Arthropoda Selecta 33(2): 193–206

A new species of the genus *Ctenapseudes* Bamber, Ariyananda et Silva, 1997 (Tanaidacea: Parapseudidae) from the Cần Giờ mangrove area in South Vietnam

Новый вид рода *Ctenapseudes* Bamber, Ariyananda et Silva, 1997 (Tanaidacea: Parapseudidae) из мангровых болот Канзе Южного Вьетнама

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KEY WORDS: diversity, Crustacea, Peracarida, taxonomy, new species, mangrove swamp, Indo-West Pacific, Indochina.

КЛЮЧЕВЫЕ СЛОВА: разнообразие, Crustacea, Peracarida, таксономия, новые виды, мангровые болота, Индо-Западная Пацифика, Индокитай.

ABSTRACT. A new species of the genus *Ctenapseudes* Bamber, Ariyananda et Silva, 1997 (Tanaidacea: Parapseudidae) is described from the deep mangrove swamps of the Cần Giờ Biosphere Reserve in South Vietnam. The new species is closely related to *Ctenapseudes sapensis* (Chilton, 1926), known from the Upper Songkhla Lagoon in Thailand (Siam Bay), but can be well separated from this species and other congeners by the features of the antennular flagellum, maxilliped, cheliped and pereopods. The calculated density of this species, which is about 1,323±189 inds/m^2 and the observed label of stable isotopes $\delta^{13}C/\delta^{15}N$, suggests that these tanaidaceans are among the most abundant primary consumers (C1) in the studied lagoon, probably feeding on the leaves of the mangrove *Rhizophora apiculata* Blume (Rhizophoraceae). The article also discusses the diversity, the role in trophic interactions and ecological impact of tanaidaceans in mangrove habitat.

How to cite this paper: Marin I.N., Palatov D.M., Nguyễn T.V. 2024. A new species of the genus *Ctenapseudes* Bamber, Ariyananda et Silva, 1997 (Tanaidacea: Parapseudidae) from the Cần Giờ mangrove area in South Vietnam // Arthropoda Selecta. Vol.33. No.2. P.193–206. doi: 10.15298/arthsel.33.2.06

РЕЗЮМЕ. Новый вид рода *Ctenapseudes* Bamber, Ariyananda et Silva, 1997 (Tanaidacea: Parapseudidae) описан из мангровых болот биосферного заповедника Канзе в Южном Вьетнаме. Новый вид наиболее близок к *Ctenapseudes sapensis* (Chilton, 1926), который известен из верхней лагуны Сонгкхла в Таиланде (Сиамский залив), но хорошо отличим от этого вида и других видов рода по особенностям жгутика антеннул, максиллипед, хелипед и переопод. Рассчитанная плотность этого вида, которая составляет около 1,323±189 особей/м^2, и наблюдаемая метка стабильных изотопов $\delta^{13}C/\delta^{15}N$, позволяют предположить, что эти ракообразные являются одними из наиболее массовых первичных консументов (C1) в исследуемой лагуне, вероятно, питаясь листьями мангровых деревьев *Rhizophora apiculata* Blume (Rhizophoraceae). В статье также обсуждается разнообразие, роль в трофических взаимодействиях и экологическое воздействие ракообразных-танаид в мангровых зарослях.

Introduction

The tanaid crustaceans, or tanaidaceans (order Tanaidacea Dana, 1849), currently including more than 1,200 living species, are widely distributed in the World Ocean from littoral to abyssal depths [Błażewicz-Paszkowycz *et al.*, 2012; Anderson, 2016]. These tiny crustaceans, with body sizes typically only a few millimeters long, exhibit a variety of lifestyles, from free-living to adapting to an interstitial lifestyle, living in empty gastropod shells, similar to hermit crabs, others build tubes on various substrates or on other organisms [Hassack, Holdich, 1987; Błażewicz-Paszkowycz *et al.*, 2012; Kakui, Hiruta, 2014; Błażewicz-Paszkowycz, 2014]. These crustaceans play

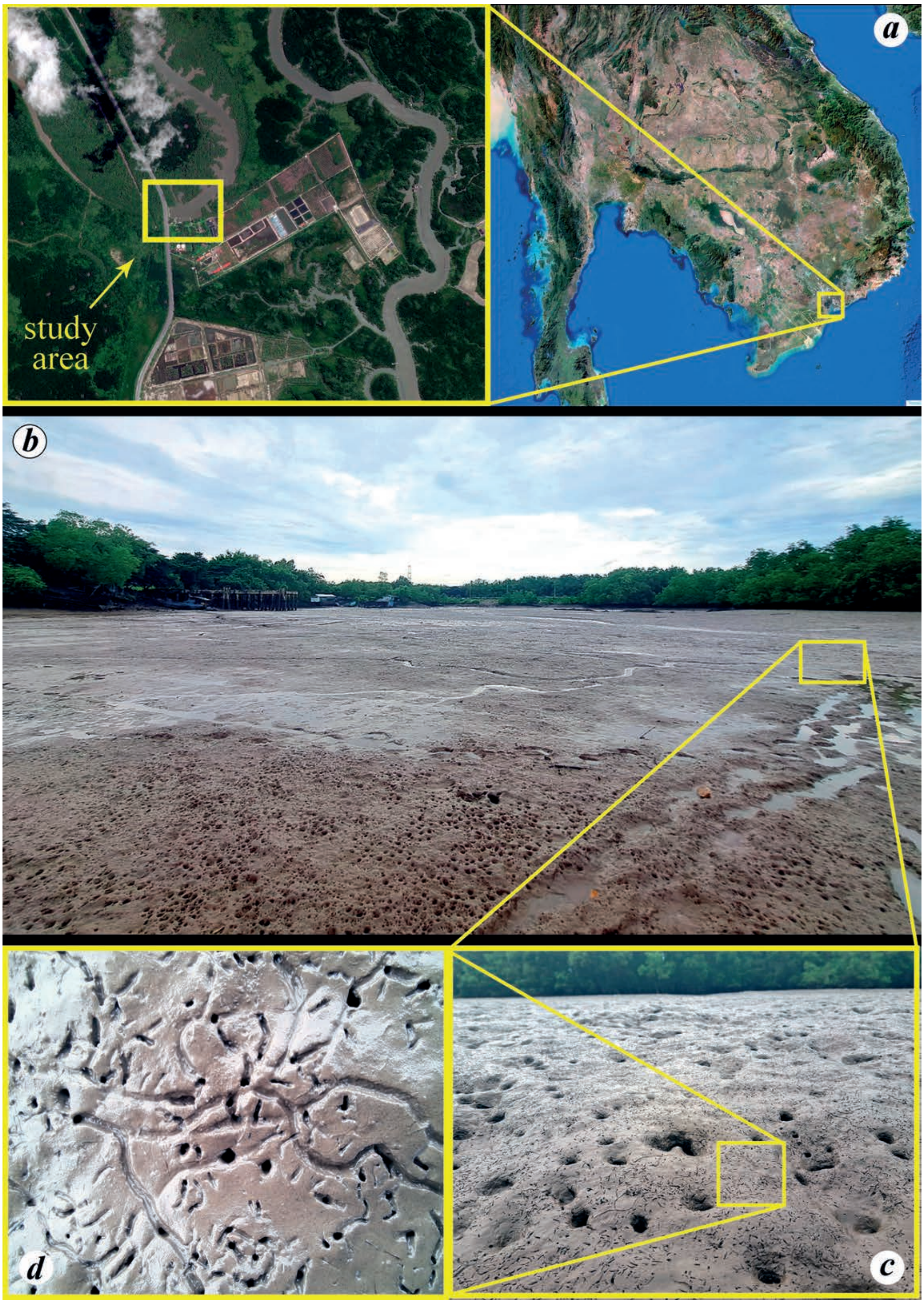

Fig. 1. The habitat of *Ctenapseudes vuxuankhoi* sp.n. in the mangrove swamps of the Cần Giớ Biosphere Reserve, South Vietnam: *a* — general map of the location of the study area in the Cần Giớ Biosphere Reserve; *b* — general view of the lagoon during the lowest level of the tide; *c* — bottom of the lagoon with *Wolffogebia cangioensis* Kolevatov et Marin, 2022 (Decapoda: Upogebiidae) (large) and tanaidacean burrows; *d* — tanaidacean burrows on the surface mud of the bottom of the lagoon. Photocredits: *b, c, d* — from Tien Tran Van.

