RESEARCH ARTICLE



Six new species of Diostracus Loew (Diptera, Dolichopodidae) from Tibet

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Abstract

Six species of *Diostracus* from Tibet are described as new to science: *D. concavus* **sp. nov.**, *D. fasciculatus* **sp. nov.**, *D. laetus* **sp. nov.**, *D. polytrichus* **sp. nov.**, *D. strenus* **sp. nov.**, and *D. translucidus* **sp. nov.** A key to the species from Tibet of the genus is provided. The distribution of the genus in Tibet is also discussed.

Keywords

Key, long-legged fly, morphology, The Himalayan region

Introduction

Diostracus belongs to the subfamily Hydrophorinae of Dolichopodidae. These flies are usually stout and larger than other dolichopod flies. They prefer to live on the vertical or oblique surfaces of rocks at altitudes 1000 m to 3500 m, with slow water flow, or a thin water layer on the surface, or just wet, but they do not like those rocks behind streams or waterfalls.

Before our study, 101 species of the genus had been reported (Zhu 2006; Zhu et al. 2007a, b; Grichanov 2013, 2015, 2017; Pusch 2014; Wang et al. 2015). The first *Diostracus*, *D. prasinus* Loew, was named in 1861 from the Nearctic Region, whereas most species of the genus were reported from the Palaearctic and Oriental realms.

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Remarkably, *Diostracus* shows great diversity in the Himalayas, which is the junctions of the two realms, and 39 species have been reported from this area (Zhu 2006; Wang et al. 2015). Tibet is located in the east of the Himalaya Mountains. However, there were only three species of *Diostracus* known from Tibet: *D. nebulosus* Takagi, 1972 is widely distributed in the Himalayas, while *D. acutatus* Wang et al., 2015, and *D. tibetensis* Wang et al., 2015 were reported in Nyingchi, Tibet.

Here we provide an investigation of the diversity of *Diostracus* in Tibet and six new species are reported.

Materials and methods

This work is based on the material collected by sweep netting from Tibet in 2013 and 2018. The main locality is Yadong County (88°52'–89°30'E, 27°23'–28°18'N), located on the southern slope of the Himalaya Mountains. All the altitudes of localities are approximately 3000 m a.s.l. The specimens are deposited in the Entomological Museum of China Agricultural University, Beijing (CAU). The information about the specimens studied in the paper are presented in Table 1. Morphological terminology for adult structures mainly follows Cumming and Wood (2017).

The following abbreviations are used:

acr	acrostichal,	MSSC	male secondary sexual characters,
ad	anterodorsal bristle (s),	pvt	postrovertical bristle (s),
av	anteroventral bristle (s),	npl	notopleural bristle (s),
dc	dorsocentral bristle (s),	oc	ocellar bristle(s),
CI	fore coxa,	pd	posterodorsal bristle(s),
CII	mid coxa,	ph	postohumeral bristle,
CIII	hind coxa,	psa	postosupraalar bristle,
FI	fore femur,	pv	postoventral bristle(s),
FII	mid femur,	TI	fore tibia,
FIII	hind femur,	TII	mid tibia,
It	fore tarsomeres,	TIII	hind tibia,
h	humeral bristle,	sa	supraalar bristle,
IIt	mid tarsomeres,	sc	scutellar bristle(s),
IIIt	hind tarsomeres,	t	tarsomeres,
LI	fore leg,	vt	vertical bristle(s).

Each holotype male was submitted to barcode sequencing, using the primers LCO1480/ HCO2198 (Folmer et al. 1994), under the following experimental procedures: 3 min at 95 °C for the first cycle, reactions were amplified through 35 cycles at following paraments, 30 s at 95 °C, 30 s at 55 °C, and 90 s at 72 °C, then elongation for 1 cycle at 72 °C for 10 min. The sequences were uploaded to GenBank (Table 2). Females were also sequenced to pair them to males, in addition to examination of their morphological characters.

Species name	Number	Locality	Altitude	Geographical	Type or other
1	and sex			coordinates	material
Diostracus	3 8 8 6 9 9	Tibet, Shigatse, Yatung County	2700–3200 m	27°48'N, 88°90'E	Other material
acutatus	2 8 8 1 9	Tibet, Shigatse, Yatung County,	ca 3350 m	27°48'N, 88°90'E	Other material
		Pamaimang			
D. concavus	18	Tibet, Bomi, Gagela Mt.	3026 m	/	Holotype
D. fasciculatus	18	Tibet, Shigatse, Yatung County	2700–3200 m	27°48'N, 88°90'E	Holotype
	3 8 8 2 9 9	Tibet, Shigatse, Yatung County	2700–3200 m	27°48'N, 88°90'E	Paratypes
	11884	Tibet, Shigatse, Yatung County,	ca 3350 m	27°48'N, 88°90'E	
	<u></u> 22	Pamaimang			
D. laetus	18	Tibet, Shigatse, Yatung County	2700–3200 m	27°48'N, 88°90'E	Holotype
D. polytrichus	18	Tibet, Shigatse, Yatung County,	ca 3350 m	27°48'N, 88°90'E	Holotype
		Pamaimang			
	2 8 8 2 2 2 2	Tibet, Shigatse, Yatung County,	ca 3350 m	27°48'N, 88°90'E	Paratypes
		Pamaimang			
D. strenus	18	Tibet, Shigatse, Yatung County	2700–3200 m	27°48'N, 88°90'E	Holotype
	1 👌	Tibet, Shigatse, Yatung County,	ca 3350 m	27°48'N, 88°90'E	Paratype
		Pamaimang			
D. translucidus	18	Tibet, Medog	/	/	Holotype
	2 9 9	Tibet, Medog	/	/	Paratypes

Table 1. List of materials studied in this paper.

Table 2. Barcode label data for *Diostracus* species reported in this paper.

Species	Specimen catalog code	Sex	GenBank code	GenSeq
D. acutatus	Di03M	male	MT447459	Genseq-5 COI
	Di03F	female	MT462596	Genseq-5 COI
D. concavus	Di06M	male	MT452300	Genseq-1 COI
D. fasciculatus	Diostracus sp1	male	MT080656	Genseq-2 COI
	Di01F	female	MT462594	Genseq-2 COI
D. laetus	Di05M	male	MT452307	Genseq-1 COI
D. polytrichus	Di02M	male	MT438694	Genseq-2 COI
	Di02F	female	MT462595	Genseq-2 COI
D. strenus	Di04M	male	MT447458	Genseq-2 COI
D. translucidus	Diostracus sp7 male	male	OP249496	Genseq-1 COI
	Diostracus sp7 female	female	OP249495	Genseq-2 COI

Taxonomic accounts

Genus Diostracus Loew, 1861

Diostracus Loew, 1861: 44. Type species: Diostracus prasinus Loew, 1861 (monotypy).

- Sphyrotarsus Mik, 1874: 342. Type species: Sphyrotarsus argyrostomus Mik, 1874 (monotypy).
- Asphyrotarsus Oldenberg, 1916: 193. Type species: Liancalus leucostomus Loew, 1861 (original designation).
- *Takagia* Negrobov, 1973: 1520 (as subgenus of *Sphyrotarsus* Mik, 1874) (not Matsumura, 1942). Negrobov 1978: pl. CLXI (as genus, in error). Type species: *Sphyrotarsus stackelbergi* Negrobov, 1965 (original designation).

