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Surveys of Afrotemperate forests yields two new freshwater crabs (Decapoda: Potamonautidae: *Potamonautes* MacLeay, 1838) from South Africa

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Abstract. Sampling of remote inland aquatic habitats in South Africa has constantly been yielding novel endemic freshwater crab species (*Potamonautes* MacLeay,1838). During the present study, we report on the discovery and description of two new freshwater crab species (*Potamonautes baziya* sp. nov., and *P. mariepskoppie* sp. nov.) from Afrotemperate forested mountain regions in the Eastern Cape and Mpumalanga provinces of South Africa, respectively. Phylogenetic evidence derived from DNA sequence data of three partial mitochondrial loci (12S rRNA, 16S rRNA and cytochrome oxidase subunit one, COI) corroborates the evolutionary distinction of the two novel species. In addition, morphological and ecological data for the two new species further delineate their evolutionary distinction from congeneric sister species. A comparison of the taxonomically important gonopods 1 and 2 and carapace features among the sister species and other known freshwater crabs of South Africa was further used to provide evidence for the distinction of the two novel species. The discovery of two new species suggest that remote mountainous areas or unsampled regions in South Africa likely harbor several novel species, reiterating a call to document aquatic inland biodiversity in forested and mountainous regions of the country.

Keywords. Aquatic biodiversity, Decapoda, evolutionary relationships, novel lineages.

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Introduction

The alpha taxonomy of South African freshwater crabs (*Potamonautes* MacLeay, 1838) is well-established and an exemplar of one of the best studied inland aquatic crustacean groups in the Afrotropical region (Daniels 2017; Daniels *et al.* 2012, 2019; Peer *et al.* 2015, 2017; Phiri & Daniels 2014, 2016). The discovery of new freshwater crab species was largely galvanized by the application of molecular tools such as allozyme electrophoresis and more recently DNA sequencing (Daniels 2017; Daniels *et al.* 2014, 2019, 2020b; Gouws *et al.* 2000, 2001; Peer *et al.* 2015, 2017; Phiri & Daniels 2014, 2016). In addition, a new species is currently being described from Hogsback in the Eastern Cape Province (Peer pers. comm.). All of the recently documented diversity appears to be narrow endemic species, suggesting that fine-scale sampling is required to document the true taxonomic diversity of the group. Furthermore, the continued discovery of new freshwater crab species can be attributed to the fact that large areas of the country remain unsampled. These areas should be the focus of future systematic surveys, particularly in areas or biomes where habitats are naturally fragmented, creating an ideal template for allopatric speciation.

Currently, 24 *Potamonautes* species are known from South Africa, with inland aquatic habitats of the Eastern Cape and Mpumalanga provinces remaining particularly poorly sampled and likely harboring undescribed species. In the Eastern Cape, four freshwater crab species are present: *P. barbarai* Phiri & Daniels, 2014, *P. danielsi* Peer & Gouws, 2017, *P. mhlophe* Daniels, 2017, and the new, as yet undescribed freshwater crab species from Hogsback, along the Amathola Mountains (Peer pers. comm.). In Mpumalanga, five freshwater crab species are present: *P. sidneyi* Rathbun, 1904, *P. warreni* Calman, 1918, *P. calcaratus* Gordon, 1929, *P. unispinus* Stewart & Cook, 1998 and *P. flavusjo* Daniels, Phiri & Bayliss, 2014. Unpublished DNA sequence data indicate that *P. danielsi* is confined to southern KwaZulu-Natal and the Eastern Cape provinces and does not occur in Mpumalanga province, as suggested by Peer *et al.* (2017) (Daniels unpubl.). *Potamonautes sidneyi* is a species complex that contains several cryptic lineages and is currently the focus of an ongoing study (Gouws *et al*. 2015; Daniels unpubl.). Recent surveys of inland freshwater systems in the Eastern Cape and Mpumalanga provinces resulted in the collection of morphologically distinct specimens that could not be assigned to any of the above or other described species. The specimens from Baziya forest station in the Eastern Cape were initially collected during a Foundational Biodiversity Initiative Program, funded by the National Research Foundation, that focused on forest biodiversity in the province. Initial genetic data from the Baziya freshwater crab specimens indicated that these were distinct from known species; however, the original specimens were subsequently lost, requiring resampling during the present study. While sampling wetlands, the second species was collected from the lowveld section of the Blyde Canyon Nature Reserve in the shadow of the Mariepskop Mountains in Mpumalanga Province. The purpose of the present study is to describe the two novel freshwater crab species, to determine their phylogenetic placement and compare their morphology with congeneric species present in South Africa.

Material and methods

Freshwater crabs were hand collected from under stones in streams in Afrotemperate forested areas at Baziya forest station in the Eastern Cape Province of South Africa. A total of 22 specimens were collected from Baziya. In addition, specimens were hand collected from forests at the Blyde Canyon Nature Reserve at Mariepskop in Mpumalanga Province. Only two adult males and four male juveniles were collected at Blyde Canyon Nature Reserve; no females were found. In addition, Dr N. Peer provided a tissue sample of the new, as yet undescribed species from Hogsback, allowing us to determine the phylogenetic position of the species. A handheld GPS was used to record latitude and longitude, and freshwater crabs were preserved in absolute ethanol. Both new species were photographed in the laboratory, while images of the live Baziya specimens were also captured in the field with a Canon EOS

90D camera with a Sigma 105 mm f2.8 Macro USM lens. The image of the live Blyde Canyon Nature Reserve species was captured with the use of a Huawei P20 Lite cellular phone.

DNA extraction, PCR and sequencing

Muscle tissue, extracted from walking legs, was subjected to DNA extraction using a Nucleospin kit (Macherey-Nagel, Duren, Germany), following the manufacturers protocol. Extracted DNA was stored in a refrigerator at -20ºC until required for PCR. Generally, a 1 µl DNA in 19 µl water dilution was performed prior to use. Three partial mtDNA gene fragments were selected for the present study; these included cytochrome oxidase subunit one (COI), 12S rRNA and 16S rRNA. These three loci were selected because each has a different mutational rate and have been successfully used for reconstructing evolutionary relationships among freshwater crabs (Daniels *et al*. 2002a, 2002b, 2006, 2015, 2019, 2020a, 2020b; Phiri & Daniels 2014, 2016; Gouws *et al*. 2015; Wood & Daniels 2016; Daniels & Klaus 2018). Primer pairs are outlined in Daniels *et al*. (2002b, 2006, 2015). Standard PCR conditions for amplification and DNA sequencing protocols were followed (Daniels *et al*. 2006, 2015, 2019, 2020a, 2020b; Daniels 2017). Sequences of each of the three mitochondrial gene regions were downloaded from GenBank for all the described southern African freshwater crab species (Daniels *et al.* 2002b, 2014, 2019; Daniels & Bayliss 2012; Phiri & Daniels 2014; Peer *et al.* 2015, 2017; Wood & Daniels 2016; Daniels 2017) and included to understand the phylogenetic placement of the two new species from the present study and the undescribed species from Hogsback. Four species of *Liberonautes* Bott, 1955 (*L. latidactylus* (De Man, 1903), *L. rubigimanus* Cumberlidge & Sachs, 1989, *L. lugbe* Cumberlidge, 1999 and L. *nimba* Cumberlidge, 1999) were used as outgroups, since this genus is sister to *Potamonautes* (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 three gene fragments. No insertions or deletions were evident for the protein-coding COI locus and sequences for this locus were aligned manually. The 12S rRNA and 16S rRNA loci were aligned using Clustal X ver. 2.1 (Thompson *et al*. 1997). Since all three fragments occur on the mitochondria and are linked, we combined the DNA sequence data for the three fragments into a single data matrix and conducted all analyses on the combined data set. Maximum Likelihood (ML) and Bayesian approaches were used to estimate evolutionary relationships. jModelTest (Posada 2008) was used to obtain the best-fit substitution model for each of the three gene loci (results not shown). These substitution models were used in a partitioned Bayesian analyses. The best-fit substitution models were chosen using the Akaike Information Criteria (AIC) (Akaike 1973). Maximum likelihood tree inference was conducted on the concatenated data set using the IQ-Tree web server (ver. 1.4.3, http://iqtree.cibiv.univie.ac.at/, Trifinopoulos *et al*. 2016). A single replicate search was conducted for the best tree. Branch support values were estimated using an ultrafast bootstrap analysis with 10 000 pseudoreplicates and parameters set to default. Bootstrap values > 75% were deemed as sufficient support for nodes. Analyses were performed using a heuristic search algorithm starting at a random tree. Four rate categories were included for gamma and base frequencies were estimated. Bootstrap values were discerned during the online analysis and incorporated into the consensus tree generated. Bayesian inferences was used to investigate optimal tree space using the program MRBAYES ver. 3.2.6 (Ronquist *et al.* 2012). Four Markov chains were run, with each chain starting from a random tree and run for fifty 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. A 50 % majority rule consensus tree was generated from the trees retained (after the trees from the burn-in determined using likelihood plots were discarded) with posterior probabilities (pP) for each node estimated by the percentage of time the node was recovered. Posterior probability values < 0.95 pP were regarded as poorly resolved (Daniels *et al*.

2019). Uncorrected 'p' distances among sister species were calculated for the COI locus in PAUP ver. 4.0b10 (Swofford 2002).

