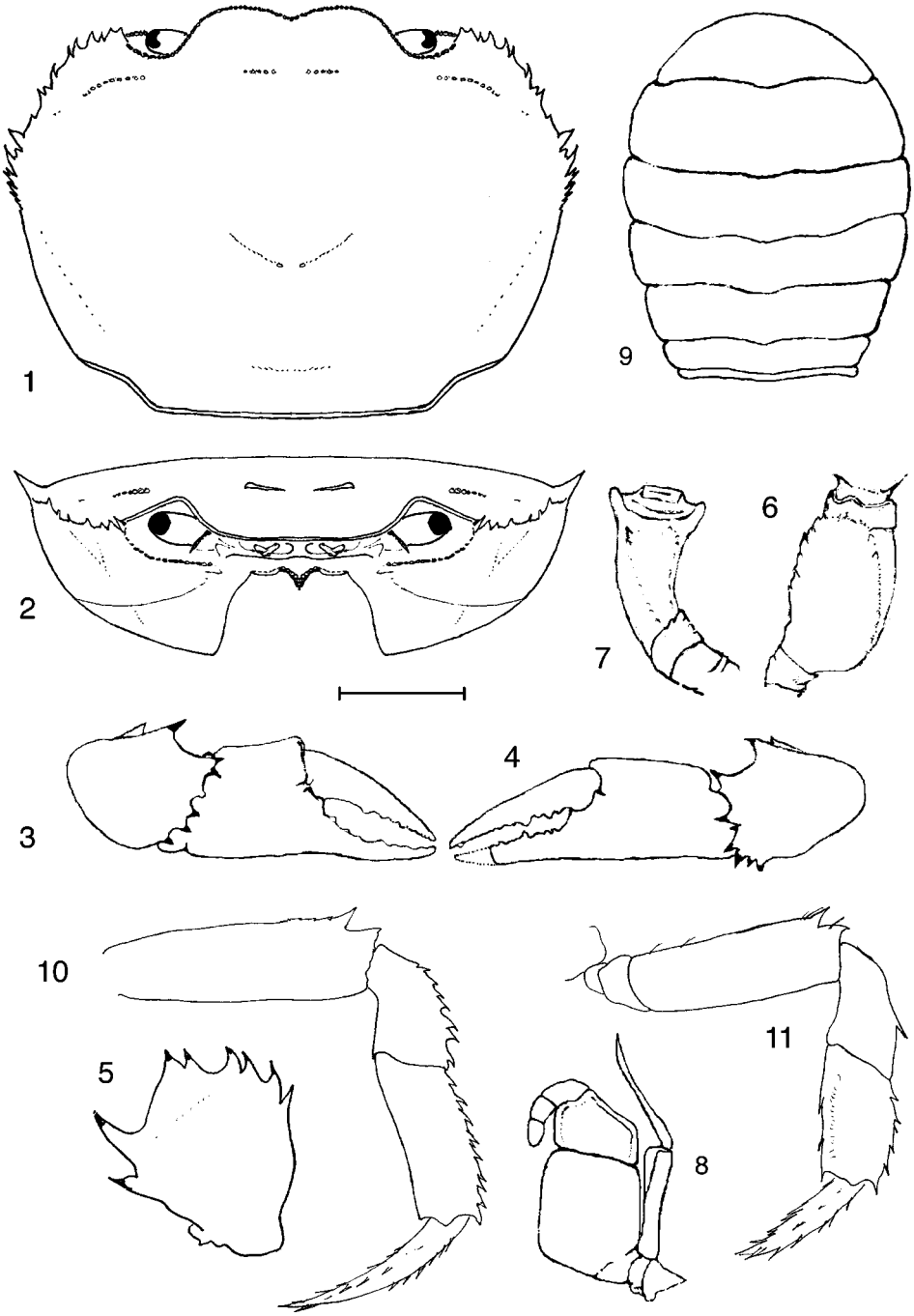
– Frontal margin either straight or only faintly indented in center; eyestalk normal length, not tapering distally; cornea not reduced, pigment dorsal and ventral; margins of meri of P2–P5 lined by dense hair-like setae; second carpal tooth of P1 reduced (much smaller than first carpal tooth); carapace very flat (ch/fw 0.9); carapace height less than front width; anterolateral margin of carapace behind exorbital tooth forming deep sinus before meeting epibranchial tooth..... *E. vandenbrandeni* **n. comb**.

1. Erimetopus brazzae (A Milne-Edwards, 1886) (Figs. 1–17, 42)

Thelphusa brazzae A. Milne-Edwards, 1886: 148; Ortmann, 1897: 300
Parathelphusa brazzae brazzae: A. Milne-Edwards, 1887: 142, pl. 8, fig. 6; de Man, 1898: 438.
Erimetopus spinosus Rathbun, 1894: 26; 1900: 285
Potamon (Acanthothelphusa) brazzae: Ortmann, 1903: 300.
Potamonautes (Erimetopus) brazzae brazzae: Bott, 1955: 224–225, fig. 7a–b, pl. III, fig. 1a–c.
Potamonautes (Erimetopus) brazzae frontospinulosa Bott, 1955: 225–226, fig. 8a–b, pl. III, fig. 2a–c.
Erimetopus brazzae: Rathbun, 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.

Type material examined: Republic of the Congo (formerly French Congo): *Thelphusa brazzae* A. Milne-Edwards, 1886 (illustrated here, designated the lectotype), female adult (cw 23.5, cl 18.5, ch 8, fw 7 mm) Ngancin (=Ngabé) 3°18’S, 16°6’E, on right bank of the river Congo opposite Kwamouth in the D. R. Congo, iv.1884, coll. M. de Brazza (MNHN-B5069). **Democratic Republic of Congo:** Paratype of *Erimetopus spinosus* Rathbun, 1894 (MCZ 4255), female, ovigerous adult (cw 38, cl 30.5 mm) Malebo Pool (formerly Stanley Pool), 2°27’0”S, 16°28’60”E, coll. J.-H. Camp, in mud under boards and timbers; paratype of *Erimetopus spinosus* Rathbun, 1894, female, ovigerous adult (cw 33.5, cl 27, ch 11.5, fw 8.5 mm), plus 13 other female paratypes, Malebo Pool, coll. J.-H. Camp, in mud under boards and timbers (USNM 18066).