- Lagodechia Negrobov & Tsurikov, 1996: 632. Type species: Diostracus spinulifer Negrobov & Tsurikov, 1988 (monotypy).
- Ozmena Özdikmen, 2010: 265 (new name for *Takagia* Negrobov, 1973, not Matsumura, 1942) (as subgenus of *Sphyrotarsus* Mik, 1874).

Diagnosis. Medium to huge dolichopodid flies (males body length 3.4–7.6 mm, usually larger in females). Body stout, metallic green, always with pollinosity. Vertex weakly concave; upper occiput slightly concave. Scape with or without dorsal seta; arista subapical or sub-basal. Palpus rather large and loosely applied on proboscis, sometimes elongated, beyond the apex of proboscis in males, and relatively smaller in females. Proboscis bulky. Acr absent; four or six pairs of dc; one or two strong npl; scutellum with two strong sc, sometimes with marginal hairs. Crossvein m-cu longer than final section of 5th longitudinal vein. Legs and wings are often modified in males, which are usually the identical characters for groups or species. Abdomen cylindrical, with five visible segments; Sternite I or IV sometimes with produced process, and Sternite V usually split into pair of sclerites in males.

Key to species (males) of *Diostracus* from Tibet

Palpus normal, not reaching apex of proboscis; scutellum with pair of sc and 1 four or five pairs of marginal hairs; CI with row of anterior hairs and two strong recurved spines at extreme apex; FI with a deep hollow at base; wing indistinctly tinged grayish, apically with three translucent windows; FII with row of dense ad on apical 2/5**D.** translucidus sp. nov. Palpus prolonged, reaching apex of proboscis; scutellum with pair of sc, without Empodium and pulvilli reduced into minute protuberance (fenestratus group)..... 5 2 Wing with a dark square marking on vein M near crossvein; five dc..... 3 D. nebulosus Takagi Wing with a small round black nodule at middle of crossvein; six dc......4 Cercus finger-like, straight, with long yellow hairs D. tibetensis Wang et al. 4 Cercus lamellate with broad basal half......D. polytrichus sp. nov. Wing with dark and yellow markings at middle; discal crossvein strongly sinuate, 5 S-shaped; anterodistal corner of discal cell with an accessory cellula (pulchripennis Wing without distinct marking; discal crossvein nearly straight; anterodistal corner of discal cell without accessory cellula (flex subgroup)6 6 Posterior margin of wing somewhat prolonged along vein CuA,; apex of TII swollen with two rows of narrow flat willow leaf-like ventral bristles, row of long av (anterior ones somewhat curved), rows of pale long ventral hairs $(2-3 \times$ longer than TII depth, curved), row of erect pv along whole length (as long as Posterior margin of wing normal; TII normal, not swollen......7

7	Crossvein m-cu elongated, strongly bent, margined with black on long anterior
	portion, and with blackish spot at short posterior portion; FI slightly thickened; It,
	with acute apicoventral corner, It, with an acute ventral process near extreme base;
	abdominal sternite I with a nearly acute process at middle; sternite IV medially
	with an obtuse anterior process and two short thin, contiguous posterior processes
	bearing bundle of brown hairs
_	Crossvein m-cu not elongated, acutely and deeply arched to vein M ₁ , forming a
	'h'-shaped curve, with a jet-black brand inside curve; FI distinctly thickened; It,
	shortened, without acute apicoventral corner; abdominal sternite without such
	appendage
8	Propleuron with two or three sparse short pale hairs on upper portion and one
	or two short pale hairs on lower portion; It _{3.5} normal, without ventral suture
	D. strenus sp. nov.
_	Propleuron with group of seven long pale hairs on upper portion and group of
	nearly 20 long pale hairs on lower portion; It_{3-5} with a ventral suture

Diostracus acutatus Wang, Wang & Yang, 2015

Figs 1, 2, 31A, B, 32A, B

Diostracus acutatus Wang, Wang & Yang, 2015: 96, figs 1-6.

Diagnosis. The species belongs to the *fenestratus* group, characterized by specialized It₁ and It₂ (MSSC). It₁ distinctly shortened, with a nearly acute apicoventral process; It₂ basally bent with a short finger-like ventral process near extreme base. Females of *D. acutatus* are characterized by the apical or subapical antenna, oblique crossvein, m-cu oblique, and brownish trochanters.

Male (Fig. 1A). Same as description of Wang et al. (2015).

Female (Fig. 1B). Body length 6.0–6.4 mm; wing length 6.9–7.8 mm. Antennal scape with two short dorsal bristles, first flagellomere somewhat prolonged, 1.2 × longer than width, arista apical or subapical, 4.6 × longer than first flagellomere (Fig. 31A, B). Proboscis yellowish brown with blackish edge; palpus relatively smaller than males, not reaching apex of proboscis. six dc, anterior four short and weak, 5th long and weak. Propleuron with a single pale hair on upper portion, and group of 5–7 long pale hairs on lower portion. Legs black, except trochanters yellowish brown. CI without distinctive bristle or hair, but with short pale anterior hairs on lower portion; FI without distinct bristles; TI with an ad at basal 1/4, four pd, apically with one bristle and comb of anterior bristles; FII with two anterior bristles on apical 1/3; TII with three ad, two pd, apically with five bristles; FIII with three anterior bristles on apical 1/3; TIII with four



Figure 1. Diostracus acutatus A male; lateral view B female, lateral view. Scale bars: 1 mm.



Figure 2. D. acutatus female, abdomen A dorsal view B lateral view C ventral view. Scale bar: 1 mm.

ad, two pd, 4–6 weak v, apically with two bristles. Wing (Fig. 32A, B): m-cu somewhat curved, forming right angle with CuA₁. Halter yellow.

Female terminalia (Fig. 2): Abdominal tergite VIII split into pair of sclerites; epiproct split into pair of triangular hemitergites, apically with row of seven strong curved spines; dorsal lobes of cercus rounded in lateral view, with yellow bristles; ventral lobes of cercus membranous.

Remarks. *Diostracus acutatus* is similar to *D. nishidai* Saigusa, in that they both have acute apico-ventral corners of It_1 and It_2 and the shapes of wings and the appendages on abdominal sternite IV are nearly identical. But for males, they are different in the shapes of the main lobe of surstylus, and the apicoventral corner of It_1 in *D. acutatus* is sharper.

Diostracus concavus sp. nov.

https://zoobank.org/916C3BDC-2FA0-4862-807F-B799C54D4A06 Figs 3–6

Type material. *Holotype*: CHINA • ♂, Tibet, Nyingchi, Bomi, Gagela Mountain, 3026 m, 2013. VII. 13, leg. Xiaoyan Liu.