Morphology

Characters for male and female specimens from Baziya were considered separately, since freshwater crabs exhibit sexual dimorphism. As no females were sampled at the Blyde Canyon Nature Reserve, no differences between the sexes were quantified. The following measurements were taken with digital callipers: carapace length (CL); the carapace width at widest point (CWW); the width of the posterior margin of the carapace (CWP); the distance between the postfrontal crest and the anterior margin of the carapace (PFCD); the frontal width, measured between the medial margins of the orbits (FW); the distance between the exorbital teeth (CWA); the carapace height (CH); the length and width of the merus of pereiopods 2 and 5 (PML and PMW); the length of the propodus of the major cheliped (MCPL); as well as the major cheliped dactylus length (MCDL). All measurements are given in millimetres (mm). Samples have been deposited in the South African Museum of Natural History, Iziko Museums of Cape Town (SAM A). The structure of gonopods 1 and 2 of the two new species are compared to that of other congeneric species. In addition, the major and minor cheliped of the new species were photographed with a 31 mm extension tube to the aforementioned setup to increase magnification.

Results

New sequences were deposited in GenBank (COI accession numbers OK489797–OK489798, 12S rRNA accession numbers OK482906–OK482907 and 16SrRNA accession numbers OK482901–OK482902). The ML and BI tree topologies were nearly identical; hence only the ML tree topology is shown. The ML and BI phylogenetic analyses based on the 1278 nucleotides of the three combined mtDNA loci, comprising 600 bp, 316 bp and 362 bp fragments for COI, 12S rRNA and 16S rRNA, respectively, retrieved a monophyletic and statistically well-supported *Potamonautes* MacLeay, 1838 (Fig. 1). Since the tree topologies for the ML and BI analyses were nearly identical, we show only the ML tree topology, comprising three distinct clades. Clade 1 (>75% / >0.95pP) contained five East African freshwater crab species, with *P. namuliensis* Daniels & Bayliss, 2012 being basal to a clade containing *P. choloensis* Chace, 1953 sister to *P. licoensis* Daniels, Bittencourt-Silva, Muianga & Bayliss, 2020 while the latter clade was sister to *P. calcaratus* Gordon, 1929 and *P. obesus* A. Milne-Edwards, 1868. *Potamonautes bellarussus* Daniels, Phiri & Bayliss, 2014 was equidistant between clades 1 and 2. Clade 2 also comprised species from East Africa, with *P. niloticus* H. Milne-Edwards, 1837 being basal to a clade comprised of *P. odheri* Colosi, 1924 sister to *P. subukia* Cumberlidge & Dobson, 2008, while the latter clade was in turn sister to *P. raybouldi* Cumberlidge & Vannini, 2004 sister to *P. platynotes* Cunnington, 1907, and the latter two species sister to *P. supracilcatus* Hilgendorf, 1898 and *P. lirrangensis* Rathbun, 1904. Clade 3 (>75% / >0.95pP) contained southern African freshwater crab species exclusively. The southern African mountain stream species comprised one clade, with *P. baziya* sp. nov., from the Baziya forest station in the Eastern Cape as sister to two Drakensberg Mountain endemic species, *P. clarus* Gouws, Stewart & Coke, 2000 and *P. depressus* Krauss,1843. The latter clade was in turn sister to species from the Cape Folds Mountain (CFM), with *P*. sp. nov. from Hogback as sister to *P. parvispina* Stewart, 1997, and this clade was sister to *P. parvicorpus* Daniels, Stewart & Burmeister, 2001 sister to *P. brincki* Bott, 1960 sister to *P. tuerkayi* Wood & Daniels, 2016. The three forest-living species was basal to a large-bodied riverine dwelling clade and comprised *P. danielsi* sister to *P. lividus* Gouws, Stewart & Reavell, 2001 and *P. isimangaliso* Peer & Gouws, 2015. This large-bodied riverine clade comprised *P. bayonianus* Brito-Capello, 1864 sister to *P. unispinus* Stewart & Cook, 1998 and *P. warreni* Calman, 1918, and these species were in turn sister to *P. sidneyi* Rathbun, 1904 sister to *P. perlatus* H. Milne Edwards, 1837, *P. granularis* Daniels, Stewart & Gibbons, 1998, *P. barnardi* Phiri & Daniels, 2014 and *P. barbarai* Phiri & Daniels, 2014. The final clade comprised mainly temperate/ tropical freshwater crab species with *P. mhlophe* Daniels, 2017 sister to *P. dentatus* Stewart, Cook & Coke, 1995, and this clade

was sister to a larger clade containing *P. gorongosa* Cumberlidge, Naskrecki & Daniels, 2017 sister to *P. mutareensis* Phiri & Daniels, 2013; while *P. flavusjo* Daniels, Phiri & Bayliss, 2014 was sister to a clade containing *P. mulanjeensis* Daniels & Bayliss, 2012 sister species to *P. ntendekaensis* Daniels, Busschau & Cumberlidge, 2019 and *P. mariepskoppie* sp. nov., sister to *P. ngoyensis* Daniels, Busschau & Cumberlidge, 2019.

The average uncorrected COI sequence 'p' distance between *P. baziya* sp. nov. and its two sister species was 13.03%. The uncorrected COI 'p' distance between *P. mariepskoppie* sp. nov. and *P. ngoyensis* was 8.65%, while the 'p' distance between *P. mariepskoppie* sp. nov. and *P. ntendekaensis* was 10.90%. The 'p' distance between *P. ngoyensis* and *P. ntendekaensis* was 8.10%. The uncorrected distance between *P. licoensis* and *P. choloensis* was 8.67%. Among the small-bodied, mountain-living freshwater crab species endemic to the Cape Fold Mountains, the COI 'p' distance between *P. parvispina* and *P. parvicorpus* was 7.36% and 8.56% between *P. brincki* and *P. tuerkayi*. Finally, the uncorrected distance between *P. parvispina* and its sister, the new as yet undescribed species from Hogsback, was 7.81%. The uncorrected COI sequence distance we observed between the two putative novel lineages in the present study, >7.30%, is comparable to what has been observed in previous studies. The phylogenetic results, together with the marked COI 'p' distance values, and the morphological differences, support the recognition of two novel freshwater crab species, the description of which follows.

Infraorder Brachyura Latreille, 1802
Superfamily Potamoidea Ortmann, 1896
Family Potamonautidae Bott, 1970
Subfamily Potamonautinae Bott, 1970
Genus *Potamonautes* MacLeay, 1838

Potamonautes mariepskoppie sp. nov.
urn:lsid:zoobank.org:act:C0AE6C3E-5460-450C-87D4-87D24DC47862
Figs 1–6

Diagnosis

Measurements for the holotype as follows: CL = 19.07 mm; CWW = 26.76 mm; CWP = 11.56 mm; FW = 11.58 mm; PFCD = 2.89 mm; CH = 10.63 mm; MCPL = 16.44 mm; MCDL = 10.14 mm; P2ML = 11.06 mm; P2MW = 4.65 mm; P5ML = 9.34 mm; P5MW = 3.61 mm.

Carapace. Highly arched (CH/CL = 0.55) postfrontal crest well-defined, complete, lateral ends meeting anterolateral margins; epigastric crests faint, median sulcus between crests short, not forked posteriorly; exorbital, epibranchial teeth reduced to granules; anterolateral carapace margin with no tooth on epibranchial (Fig. 2A–C).

Third maxilliped. Ischium with distinct vertical sulcus; s3/s4 complete, V-shaped, deep, midpoint almost meeting anterior margin of sterno-pleonal cavity; margins of s4 low, not raised (Fig. 2B).

Cheliped. Dactylus (moveable finger) slim, highly arched, enclosing oval interspace, with three larger teeth interspersed by smaller teeth along length; propodus (fixed finger) with four larger teeth interspersed by smaller teeth along length (Fig. 2C); carpus inner margin distal tooth large, pointed, proximal tooth reduced to granules; medial inferior margin of merus lined with series of small granules terminating distally at small, low distal meral tooth, lateral inferior margin smooth.

G1 terminal article. ⅓rd length of subterminal; first third straight in line with longitudinal axis of subterminal, middle part directed outward at 45°, widened by raised rounded ventral lobe, tip curving sharply upward (Fig. 3A–B).