Рис. 1. Биотоп *Ctenapseudes vuxuankhoi* sp.n. в мангровых болотах биосферного заповедника Канзе, Южный Вьетнам: *a* — общая карта расположения исследуемой территории в биосферном заповеднике Канзе; *b* — общий вид лагуны во время максимального отлива; *c* — дно лагуны с норами *Wolffogebia cangioensis* Kolevatov et Marin, 2022 (Decapoda: Upogebiidae) (крупные) и танаид; *d* — норы танаид на поверхности ила дна лагуны. Фотографии: *b, c, d* — от Тьен Тран Вана.

a crucial role in a wide range of marine ecosystems by connecting primary producers and higher trophic levels. This is attributed to their high abundance (reaching up to 146,000 inds/m^2) in some habitats [Barnard, 1970; Delille *et al.*, 1985; Bouillon *et al.*, 2002; Lee, 2008; Angsupanich *et al.*, 2010; Li *et al.*, 2022]. Devoid of a dispersal phase, such as planktonic larvae in their life cycle, allopatric speciation and high regional diversity dominate in this typical peracarid group of crustaceans, making a cosmopolitan distribution unlikely or even non-existent [Bamber, 1998; Blazewicz-Paszkowycz *et al.*, 2012].

The suborder Apseudomorpha is considered as the most plesiomorphic group within the order Tanaidacea, having been present since the Lower Carboniferous, the Triassic and the Jurassic [Schram, 1986; Błażewicz-Paszkowycz *et al.*, 2012]. This group displays high morphological diversity, adapted to a variety of specific and specialized habitats; most apseudomorph tanaidaceans are burrowers [Błażewicz-Paszkowycz *et al*., 2012; Kakui, 2017]. As opportunistic feeders, especially representatives of the family Parapseudidae, these peracarid crustaceans form dense populations and serve as a food source for many local fish species in mangrove communities and shallow water coastal lagoons of the Indo-Western Pacific region [Angsupanich, Siripech, 2001; Angsupanich *et al.*, 2005a, b, 2010]. Most species in mangrove communities are confined to non-marine habitats with narrow distribution ranges, primarily due to the absence of a dispersal phase and limited capacity to settle across large open oceanic areas. Consequently, the diversity within genera is typically defined by numerous allopatric species residing in distant and well-isolated mangrove communities or brackish water habitats, where they form similar complexes with unrelated species. [Kakui, Angsupanich, 2012, 2013; Angsupanich *et al.*, 2005a, 2010].

A detailed study of the crustacean biodiversity in the deep mangrove swamps of the Cần Giờ Biosphere Reserve also revealed the high diversity of tanaidaceans, forming a specific infaunal complexes associated with muddy habitats (see Fig. 1) [Marin, 2021a, b; Kolevatov, Marin, 2022; Marin, Palatov, 2022; Marin *et al.*, 2023]. Herewith, we describe a new species from the genus *Ctenapseudes* Bamber, Ariyananda et Silva, 1997, which sympatrically coexisting with several others tanaidaceans (see Marin *et al.*, 2024) in such specific habitats of deep mangrove swamps of this area.

Material and methods

SAMPLING. Tanaidaceans were manually collected using a hand net from the muddy bottom of the mangrove swamps located at 10°27′30.7″N 106°53′35.7″E (Fig. 1) in the Cần Giờ Mangrove Biosphere Reserve, South Vietnam during the period of September–October 2022–2023. All the collected samples were preserved in 90% ethanol for subsequent DNA analysis. At least one crustacean specimen from each location was used for molecular analysis in order to understand their genetic diversity in the region as much as possible. All collected animals were identified to the species level using a light microscope. The type material has been deposited at the collection of the Zoological Museum of Moscow State University, Moscow (ZMMU), while additional material is stored in the personal authors' collection (LEMMI).

MORPHOLOGICAL STUDY. Alive animals were relaxed in a clove oil and then photographed using CanonG16 digital camera. The light microscopy photographs of morphological features were captured using a digital camera attached to Olympus ZX10 and Olympus CX21 light microscopes. The scanning electron microscopy (SEM) images were obtained at the Paleontological Museum of the Paleontological Institute of the Russian Academy of Sciences, Moscow, using the Vega3 Tescan microscope. Tanaidaceans were placed in 95% ethanol, cleaned in an ultrasonic cleaner, followed by dehydration with acetone and critical-point drying (CPD). Subsequently, they were affixed to specimen stubs with double-sided tape, and finally coated with gold through sputtering using the Polaron PS 100. The standard measurement of the body length (bl., in mm) is defined as the dorsal length from the distal margin of the head (rostrum) to the posterior margin of the telson, excluding the length of the uropod and antenna.

ECOLOGICAL ANALYSIS. The density analysis of the studied crustaceans was carried out using a PVC pipe with a diameter of 13 cm. The pipe was immersed deeply into the muddy bottom, and then carefully removed from the substratum. Then the collected substratum was placed on a sieve with a mesh of 2 mm, and all animals from one sample were transferred to a separate tube, identified, and carefully counted. A total of 23 quantitative samples were used in this study.

STABLE ISOTOPE ANALYSIS. The organic matter (leaves of mangroves) and tanaidaceans for the stable isotope analysis were collected in the same studied locality, 10°27′30.7″N 106°53′35.7″E, in South Vietnam (see above). The muscle tissue of collected animals and plant material was oven-dried at 50°C for 4–5 days and then wrapped in tin foil (1200–1500 μg and 400–600 μg, respectively). The composition of stable isotope ($\delta^{13}C/\delta^{15}N$) was determined using a Thermo–Finnigan Delta V Plus continuous-flow mass spectrometer (Thermo Electron GmbH, Bremen, Germany) coupled with an elemental analyzer (Thermo Flash 1112, Thermo Electron) at the Joint Usage Center at the A.N. Severtsov Institute of Ecology and Evolution of the Russian Academy of Sciences. The isotopic composition of nitrogen and carbon was expressed in the δ-notation relative to the international standard (atmospheric nitrogen or VPDB): $\delta X(‰)=[(Rsample/Rstandard)-1]\times1000$, where R is the ratio of the heavier isotope to the lighter isotope. Samples were analyzed with reference gases calibrated against IAEA (Vienna, Austria), reference materials USGS 40 and USGS 41(glutamic acid). The drift was corrected using internal laboratory standards (acetanilide, ca-sein). The standard deviation of $\delta^{15}N/\delta^{13}C$ values in our laboratory standards (n=8) was <0.15‰.

Results

TAXONOMIC PART

Order Tanaidacea Dana, 1849
Suborder Apseudomorpha Sieg, 1980
Family Parapseudidae Guţu, 1981
Genus *Ctenapseudes* Bamber, Ariyananda et Silva, 1997

***Ctenapseudes vuxuankhoi* sp.n.**

Figs 2–7.

MATERIAL EXAMINED. Holotype ♀, bl. 5.5 mm, ZMMU Mh-4 — VIETNAM, Ho Chi Minh District, Cần Giớ Mangrove Biosphere Reserve, 10°27′30.7″N 106°53′35.7″E, the extended cut part of one of

Fig. 2. *Ctenapseudes vuxuankhoi* sp.n., general dorsal and lateral views. Scale bar — 0.5 mm.
Рис. 2. *Ctenapseudes vuxuankhoi* sp.n., общий вид сверху и сбоку. Шкала — 0,5 мм.

the channels connected to the estuary, deep muddy bottom, hand net sampling coll. D. Palatov & I. Marin, 25.09.2022.