Additional material examined: Democratic Republic of Congo (formerly Zaire): Kinshasa (formerly Leopoldville), female, ovigerous adult (cw 26.9 mm; egg diameter 1.4 mm), 4°17’60”S, 15°18’0”E, 1926, coll. D. van den Branden (MRAC 201); Kinshasa, female, ovigerous adult (cw 31.5 mm), 1933, coll. A. Tinant (ZSM 1528/1); Kinshasa, female adult (cw 26 mm), 7.vi.1921, coll. H. Schouteden (MRAC 1302); female adult, Malebo Pool, coll. J.-H. Camp (MCZ 4255); near Kinshasa, 2 females, coll. Dr. Christy (NHML 1904.6.2.1-2).



FIGURES 1–11. *Erimetopus brazzae* (A. Milne-Edwards, 1886), adult female lectotype, cw 23.5 mm, MNHN-B5069. 1, carapace and eyes, dorsal view; 2, cephalothorax, carapace and eyes, frontal view; 3, carpus. propodus, and dactylus of right cheliped, frontal view; 4, carpus. propodus, and dactylus of left cheliped, frontal view; 5, carpus of cheliped, superior view; 6, merus of right cheliped, dorsal view; 7, merus of right cheliped, inferior view; 8, left third maxilliped; 9, abdomen; 10, right pereopod 3; 11, right pereopod 5. Scale = 5 mm (1–2, 5, 9–11); 10 mm (3, 6–8).

FIGURES 12–14. *Erimetopus brazzae* (A. Milne-Edwards, 1886), photographs of adult female lectotype of *Thelphusa brazzae* A. Milne-Edwards, 1886, cw 23.5 mm, MNHN-B5069. 12, frontal view; 13, dorsal view; 14, underside, ventral view.

FIGURES 15–17. *Erimetopus brazzae* (A. Milne-Edwards, 1886), photographs of adult female lectotype of *Erimetopus spinosus* Rathbun, 1894 cw 33.5 mm, USNM 18066. 15, frontal view; 16, dorsal view; 17, underside, ventral view.

Diagnosis. Frontal margin deeply indented in center forming two rounded frontal lobes; eyestalk short, tapering; cornea reduced, pigment dorsal only; margins of meri of P2–P5 either smooth or with sparse hair-like setae; second carpal tooth of cheliped large (subequal to first carpal tooth); carapace medium height (ch/fw 1.4); carapace height greater than front width; anterolateral margin of carapace behind exorbital tooth lacking sinus, curving evenly to meet epibranchial tooth.

Redescription. Carapace outline subhexagonal/rounded; anterolateral margin of carapace between exorbital, epibranchial teeth very long, with several irregular pointed teeth, lacking identifiable intermediate tooth; anterolateral margin behind exorbital tooth long, curving evenly to meet epibranchial tooth; anterolateral margin posterior to epibranchial tooth with row of five small teeth, continuous with posterolateral margin. Frontal margin smooth, distinctly indented in center forming two rounded frontal lobes; front horizontal (not deflexed); postfrontal crest incomplete, epigastric lobes prominent, significantly separated from weak postorbital crests; lateral ends of postorbital crests not meeting anterolateral margins. Exorbital tooth large, pointed, bifurcated (with second smaller tooth immediately behind it); epibranchial tooth large, sharp, pointing forward, positioned well behind postorbital crest; eyestalk short, tapering distally, cornea reduced, pigment dorsal only; orbit narrow (1/7 cw), upper orbital margin semi-circular. Carapace medium height (ch/fw 1.4), height greater than front width; front width almost one-third carapace width (fw/cw 0.3); carapace sidewall with distinct vertical sulcus, ending before meeting anterolateral margin midway between exorbital and epibranchial teeth, dividing sidewall into three parts. Exopod of third maxilliped with long flagellum; ischium smooth, lacking vertical sulcus. Epistomial tooth triangular, margin granulated; antennular fossae very wide, angled upward at lateral margins; second antennal segments broad, filling lateral margins of antennular fossae. Thoracic sternal sulcus s1/s2 either faint or absent; thoracic sternal sulcus s2/s3 deep, v-shaped, completely crossing sternum; thoracic sternal sulcus s3/s4 reduced to two small side notches; sternum in this region completely smooth. Episternal sulci s4/e4, s5/e5, s6/e6 and s7/e7 each marked by visible groove.

Chelipeds of adult female slim, slightly heterochelous, both fingers long, narrow, with small even teeth; dactylus not arched. First carpal tooth on inner margin of carpus of cheliped large, slender, pointed, curving forward; second carpal tooth pointed, subequal to first tooth, directed inward; outer margin of carpus of cheliped with up to seven pointed teeth, two close to condyle of propodus. Lateral, medial inferior margins of merus of cheliped smooth, with single small, pointed tooth at distal end. Carpi of P2–P4 with spines on anterior margins, posterior margins smooth; carpus of P5 with single spine on anterior margin, posterior margin smooth; propodi of P2–P4 with spines on anterior margins, posterior margins smooth; propodus of P5 with spines on anterior and posterior margins. Dactyli of P2–P5 with rows of strong spines. *Erimetopus brazzae* is a small species with an adult size range between cw 23.5–33.5 mm.

Distribution. Central Africa, associated with the lower reaches of the Congo River from Ngancin (=Ngabé, Republic of the Congo) to Gombe–Matadi (D. R. Congo) 4°58'60"S, 14°43'0"E and in the southeastern tributaries of the Congo River (the Kwa, Kwilu, and Kwango rivers) in the D. R. Congo (Fig. 45). We have included here a number of localities taken from Bott (1955) who listed material from Kidzueme (= Kidzweme) 3°58'0"S, 18°26'60"E, Moluma stream, Kwilu river, a tributary of the river Kwango in the D. R. Congo collected by E. Dartevelle in 1947 (MRAC 31964–31967, 33042–33045, 33082–33084). We have been unable to confirm the report by Rathbun (1894) that this species occurs in Gabon. This species has a relatively narrow distribution, is not well represented in museum collections, and has not been collected (to our knowledge) since 1947. For these reasons we would judge its conservation status to be in the Critically Endangered category (Red List Criteria A2) of the Red List Assessment (IUCN 2001).

Discussion. Rathbun (1894, 1921) and Capart (1954, fig. 43) each provided a brief description and illustration of the dorsal carapace of the female lectotype from Ngancin (Ngabé, Republic of the Congo), while Bott (1955) provided a detailed description, illustrations, and photographs of a specimen of *E. brazzae* from Kidzueme (= Kidzweme, D. R. Congo). It should be noted that there is a difference between the carapace characters of the specimen of *E. brazzae* from Kidzueme illustrated by Bott (1955: Fig. 7a–b) and the type of *E. brazzae* from Ngancin (=Ngabé) examined in the present study. For example, the postfrontal crest of *E. brazzae* from Kidzueme completely crosses the carapace in the sketch by Bott (1955: Fig. 7a–b), but the crest is incomplete (see Fig. 1; Capart 1954, fig. 43) in the lectotype from Ngancin.