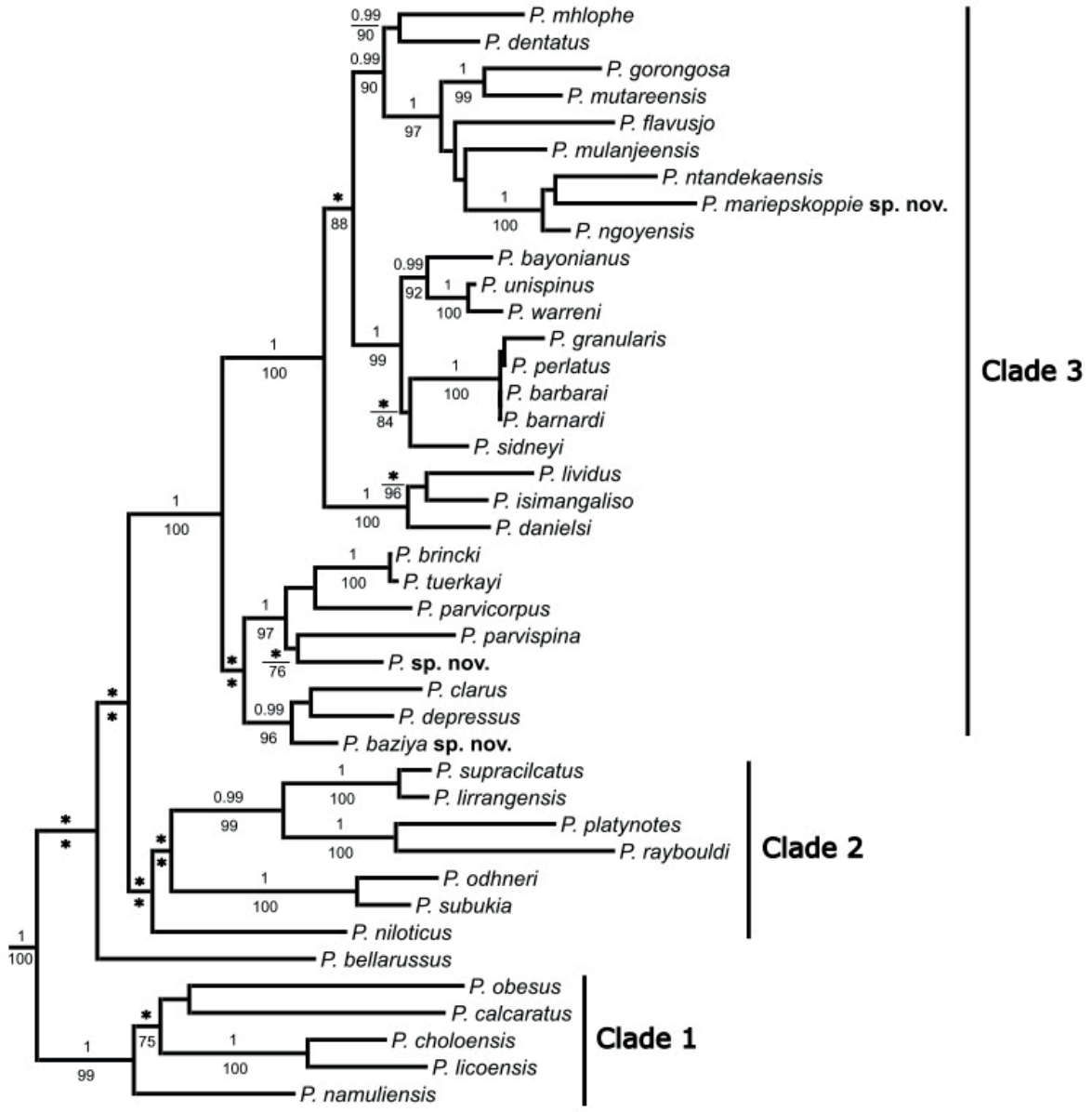

Fig. 1. A Maximum Likelihood tree topology derived for the three mtDNA loci (12S rRNA +16S rRNA + COI) for the eastern and southern African freshwater crab genus *Potamonautes*, with the outgroups removed. Bootstrap values > 75% are indicated below each node while posterior probability values > 0.95 p*P* are shown above each node. An asterisk (*) above or below a node indicates the lack of statistical support. The new, as yet undescribed species from Hogsback is demarked as *P*. sp. nov. on the phylogenetic tree. Clades 1 and 2 refers to predominantly East African species, while clade 3 refers to the southern African clade.

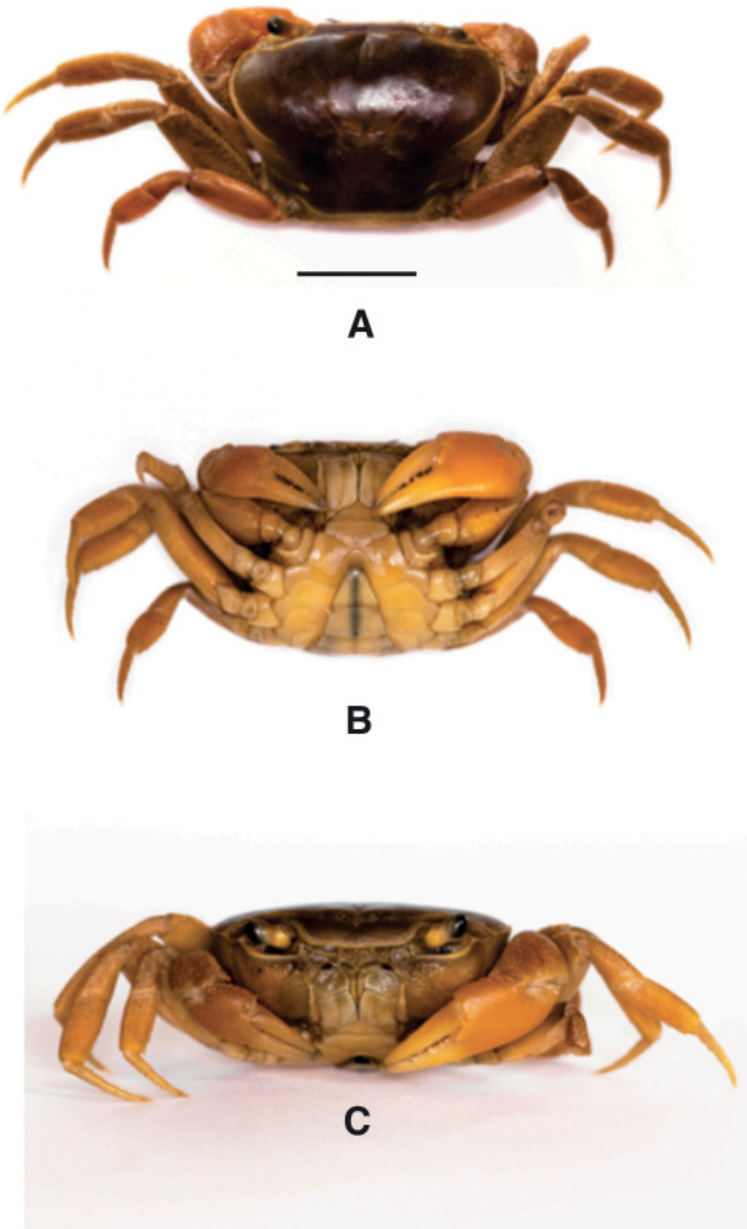

Fig. 2. *Potamonautes mariepskoppie* sp. nov., ♂, holotype (CL = 19.07 mm) (SAM A-094471). **A**. Entire animal, dorsal aspect. **B**. Entire animal, ventral aspect. **C**. Cephalothorax, frontal aspect. Scale bar = 10 mm.

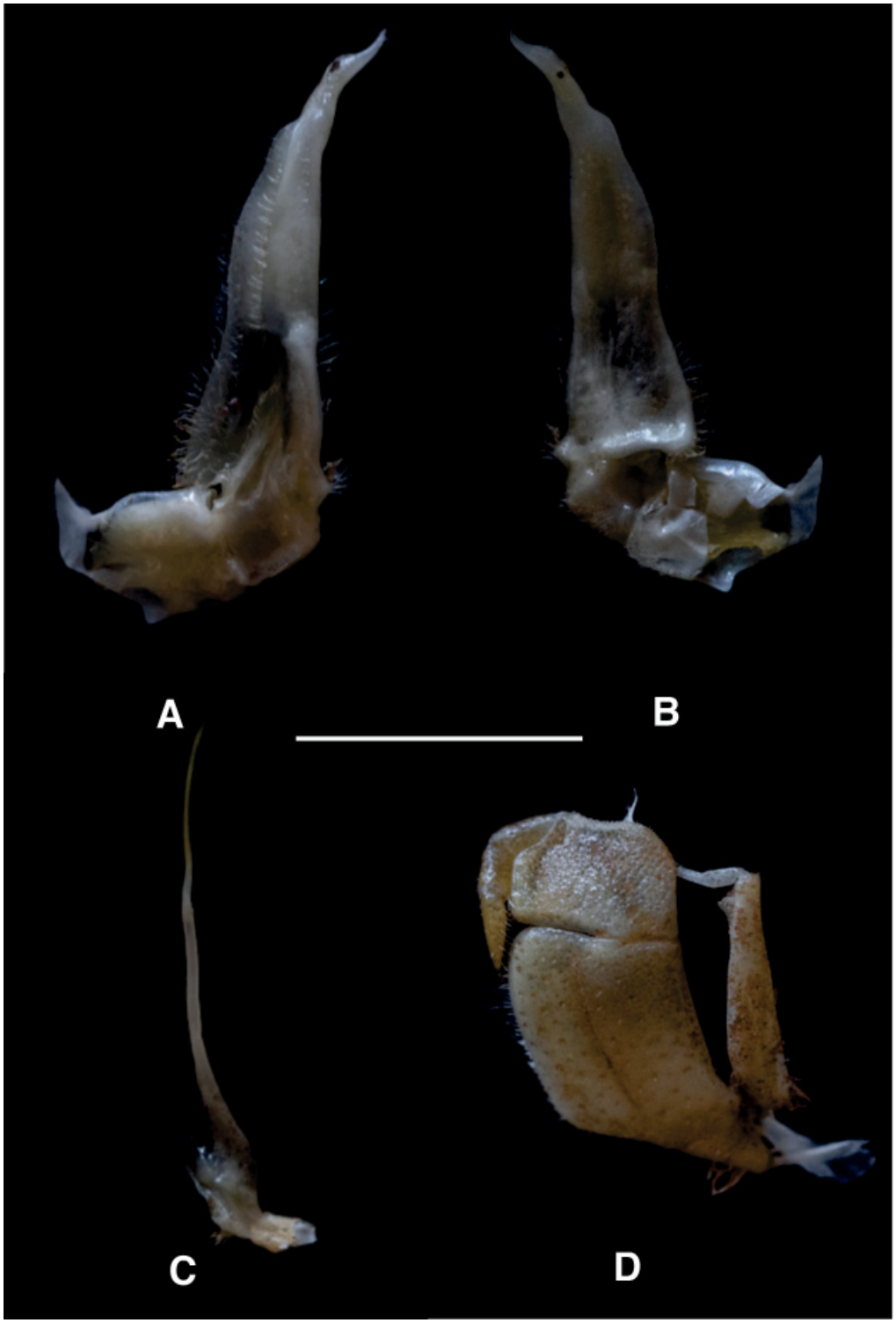

Fig. 3. *Potamonautes mariepskoppie* sp. nov., ♂, holotype (SAM A-094471) **A**. Left gonopod 1, anterior view. **B**. Left gonopod 1, posterior view. **C**. Left gonopod 2, anterior view. **D**. Right third maxilliped. Scale bar = 10 mm.