Allotype ♂, bl. 6.5 mm, ZMMU Mh-5 — same location and date as for holotype.

Paratype, 2♀♀ (bl. 5.5 and 5.4 mm and 2 ♂♂ (bl. 6.2 and 6.3 mm), ZMMU Mh-6 — same location and date as for holotype.

ETYMOLOGY. The new species is named after Dr. Vu Xuan Khoi, the former chief of the Laboratory of Ecology in the Southern Branch of the Joint Vietnam–Russia Tropical Research and Technological Center, Ho Chi Minh, Vietnam.

DIAGNOSIS. Body dorsoventrally flattened. Carapace barrel-shaped, with acute sharp triangular rostrum, eyes present. Pereon with free pereonites. Pleon with 5 short broad triangular pleonites; pleonite I with a transverse row of long plumose setae; pleonites I–IV with 3–4 long lateral plumose setae on each side, exceeding the length of the corresponding segment. Pleotelson about 1.5 times longer than wide, with posterior margin triangular. Inner antennular flagellum longer than outer flagellum in ♂♂, equal in ♀♀. Maxilliped endite bearing 9 strong plumose setae along inner margin; maxilliped palp article II without spines on outer margin. Carpus of cheliped stout in ♀♀, about 5.5 times longer than wide. Propodus of pereopod I stout and significantly distodorsally expanded, with 2–3 ventral spines. Ischium of pereopod II unarmed. Uropodal exopodite with 8 articles, endopodite with about 34–35 articles, about 3.5 times longer than exopodite in ♀♀; exopodite composed of 10–11 articles and endopodite composed of approximately 36–39 articles in ♂♂.

DESCRIPTION. Based on holotype ♀. Body (Figs 2, 7*b*); dorsoventrally flattened; about 5 times longer than carapace width; carapace about as wide as long, with acute triangular rostrum (Fig. 7*c*); ocular lobes distinctly anterolaterally produced, eyes well pigmented, brightly white; epistome pointed with small upturned spiniform seta; pereonites I to VI, respectively 2.7, 2.1, 1.6, 1.4, 1.4 and 1.3 times wider than long; pereonites

III–VI with small mid-ventral spinous processes (hyposphenia) (Fig. 7*k*); pleonite I with a transverse row of long plumose setae; pleonites I–V subequal in length, with small mid-ventral acute thick tubercle, dorsally smooth; pleonites I–IV with 3–4 long lateral plumose setae on each side, exceeding the length of the corresponding segment; pleonite V on the lateral surfaces with 1–2 short plumose setae; (Fig. 6*a*); epimeral plates pointed and directed backward, most prominent on pleonite V; pleotelson about 1.5 times longer than wide (Figs 6*a*, *b*, 7*e*).

Antennula (Fig. 3*a*) different between male and female, significantly longer in male (Fig. 3*b*). Article I of peduncle about 2.5 times longer than wide and about 0.4 times as long as carapace in female (Fig. 3*a*), with long simple and short broom setae along lateral margins; article II about 2.6 times longer than wide, about 0.6 times as long as article I and about 3 times longer than article III, with long setae along lateral margins; article III about as long as wide; article IV short, as long as article III; with subequal flagella: inner flagellum with 10–13 articles, and 12–15 articles in outer flagellum.

Antenna (Fig. 3*c, d*) about as long as antennular peduncle; article I short, about as long as wide, spine-like, slightly curved distally; article II about 1.5–1.8 times longer than wide, oblong squama bearing 7 long setae; article III short, about 0.7–0.9 times as long as wide; article IV considerably shorter than article V, about as long as wide; article V about 1.6 times longer than wide; flagellum with 8 articles, bearing long simple setae along outer margin and shorter setae along inner margin.

Labrum (Fig. 3*e*) anterior part bluntly convex with marked blunt tip, with three tufts of fine setules on anterior margin.

Labium (Fig. 3*f*) lateral margins smooth, terminal lobes bearing 1 distal spiniform seta and dense long setules on anterolateral corner and the surface of medial half.

Mandible (Fig. 4*a*, *c*) molar process distally with rugose grinding surface; pars incisiva and lacinia mobilis (on left mandible only) with 5 blunt denticles and 5 spine-like accessory setae on setiferous lobe (Fig. 4*b*, *d*); palp stout, 3-articulated, ratio of articles I–III about 1.0/2.0/1.4, with many long simple setae along inner margins, articles II and III with comb of leaf–like stout setae on inner margin.

Maxillula (Fig. 3*e*) outer endite with 9–10 terminal and 2 strong subapical spiniform setae; inner endite with 4 long and 2 smaller ciliate setae on distal margin; palp 2-articulated, distal article slightly longer than basal one, with 2 long distal and 4 unequal subdistal setae.

Maxilla (Fig. 3*f*) outer lobe of movable endite bearing 6 long pinnate setae; inner lobe of movable endite with dense row of sickle-shaped setae, 4 pinnate and 2 ciliate setae; outer lobe of fixed endite with 3 pinnate, 1 palm leaf-like, 1 strong lower and about 6–7 smaller sickle shaped setae on apical margin; inner lobe of fixed endite with row of ciliate and simple setae.

Maxilliped (Fig. 3*g*) basis subquadrate, as long as wide; endite with 8 strong plumose setae along its inner side, 5 coupling hooks, and row of spiniform setae on anterior margin (Fig. 6*f*); palp 4-articulated, article I short and wide with 3 long simple setae on inner margin, article II about 3 times longer than article I, with 5 long distal simple setae on outer margin, with row of long setae along inner margin, article III small, oval, covered with long simple setae on inner margin; article IV very small, oval, bordered with long simple setae.

Epignath (Fig. 3*g*) cup-shaped, with strong spiniform setae bearing 9 strong apical plumose setae.

Cheliped (Fig. 5*a*, *b*) with 3-articulated exopodite, distal article of which with 3 plumose setae and 1 subdistal seta. Cheliped in female (Fig. 5*a*) with basis narrow, swollen distally, about 3.2 times longer than maximal width, with 7–8 distoventral setae; merus about 2.5–3 times longer than maximal width, with several rows of ventral simple setae; carpus about 5.5 times longer than wide, as long as basis, with several rows of setae; propodus about half as long as carpus, fixed finger slender, about 5 times as long as wide, bearing row of spinules along distal part of cutting margin; dactylus as long as fixed finger and propodus (palm), curved downward, with smooth cutting margin.

Pereopod I (Fig. 5*c*) wide (swimming-type); exopodite 3-articulated with 6 plumose setae on distal article; coxal plate oval, slightly wider than long; basis about 2.5 times as long a wide, with several simple setae distoventrally; ischium short, 3 times wider than long, with many long setae distoventrally; merus oblong, as long as carpus, covered with numerous simple setae and 1 distoventral small stout spiniform seta; carpus expanding distodorsally, with numerous long setae simple setae on dorsal and ventral margins and lateral surface, with 1 long distodorsal and 1 stout ventral spiniform setae; propodus oblong, as long as carpus, with numerous long setae on both margins, with 1 long distodorsal and 1 stouter ventral spiniform setae; dactylus short and slender, spiniform, about twice longer than adjacent spiniform setae, with some ventral denticles and sharp tip.

Pereopods II (Fig. 5*d*) and III (Fig. 5*e*) mostly similar; coxal plate wider than long; basis about 3.3 times longer than wide, subequal to combined length of ischium, merus and carpus, with several simple setae distoventrally; ischium small, wider than long, with many distoventral setae; merus shorter than carpus, with long slender distoventral spiniform setae, 1 small distodorsal setae, numerous long setae along ventral margin and 2 tufts of strong simple setae on lateral surface; carpus with 3–4 long spiniform setae on ventral margin and 2 short distodorsal spiniform setae, with numerous setae along ventral margin and row of strong setae on lateral surface; propodus with 2–3 ventral spiniform setae and 2 long distodorsal spiniform setae and row of long setae on lateral surface; dactylus long, spiniform, slightly longer than adjacent spiniform setae, about 0.7 times as long as propodus, with sharp tip.