Diagnosis. MSSC: first flagellomere $1.5 \times \text{longer}$ than wide; propleuron with group of seven long pale hairs on upper portion and group of ~ 20 long pale hairs on lower portion; It₁ shortened and expanded, concave ventrally, forming a hollow with an expanded It₂. Wing (Fig. 4B) hyaline, m-cu acutely and deeply arched to vein M₁, forming an 'h'-shaped hairpin with a slender jet-black mark inside.

Description. Male (Fig. 3). Body length 5.7 mm; wing length 6.8 mm.

Head (Fig. 4A) dark metallic green with pale gray pollinosity. Eyes separated; face widened towards clypeus. Hairs and bristles on head black; lower postocular bristles including posteroventral hairs pale. Ocellar tubercle distinct, with pair of strong oc, without posterior hairs; vt short, $0.7 \times as$ long as oc, nearly as long as pvt. Antenna black; scape without dorsal bristle; first flagellomere subtriangular, $1.5 \times$ longer than wide; arista subapical, $5.2 \times as$ long as first flagellomere, nearly bare. Proboscis black-ish with pale hairs; palpus lobate, $3 \times as$ long as broad, blackish with a purple luster, without distinctive bristle.

Thorax dark metallic green with pale gray pollinosity. Hairs and bristles on thorax black; six mostly hair-like dc except posterior most one dc longest and thick; acr absent; two h, one ph, two npl, one sa, one psa; scutellum with pair of long sc. Propleuron with group of seven long pale hairs on upper portion and group of nearly 20 long pale hairs on lower portion.

Legs nearly entirely black except fore trochanter dark yellow; claws well developed, empodium and pulvilli reduced. Hairs and bristles on legs black except those on coxae pale. CI with cluster of anterior dense, erect, long, pale hairs on apical 1/4 (nearly as long as CI) and comb of pale hairs along anterior margin; CII and CIII nearly bare. Fore trochanter with rows of tiny ventral spines and a hook-like posterior process.



Figure 3. D. concavus, male; lateral view. Scale bar: 1 mm.



Figure 4. *D. concavus* male **A** head, lateral view **B** apex of wing **C** apex of TI and $It_{1,2}$, posterior view **D** apex of FI TI and $It_{1,2}$, anterior view. Scale bars: 1 mm.

FI distinctly thickened, with cluster of four or five erect ventral bristles at extreme base; TI distinctly thickened, weakly curved, with 3 ad, two pd, row of six long pv on apical 1/4; It, shortened and expanded, concave ventrally, forming a hollow with expanded It₂, anterior margin expanded into two dentiform lobes with row of four or five bristles, ventral margin expanded into a lobe at base (corresponding to the lobe of It₂), with a subapical pv (Fig. 4C, D); basal half of It₂ expanded and concave ventrally, anterior margin expanded into a pale dentiform lobate and a rectangular lobate, posterior ventral margin expanded into a finger-like lobe at extreme base, apical half with rows of erect ventral bristles, apical half of $I_{1,2}$, $I_{1,2,5}$ with a ventral suture. FII somewhat flattened laterally, with three ad on apical 1/3; TII with three weak ad, three weak pd, apical 1/5 with two rows of long pale anteroventral hairs (longest ones nearly as long as 1/4 of TII) and row of erect short pv (nearly as long as TII depth), and row of long pale posteroventral hairs along whole length (nearly as long as FII depth), apically with three long bristles. FIII with an anterior bristle and two curved av subapically; TIII with four ad and four pd, apically with two strong long bristles. Relative lengths of tibia and five tarsomeres: LI 5.0: 0.7: 2.5: 2.0: 1.0: 1.3; LII 9.0: 6.1: 2.2: 1.3: 0.7: 1.0; LIII 10.3: 5.2: 3.0: 1.5: 0.7: 1.0.



Figure 5. *D. concavus* male **A** abdominal Sternite IV and V, male genitalia removed, ventral view **B** male genitalia, lateral view **C** male genitalia, ventral view. Scale bar: 1 mm.



Figure 6. *D. concavus* male **A** abdominal Sternite IV and V, male genitalia removed, ventral view **B** male genitalia, lateral view **C** male genitalia, ventral view. Scale bar: 1 mm.

Wing (Fig. 4B) hyaline, indistinctly tinged grayish; veins dark brown; crossvein m-cu not elongated, acutely and deeply arched to vein M_1 , forming a 'h'-shaped curve with M_1 , with a slender jet-black brand inside hairpin curve; posterior margin somewhat prolonged along vein CuA₁. Squama brown with brown hairs. Halter pale (somewhat faded).

Abdomen nearly as long as head and thorax combined, dark metallic green with pale gray pollinosity. Abdomen with pale pubescence. Sternite IV medially with an obtuse anterior process and a tubercle bearing bundle of brown bristles, each lateroposterior corner with a tubercle bearing bundle of brown bristles (Figs 5A, 6A). Sternite V split into pair of sclerites, each sclerite ginkgo leaf-like in shape (Figs 5A, 6A).

Male genitalia (Figs 5B, C, 6B, C): Epandrium slightly longer than wide. Epandrial lobe long, wavy, band-like, with an acute basal process, a short bristle at tip. Surstylus thick, lamellated, with two short spines. Hypandrium short thick, apically with a shallow, V-shaped apical incision. Cercus rather short (1/3 as long as epandrium), spoon-shaped, with dark yellow hairs on outer surface, apical one long (nearly as long as cercus), and subapically with group of dense erect dark yellow bristles on inner surface.

Female. Unknown.

Distribution. China (Tibet).

Remarks. The new species belongs to the *flexus* subgroup of *D. fenestratus* group. This new species has wing characteristics similar to that of *D. strenus* sp. nov., but the latter can be separated from *D. concavus* by It_{3-5} , which is normal and has no ventral suture (MSSC).

Etymology. New species name refers to the concave It, of males.

Diostracus fasciculatus sp. nov.

https://zoobank.org/49078BA3-AAB9-4799-B295-B557A671788D Figs 7–11, 31C, 32C

Type material. *Holotype:* CHINA • \Diamond , China: Tibet, Shigatse, Yatung County (27°48'N, 88°90'E), 2700–3200 m, 2018. VII. 13, leg. Yajun Zhu. *Paratypes:* • 3 $\Diamond \Diamond$ 2 $\Diamond \Diamond$, same data as for holotype; 11 $\Diamond \Diamond$, 4 $\Diamond \Diamond$, same data as for preceding, but Pamaimang, 3350 m, 2018. VII. 14.

Diagnosis. MSSC: posterior margin of wing somewhat prolonged along vein CuA_1 . TII and TIII prolonged; apex of TII swollen with two rows of narrow, flat, willow leaf-like ventral bristles, row of long av and pale curve ventral hairs, row of erect pv along whole length, apically with three long bristles; It₁ swollen at extreme base, with rows of long curved posterior bristles.

Description. Male (Fig. 7A). Body length 5.0–5.4 mm; wing length 5.8–6.2 mm.

Head (Fig. 8A) dark metallic green with pale gray pollinosity. Eyes separated; face widened towards clypeus. Hairs and bristles on head black; lower postocular bristles including posteroventral hairs pale. Ocellar tubercle distinct, with pair of strong oc,



Figure 7. D. fasciculatus A male; lateral view B female, lateral view. Scale bars: 1 mm.