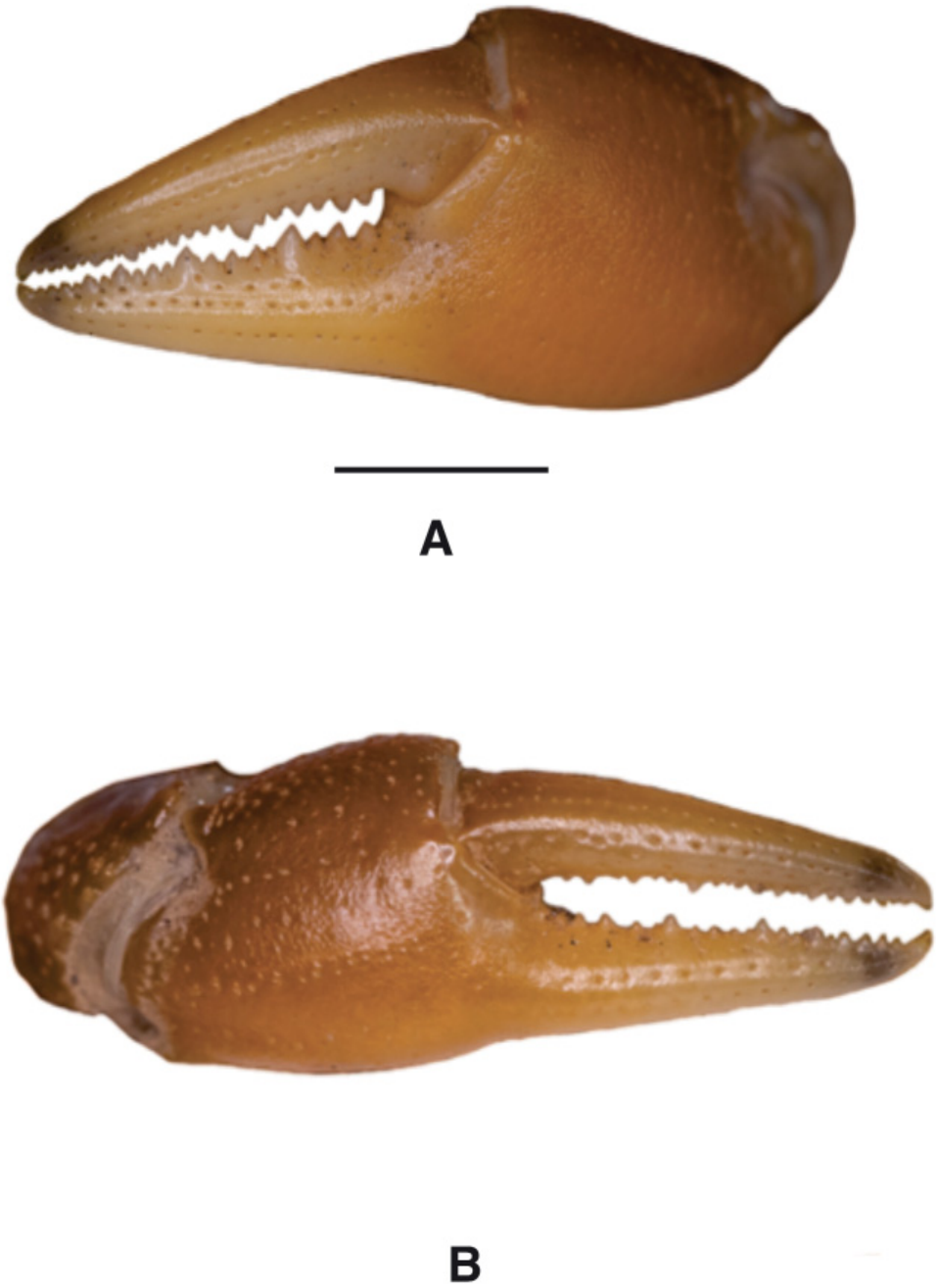

Fig. 4. *Potamonautes mariepskoppie* sp. nov., ♂, holotype (SAM A-094471) **A**. Major right cheliped. **B**. Minor left cheliped. Scale bar = 10 mm.

Etymology

Named after Mariepskop since it occurs in close proximity to the mountain. The specific epithet is used as a Latin noun in apposition.

Material examined

Holotype

SOUTH AFRICA – **Mpumalanga Province** • ♂; Blyde Canyon Nature Reserve, lowveld section, forest wetland; 24º42′36.36″ S, 30º54′11.664″ E; 733 m a.s.l.; 21 May 2021; H. Marais leg.; SAM A-094471.

Paratype

SOUTH AFRICA – **Mpumalanga Province** • 1 ♂; same collection data as for holotype except 17 Jun. 2020; SAM A-094472.

Other material

SOUTH AFRICA – **Mpumalanga Province** • 4 juvs; same collection data as for paratype; SAM A-094473.

Description

Based on the adult male holotype (CWW 26.76 mm).

Carapace. Smooth with no tooth on the anteriolateral margins; widest anteriorly, narrowest posteriorly (CWP/CL 0.60); vaulted (CH/CL 0.55) (Fig. 2A); front broad, one-third of CWW (FW/CWW 0.43); urogastric, cardiac grooves distinct, other grooves faint or missing; postfrontal crest complete, anterolateral margin posterior to epibranchial corner finely granulated, epigastric crests faint, median sulcus between crests short, forked posteriorly; exorbital, epibranchial teeth each reduced to granules; anterolateral margin between exorbital, epibranchial teeth faintly granulated, curving slightly outward, lacking intermediate tooth (Fig. 2B–C); branchiostegal wall vertical sulcus faint, meeting longitudinal sulcus, dividing branchiostegal wall into 3 parts, suborbital, dorsal pterygostomial regions granulated, hepatic region smooth; suborbital margin faintly granulated.

Third maxilliped. Filling entire buccal frame, except for respiratory openings; exopod with long flagellum, ischium with faint vertical groove (Fig. 3D). Epistomial tooth large, triangular, margins lined by large granules.

Mandible. Palp two-segmented; terminal simple; tuft of setae at junction between segments.

Sternum. s1, s2 fused; s2/s3 deep, completely crossing sternum; s3/s4 complete, V-shaped, deep, midpoint almost meeting anterior margin of sterno-pleonal cavity; margins of s4 low, not raised.

Cheliped. Dactylus (moveable finger) slim, arched, with two teeth interspersed by smaller teeth along length; propodus (fixed finger) with two teeth interspersed by several smaller teeth along length (Fig. 4A–B), tips of both propodus and dactylus black; carpus distal tooth large, pointed, proximal tooth small but distinct, followed by granule; both inferior margins of merus lined with series of small granules, distal meral tooth small, pointed.

Pereopods. Walking legs slender, 3 longest, 5 shortest; dorsal margins of pereopods with fine sharp bristles, dactyli of walking legs ending in sharp point, with rows of spine-like bristles.

Pleon. Outline broadly triangular with straight margins.

G1 TERMINAL ARTICLE. Short (⅓ length of subterminal), curving away from midline, first third straight in line with longitudinal axis of subterminal segment, middle part directed outward at 45°, widened by low raised rounded ventral lobe, tip curving gently upward. G1 subterminal broad at base, tapering to slim junction with terminal article distally where these two parts have same width, ventral side with heavily setose margins; with setae-fringed flap covering lateral half of segment; dorsal side smooth, no flap, with broad membrane on dorsal side of suture marking junction between terminal, subterminal parts (Fig. 3A–B).

G2 TERMINAL ARTICLE. Long, flagellum-like, 0.5 times length of subterminal (Fig. 3C).

Size

A small-bodied species, CL = 19.07 mm, and wide, CWW = 26.76 mm.

Colour in life

Dorsal carapace chocolate brown with a glossy shine, while the chelipeds and ventral surface are light orange in colour (Fig. 5A).

Distribution

Known only from the lowveld section of the Blyde Canyon Nature Reserve, east of Mariepskop, Mpumalanga Province, South Africa. However, a digital photographic record from iNaturalist (posted by Werner Conradie) suggests the species is also present around Haenertsburg, in Limpopo Province, South Africa (Fig. 5B). Surveys of the latter area are required to confirm this observation.