Pereopods IV (Fig. 5*f*) and V (Fig. 5*g*) are also mostly similar; coxal plate wider than long, with bluntly convex ventral margin; basis swollen, about 3 times longer than wide, with several simple setae on distal half of ventral margin; ischium small, about as long as wide, with some distoventral setae; merus about 1.5 times longer than wide, about half as long as carpus, with 2 long spiniform setae and numerous long setae on ventral margins; carpus about 3 times longer than wide, with 5–6 long spiniform setae and numerous long simple setae on ventral margins; propodus shorter and slender than carpus, with subdistal row of slender long spiniform setae and simple setae, with 6–8 strong spiniform setae distodorsally; dactylus slender, slightly shorter than propodus, spiniform, with sharp tip.

Pereopod VI (Fig. 5*h*) with basis swollen, about 3.5 times longer than wide, dorsal marginal with row of long plumose setae, ventral margin with 6–7 plumose setae distally; ischium short, about as long as wide, with some simple distoventral setae; merus equal to ischium, short, about as long as wide, with several plumose setae along dorsal margin and several simple setae along ventral margin; carpus about 3 times longer than wide, about 3 times longer than merus and 1.5 longer than propodus, with row of dorsal plumose setae, ventral margin with several fine long spiniform setae and simple setae; propodus about 2.5 times as long as wide, with distal row of numerous plumose spine-like setae, 2–3 distodorsal long and 6–7 ventral long spiniform setae; dactylus slender, as long as propodus, spiniform, with sharp tip.

Oostegites oval or oblong, on cheliped and pereopods II–IV.

Pleopods (Fig. 6*d*) similar and biramous; basal article subcylindrical, about 2.5 times longer than wide; both rami oval,

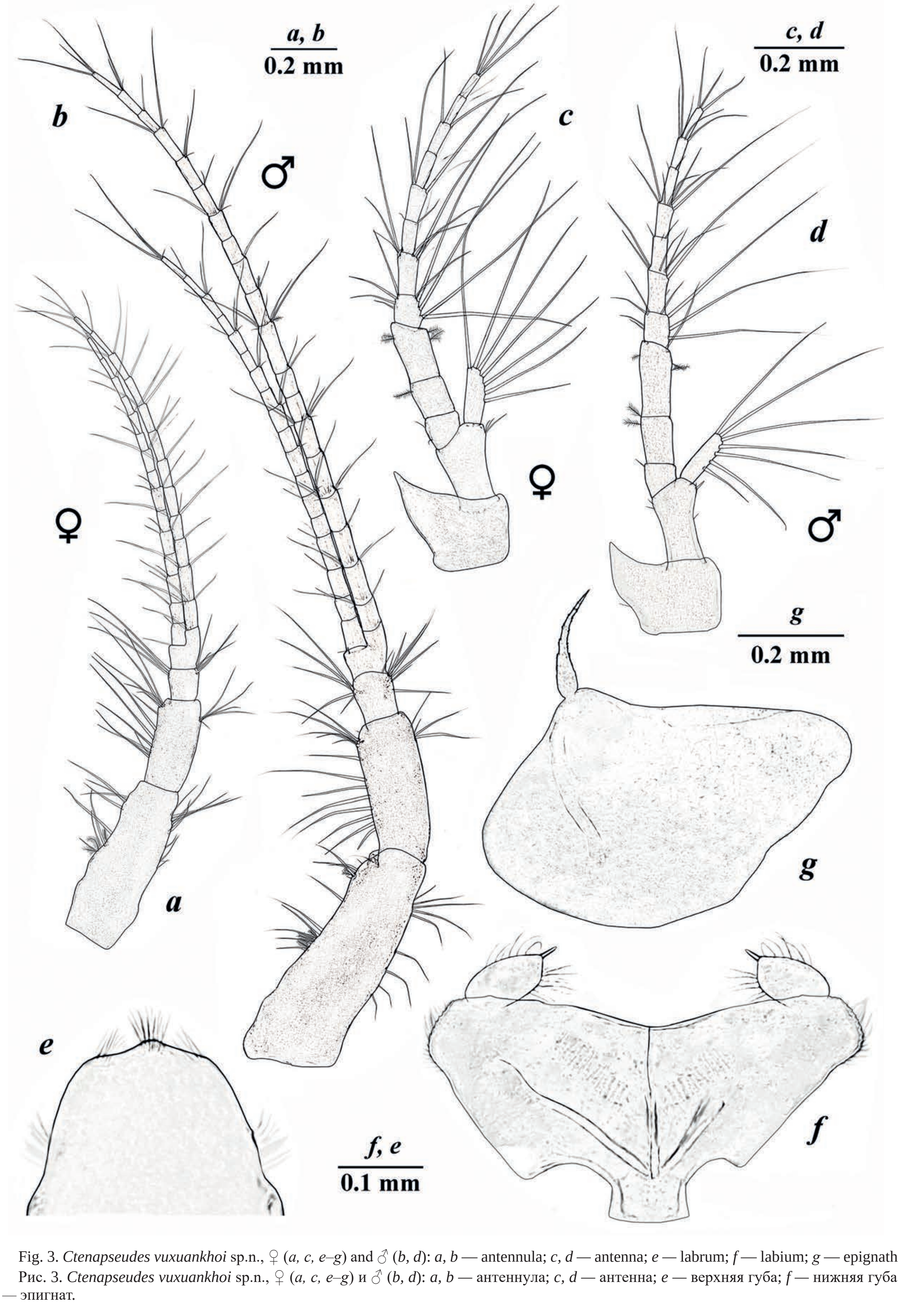

Fig. 3. *Ctenapseudes vuxuankhoi* sp.n., ♀ (*a, c, e–g*) and ♂ (*b, d*): *a, b* — antennula; *c, d* — antenna; *e* — labrum; *f* — labium; *g* — epignath.

Рис. 3. *Ctenapseudes vuxuankhoi* sp.n., ♀ (*a, c, e–g*) и ♂ (*b, d*): *a, b* — антеннула; *c, d* — антенна; *e* — верхняя губа; *f* — нижняя губа; *g* — эпигнат.