Here we follow the opinion of other authors (Rathbun 1905, 1921; Balss 1936; Bott 1955) and treat *E. spinosus* as a junior synonym of *E. brazzae* following our comparison of the two paratypes of *E. spinosus* Rathbun, 1894 (USNM 18066, adult female, cw 33.5 mm; MCZ 4255, cw 30.4 mm) with the lectotype of *E. brazzae* (MNHN-5069, adult female, cw 23.5 mm). For example, the carapace height, incomplete postfrontal crest, size of the exorbital and epibranchial teeth, the lack of a deep sinus on the anterolateral margin before it meets the epibranchial tooth, the tooth patterns on the margins of the meri, carpi, propodi, and dactyli of P2–P5, the eyestalk length, cornea size, and orbit shape of *E. spinosus* are all essentially the same as in *E. brazzae*. In addition, although the carapace height of *E. brazzae* (ch/fw 1.4) indicates a possible difference from that of *E. spinosus* (ch/fw 1.1), both values fall within the range of those freshwater crabs that have a carapace of medium height (ch/fw 1.1–1.4) (Cumberlidge 1999). These two taxa differ in the toothing on the anterior margin of the carpus of P5 (which has a single tooth in *E. brazzae* but several teeth in *E. spinosus*), and in the toothing on the anterior face of the carpus of P1 (which has three teeth in *E. brazzae* but five teeth in *E. spinosus*). We consider that these differences between *E. brazzae* and *E. spinosus* represent intraspecific variability and that they are not substantial enough to warrant the recognition of separate taxa.

Unfortunately, all known specimens of *P. (E.) b. frontospinulosa* described by Bott (1955) (the holotype, cw 26, cl 20, ch 8, fw 7 mm, MRAC 38391, and all 17 paratypes, MRAC 38391–38400, 38366–38372), collected by E. Dartevelle in March 1948 from the Luari River, Gombe–Matadi in the D.R. Congo are apparently lost. In the absence of these specimens, our conclusions regarding the taxonomic status of *P. (E.) b. frontospinulosa* Bott, 1955 are based on our study of the photographs and sketches provided by Bott (1955). *Potamonautes (E.) b. frontospinulosa* is similar in many respects to *E. brazzae*. For example, the incomplete postfrontal crest, the relative sizes of the exorbital and epibranchial teeth, the large and pointed second carpal tooth of the cheliped, the presence of, and the arrangement of teeth on the margins of the meri, carpi, propodi, and dactyli of P2–P5, the reduced eyestalk length and cornea size, and the semi-circular upper orbital margin of *P. (E.) b. frontospinulosa* are all essentially the same as in *E. brazzae*. In addition, the carapace proportions of *E. brazzae* (ch/fw 1.4) and *P. (E.) b. frontospinulosa* (ch/fw 1.1) fall within the range of those freshwater crabs with a carapace of medium height (ch/fw 1.1–1.4) (Cumberlidge 1999).

Potamonautes (E.) b. frontospinulosa differs from *E. brazzae* (and is closer to *E. vandenbrandeni*) in its possession of the following characters. The frontal margin is distinctly indented in *E. brazzae*, but this margin is either straight and not indented (as in the photograph of *P. (E.) b. frontospinulosa*), or it is indented (as in the illustration of the same specimen by Bott (1955: fig. 8a,b)); and the front is of medium width in *E. brazzae* (fw/cw 0.4), but more narrow in *P. (E.) b. frontospinulosa* (fw/cw 0.3) (Cumberlidge 1999). The vertical groove on the carapace sidewall meets the base of the epibranchial tooth in *P. (E.) b. frontospinulosa*, and there is a deep sinus on the anterolateral margin before it meets the epibranchial tooth (this sinus is lacking in *E. brazzae*). Bott (1955) presumably named this taxon because of its possession of spines on the frontal margin. However, although Bott's (1955, fig. 8a,b) sketch shows distinct teeth on the frontal margin of *P. (E.) b. frontospinulosa*, Bott's (1955: Pl. 3, figs. 2a–c) photographs show this margin to be granular. It is possible that Bott's sketches and photographs depict different specimens of *P. (E.) b. frontospinulosa*, and that this character (which Bott (1955) considered to be diagnostic of the subspecies) is variable.

In the absence of the opportunity to examine actual specimens of *P. (E.) b. frontospinulosa*, we hesitate to offer further opinion on the taxonomic position of *P. (E.) b. frontospinulosa*. We therefore follow the opinion of Bott (1955) and provisionally treat this taxon as a subspecies of *E. brazzae* until more material becomes available.

Natural history. The type locality of *E. brazzae* is from Ngancin (=Ngabé) in the Republic of the Congo, which is on the right bank of the lower Congo River, at a stretch where the river banks are up to 1.5 km apart. Ngancin (=Ngabé) is directly opposite Kwamouth in the D. R. Congo (Fig. 45). Here the river is deep and fast flowing, and the volume of water very high, because this section of the river is where the Congo is joined by the Ubangi, Sangha, and Kwa Rivers. Close to Kinshasa the Congo River forms the

Malebo Pool, a large lake-like stretch of water about 25 km by 30 km. All the adult egg-bearing females of *E. brazzae* known so far have been found either in the swampy areas of the lower Congo River and its tributaries, or on the banks of Malebo Pool, rather than in the river itself (Fig. 45). The fact that only egg-bearing females have been collected between April and June, and that these were all taken from muddy ground near the river banks (either under stones, under boardwalks, or tangled in water plants) has given rise to speculation that this species releases its hatchlings in such habitats, but spends the rest of its lifecycle elsewhere. At Malebo Pool *E. brazzae* occurs together with *Potamonautes paecilei* (A. Milne-Edwards, 1886) in mud under boards and timbers.