Ecology

The type locality is located 12 km southeast of Mariepskop Mountain and forms part of the Great Drakensberg Mountain escarpment. The swamp forest receives annual rainfall averaging 1500 mm on top of the mountain and 750 mm at the bottom (Ngwenya *et al*. 2019). The swamp forests in these areas are all channelled valley-bottom wetlands with connected seeps. The wetland of the type locality is on a shallow gradient that allows the water to seep out slowly into shallow channels and forms shallow muddy puddles, which the crab species prefers. *Potamonautes mariepskoppie* sp. nov., occurs sympatrically with *P. sidneyi* sensu stricto. The soils are predominantly organic soils of 15-100 cm deep (Van Rooyen *et al.* 2020). The presence of large water berries, *Syzygium cordatum*, is diagnostic of these swamp forests. There are other wetland species present, such as *Carex spicata-paniculata*, *Commelina benghalensis*, *Cyperus denudatus*, *Cyclosorus interruptus*, *Cyperus dives*, *Isolepis fluitans*, *Kyllinga odorata*, *Leersia hexandra*, *Persicaria decipiens*, *Selaginella kraussiana*, *Schoenoplectus brachyceras*, *Setaria megaphylla*, *Scleria transvaalensis* and *Thelypteris confluens*.

Remarks

Potamonautes mariepskoppie sp. nov., can be distinguished from its two sister species, *P. ngoyensis* and *P. ntendekaensis*, using colour when alive. *Potamonautes mariepskoppie* sp. nov. has a chocolate brown carapace and orange chelipeds that vary to rust brown as does the specimen from Haenertsburg, Limpopo (Fig. 5B). *Potamonautes ngoyensis* has a pale-white carapace and chelipeds; *P. Potamonautes ntendekaensis* has a chocolate-coloured carapace with red pereopods; the entire animal fades to bright orange/red when preserved in absolute ethanol (Daniels *et al.* 2019). In addition, *P. mariepskoppie* sp. nov. is a small-bodied species (CWW = 26.76 mm) with a highly arched carapace (CH/CL = 0.60), while *P. ngoyensis* is a large-bodied (CWW = 32.8 mm) and flat species (CH/CL = 0.50). Similarly, *P. ntendekaensis* is a large-bodied species (CWW = 37.56 mm), that is highly arched (CH/CL = 0.55). All three species appear to be narrow-endemic forest-dwelling species and are poorly collected based on current distribution records. *Potamonautes mariepskoppie* sp. nov. appears to be confined

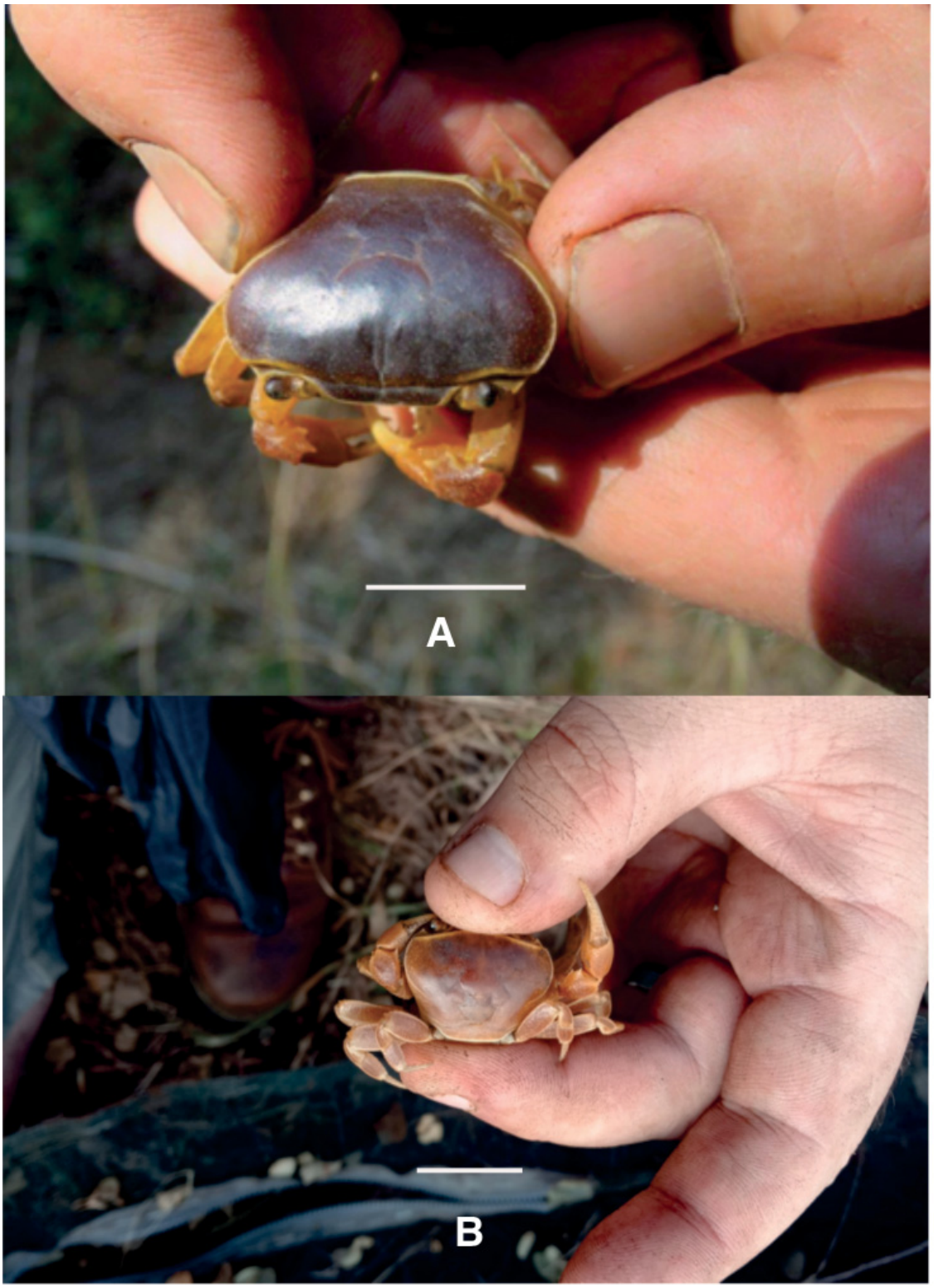

Fig. 5. A. Dorsal image of *Potamonautes mariepskoppie* sp. nov., when alive taken at the Blyde Canyon Nature Reserve, Mpumalanga Province, South Africa. **B**. Dorsal image of *P. mariepskoppie* sp. nov., of the specimen collected at Haenertsburg, Limpopo Province, South Africa. Scale bars = 10 mm.

to swamp forest patches east of Mariepskop and possibly at Haenertsburg, Limpopo province, while *P. ntendekaensis* is endemic to the Ntendeka Wilderness (Ngome forest – representing Eastern Scarp forest) area of KwaZulu-Natal, and *P. ngoyensis* is endemic to the Ngoye forest, part of the greater IOCB forest of KwaZulu-Natal (Daniels *et al.* 2019). Phylogenetically, *Potamonautes mariepskoppie* sp. nov. is not closely related to the five other species that occur in Mpumalanga province and can also easily be distinguished from these. Both *P. unispinus* and *P. calcaratus* have a single tooth on the anterolateral carapace margin, which is nearly spike-like in *P. calcaratus*. In *P. unispinus* the tooth on the anterolateral margin is sharp, pointed and prominent, similar to the exorbital tooth, and the species is large (CL= 49.83 mm) and broad (CWW = 64.88 mm). *Potamonautes unispinus* is a riverine species that is widespread in southern Africa and known from South Africa, Zimbabwe and Zambia (Stewart & Cook 1998), while *P. calcaratus* occurs exclusively around ephemeral pans in the Kruger National Park in South Africa, where it burrows into the clay sidewalls up to 1 m (Daniels *et al*. 2002a). The latter species is also found in Mozambique and Zimbabwe (Reed & Cumberlidge 2004). Additionally, the chelipeds of *P. calcaratus* are highly modified and nearly flattened for burrowing. The latter species has a vaulted carapace, indicative of its semi-terrestrial mode of life (Daniels pers. obs). In *Potamonautes warreni*, the dentition on the anterolateral margin of the carapace varies from a single tooth to a series of five to ten teeth (Daniels 2001). *Potamonautes warreni* is a riverine species widespread in South Africa, Botswana and Namibia where it occurs in the Orange River and its major tributaries such as the Vaal River. *Potamonautes flavusjo*, a Mpumalanga Highveld endemic, is semi-terrestrial and occurs in vlei (wetland) and lake areas, where it burrows into peat soils (Daniel *et al*. 2014). This species has characteristic sulphur-yellow patches on its dorsal carapace surface and the ventral surface is bright

Fig. 6. Swamp forest habitat where *P. mariepskoppie* sp. nov., was collected at the Blyde Canyon Nature Reserve, below the Mariepskop Mountains, Mpumalanga Province, South Africa.

yellow and the species has a highly vaulted carapace (CH/CL = 0.61) (Daniels *et al*. 2014). *Potamonautes sidneyi* sensu stricto is generally large-bodied (CWW > 52.4 mm) and the cephalothorax is flat (CH/CL = 0.54), while the anterolateral margins of the carapace are heavily granulated. The species is common in large rivers, streams and swamp habitats throughout KwaZulu-Natal, Mpumalanga, Gauteng, Limpopo, the North-West and Northern Cape provinces of South Africa (Barnard 1950; Peer *et al*. 2017; Daniels unpubl).