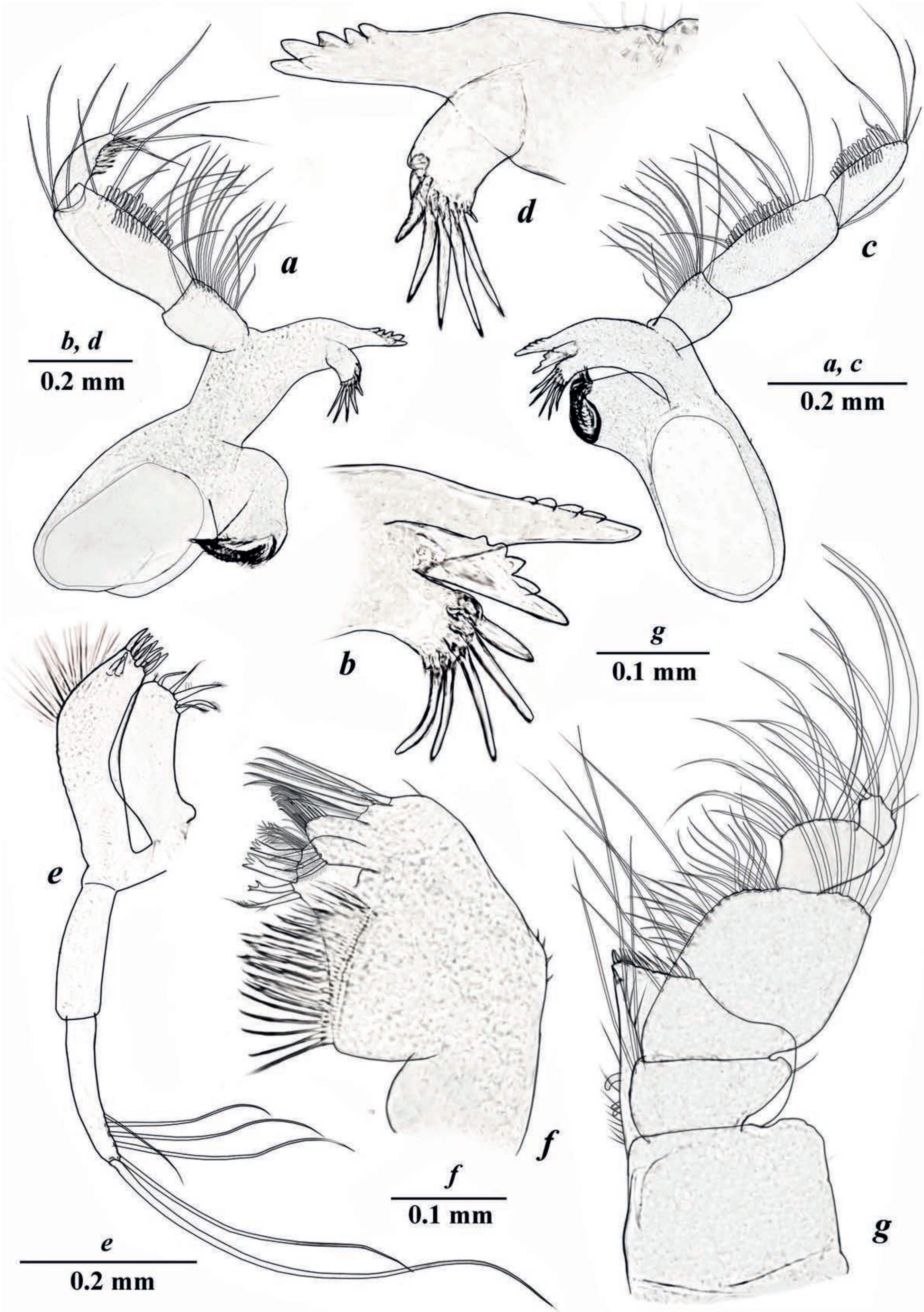

Fig. 4. *Ctenapseudes vuxuankhoi* sp.n., ♀: *a* — left mandible; *b* — same, incisor process; *c* — right mandible; *d* — same, incisor process; *e* — maxillula; *f* — maxilla; *g* — maxilliped.

Рис. 4. *Ctenapseudes vuxuankhoi* sp.n., ♀: *a* — левая мандибула; *b* — то же самое, резцовый отросток; *c* — правая мандибула; *d* — то же самое, резцовый отросток; *e* — максиллула; *f* — максилла; *g* — максиллипед.

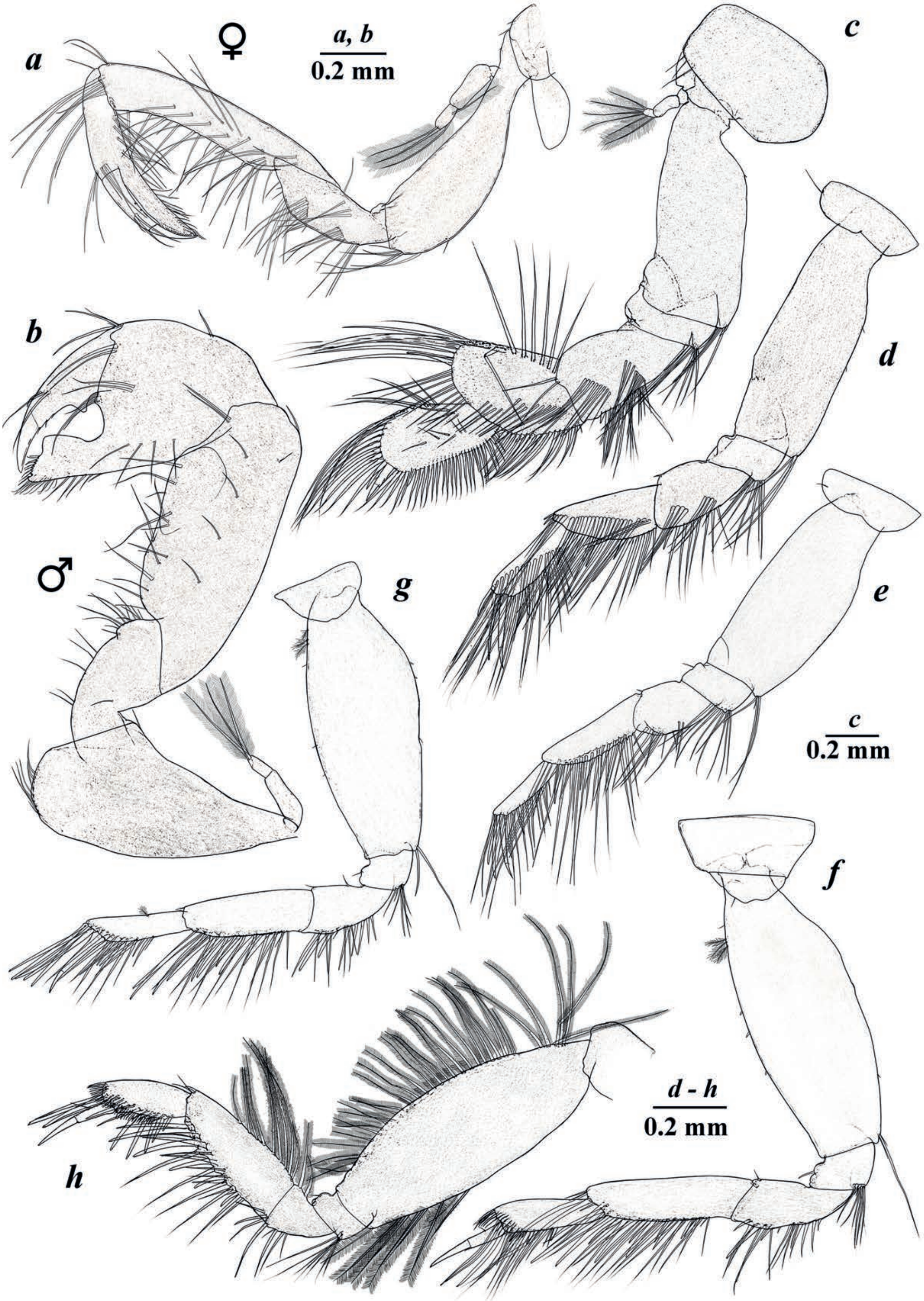

Fig. 5. *Ctenapseudes vuxuankhoi* sp.n., ♀ (*a, c–h*) and ♂ (*b*): *a, b* — cheliped; *c* — pereopod I; *d* — pereopod II; *e* — pereopod III; *f* — pereopod IV; *g* — pereopod V; *h* — pereopod VI.

Рис. 5. *Ctenapseudes vuxuankhoi* sp.n., ♀ (*a, c–h*) и ♂ (*b*): *a, b* — хелипеда; *c* — переопода I; *d* — переопода II; *e* — переопода III; *f* — переопода IV; *g* — переопода V; *h* — переопода VI.