Figure 8. *D. fasciculatus* male **A** head, lateral view **B** thorax, lateral view, show the bristles **C** wing **D** FI, anterior view **E** part of TII and IIt, anterior view. Scale bars: 1 mm.

without posterior hairs; vt rather short, $0.5 \times as$ long as oc, nearly as long as pvt. Antenna black; scape without dorsal bristle; first flagellomere subtriangular, $1.5 \times longer$ than wide; arista apicodorsal, $4.5 \times as$ long as first flagellomere, nearly bare. Proboscis blackish with pale hairs; palpus lobate, $4 \times as$ long as broad, blackish with a purple luster, without distinctive bristle.

Thorax (Fig. 8B) dark metallic green with pale gray pollinosity. Hairs and bristles on thorax black; six mostly hair-like dc except posterior most one dc longest and thick; acr absent; one h, one ph, two npl, one sa, one psa; scutellum with pair of long sc. Propleuron with two or three sparse short pale hairs on upper portion and one or two short pale hairs on lower portion.

Legs nearly entirely black except fore trochanter dark yellow; claws well developed, empodium and pulvilli reduced. Hairs and bristles on legs black except those on coxae pale. CI without distinctive bristle, but with dense erect anterior pale hairs on apical 1/4; CII nearly bare; CIII with blackish bristle at extreme apex. Fore trochanter elongated, with hook-like posterior process (Fig. 8D). FI distinctly thickened (Fig. 8D); TI slightly thickened, weakly curved, with one ad at basal 1/3, two pd (one at apical 1/3 outstanding), row of weak pv along whole length; It₁ shortened, concave ventrally, anterior ventral margin expanded into a lobe and recurved, with short bristles apically

(Fig. 8D); I_2 with a finger-like lobe at extreme base, corresponding to the cavity of I_1 , apical half thickened with short dense pv. FII somewhat flattened laterally, with three ad on apical half; apex of TII swollen with two rows of narrow flat willow leaf-like ventral bristles, row of long av (anterior ones somewhat curved), rows of pale long ventral hairs (2–3 × longer than TII depth, curved), row of erect pv along whole length (as long as TII depth), apically with three long bristles (Fig. 8E); I_1 swollen at extreme base, with rows of long curved posterior bristles (Fig. 8E). FIII with two av on apical 1/3, rows of sparse pale ventral hairs along whole length (less than FIII depth); TIII with four ad, three pd, without outstanding ventral bristle, apically with two strong long bristles. Relative lengths of tibia and five tarsomeres: LI 5.3: 0.8: 1.5: 1.8: 0.7: 0.75; LII 7.3: 2.9: 1.4: 0.85: 0.45: 0.75; LIII 8.9: 3.3: 2.3: 1.2: 0.65: 0.85.

Wing (Fig. 8C) hyaline, indistinctly tinged grayish; veins dark brown, R_{4+5} curved at apical 1/3; crossvein m-cu acutely and deeply arched to vein M_1 , forming a hairpin curve, with a slender jet-black brand inside hairpin curve; posterior margin somewhat prolonged along vein CuA₁. Squama brown with brown hairs. Halter brown.

Abdomen (Fig. 9A) nearly as long as head and thorax combined, dark metallic green with pale gray pollinosity. Abdomen with pale pubescence. Sternite IV medially with pair of obtuse anterior process (very close), bearing bundle of brown hairs (Fig. 10A). Sternite V split into pair of sclerites, each sclerite ginkgo leaf-like (Fig. 10A).

Male genitalia (Figs 9B, C, 10B, C): Epandrium slightly longer than wide. Epandrial lobe pale and lamellated, band-like, elongated, apically with short hairs. Surstylus thick, bent inwards, apically furcated. Hypandrium thick, apically with a deep, U-shaped incision in ventral view. Cercus broad, leaf-like, nearly as long as epandrium, with long dark yellow hairs along margins.

Female (Fig. 7B). Body length 4.9–6.7 mm; wing length 6.1–7.9 mm. Nearly as same as male, but: antenna (Fig. 31C) scape with two short dorsal bristles, first flagellomere somewhat prolonged, 1.2 × longer than width, arista apicobasal, 4.6 × longer than first flagellomere. Proboscis yellowish brown with blackish edge; palpus relatively smaller than males, not reaching apex of proboscis. Six weak dc, except posterior most dc longest and thicken. Propleuron with one or two pale curved hairs on lower portion. Legs black, except trochanters yellowish brown. CI without distinctive bristle or hair, but with short pale anterior hairs on lower position; FI without distinct bristles; TI with one ad at basal 1/4, four pd, apically with a bristle and comb of anterior bristles; FIII with two anterior bristles on apical 1/3; TII with three ad, two pd, apically with five bristles; FIII with two bristles. Wing (Fig. 32C): m-cu straight, forming acute angle with CuA₁. Halter yellow.

Female terminalia (Fig. 11): Abdominal tergite VIII divided into two sclerites; epiproct split into pair of triangular hemitergites, apically with row of nine strong curved spines; dorsal lobes of cercus triangulated, with dark yellow bristles; ventral lobes of cercus short, apex rounded, with long yellow hairs.

Distribution. China (Tibet).



Figure 9. *D. fasciculatus* male **A** abdomen, lateral view **B** male genitalia, lateral view **C** male genitalia, ventral view. Scale bars: 1 mm.



Figure 10. *D. fasciculatus* male **A** abdominal Sternite IV and V, male genitalia removed, ventral view **B** male genitalia, lateral view **C** male genitalia, ventral view **D** surstylus, ventral view. Scale bars: 0.2 mm.

Remarks. The new species belongs to the *flex* subgroup *D. fenestratus* group. The species is unique for the shape of wings and It_{1-2} , and the prolonged TII and TIII which have relatively short IIt_1 and $IIIt_1$. Females are characterized by an arched cross-vein m-cu, and the crossvein vertical adjunct to vein CuA₁; the trochanters are black.

Etymology. The new species name refers to the cluster of bristles on apex of TII of males.



Figure II. D. fasciculatus female, abdomen A dorsal view B lateral view C ventral view. Scale bar: 1 mm.

Diostracus laetus sp. nov.

https://zoobank.org/43CC31E5-3F0A-4277-8734-A41164D50B41 Figs 12–15

Type material. *Holotype*: CHINA • ♂, China: Tibet, Shigatse, Yatung County (27°48'N, 88°90'E), 2700–3200 m, 2018. VII. 13, leg. Yajun Zhu.

Diagnosis. MSSC: Wings with dark and yellow markings at middle. CI with a brown curved anterior spine at extreme apex; CII with row of four brown anterior spines along apical edge; fore trochanter with row of upwards curved bristles along basal edge. FI with short upwards curved ventral bristles on basal 1/4; TI thickened, with rows of pale ventral hairs on apical 3/4, and apically with two long wavy posterior bristles; FII with row of long av and posteroventral hairs.

Description. Male (Fig. 12). Body length 7.4 mm; wing length 8.2 mm.