In general, species of African freshwater crabs that have extensive spines on their carapace margins (such as *P. niloticus, L. chaperi*, and *P. armata*) are aquatic animals that typically live in rivers and lakes rather than in small streams, or on land (Balss 1936; Cumberlidge 1999; Cumberlidge & Sternberg 1999). Species of crabs that have reduced eyestalks and corneas typically live in habitats such as caves where light intensity is low (Ng 1989a,b; 1990, 1992; Ng & Goh 1987; Ng & Guinot 1998; Ng & Trontelj 1996; Ng & Whitten 1995; Ng & Yussof 1990; Ng *et al*. 1994; Takeda & Ng 2001), or even in the darkness of deep-sea hydrothermal vents (Williams 1980; Guinot 1989). Bott (1955) interpreted the spines on the margins of the carapace, chelipeds, and walking legs, and the reduced eyestalks and corneas of *E. brazzae* as indicators that these crabs burrowed into muddy substrata where the light intensity was low. Rathbun (1921) and Bott (1955) speculated that the egg-bearing females of *E. brazzae* moved to more oxygen-rich, plant-filled waters during the breeding season in order to meet the greater oxygen demands of the developing hatchlings. Bott (1955) considered that the original function of the spines on the carapace margins and walking legs of the ancestors of freshwater crabs somehow prevented these animals from sinking into soft muddy substrata. Cumberlidge (1999) considered that it would be equally likely that spines on the carapace margins and legs served to deter attacks by soft-mouthed aquatic predators (such as fish).

2. Erimetopus vandenbrandeni (Balss, 1936) n. comb. (Figs. 18–45)

Potamon (Potamonautes) vandenbrandeni Balss, 1936: 190, fig. 26.
Potamon vandenbrandeni: Chace, 1942: 223.
Potamonautes (Longipotamonautes) vandenbrandeni: Bott, 1955: 240–241, fig. 22A, 69A,a–b, pl. III, fig. 3a–b.

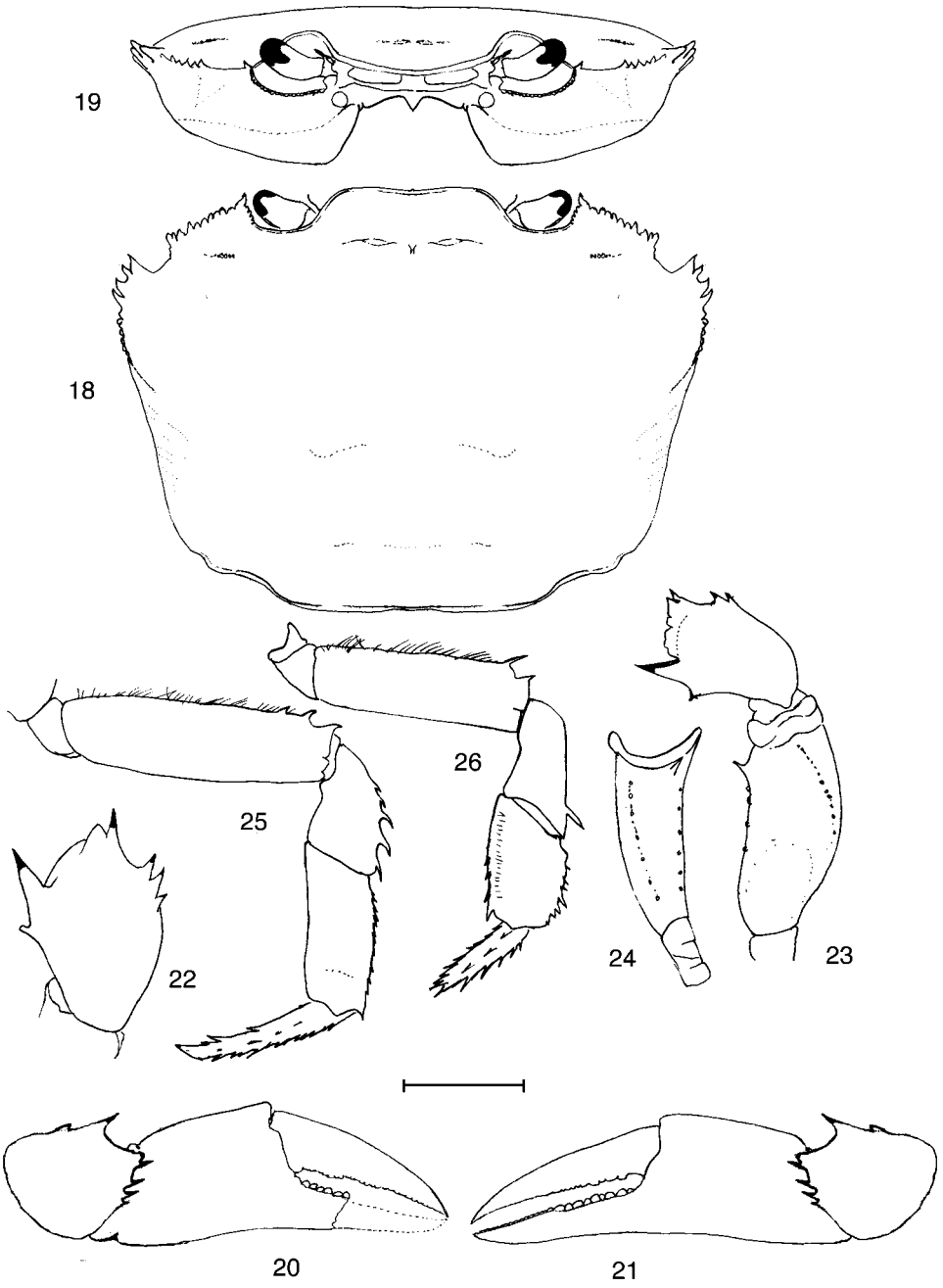
Type material: Democratic Republic of Congo (formerly Zaire): Lectotype (here designated), male subadult (cw 16.8, cl 12.4, ch 4, fw 4.4 mm) Kinshasa, 04°17’60”S, 15°18’ E, coll. G. F. de Witte, 31.viii.1930 (MRAC 1273). Paratypes, 2 females, both ovigerous (cws 30.4, 28.5 mm) Kinshasa S 04°19’, E 015°19’, 1926, coll. Dr. van den Branden (MRAC 247-248). Paratype, female, ovigerous (cw 35.5 mm) coll. Dr. van den Branden,

1926 (MRAC 251); paratype, female, ovigerous (cw 29.8 mm), Kinshasa, coll. Dr. van den Branden, 1926 (MRAC 252); paratype, female, ovigerous, Kinshasa, 1931, coll. C. Henrard (MRAC 1640).