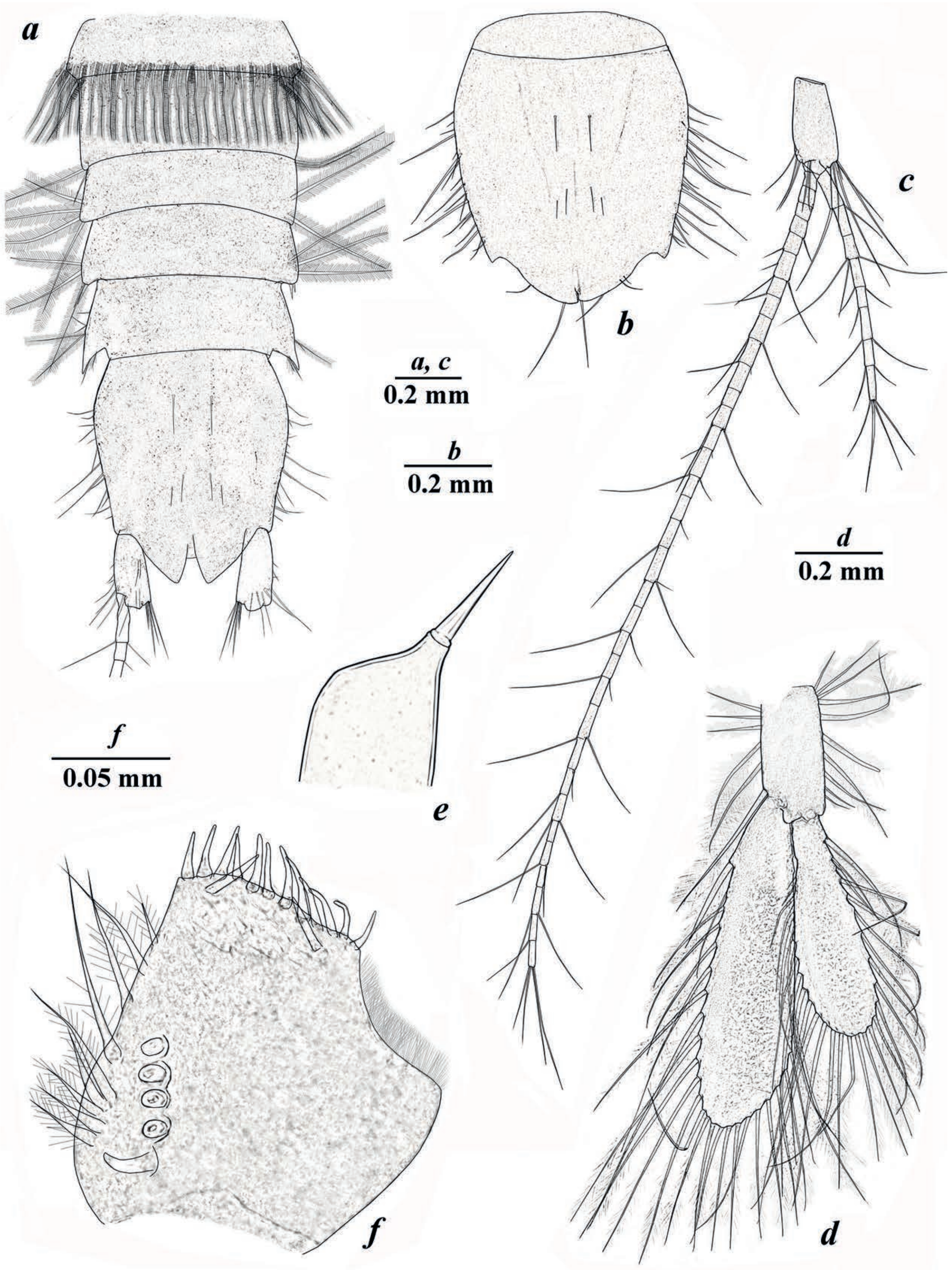

Fig. 6. *Ctenapseudes vuxuankhoi* sp.n., ♀: *a* — abdominal somites and pleotelson; *b* — pleotelson; *c* — uropod; *d* — pleopod; *e* — penis; *f* — endite of maxilliped.

Рис. 6. *Ctenapseudes vuxuankhoi* sp.n., ♀: *a* — брюшные сомиты и плеотельсон; *b* — плеотельсон; *c* — уропода; *d* — плеопода; *e* — пенис; *f* — эндит максиллипеды.

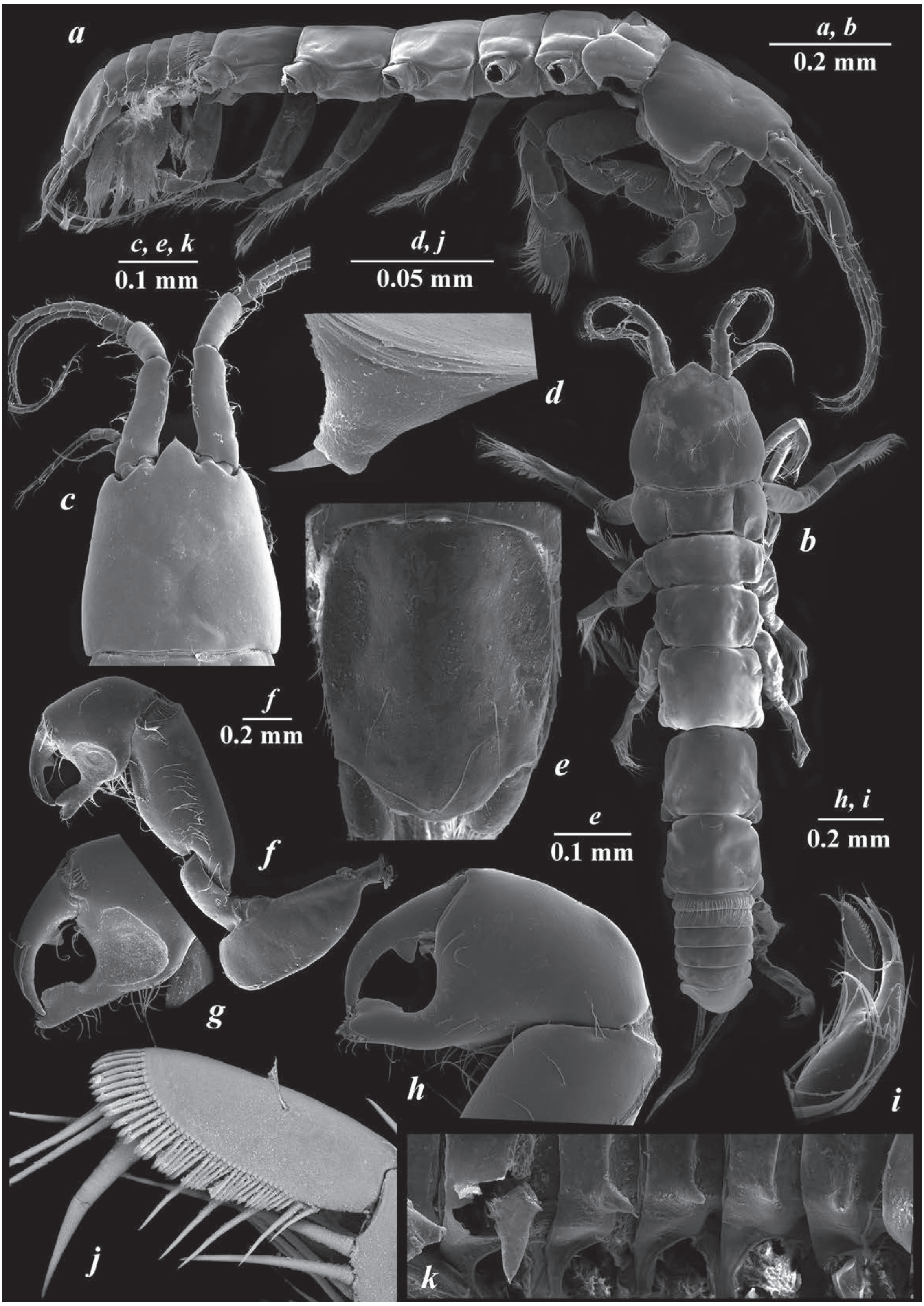

Fig. 7. *Ctenapseudes vuxuankhoi* sp.n., ♂ (*a, c–h, j, k*) and ♀ (*b, i*), SEM photographs: *a* — general lateral view; *b* — general dorsal view; *c* — head, dorsal view; *d* — hyposphenia of pereonite V; *e* — pleotelson; *f* — cheliped; *g–i* — same, chela (propodus); *j* — distal segments of pereopod VI; *k* — pereonites, ventral view.