Head (Fig. 13A) dark metallic green with pale brown pollinosity. Eyes separated; face widened towards clypeus. Hairs and bristles on head black; lower postocular bristles including posteroventral hairs pale. Ocellar tubercle distinct, with pair of oc (broken), pair of posterior hairs; vt weak, slightly shorter than pvt. Antenna black; scape without dorsal bristle; first flagellomere subrectangular, $1.3 \times$ longer than wide; arista apicodorsal, $5.3 \times$ as long as first flagellomere, nearly bare. Proboscis yellowish brown with blackish edge; palpus lobate, $2.3 \times$ as long as broad, blackish with a purple luster, without distinctive bristle.



Figure 12. D. laetus, male, lateral view. Scale bar: 1 mm.



Figure 13. *D. laetus* male **A** head, lateral view **B** abdomen, lateral view **C** base of FII, anterior view **D** LI, anterior view **E** part of wing. Scale bars: 1 mm.

Thorax dark metallic green with pale brown pollinosity. Hairs and bristles on thorax black; six mostly hair-like dc except posterior most one dc longest and thick; acr absent; one h, one ph, two npl, one sa, one psa; scutellum with pair of long sc. Propleuron with two or three sparse short pale curved hairs on upper portion and two long pale curved hairs on lower portion.

Legs nearly entirely black except extreme apexes of coxae and trochanters brownish yellow; claws well developed, empodium and pulvilli reduced. Hairs and bristles on legs black. CI with short sparse pale hairs on anterior surface, and a brown curved anterior spine at extreme apex (Fig. 13D); CII with row of four brown anterior spines along apical edge; CIII nearly bare. Fore trochanter with ridge and row of upwardly curved bristles along basal edge (Fig. 13D). FI distinctly thickened, with short upwards curved ventral bristles on basal 1/4; TI thickened, with four ad, one pd at middle, rows of pale ventral hairs on apical 3/4, and apically with two long wavy posterior bristles (Fig. 13D); It₁ shortened, apex expanded, concave ventrally, anterior ventral margin expanded into a lobate, with comb of bristles on anterior surface (Fig. 13D); It₂ with a finger-like lobe at extreme base, with a posteroventral ridge on basal half (Fig. 13D). FII thickened, with row of seven short av spines, row of three long anteroventral hairs



Figure 14. *D. laetus* male **A** abdominal Sternite IV and V, male genitalia removed, lateral view **B** abdomen, male genitalia removed, ventral view **C** male genitalia, lateral view **D** male genitalia, ventral view. Scale bar: 1 mm.



Figure 15. *D. laetus* male **A** abdominal Sternite IV and V, male genitalia removed, ventral view **B** male genitalia, lateral view **C** male genitalia, ventral view. Scale bar: 1 mm.

and row of long posteroventral hairs (as long as FII depth, somewhat curved on basal 2/3) (Fig. 13C); TII with two ad, apically with two long bristles. FIII without conspicuous hairs and bristles; TIII with three ad, two pd, without outstanding ventral bristle. Relative lengths of tibia and five tarsomeres: LI 5.5: 1.2: 3.0: 3.3: 1.8: 1.0; LII 10.2: 6.4: 3.2: 1.8: 0.9: 1.0; LIII 11.8: 6.2: 4.2: 1.8: 0.9: 1.0.

Wing (Fig. 13E) hyaline, anterior half and area around crossvein m-cu yellowish, with dark cloud on middle of cell R_{2+3} , and a stripe of dark cloud along M_1 and expanding along posterodistal corner of distal cell, dark cloud in subapical portion of distal cell prominent; veins dark brown, R_{4+5} curved at middle, M_1 curved at apical 1/3; crossvein m-cu acutely and deeply arched to vein M_1 , forming a hairpin curve, with a slender jet-black brand inside hairpin curve, accessory cellula 1.3 × longer than width. Squama brown with brown hairs. Halter yellow with blackish apex.

Abdomen (Fig. 13B) nearly as long as head and thorax combined, dark metallic green with pale brown pollinosity, except edge of sternites, apex of epandrium and base of cercus pale. Abdomen with short sparse pale pubescence. Posterior edge of sternite IV forwards recurved with row of short curve spines (Figs 14A, B, 15A). Lateroposterior corner of tergite V elongated into a triangular process. Sternite V split into pair of sclerites, each sclerite ginkgo leaf-like (Figs 14A, B, 15A).

Male genitalia (Figs 14C, D, 15B, C): Epandrium slightly longer than wide. Epandrial lobe and surstylus pale and lamellated. Epandrial lobe short, band-like, apically with one long and one short bristles. Surstylus irregular in shape, with irregular processes and bristles. Process of subepandrial sclerite exceeding epandrium margin, with short fine pubescence. Hypandrium thick, apically with a shallow, U-shaped incision. Cercus band-like, somewhat bent, with long dark yellow hairs around cercus.

Female. Unknown.

Distribution. China (Tibet).

Remarks. The new species belongs to *pulchripennis* subgroup and is quite similar to *D. emotoi*. Both species have same chaetotaxy on FII and they are similar in wing style. However, the new species has no posterior bristles on FI, long ventral hairs and two wavy bristles on TI, and relatively smaller wing accessory cellula (2.5 × as long as wide).

Etymology. The name of new species refers to the bright coloration of male wings.

Diostracus polytrichus sp. nov.

https://zoobank.org/4318BDD9-0AE4-4A15-96DE-549267680311 Figs 16–20, 31D, 32E

Type material. *Holotype:* CHINA • \Diamond , China: Tibet, Shigatse, Yatung County (27°48'N, 88°90'E), Pamaimang, 3350 m, 2018. VII. 14, leg. Yajun Zhu. *Paratypes:* • 2 $\Diamond \Diamond$ 2 $\bigcirc \Diamond$, same data as for holotype.

Diagnosis. MSSC: palpus black; wing crossvein m-cu nearly straight, with jetblack nodule; halter yellow, with blackish apex. Abdomen with dense ventral hairs.

Description. Male (Fig. 16A). Body length 6.6–7.0 mm; wing length 9.4–9.8 mm.



Figure 16. D. polytrichus A male; lateral view B female, lateral view. Scale bars: 1 mm.

Head (Fig. 17A) dark metallic green with pale gray pollinosity. Eyes separated; face widened towards clypeus. Hairs and bristles on head black; lower postocular bristles including posteroventral hairs brownish. Ocellar tubercle distinct, with pair of strong oc, without posterior hairs; vt rather short, $0.3 \times$ as long as oc, sometimes hair-like; pvt slight shorter than oc. Antenna black; scape bare, or with three or four dorsal bristles; first flagellomere semicircular to subtriangular, $1.2-1.6 \times$ longer than wide; arista apico-dorsal, $4.2-7.5 \times$



Figure 17. *D. polytrichus* male **A** head, lateral view **B** abdomen, lateral view **C** wing **D** I_1 , anterior view. Scale bars: 1 mm.

as long as first flagellomere, nearly bare. Proboscis blackish with pale hairs; palpus lobate, $2.2-2.5 \times as$ long as broad, blackish with a purple luster, without distinctive bristle.