The three remaining sister species to the clade containing *P. mariepskoppie* sp. nov. are all found in neighboring Southern African countries. *Potamonautes gorongosa* occurs at Gorongosa National Park in Mozambique, *P. mutariensis* occurs in the Zimbabwean Highlands and *P. mulanjeensis* occurs on Mount Mulanje in Malawi. Phylogenetically, *P. mariepskoppie* sp. nov. is distantly related to the two remaining swamp forest dwelling South African freshwater crab species, *P. lividus* and *P. isimangaliso* (Fig.1), although it does bear a superficial resemblance to these two species. *Potamonautes lividus* occurs in swamp forest patches in Eastern Cape province, at Dwesa Nature Reserve, Mazeppa Bay and Manubi State forest, and in the IOCB forests from Amatikulu Nature Reserve, Richards Bay, Empangeni, Tugela River Mouth, the University of Zululand campus, and Mapelane Nature Reserve in KwaZulu-Natal (Gouws *et al*. 2001; Daniels *et al*. 2020a). *Potamonautes isimangaliso* is confined to iSimangaliso Wetland Park in northern KwaZulu-Natal (Peer *et al*. 2015). *Potamonautes lividus* was originally described from *Ficus* and *Barringtonia* dominated forests, and the carapace of the species is blue or light blue (Gouws *et al.* 2001). Furthermore, the cephalothorax is ovoid with no epibranchial tooth and the carapace is highly vaulted (CH/CL = 0.64), indicative of a semi-terrestrial mode of life (Gouws *et al*. 2001). In *P. isimangaliso*, the cephalothorax is also ovoid, and the carapace is highly vaulted (CH/CL = 0.57) and light brown, maroon, purple or brown–black in colour (Peer *et al*. 2015). The species lives in ephemeral pans in sand forest where it burrows into the soil to a depth of 30–50 cm (Peer *et al.* 2015). *Potamonautes mariepskoppie* sp. nov., is distantly related to the undescribed species from Hogsback and the four mountain-living freshwater crab species from the Cape Fold Mountains (*P. brincki*, *P. parvicorpus*, *P. parvispina* and *P. tuerkayi*), and the three Great Drakensberg Escarpment species (*P. clarus*, *P. depressus* and *P. baziya* sp. nov).

Taxonomic note

H. Milne-Edwards (1853) described *Thelphusa inflata* from Durban, KwaZulu-Natal (formerly Port of Natal, Natal province). Barnard (1950) was of the opinion that *Potamonautes inflatus* is a variant of *P. perlatus*. In addition to Durban, Barnard (1950) also listed *P. inflatus* as being present at Belfast, Haenertsburg and Mariepskop in the former Transvaal province (notably, the last two localities are also where *P. mariepskoppie* sp. nov. occurs). Bott (1955) recognized *P. inflatus* as a junior subjective synonym of *P. depressus*, noting that the "type" is unknown or lost. Our phylogenetic results refute a close relationship between *P. mariepskoppie* sp. nov. and *P. depressus*. A search of the digital records of the Muséum national d'Histoire naturelle, Paris, France failed to identify the type specimen of *P. inflatus*, suggesting the holotype is lost. Similarly, an exhaustive search of the South African Museum of Natural History, Cape Town, failed to retrieve the material from Belfast, Mariepskop and Haenertsburg that Barnard (1950) assigned to *P. inflatus*. Researchers consider *P. inflatus* as an invalid taxon (Stewart *et al*. 1995; Gouws & Stewart, 2001; Ng *et al.* 2008). A recent redescription of *P. sidneyi* suggests that the type material was likely originally collected from the region of Port Natal (Peer *et al.* 2017). The original description of *P. inflatus* is inadequate to differentiate it from *P. sidneyi*. Considering the absence of type material for *P. inflatus* and its confusing taxonomic status, the species name a *nomen nudum*. In recent years, six freshwater crab species, *P. dentatus*, *P. lividus*, *P. isimangaliso*, *P. danielsi*, *P. ntendekaensis* and *P. ngoyensis*, have been described from KwaZulu-Natal. Apart from *P. sidneyi,* no other species occurs in close geographic proximity to Durban (Port Natal) (Stewart *et al.* 1995; Peer *et al.* 2015, 2017; Daniels et *al.* 2019). The specimens from Mariepskop are recognized as *P. mariepskoppie* sp. nov., rather than *P. inflatus*, to limit any potential future confusion.

Potamonautes baziya sp. nov.

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Figs. 1,7–10;Table 1

Diagnosis

Carapace. Ovoid, highly flat (CH/CL = 0.45) (Table 1); postfrontal crest well-defined, complete, lateral ends meeting anterolateral margins; epigastric crests faint, median sulcus between crests short, not forked posteriorly; exorbital, epibranchial teeth reduced to granules; anterolateral carapace margin smooth (Fig. 7A).

Third maxilliped. Ischium with distinct vertical sulcus (Fig. 7B–C); s3/s4 complete, V-shaped, deep, midpoint almost meeting anterior margin of sterno-pleonal cavity; margins of s4 low, not raised (Fig. 7B).

Cheliped. Dactylus (moveable finger) slim, highly arched, enclosing oval interspace, with three larger teeth interspersed by smaller teeth along length; propodus (fixed finger) with four larger teeth interspersed by smaller teeth along length (Fig. 8A); carpus inner margin distal tooth large, pointed, proximal tooth reduced to granules (Fig. 8B); medial inferior margin of merus lined with series of small granules terminating distally at small, low distal meral tooth, lateral inferior margin smooth.

G1 terminal article. ⅓ length of subterminal segment; first third straight in line with longitudinal axis of subterminal, middle part directed outward at 45°, widened by raised rounded ventral lobe, tip curving sharply upward (Fig. 9A–B).

Etymology

Named after the Baziya forest station. The specific epithet is used as a Latin noun in apposition.

Material examined

Holotype

SOUTH AFRICA – **Eastern Cape Province** • ♂; Baziya Forest station, Afrotemperate forest streams; 31º33.917, S, 28º25.176′ E; 999 m a.s.l.; 19 May 2021; S.R. Daniels and A. Barnes; SAM A-094474.

Paratype

SOUTH AFRICA – **Eastern Cape Province** • 1 ♂; same collection data as for holotype; SAM A-094475.

Other material

SOUTH AFRICA – **Eastern Cape Province** • 8 ♀♀, 8 ♂♂, 4 juvs; same collection data as for holotype ; SAM A-094476.

Description

Based on male holotype (CWW = 40.30 mm, Table 1).

Carapace. Lacking dentition on the anteriolateral margins; widest anteriorly, narrowest posteriorly (CWP/CL = 0.47); flattened (CH/CL = 0.45) (Fig. 7A); front broad, one-third of CWW (FW/CWW = 0.35); urogastric, cardiac grooves distinct, other grooves faint or missing; postfrontal crest complete, anterolateral margin posterior to epibranchial tooth smooth, meeting epibranchial teeth; epigastric crests faint, median sulcus between crests short, forked posteriorly; anterolateral margin between exorbital, epibranchial teeth faintly granulated, curving slightly outward, lacking intermediate tooth (Fig. 7B–C); branchiostegal wall vertical sulcus faint, meeting longitudinal sulcus, dividing branchiostegal wall into

3 parts, suborbital, dorsal pterygostomial regions granulated, hepatic region smooth; suborbital margin faintly granulated.

Third maxilliped. Filling entire buccal frame, except for respiratory openings; exopod with long flagellum, ischium with faint vertical groove (Fig. 9D). Epistomial tooth large, triangular, margins lined by large granules.

Mandible. Palp two-segmented; terminal simple; tuft of setae at junction between segments.

Sternum. s1, s2 fused; s2/s3 deep, completely crossing sternum; s3/s4 complete, V-shaped, deep, midpoint almost meeting anterior margin of sterno-pleonal cavity; margins of s4 low, not raised.

Cheliped. Dactylus (moveable finger) slim, arched, enclosing oval interspace, with three larger teeth interspersed by smaller teeth along length; propodus (fixed finger) with four larger teeth interspersed by smaller teeth along length (Fig. 8A–B); carpus distal tooth large, pointed, proximal tooth small but distinct, followed by granule; both inferior margins of merus lined by series of small granules, distal meral tooth small, pointed.

Pereopods. Walking legs slender, pereopod 3 longest, 5 shortest; dorsal margins with fine sharp bristles, dactyli of walking legs ending in sharp point, with rows of spine-like bristles along segment.

Pleon. Outline broadly triangular with straight margins.

G1 terminal article. Short (⅓ length of subterminal segment), curving away from midline, first third straight in line with longitudinal axis of subterminal, middle part directed outward at 45°, widened by low raised rounded ventral lobe, tip curving gently upward. G1 subterminal broad at base, tapering to slim junction with terminal article distally where these two parts have same width, ventral side of segment with heavily setose margins; with setae-fringed flap covering lateral half of segment; dorsal side smooth, no flap, with broad membrane on dorsal side of suture marking junction between terminal, subterminal parts (Fig. 9A–B).

G2. Terminal article long, flagellum-like, 0.5 times length of subterminal article (Fig. 9C).

Size

A medium-bodied species (CL= 29.28 mm for holotype) and wide (CWW = 40.30 mm).

Colour in life

Dark brown carapace when alive (Fig. 10A).

Distribution

To date, the species has only been collected from Baziya forest station. It is likely to also occur at other localities along the Great Drakensberg Escarpment in the Eastern Cape.