Рис. 7. *Ctenapseudes vuxuankhoi* sp.n., ♂ (*a, c–h, j, k*) и ♀ (*b, i*), SEM фотографии: *a* — общий вид сбоку; *b* — общий вид сверху; *c* — голова, вид сверху; *d* — гипосфения переонита V; *e* — плеотельсон; *f* — хелипеда; *g–i* — то же самое, клешня (проподус); *j* — дистальные сегменты переопода VI; *k* — переониты, вид снизу.

long and narrow, bearing long plumose setae, endopodite about 1.6 times longer than exopodite.

Uropod (Fig. 6*c*) biramous, filiform; basal article subcylindrical, about 2.5 times longer than wide; rami with indistinct articulations, exopodite with 8 articles, endopodite with about 34–35 articles, about 3.5 times longer than exopodite.

MALE ALLOTYPE shows some differences in morphology from holotype female. Body slightly pronounced, about 5.6 times longer than wide (Figs 2, 7*a*). Carapace is about 1.1 times longer than width. Antennule with peduncular article about 3 times longer than wide and about 0.7 times as long as carapace in male (Fig. 3*b*); peduncular article IV slightly longer inner than outer flagella, which with 19 (inner) and 18 (outer) articles, respectively. Antenna with article V about 1.6 times longer than wide and flagellum 7-articlulated. Cheliped in male (Figs 5*b*, 7*f*) significantly stronger and more robust than in female, with basis greatly swollen distally, about 2.5 times longer than maximal width, with 7–8 distoventral setae; merus about 2 times longer than maximal width, with row of subdistal ventral simple setae on inner margin; carpus strong, about 2.5 times longer than, as long as basis, with simple setae along inner margin; propodus (Fig. 7*g, h*) swollen distally, subquadrate, about as long as wide, with strong and stout fixed finger about 2 times longer than wide, bearing well-marked subdistal crest and a row of small distal spinules along subdistal part on cutting margin; dactylus as long as fixed finger and propodus , sharpening distally, curved downward, with triangular blunt proximal tooth and distally smooth cutting margin. Ventral margin of pereopod VII bears only 1–3 short plumose setae distally. Uropods longer, with the exopodite composed of 10–11 articles and endopodite composed of approximately 36–39 articles.

COLORATION. The body, antenna and appendages are milky white, with bright white spots on dorsolateral margins of the anterior part of the carapace and the dorsolateral margins of the pereonites; eyes are brightly white; pleotelson milky white with bright white spots on dorsolateral margins in ♂♂, and brightly white in ♀♀ (see Fig. 2).

ECOLOGY AND DISTRIBUTION. The species is currently known only from the type locality, the Cần Giờ Mangrove Biosphere Reserve, South Vietnam, where it lives in the upper layer of alluvial silt. The most significant aggregations of the species, up to 1,323±189 inds/m^2, are observed in the cut part of the mangrove channel within peculiar lacunae surrounded by mangrove forest. It also occupies the silt along the entire length of the channel but does not extend to the estuary part of the bay.

TAXONOMIC REMARKS. Currently, the genus *Ctenapseudes* incudes 4 valid species, namely *Ctenapseudes chilkensis* (Chilton, 1924), *Ctenapseudes extravaganza* Bamber, Ariyananda et Silva, 1997, *Ctenapseudes indiana* Pandiyarajan et Biju, 2017 an *Ctenapseudes sapensis* (Chilton, 1926). All species are known from mangrove lagoons or brackish waters in the river estuary of India, Sri Lanka and Thailand (see below).

The new species closely resembles *C. sapensis*, as re-described by Angsupanich *et al.* [2010] from the Upper Songkhla Lagoon (Siam Bay) in Thailand. However, it can be distinguished by the following characteristics: 1) maxilliped endite bearing 9 strong plumose setae along inner margin (compared to 6 strong plumose setae in *C. sapensis*); 2) maxilliped palp article II without spines on outer margin (compared to 3 well-marked spines in *C. sapensis*); 3) stouter carpus of cheliped in ♀♀, about 5.5 times longer than wide (compared to 8 times longer than wide in *C. sapensis*); 4) smooth dorsal and ventral margins of basis of pereopod I (compared to both margins covered with small but well-marked setae in *C. sapensis*; and 5) with only three plumose setae on ventral margin of basis of pereopod VI (compared to a dense row of plumose setae in *C. sapensis*).

The new species is also morphologically similar to *C. chilkensis,* known from the Chilika Lake, located in the Odisha state on the east coast of India at the mouth of the Daya River, and *C. extravaganza* from Sri Lanka. However, it can be differentiated from these two species by the following features: 1) a stout and significantly distodorsally expanded propodus of pereopod I, similar to that of *C. sapensis,* with 2–3 ventral spines (in contrast to 5 spines in *C. chilkensis* and *C. extravaganza*, as well as some minimal features such as 2) much stouter antenna; 3) different profile of rostrum; and 4) shorter and stouter dactylus of cheliped [Chilton, 1924; Barnard, 1935; Bamber *et al.*, 1997; Angsupanich *et al.*, 2010].

Lastly, the new species can be distinguished from *C. Indiana*, inhabiting the Kochi Backwaters estuary, located in Kerala state, south-western India, by the following characteristics: 1) inner antennular flagellum longer than outer in ♂♂ (vs. inner and outer antennular flagella are similar in both sexes); 2) outer antennular flagellum with 12–15 articles (vs. 19–25 articles); 2) significantly slender distal segments of cheliped in ♀♀; and 3) unarmed ischium of pereopod II (vs. with one ventral spiniform setae in *C. indiana*) [Pandiyarajan *et al.*, 2017].

ECOLOGICAL PART

The bottom habitats in deep areas of mangrove forests and swamps that we investigated are characterized by an accumulation of alluvial deposits with a relatively low oxygen content at the depth of silty substrates. This low oxygen content is primarily attributed to the activity of anaerobic sulfur-reducing bacteria [Ng, Sivasothi, 2002; Hossein, Nuruddin, 2016]. On the other hand, the upper layer of the substrate, about 1 centimeter, likely provides optimal conditions for life, supporting a large population of crustaceans. The diversity of benthic organisms in that area is relatively low; however, most species show high population densities. The most abundant inhabitants of the studied lagoon are the peracarid crustaceans described

Table 1. Stable isotope ($\delta^{13}C/\delta^{15}N$±SD) values (‰) for the studied tanaidaceans and their probable food source from the Cần Giờ mangrove area in South Vietnam.

Таблица 1. Значения стабильных изотопов ($\delta^{13}C/\delta^{15}N$±SD) (‰) для изученных видов танаид и их вероятного источника пищи в мангровом районе Канзе в Южном Вьетнаме.