Thorax dark metallic green with pale gray pollinosity; mesoscutum with two dark brown longitudinal stripes. Hairs and bristles on thorax black; six weak dc except posterior most one dc longest and thick, occasionally with excess dc; acr absent; one weak and one strong h, one ph, two npl, one sa, one psa; scutellum with pair of long sc. Propleuron with one or two sparse long pale hairs on upper portion and group of long pale hairs on lower portion.

Legs nearly entirely black except fore trochanter dark brown; claws well developed, empodium and pulvilli reduced. Hairs and bristles on legs black except those on coxae pale. CI with group of pale curved anterior hairs on basal 1/3, upper ones long, and cluster of erect bristles on apical 1/4; CII nearly bare; CIII with blackish bristle at extreme apex. FI thickened, with two rows of ventral hairs (as long as FI depth), basal ones pale, and one posterior bristle at extreme base; TI with two pd, three d, row of six or seven long pv on apical half, apically with two bristles and comb of anterior bristles; It₁₋₂ with rows of pd and pv, ventral surface with short dense fine hairs, It₁ with row



Figure 18. *D. polytrichus* male **A** abdominal Sternite IV and V, male genitalia removed, ventral view **B** male genitalia, lateral view **C** male genitalia, ventral view. Scale bars: 1 mm.



Figure 19. *D. polytrichus* male **A** abdominal Sternite IV and V, male genitalia removed, ventral view **B** abdominal Sternite IV and V, male genitalia removed, lateral view with some angles **C** male genitalia, lateral view **D** male genitalia, ventral view. Scale bars: 1 mm.

of av spines, extending to It_2 (Fig. 17D); FII with two rows of av on basal half, one distinct v at middle, row of short av on apical 1/3, row of pale long pv on basal 2/3 (longest ones 2.5 × longer than FII depth); TII with two ad, two pd, apically with four bristles. FIII with four av on middle 1/3, apically with one av; TIII with four ad, four pd, four short ventral bristles, apically with three long bristles and comb of short anterior bristles. Relative lengths of tibia and five tarsomeres: LI 6.9: 3.1: 3.2: 1.7: 1.1: 1.0; LII 5.8: 3.2: 1.4: 0.9: 0.5: 0.8; LIII 7.8: 3.4: 2.5: 1.5: 0.8: 0.9.

Wing (Fig. 17C) hyaline, indistinctly tinged grayish; veins dark brown; crossvein m-cu nearly straight, curved around nodule, with a jet-black nodule. Squama brown with brown hairs. Halter yellow with blackish apex.

Abdomen (Fig. 17B) nearly as long as thorax, dark metallic green with pale gray pollinosity, bent upwards medially. Abdomen with dense long pale pubescence. Sternite V split into pair of sclerites (Figs 18A, 19A, B).



Figure 20. D. polytrichus female, abdomen A dorsal view B lateral view C ventral view. Scale bar: 1 mm.

Male genitalia (Figs 18B, C, 19C, D): Epandrium swollen, slightly longer than wide. Epandrial lobe tiny and pale, lamellate, apically with two pale bristles. Surstylus bifurcated, dorsal lobe broad and lamellated, inner surface with dense dentiform bristles, ventral lobe elongated, broad and leaf-like, apical margin pale, with one long inner bristle at middle. Hypandrium relatively small, apically with a deep U-shaped incision in ventral view. Cercus band-like, apical 1/3 becoming narrower, with long yellow hairs along margins.

Female (Fig. 16B). Body length 5.4–6.0 mm; wing length 6.8–7.9 mm. Nearly as same as male, but: ocellar tubercle without posterior hairs, antenna (Fig. 31D) scape with two short dorsal bristles, first flagellomere semicircular, nearly as long as width, arista apicobasal, 5.6 × longer than first flagellomere. Proboscis blackish; palpus relatively smaller than males, not reaching apex of proboscis. Seven weak dc, except posterior most dc longest and thicken. Propleuron with two or three sparse short pale curved hairs on upper portion and group of five or six sparse long pale curved hairs on lower portion. Legs black. CI with erect pale hairs on anterior surface, ones on lower portion black and thick; FI with one preapical pv; TI with four pd, two pv, apically with three bristles and comb of short anterior bristles; FII with one strong preapical av and one weak preapical pv; TIII with three ad, apically with three bristles. Wing (Fig. 32E): m-cu straight, forming obtuse angle with CuA₁; area around m-cu tingled with blackish ash. Halter yellow with blackish apex.

Female terminalia (Fig. 20): Abdominal segments VII and VIII slender; tergite VIII divided into two sclerites; epiproct split into pair of hemitergites, apically with row of five strong curved spines; dorsal lobes of cercus finger-like, somewhat elongated, with dark yellow bristles; ventral lobes of cercus short, apex rounded.

Distribution. China (Tibet).

Remarks. The new species is quite similar to *D. tibetensis*, but the cerci of new species are lamellate with broad base. Females of the new species are characterized by the semicircular first flagellomere of antenna, the straight crossvein m-cu, and the blackish apex of halter.

Etymology. The name of the new species refers to the dense abdominal ventral hairs.

Diostracus strenus sp. nov.

https://zoobank.org/DD9B81DF-05D1-485A-81E8-572D667BA73F Figs 21–24

Type material. *Holotype*: CHINA • ♂, Tibet, Shigatse, Yatung County (27°48'N, 88°90'E), 2700–3200 m, 2018. VII. 13, leg. Yajun Zhu. *Paratype*: • 1 ♂, same data as for holotype but Pamaimang, 3350 m, 2018. VII. 14.

Diagnosis. MSSC: dark and robust fly; FI and TI distinctly thickened; posterior ventral margin of It_1 and anterior ventral margin of It_2 expanded into auriform lobes; crossvein m-cu acutely and deeply arched to vein M_1 , forming a 'h'-shaped curve, with a jet-black mark inside curve.



Figure 21. D. strenus, male; lateral view. Scale bar: 1 mm.

Description. Male (Fig. 21). Body length 6.0 mm; wing length 8.0 mm.

Head (Fig. 22A) dark metallic green with pale brown pollinosity. Eyes separated; face widened towards clypeus. Hairs and bristles on head black; lower postocular bristles including posteroventral hairs pale. Ocellar tubercle distinct, with pair of strong oc, without posterior hairs; vt short, $0.7 \times as$ long as oc, nearly as long as pvt. Antenna black; scape with a weak dorsal bristle at basal 1/3; first flagellomere subtriangular, 1.5 × longer than wide; arista apicodorsal, $3 \times as$ long as first flagellomere, nearly bare. Proboscis blackish with pale hairs; palpus lobate, $3.5 \times as$ long as broad, blackish with a purple luster, without distinctive bristle.

Thorax dark metallic green with pale brown pollinosity. Hairs and bristles on thorax black; six mostly hair-like dc except 1st and 6th dc long and thick; acr absent; one h, one ph, two npl, one sa, one psa; scutellum with pair of sc. Propleuron with two or three sparse, short, pale hairs on upper portion and one or two short pale hairs on lower portion.