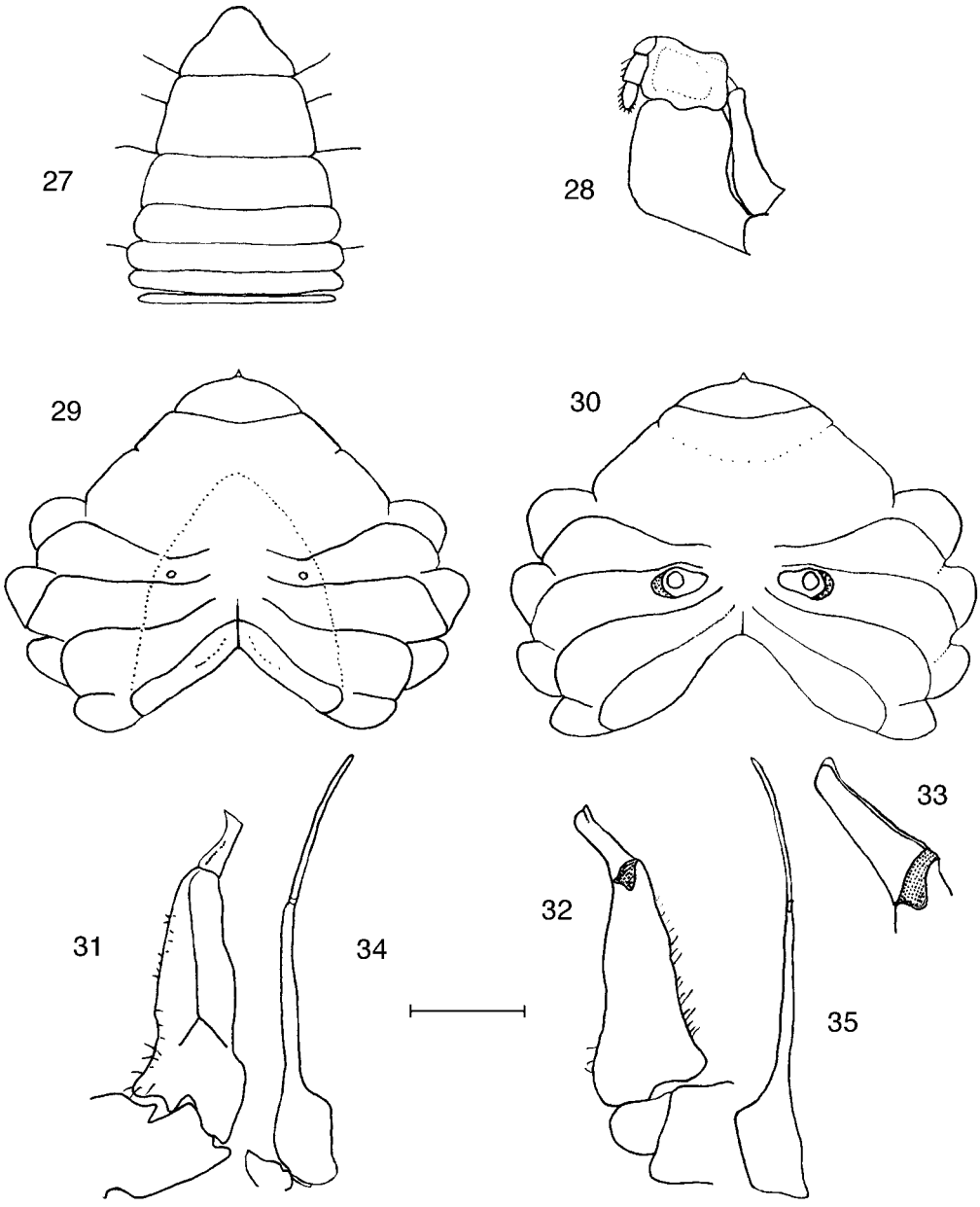
Additional material. Democratic Republic of Congo: female, ovigerous (cw 30 mm) Kinshasa, coll. Dr. van den Branden, 1926 (MRAC 249); female, ovigerous (cw 33.8 mm), Kinshasa, coll. Dr. van den Branden, 1926 (MRAC 250); female, ovigerous (cw 35.1 mm), Kinshasa, coll. Dr. van den Branden, 1926 (MRAC 253); female, ovigerous (cw 38 mm), Kinshasa, coll. Dr. van den Branden, 1925 (MRAC 1557); female, ovigerous (cw 35.2 mm), Kinshasa, coll. Dr. van den Branden, 1925 (MRAC 1559); 3 females, all ovigerous (cws 24.9, 22.7 mm, one damaged), Kinshasa, coll. Dr. van den Branden, 1930 (MRAC 1566–1568); 2 females, both ovigerous (cws 24, 22.6 mm), Kinshasa, coll. C. Henrard, 1931 (MRAC 1634–1635); 4 females, all ovigerous (cws 31.2, 25.8, 25.8, 22.6 mm), Kinshasa, coll. C. Henrard, 1931 (MRAC 1636–1639).

Diagnosis. Frontal margin smooth; either straight or only faintly indented in center; eyestalk normal length, not tapering distally; cornea not reduced, pigment dorsal and ventral; margin of meri of P2–P5 lined by dense hair-like setae; second carpal tooth of P1 reduced (much smaller than first carpal tooth); carapace very flat (ch/fw 0.9); carapace height less than front width; anterolateral margin between exorbital, epibranchial teeth very long, straight, directed outward then curving sharply inward, forming deep sinus before meeting epibranchial tooth; terminal article of gonopod 1 one-third as long as subterminal segment, terminal article tubular with parallel sides, medial and lateral folds low and even throughout length, tip of terminal article broad, with distinct triangular medial corner; distal margin of subterminal segment of gonopod 1 distinctly indented in middle; dorsal membrane broadest in middle, tapering sharply at both sides, narrowest at lateral and medial margins; gonopod 2 long, terminal article long, slender, flagellum-like.

Redescription. Carapace outline subhexagonal/rounded. Frontal margin smooth, either straight or faintly indented in center; front horizontal or only slighlty deflexed; front narrow (fw/cw 0.3); postfrontal crest incomplete, epigastric lobes continuous with postorbital crests, but lateral ends of postorbital crests not meeting anterolateral margins. Exorbital tooth small, pointed; epibranchial tooth large, sharp, directed forward, positioned well behind postfrontal crest. Eyestalks normal length, not tapering distally; cornea not reduced, pigment dorsal and ventral; orbit narrow (1/7 cw), upper orbital margin semi-circular; carapace flat, height less than front width (ch/fw 0.9). Anterolateral margin of carapace between exorbital and epibranchial teeth lacking intermediate tooth; margin granulated, very long, straight, directed outward, then curving sharply backward, forming deep sinus before meeting epibranchial tooth; anterolateral margin of carapace posterior to epibranchial tooth with two small teeth behind epibranchial tooth; margin continuous with posterolateral margin. Carapace sidewall with vertical sulcus, curving upward from longitudinal groove to meet anterolateral margin at exorbital tooth, dividing sidewall into three parts. Second antennal segments broad, filling lateral margins of antennular fossae.