Sample	$\delta^{13}C$	$\delta^{15}N$	Mean±SD ($\delta^{13}C$)	Mean±SD ($\delta^{15}N$)	Number
Ctenapseudes vuxuankhoi sp.n.	−25.62	4.58	0.27	0.18	10
Pseudohalmyrapseudes alexeitiunovi	−24.85	4.34	0.38	0.19	5
Mangrove *Rhizophora apiculata* (source)	−31.1	4.8	2.0	0.1	5

above, *Ctenapseudes vuxuankhoi* sp.n., *Pseudohalmyrapseudes alexeitiunovi* [Marin *et al*., 2024] and one unidentified species reaching the density values for 1,323±189 inds/m^2, 124±17 inds/m^2 and 49±17 inds/m^2 respectively (totally 1,499±192 inds/m^2 for all tanaidacean species), the burrowing shrimps *Wolffogebia cangioensis* Kolevatov et Marin, 2022 (Decapoda: Gebiidea: Upogebiidae) (635±68 inds/m^2); several species of amphipod crustaceans (Crustacea: Amphipoda) (about 119±19 inds/m^2 totally for all amphipods), preliminary identified as *Melita* sp. (Melitidae) (7±4 inds/m^2), *Victoriopisa* sp. (Eriopsidae) (36±14 inds/m^2), and *Grandidiniella* sp. (Photidae) (56±27 inds/m^2); and *Alpheus* sp. (Decapoda: Caridea: Alpheidae) (possibly two different species); polychaetes (Polychaeta) and burrowing anemones (Hexacoralia), which were unidentified density values were not calculated. This complex of the species (primary consumers) actually forms the trophical basis of this community, representing the majority of the abundance and biomass of local benthic fauna.

The results obtained from the stable isotope composition ($\delta1^3C/\delta^{15}N$) indicate that the examined crustaceans, *Ctenapseudes vuxuankhoi* sp.n. and other species under study are primary consumers feeding on organic matter, presumably derived from the leaves of the local mangrove *Rhizophora apiculata* (see Table 1). A detailed study of the trophic structure of this community will be presented in a forthcoming publication [Marin *et al*., in prep.].

Discussion

Beyond its taxonomic significance, this work also highlights the crucial ecological functions of coastal mangrove flooded plains (swamps). These areas concentrate primary organic matter, fostering conditions for its processing and the formation of a high biomass of primary nutrients. Studies have demonstrated that silty sediments in the depths of mangrove forests usually support a higher density of bottom organisms compared to adjacent, non-vegetation-covered sediments [Edgar, 1990; Sasikumar, Chong, 1998]. In these habitats, peracarid crustaceans (tanaidaceans, amphipods, isopods) commonly dominate, and they seem to have the ability to utilize primary plant products, subsequently serving as a food source for fish. Studies conducted in temperate zones also indicate the importance of tidal mudflats in the life cycle of many fish species [Laffaille *et al*., 1998; Morrison *et al*., 2002; Almeida, 2003; Carpentier *et al*., 2014].

In the present study, several species of crustaceans, including tanaidaceans, amphipods and decapods (see above), predominate in this lagoon in terms of abundance and biomass. The abundance of these opportunistic feeders usually indicates a significant accumulation of organic matter in the area [Pearson, Rosenberg, 1978]. For example, *Ctenapseudes sapensis* is the dominant species widespread in the Songkhla Lagoon, Thailand, reaching its peak density of 5,044 inds/m^2 in the period following the rainy season (February) [Angsupanich, Siripech, 2001; Jombodin *et al*., 2022]. This species is a major food source for the locally dominant ariid catfishes, *Osteogeneiosus militaris* (Linnaeus, 1758) and *Arius maculatus* (Thunberg, 1792) (Siluriformes: Ariidae) [Angsupanich *et al*., 2005b]. In the case of the mangrove ecosystem in Cochin, Southern India, the density of *Ctenapseudes chilkensis* reaches a density of 29,419 inds/m^2 [Joseph *et al*., 2021]. Meanwhile, another parapseudid tanaidacean *Halmyrapseudes gutui* Kakui et Angsupanich, 2013 reaches 9,987 inds/m^2 in the mangrove environment of Lidee Island in southern Thailand [Kakui, Angsupanich, 2013]. Another example is *Halmyrapseudes spaansi* Băsescu et Gutu 1975, reaching a density of 8,736–38,528 inds/m^2 and biomass up to 37 g/m^2 in Sinnamary mudbanks of French Guiana (05°27'N 53°00'W), offering a potential rich trophic resource for many predator species [Nguyen *et al*., 2018]. The final examples are the tanaidaceans *Hargeria rapax* (Harger, 1879) and *Halmyrapseudes bahamensis* Băsescu et Gutu, 1974, which could reach a maximum density of 35,127 inds/m^2 in mangroves during April in Rookery Bay, Florida [Sheridan, 1997]. The density values of the tanaidaceans, *Ctenapseudes vuxuankhoi* sp.n. and *Pseudohalmyrapseudes alexeitiunovi* Marin, Palatov et Nguyễn, 2024, in the mangrove swamps of Cần Giờ Biosphere Reserve in South Vietnam were not so abundant during the rainy season in September–October, the period when the study was conducted. However, it is anticipated that in the spring.

Isotopic labels of both species clearly indicate that they consume primary organic matter, most likely the leaves of locally common mangrove *Rhizophora apiculata* Blume (Plantae: Rhizophoraceae) (see above). In fact, representatives of the genera *Ctenapseudes* and *Halmyrapseudes* Băsescu et Gutu, 1974 are the most numerous peracarids in mangrove and estuarine habitats across various tropical regions, where they are often the main component of the diet for many local fish species. For example, *H. spaansi* in French Guinea had the lowest trophic ratio among studied local consumers and were classified as C1 (primary consumers). The diet of the species consists of terrestrial freshwater's source (i.e., mangrove leaves) accounting for 11.5–35.54% depending on season; the remaining influence was attributed to the alternative mudflat source (64.46–88.5%) (i.e., green algae) [Nguyen, 2018]. Approximately 10% of sources in feeding of local fish and birds includes these tanaidaceans [Nguyen, 2018].

Mangrove forests are generally considered valuable feeding grounds for juvenile fish [Aburto-Oropeza *et al*., 2008]. As a result, understanding the distribution of benthic organisms in different communities is crucial for assessing the role that mangroves play in the ecology of tropical estuaries. However, some large bottom organisms, especially shrimps and different peracarids (amphipods and tanaidaceans), are concentrated not within mangrove forests, but in nearby tidal marshy areas (tidal plains). This observation suggests that feeding opportunities in the forest may be limited for many species of fish and their juveniles. As a result, it is important for reassessing the paradigm of "mangrove forests as forage lands". For example, studies conducted in Australia and New Caledonia revealed a low level of mangrove use by fish, with the majority concentrated within the first few meters of the forest [Vance *et al.*, 1996; Smith, Hindell, 2005; Dubuc *et al.*, 2019]. In our study, the high density of opportunistic feeders, such as parapseudid tanaidaceans and burrowing shrimps of the genus *Wolffogebia* spp. (see Marin & Kolevatov [2021]), on the tidal plains of mangrove forests suggests that this is the primary location of feeding grounds for many fish species.

Compliance with ethical standards

CONFLICT OF INTEREST: The authors declare that they have no conflict of interest.

Ethical approval: No ethical issues were raised during our research.

Acknowledgements. The study was carried out within the framework of the program E-3.4 of the Joint Vietnam-Russia Tropical Research and Technological Center (Hanoi, Vietnam) and, in particular, Task 8 “Study of biological diversity and functional structure of soil biota of floodplain and coastal ecosystems of the lower reaches of the Mekong River”. Authors are deeply grateful to the administration of the Southern Department of the Joint Vietnam-Russia Tropical Research and Technological Center (Ho Chi Minh City, Vietnam), especially to Dr. Cù Nguyên Định, administration of the Cần Giờ Biosphere Reserve and the stuff of the Can Gio scientific station for help during the field sampling. We are sending their special thanks to Vasily Kolevatov (Moscow State University, MSU), who make the stable isotopic analysis of our samples, Roman A. Rakitov (Paleontological Institute of RAS) for his help with obtaining SEM images, and Tien Tran Van (Tropical Centre, Ho Chi Minh) for the photographs used in Fig. 1. Authors are also very thankful to Dr. You-Wei Tzeng (National Taiwan University, Taipei (NTU)) for very valuable and useful comments to the manuscript, which greatly improved the final article.

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Responsible editor K.G. Mikhailov