Legs nearly entirely black except fore and mid trochanters dark yellow; claws well developed, empodium and pulvilli reduced. Hairs and bristles on legs black except



Figure 22. *D. strenus* male **A** head, lateral view **B** abdomen, lateral view **C** wing **D** TI and It, anterior view **E** TI and It, posterior view. Scale bars: 1 mm.

those on coxae pale. CI without distinctive bristle, but with dense, erect, pale, anterior hairs on apical 1/4; CII with cluster of black bristles at extreme apex; CIII nearly bare. Fore trochanter elongated, with lobate posterior process. FI distinctly thickened, with group of pale hairs on apical 1/5 (less than FI depth) (Fig. 22D, E); TI distinctly thickened, curved, with three ad on basal half, two pd on apical 1/3, row of five long pv on apical 1/3, apically with comb of short pale av spines (Fig. 22D, E); It, shortened, concave ventrally, posterior ventral margin expanded into a auriform lobe (Fig. 22D, E); It, thickened and recurved, somewhat flattened dorsoventrally, with anterior ventral margin at extreme base expanded into an auriform lobe, corresponding to the auriform lobe of It,, a spine-like lobe at basal 1/4, and two rows of short pv spines (Fig. 22D, E). FII with rows of pale postoventral hairs (as long as FII depth), and one ad at apical 1/8; TII with rows of curved ventral hairs on basal 2/3 (longest ones 2 × longer than TII depth), three weak ad, two weak pd, apically with two long bristles. FIII with two ad on apical 1/6, rows of sparse pale ventral hairs on basal half (less than FIII depth); TIII with five ad, three pd, without outstanding ventral bristle, apically with two bristles. Relative lengths of tibia and five tarsomeres: LI 5.7: 0.6: 2.8: 2.1: 1.0: 1.0; LII 8.8: 5.2: 2.2: 1.3: 0.8: 1.0; LIII 10.3: 4.7: 3.0: 1.4: 0.7: 1.0.



Figure 23. *D. strenus* male **A** abdominal Sternite IV and V, male genitalia removed, ventral view **B** male genitalia, lateral view **C** male genitalia, ventral view. Scale bar: 1 mm.



Figure 24. *D. strenus* male **A** abdominal Sternite IV and V, male genitalia removed, ventral view **B** male genitalia, lateral view **C** male genitalia, ventral view. Scale bar: 1 mm.

Wing (Fig. 22C) hyaline, indistinctly tinged grayish; veins dark brown; crossvein m-cu acutely and deeply arched to vein M_1 , forming a 'h'-shaped curve, with a jet-black mark inside curve. Squama brown with brown hairs. Haltere blackish with pale knob.

Abdomen (Fig. 22B) nearly as long as head and thorax combined, dark metallic green with pale gray pollinosity. Abdomen with pale pubescence. Sternite IV medially with an obtuse process, and one tubercle bearing bundle of brown bristles, lateroposterior corner with brown bristles (Figs 23A, 24A). Sternite V split into pair of sclerites, each sclerite ginkgo leaf-like (Figs 23A, 24A).

Male genitalia (Figs 23B, C, 24B, C): Epandrium slightly longer than wide. Epandrial lobe elongated, lamellated, apically with two short bristles. Surstylus thick, apex dark, bending inwards, with a finger-like inner process. Hypandrium thick, apically with a shallow, V-shaped incision. Cercus straight and clavated, inner surface somewhat hollow, with long pale hairs along margin, apical half with dense, erect, dark yellow bristles on inner surface.

Female. Unknown.

Distribution. China (Tibet).

Remarks. The new species belongs to *D. fenestratus* group. It looks like *D. flexus*, but can be separated from the latter by the following features of males: the weak acute ventral process near extreme base of It_2 , the swollen apex of It_2 , the row of erect dense strong long posterior, and the anterior ventral bristles on apex of TII.

Etymology. The name of new species refers to the strongly thickened legs.

Diostracus translucidus sp. nov.

https://zoobank.org/19498122-29A8-4F0E-8ADB-9318C2FD6101 Figs 25–30, 31E, 32D

Type material. *Holotype*: CHINA • ♂, Tibet, Nyingchi, Medog, 80 k, 2013. IX. 13, leg. Gang Yao. *Paratypes*: • 2 ♀♀, same data as for holotype.

Diagnosis. MSSC: palpus normal, not reaching apex of proboscis. Scutellum with pair of sc and four or five pairs of marginal hairs; CI with row of anterior hairs and two strong recurved spines at extreme apex; FI with a deep hollow at base; wing indistinctly tinged grayish; FII with row of dense ad on apical 2/5; wing apically with three translucent windows between vein C, vein R_{2+3} , vein R_{4+5} , and vein M_1 .

Description. Male (Fig. 25A). Body length 5.8 mm; wing length 6.0 mm.

Head (Fig. 26A) dark metallic green with pale gray pollinosity. Eyes separated; face widened towards clypeus. Hairs and bristles on head black; lower postocular bristles including posteroventral hairs pale. Ocellar tubercle distinct, with pair of oc (lost), without posterior hairs; vt rather short, $0.2 \times as$ long as pvt. Antenna brownish black; scape prolonged, without dorsal bristle; first flagellomere subtriangular, $1.3 \times longer$ than wide; arista apicodorsal, $4.8 \times as$ long as first flagellomere, nearly bare. Proboscis huge and brown, apex blackish with pale hairs; palpus lobate, not reaching apex of proboscis, without distinctive bristle.



Figure 25. D. translucidus A male; lateral view B female, lateral view. Scale bar: 1 mm.


Figure 26. *D. translucidus* male **A** head, lateral view **B** apex of wing **C** LI, anterior view **D** abdomen, lateral view. Scale bars: 1 mm.

Thorax dark metallic green with pale gray pollinosity; mesoscutum with pair of dark brown longitudinal stripe. Hairs and bristles on thorax black; six mostly hair-like dc except posterior most one dc longest and thick; acr absent; one h, one ph, one npl, one sa, one psa; scutellum with pair of sc (lost) and four or five pairs of marginal hairs (MSSC). Postnotum well developed, and convex. Propleuron with two or three sparse short pale hairs on lower portion.

Legs nearly entirely black except fore trochanter dark yellow, mid- and hind trochanters brownish black; claws prolonged (MSSC), empodium and pulvilli present. Hairs and bristles on legs black. CI depressed laterally, without distinctive bristle, but with row of anterior hairs and two strong recurved spines at extreme apex (MSSC); CII and CIII with clusters of anterior bristles at extreme apex. FI distinctly thickened, with a deep hollow at base, and row of three or four curved ventral spines and row of dense anterior bristles long the edge of the hollow (MSSC), basal 2/3 with row of four long yellow av (nearly as long as FI depth) (MSSC), apically with long thin pale hairs (MSSC) (Fig. 26C); TI slightly thickened, with row of ad along whole length, ventral surface nearly bare (MSSC); It₁ somewhat thicken, with row of long ad and pd along whole length (nearly as long as It₁ depth), apical half flattened ventrally with two rows of short curved spines and rows of bristles along the edge, apically with a strong curved pv spine (MSSC) (Fig. 26C); It₂, with row of long curved anteroventral hairs along the



Figure 27. *D. translucidus* male, apex of abdomen **A** dorsal view **B** ventral view **C** lateral view. Scale bar: 1 mm.