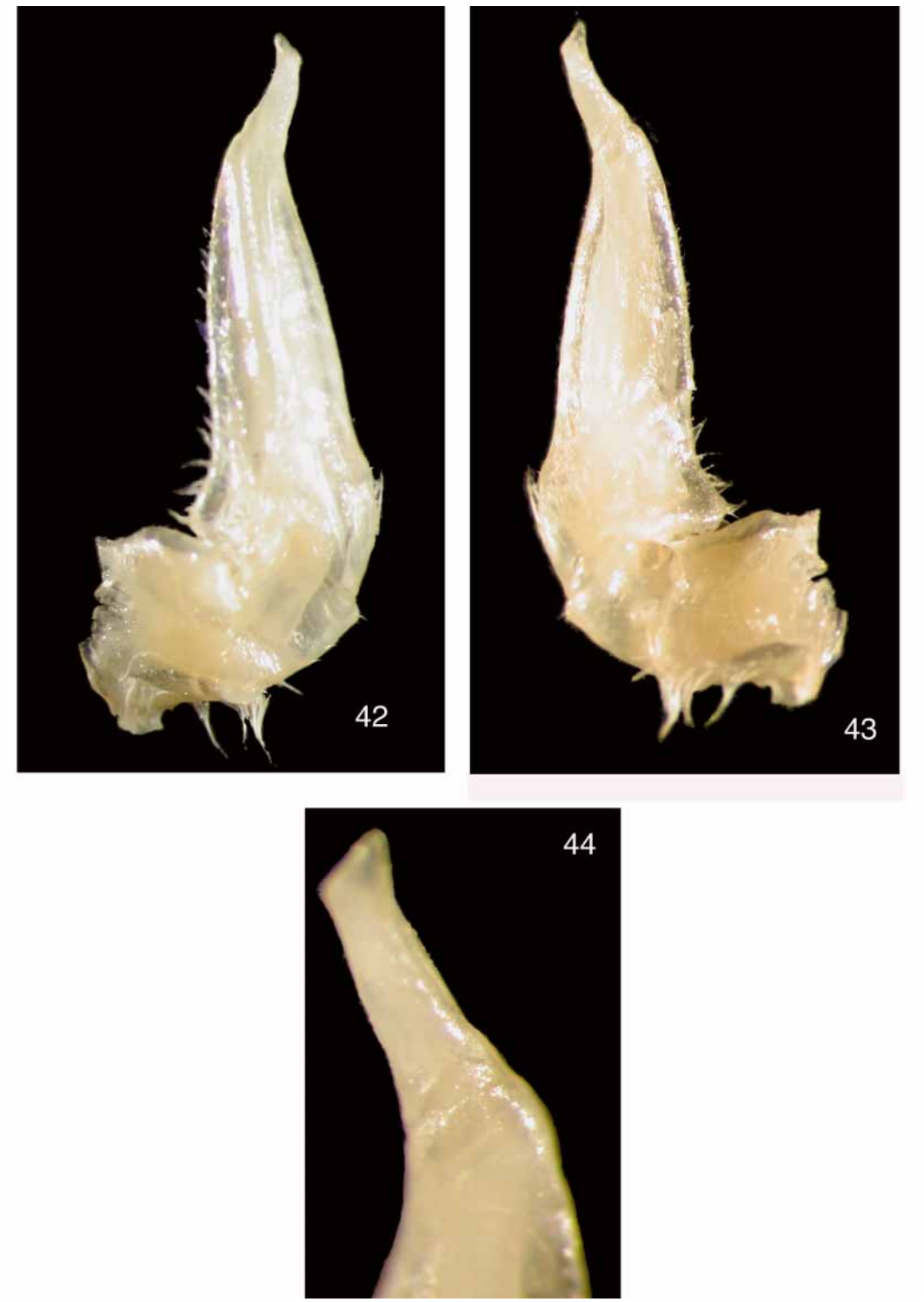
Figures 18–26. *Erimetopus vandenbrandeni* **n.comb.** (Balss, 1936) adult female paratype (cw 29.5 mm), MRAC 1273. 18, carapace and eyes, dorsal view; 19, cephalothorax, carapace and eyes, frontal view; 20, carpus. propodus, and dactylus of right cheliped, frontal view; 21, carpus. propodus, and dactylus of left cheliped, frontal view; 22, carpus of cheliped, superior view; 23, carpus and merus of right cheliped, dorsal view; 24, merus of right cheliped, inferior view; 25, right pereopod 3; 26, right pereopod 5. Scale = 5 mm (18–19, 22, 25–26); 10 mm (20–21, 23–24).



Figures 27–35. *Erimetopus vandenbrandeni* **n. comb.** (Balss, 1936). 27–29, 31–35, subadult male lectotype, cw 16.8 mm, MRAC 1273. 30, adult female paratype (cw 29.5 mm), MRAC 252. 27, abdomen; 28, left third maxilliped; 29, anterior sternum (male); 30, anterior sternum (female); 31, left gonopod 1, ventral aspect; 32, left gonopod 1, dorsal aspect; 33, left gonopod 1 terminal article, dorsal aspect, detail; 34, left gonopod 2, ventral aspect; 35, left gonopod 2, dorsal aspect. Scale = 5 mm (27–30); 3 mm (31–32, 34–35); 1 mm (33).

FIGURES 36–38. *Erimetopus vandenbrandeni* **n. comb.** (Balss, 1936), photographs of adult female paratype (cw 29.5 mm), MRAC 252. 36, frontal view; 37, dorsal view; 38, underside, ventral view.

FIGURES 39–41. *Erimetopus vandenbrandeni* **n. comb.** (Balss, 1936), photographs of subadult male lectotype (cw 16.5 mm), MRAC 1273. 39, frontal view; 40, dorsal view; 41, underside, ventral view.



FIGURES 42–44. *Erimetopus vandenbrandeni* **n. comb.** (Balss, 1936), photographs of subadult male lectotype (cw 16.5 mm), MRAC 1273. 42, first gonopod ventral view; 43, first gonopod dorsal view; 44, first gonopod terminal article, dorsal view.