Ecology

The species occurs under large boulders in small mountain streams. The sides of the streams are covered by Afrotemperate forests at Baziya forest station outside of Mthatha, Eastern Cape province, South Africa (Fig. 10B).

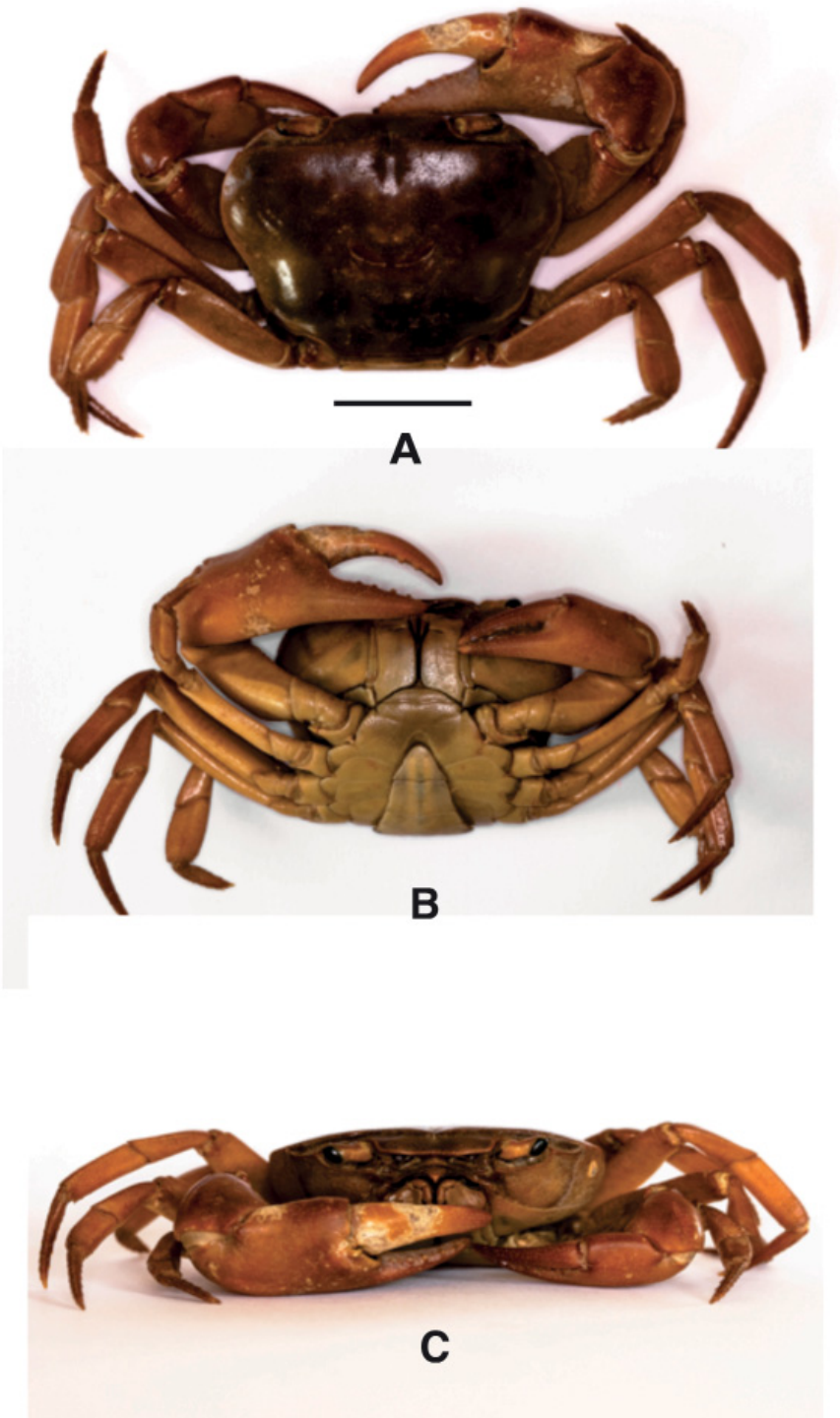

Fig. 7. *Potamonautes baziya* sp. nov., ♂, holotype (CL = 29.28 mm) (SAM A-094474). **A**. Entire animal, dorsal aspect. **B**. Entire animal, ventral aspect. **C**. Cephalothorax, frontal aspect. Scale bar = 10 mm.

Table 1. *Potamonautes baziya* sp. nov., measurements (in mm) of the holotype and the range of additional male and female specimens examined.

Variable	Abbreviation	Holotype	♂♂	♀♀
carapace length	CL	29.28	23.51–22.21	27.53–24.04
carapace width at widest point	CWW	40.30	31.70–29.47	37.30–33.30
carapace posterior margin	CWP	13.90	14.17–11.88	15.22–12.56
frontal width	FW	14.41	12.63–11.35	13.70–12.13
distance between postfrontal crest and anterior margin	PFCD	4.58	3.50–3.58	3.63–3.46
carapace height	CH	13.46	11.28–9.79	13.75–11.68
major cheliped propodus length	MCPL	34.83	24.32–18.88	21.69–20.68
major cheliped dactylus length	MCDL	20.83	14.45–10.90	12.30–11.79
pereiopod 2, merus length	P2ML	16.57	12.39–11.61	14.27–12.18
pereiopod 2, merus width	P2MW	5.30	5.05–4.73	5.48–5.04
pereiopod 5, merus length	P5ML	16.42	14.21–12.50	14.14–14.06
pereiopod 5, merus width	P5MW	5.47	5.20–4.73	5.47–5.25

Remarks

Potamonautes baziya sp. nov. is sister to *P. depressus* from the central Drakensberg Mountains, while *P. clarus* is sister to the latter clade (Fig. 1). The former pair of sister species can be differentiated based on colour when alive; *P. baziya* sp. nov. has a chocolate brown-coloured carapace, while *P. depressus* from the central Drakensberg Mountains has a dark brown to yellow brown carapace (Gouws *et al.* 2000). In addition, *P. baziya* sp. nov., has a narrower carapace dorsally (CL/CH = 2.17–2.08), while *P. depressus* has a more dorsally flattened carapace (CL/CH = 2.3–2.6) which is smooth (Peer *et al.* 2017). *Potamonautes clarus* is confined to the northern Drakensberg Mountains of KwaZulu-Natal (Gouws *et al.* 2000). *Potamonautes clarus* has a bright orange ovoid carapace when alive and viewed dorsally, while the species is cream coloured ventrally. The carapace is more vaulted (CH/CL = 0.49) and the species is small-bodied (CWW = 42.7 mm) (Gouws *et al.* 2000). The dactylus of the right cheliped is highly arched in all three species, a pattern typical of mountain-dwelling species. The terminal segment of gonopod 1 in *P. clarus* is slightly longer and more slender in comparison to *P. depressus*. Krauss (1843) only drew the dorsal aspect of *P. depressus* and did not illustrate gonopods one or two. From his original drawings, it is evident that the holotype has a highly arched right cheliped. The right cheliped of *P. baziya* sp. nov. is also arched, albeit less so than in the *P. depressus* holotype; this character is likely to vary with the age of the specimen. Bott (1955) illustrated the first gonopod of *P. depressus,* which differs from that of *P. baziya* sp. nov. in being slightly more tapered towards the tip. Cumberlidge & Tavares (2006) reported that *P. depressus* is also possibly in Eastern Cape province. An examination of *P. depressus* specimens deposited in the South African Museum of Natural History, Cape Town, revealed two localities from the southern Drakensberg that are in Eastern Cape Province and, notably, also includes specimens from Hogsback. The latter locality represents the as yet undescribed species.

Four described mountain-living freshwater crab species occur in the Cape Fold Mountains. *Potamonautes baziya* sp. nov., can easily be distinguished from *P. parvispina* which has a yellowish, green-coloured carapace when alive, with an cephalothorax that is ovoid, a carapace that is flat (CH/CL = 0.50) and which is small-bodied (CWW = 38.4 mm). The species lives in first order streams in the Cederberg where is present in the upper reaches of the Olifants and Berg River systems in Western Cape Province (Stewart 1997b). Since *P. parvispina* has a small spine on the anterolateral carapace margins, it can easily be distinguished from the three other described species (Stewart 1997b). These three remaining species

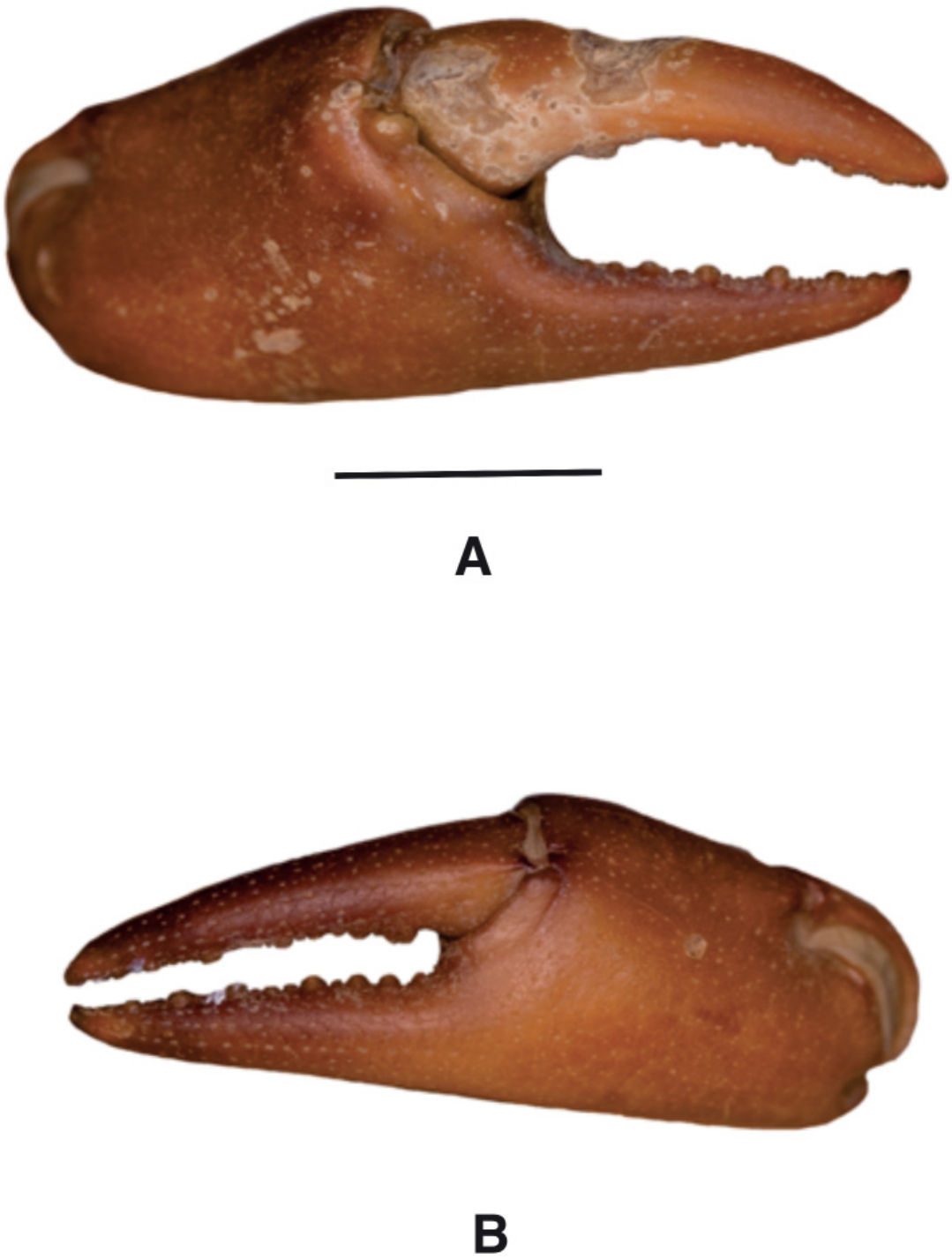

Fig. 8. *Potamonautes baziya* sp. nov., ♂, holotype, (SAM A-094474) **A**. Major right cheliped. **B**. Minor left cheliped. Scale bar = 10 mm.

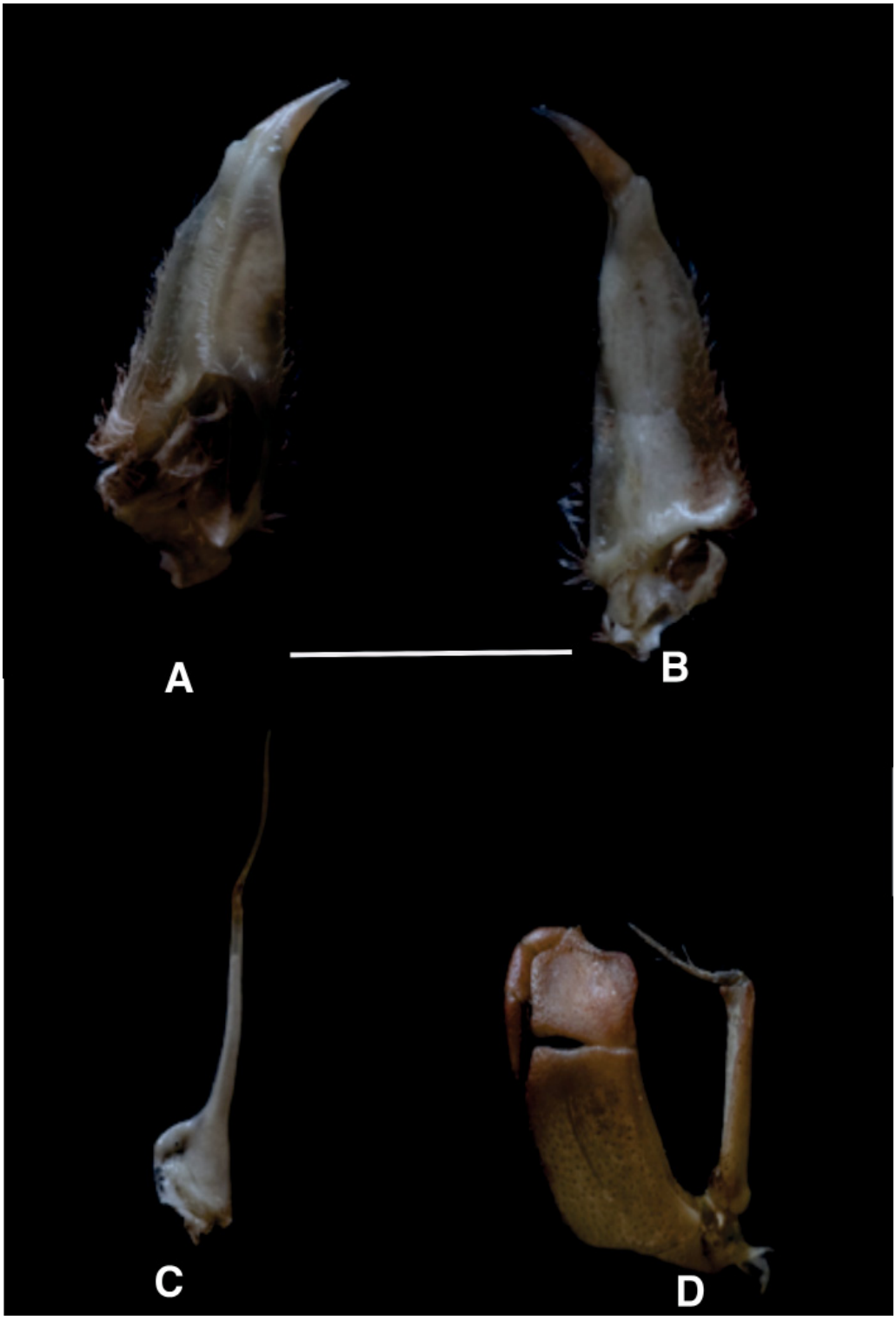

Fig. 9. *Potamonautes baziya* sp. nov., ♂, holotype (SAM A-094474) **A**. Left gonopod 1, anterior view. **B**. Left gonopod 1, posterior view. **C**. Left gonopod 2, anterior view. **D**. Right third maxilliped. Scale bar = 10 mm.

Fig. 10. A. Dorsal image of *Potamonautes baziya* sp. nov., when alive. Scale bar = 10 mm. **B**. Afrotropical forest stream habitat where *P. baziya* sp. nov. was collected at Baziya forest station in Eastern Cape Province, South Africa.

lack dentition on the anterolateral carapace margins, have an ovoid cephalothorax and are generally flat (CH/CL < 0.50), with *P. parvicorpus* being a small-bodied species (CWW = 25.31 mm) confined to the Cape Peninsula and the adjacent mountainous interior (Stewart 1997a; Daniels *et al.* 2001). *Potamonautes brincki* is also small-bodied (CWW = 32.9 mm) and known from the Hottentots Holland Mountains, while *P. tuerkayi* is also small-bodied (CWW = 30 mm) and known from the Overberg in Western Cape province, South Africa (Stewart 1997b; Daniels *et al.* 2001; Wood & Daniels 2016). Ecologically, the three latter species occur under stones in first order, fast-flowing mountains streams, and occur sympatrically with *P. perlatus* in the lower reaches. The undescribed species from Hogback is also present at Katberg and Fort Fordyce Nature Reserve in the Eastern Cape, South Africa (Daniels unpubl.). The undescribed Hogsback species occurs along steep cliffs under stones in high altitude (> 800 m a.s.l.) Afrotemperate forested areas where there is frequently very limited water flow, and it is sympatric with *P. danielsi*.

Discussion

Fine-scale sampling and the use of DNA sequence data has again helped in the discovery of two additional freshwater crab species from South Africa. Large areas of the interior of South Africa remain unsampled, particularly along mountains in Limpopo, Mpumalanga and the North West provinces of the country. Freshwater habitats in these areas should be targeted in future systematic surveys to collect crabs since they will likely harbor additional new species. In the countries neighbouring South Africa, such as Eswatini, Mozambique and Zimbabwe, limited sampling of freshwater habitats has occurred, suggesting that in these countries the diversity of freshwater crabs and other crustaceans is likely underestimated. For example, research in Mozambique has resulted in the description of four new freshwater crab species (*P. bellarussus*, *P. gorongosa*, *P. namuliensis* and *P. licoensis*) (Daniels & Bayliss 2012; Daniels *et al.* 2014, 2020b; Cumberlidge *et al.* 2017) while two additional species from high altitude mountain streams still await formal description. All four of the aforementioned species were collected from inaccessible mountain areas that have not been sampled in decades. The application of DNA sequence data has now become an integral part of understanding phylogenetics as well as in aiding the description of novel lineages. Renewed efforts to document the aquatic biodiversity of southern Africa, focusing specifically on high altitude mountains areas, is required.

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