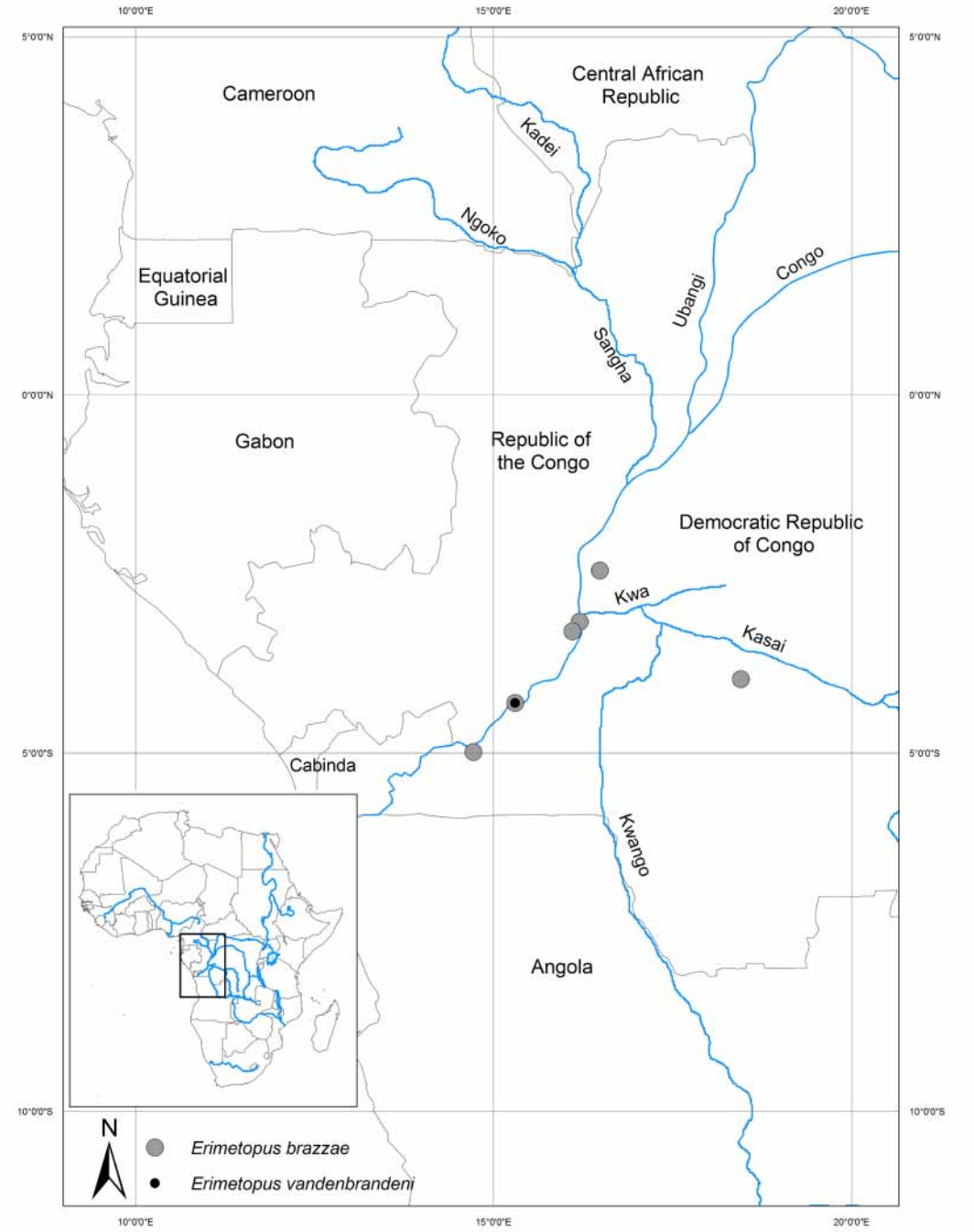


FIGURE 45. Summary of the distribution of *Erimetopus brazzae* (A. Milne-Edwards, 1886) (large grey circles) and *E. vandenbrandeni* (Balss, 1936) (small black circle). Locality data are from the present study and from the literature (Rathbun 1905, 1921; Balss 1936; Bott 1955).

Exopod of third maxilliped with long flagellum, ischium smooth, lacking vertical sulcus. Thoracic sternal sulcus s1/s2 either faint or absent; thoracic sternal sulcus s2/s3 deep,

slightly curved, running horizontally across sternum; thoracic sternal sulcus s3/s4 reduced to two small side notches. Episternal sulci s4/e4, s5/e5, s6/e6, s7/e7 each marked by visible groove.

Chelipeds of adult female and subadult male lectotype slim, slightly heterochelous, with long narrow fingers (dactylus, propodus), dactylus not arched, teeth of both fingers small, even. First carpal tooth on inner margin of carpus of cheliped large, slender, pointed, curving forward, second carpal tooth very small (0.25 x first carpal tooth); series of small teeth on outer margin of carpus of P1. Lateral, medial inferior margins of merus of cheliped faintly granular, single small pointed distal meral tooth superior surface of merus granular. Carpi of P2–P4 with spines on anterior margins, posterior margins smooth; carpus of P5 with single spine on anterior margin, posterior margin smooth; propodi of P2–P4 with spines on anterior margins, posterior margins smooth; propodus of P5 with spines on anterior and posterior margins; meri of P2–P5 with two sharp pointed distal teeth; margins of dactyli of P2–P5 with rows of strong spines. P5 shortest walking leg, propodus P5 broad, dactylus P5 very short, about half as long a dactyli of P2–P4. Terminal article of gonopod 1 one-third as long as subterminal segment, terminal article tubular with parallel sides, medial and lateral folds low and even throughout length, tip of terminal article broad, with distinct triangular medial corner; distal margin of subterminal segment of gonopod 1 distinctly indented in middle; dorsal membrane broadest in middle, tapering sharply at both sides, narrowest at lateral, medial margins. Subterminal segment of gonopod 2 broad-based, tapering sharply to long slim process, terminal article of gonopod 2 long, slender, flagellum-like. *Erimetopus vandenbrandeni* is a small species with an adult size between cw 22.6 and 38 mm. For more details, and illustrations of the type material see Balss (1936, fig. 26), for a description, photographs, and illustrations of other specimens see Bott (1955).

Distribution. *Erimetopus vandenbrandeni* is found either in, or near, the Congo River in the vicinity of Kinshasa, D. R. Congo (Fig. 45). Balss (1936) based his description on three lots of specimens, all from Kinshasa, and Bott (1955) reported on two female specimens from Kalima (near Kinshasa) collected by E. Dartevelle in 1948 (MRAC 31998, 32910). This species has a relatively narrow distribution, is not well represented in museum collections, and has not been collected (to our knowledge) since 1935. For these reasons we would judge its conservation status to be in the Critically Endangered category (Red List Criteria A2) of the Red List Assessment (IUCN 2001).

Relationships. *Erimetopus vandenbrandeni* is close to *E. brazzae* and has a similar subhexagonal carapace outline, similar tooth patterns on the carapace margins and walking legs, a large epibranchial tooth, and a long, toothed anterolateral margin of the carapace between the exorbital and epibranchial teeth. *Erimetopus vandenbrandeni* differs from *E. brazzae* as follows. The carapace of *E. vandenbrandeni* is conspicuously flattened (it is of medium height in *E. brazzae*), the second carpal tooth on the inner margin of the carpus of the cheliped of *E. vandenbrandeni* is small (this tooth is large in *E. brazzae*), and the supe-

rior margins of the meri of the walking legs P2–P5 have dense hair-like setae (these margins lack setae in *E. brazzae*). In addition, the vertical groove on the carapace sidewall of *E. vandenbrandeni* meets the base of the epibranchial tooth (this groove is not directed toward the epibranchial tooth in *E. brazzae*); there is a deep sinus on the anterolateral margin just anterior to the epibranchial tooth in *E. vandenbrandeni* (this sinus is lacking in *E. brazzae*), and the frontal margin of of *E. vandenbrandeni* is straight (this margin is distinctly indented in *E. brazzae*). *Erimetopus vandenbrandeni* shares characters such as a straight frontal margin, and a row of hair-like setae on the meri of P2–P5 with *P. (E.) b. frontospinulosa*. However, *E. vandenbrandeni* can be easily distinguished from *P. (E.) b. frontospinulosa* by the same characters outlined above that distinguish *E. vandenbrandeni* from *E. brazzae*.

Remarks. Only a single subadult male specimen (cw 16.8 mm) of *E. vandenbrandeni* is known (Figs. 27–35, 39–45). The gonopods of *E. vandenbrandeni* were not illustrated by Balss (1936) in the original description of this species, but gonopod 1 of the male of *E. vandenbrandeni* was sketched by Bott (1955: 22A), although Bott did not list this specimen in the material examined section of his work. Gonopod 1 of the male of *E. vandenbrandeni* from Kinshasa is shown in more detail in the present study (Figs. 31–33, 42–44), and gonopod 2 of this species is illustrated here for the first time (Figs. 34–35).

The general form of gonopods 1 and 2 of *E. vandenbrandeni* is the same as that found in the Old World potamonautid and potamid freshwater crabs (Bott 1955, 1970; Cumberlidge 1999). For example, gonopod one is in four parts that include a relatively well-developed terminal article and a broad dorsal membrane. This also describes the general organization of the first gonopod of a number of African genera such as *Potamonautes, Liberonautes, Sudanonautes, Potamonemus, Louisea, Afrithelphusa, Globonautes, Platythelphusa,* and *Deckenia* (Cumberlidge 1999). Similarly, gonopod two is in four parts that include a relatively well-developed flagellum-like terminal article. These characteristics also describe the general organization of the second gonopod of African genera such as *Potamonautes, Liberonautes, Louisea, Afrithelphusa, Platythelphusa* and *Deckenia* (Cumberlidge 1999).

Bott (1955) assigned *E. vandenbrandeni* to *Potamonautes* (*Longipotamonautes*) on the basis of perceived similarities between the shape of the terminal article of gonopod 1 in *E. vandenbrandeni* and *Potamonautes ballayi* (A. Milne-Edwards, 1887) (the type-species of the subgenus *Longipotamonautes* Bott, 1955). Although the terminal article of gonopod 1 of *P. ballayi* has a broad tip that is somewhat similar to that of *E. vandenbrandeni*, the terminal article in *P. ballayi* is distinctly tapered (which is typical of *Potamonautes*), rather than tubular and hose-like, as in *E. vandenbrandeni.* Moreover, the first gonopod of *E. vandenbrandeni* (Figs. 31–33, 42–44) differs from *P. ballayi* in other characters such as the shape of the dorsal membrane, the shape of the distal margin of the subterminal segment, and the position and definition of the longitudinal (seminal) groove of the terminal article (Capart 1954; Bott 1955, fig. 23).

It should be noted that the hose-like terminal article of the first gonopod of *E. vandenbrandeni* is neither identical to, nor close in organization to, the strongly-tapered terminal article of the more than 60 species of *Potamonautes* that we are familiar with. Moreover, *P. ballayi* (which is the species of *Potamonautes* that is closest to *E. vandenbrandeni* according to Bott (1955)) is in fact distinctly different from *Erimetopus* when non-gonopod diagnostic characters of the carapace, pereopods and mouthparts are considered (Bott 1955). For example, like all species of *Potamonautes*, *P. ballayi* lacks teeth on the anterolateral margin of the carapace between the exorbital and epibranchial teeth, lacks teeth on the outer margin of the carpus of the cheliped, and lacks teeth or setae on the margins of the carpi and propodi of the walking legs (P2–P4). In addition, *P. ballayi* can be further distinguished from *Erimetopus* by the former taxon's lack of teeth on the anterolateral margin behind the epibranchial tooth, by a distinctly arched dactylus of the major cheliped, and by a complete and deep sternal sulcus s3/s4.

There are only a few other species of freshwater crabs in Africa with a noticeably flat carapace similar to that found in *E. vandenbrandeni*. Examples include the completely aquatic lake-living crab *Platythelphusa maculata* (ch/fw 0.9) and the West African river crab *Liberonautes chaperi* (ch/fw 0.9) (Cumberlidge *et al*. 1999; Cumberlidge 1999). In general, African freshwater crabs with a flat carapace tend to be completely aquatic river or lake dwellers that rarely, if ever, breathe air at any point in their life cycle (Cumberlidge 1999). It remains to be seen whether this generalization applies to *E. vandenbrandeni*, and the answer to questions such as this must await data from new field collections in the lower Congo River. Given the current long-term political unrest in Central Africa, it may be a very long time before anyone is in a position to collect thoroughly enough to obtain a series of male specimens of any species of this interesting genus.

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