Figure 28. *D. translucidus* male **A** abdominal Sternite IV and V, male genitalia removed, ventral view **B** male genitalia, lateral view **C** male genitalia, ventral view. Scale bar: 1 mm.



Figure 29. *D. translucidus* male **A** abdominal Sternite IV and V, male genitalia removed, ventral view **B** male genitalia, lateral view **C** male genitalia, ventral view. Scale bar: 1 mm.



Figure 30. D. translucidus female, abdomen A dorsal view B lateral view C ventral view. Scale bar: 1 mm.



Figure 31. Female antenna, lateral view A *D. acutatus*, show apical arista B *D. acutatus*, show subapical arista C *D. fasciculatus* D *D. polytrichus* E *D. translucidus*. Scale bars: 1 mm.

whole length, apical half with two rows of long posterior bristles (MSSC); It_3 elongated, base and apex somewhat swollen, nearly bare, except with row of three or four posteroventral hairs at base and four or five dorsal bristles at apex (MSSC); It_4 with long ventral bristles apically (MSSC). FII with row of dense ad on apical 2/5 (MSSC); TII with two ad, 8 pd. FIII without outstanding bristle; TIII with row of long thin ad and long erect thin pd; $IIIt_1$ with row of thin ad long whole length. Relative lengths of tibia and five tarsomeres: LI 5.3: 1.2: 2.2: 2.6: 0.4: 0.7; LII 7.3: 5.0: 2.4: 1.2: 0.6: 0.8; LIII 8.5: 4.8: 3.4: 1.6: 0.8: 0.8.

Wing (Fig. 26B) hyaline, indistinctly tinged grayish, apically with three translucent windows between vein C, vein R_{2+3} , vein R_{4+5} , vein M_1 (MSSC); vein M with brown strip on middle section (MSSC); veins dark brown; crossvein m-cu somewhat curved. Squama yellow with yellow hairs. Halter brown.

Abdomen (Fig. 26D) nearly as long as head and thorax combined, dark metallic green with pale gray pollinosity. Abdomen with sparse pale pubescence. Tergites II–V



Figure 32. Apex of female wing A, B D. acutatus C D. fasciculatus D D. translucidus E D. polytrichus. Scale bar: 1 mm.

with triangular hyaline area on posterior margin (MSSC); Sternite II medially with a digitiform anterior process (MSSC) (Fig. 26D), Sternite IV with a pair of long brown band-like sclerites (Figs 27, 28A, 29A); Sternite V longer than Sternite IV, split into pair of sclerites (Figs 27, 28A, 29A). Hypandrium not distinctly swollen.

Male genitalia (Figs 28B, C, 29B, C): Epandrium slightly longer than wide. Epandrial lobe long, wavy, band-like, with an acute basal process, one short bristle at tip. Surstylus thick, lamellated, with two short spines. Hypandrium short thick, apically with a shallow, V-shaped apical incision. Cercus rather short (1/3 as long as epandrium length), spoon-shaped, with dark yellow hairs on outer surface, apical ones long (nearly as long as cercus length), and subapically with group of dense erect dark yellow bristles on inner surface.

Female (Figs 25B, 31E). Body length 7.4–7.6 mm; wing length 7.8–8.0 mm. Same as male, except MSSC. FI without distinct bristles; TI with three ad, two pd; FII with two ad; TII with one ad, one pd, apically with three bristles; FIII bare; TIII with four ad, apically with two bristles. Wing (Fig. 32D) hyaline, indistinctly tinged gray-ish, crossvein m-cu straight, forming acute angle with CuA₁.

Female genitalia (Fig. 30): Abdominal segments VII and VIII slender; tergite VIII divided into two sclerites; epiproct split into pair of hemitergites, apically with row of eight strong curved spines; hypoproct semicircular; dorsal lobes of cercus somewhat elongated, with dark yellow bristles; ventral lobes of cercus short, apex rounded.

Distribution. China (Tibet).

Remarks. The new species is unique. It has prolonged scapes, small palpus, and convex postnotum. But the huge proboscis, stout body and specialized structures of legs indicate that the new species belongs to *Diostracus*.

Etymology. New species name refers to the translucent windows on male wing.

Discussion

Including the species described in this work, the number of worldwide species of *Diostracus* has increased to 107, of which nine species occur in Tibet (Zhu 2006; Zhu et al. 2007a, b; Grichanov 2013, 2015, 2017; Pusch 2014; Wang et al. 2015). The six new species of *Diostracus* were found in Nyingchi and Shigatse areas of Tibet. Most of them were found at Yatung in Shigatse, which is located on the southern slope of the Himalaya Mountains (Fig. 33). As well as these two sites, we performed a five-year survey in Lhasa, Nyingchi, Shannan, and Qamdo, but there were no *Diostracus* found, although it does not mean *Diostracus* only occur in Nyingchi and Shigatse in Tibet. Due to the special habitat of the genus, it can only be collected with sweep nets after finding the flies using the naked eyes. Malaise traps collect the majority of insects in



Figure 33. Distribution of new *Diostracus* species of Tibet: black circle: *D. fasciculatus*, *D. laetus*, *D. polytrichus*, and *D. strenus*; black square: *D. translucidus*; black star: *D. concavus*.

Tibet, as its environment is often too complex to walk through, but no *Diostracus* were found in them during these surveys.

Diostracus in the Oriental realm shows great diversity in MSSC, especially in modified FI and wing. Complex structures of FI are usually associated with modified wing. The most bizarre MSSC was shown in D. fenestratus group, with It, distinctly shortened, almost triangular in shape, expanded portion concaved, and It, sinuous, with a basal denticle (Saigusa 1984). The wing in this group is always ornamented, crossvein m-cu either in S-shape or running posteriorly parallel to M₁. This species group includes 14 species all of which are distributed in the Himalayan Mountains. The species groups with partially thickened It, and modified wings (mainly the D. unisetosus group) and the species groups with simple FI and modified wings (with a jet-black nodule besides crossvein m-cu, mainly the D. unipunctatus group) are distributed also mainly in the Himalayan Mountains. The species groups with partially thickened It, and simple wings, mainly the D. nebulosus group, are distributed in the Himalayan Mountains and the Chinese mainland. Finally, the species groups with simple FI and simple wing is found in the Chinese mainland and Taiwan. Himalayan Mountains is the diversity center for the genus *Diostracus*, and species in this area show great diversity (53 species out of 107) and abundant specialized characters. The species in the Chinese mainland and Taiwan usually have low diversity (20 species of 107) and simple structures.

Besides the morphological characters, mitochondrial COI genes of females have also been sequenced to pair them with males. As a result, some females could not be matched to males, and the characters of these females are obviously different from known species found in our investigation. Therefore, we believe that more new species will be discovered in the Himalayan region in the future.

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New species of the dancing semislug Cryptosemelus Collinge, 1902 (Eupulmonata, Ariophantidae) from Loei Province, northeastern Thailand with a key to genera of mainland Southeast Asian semislugs and a key to species of the genus

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Abstract

In this study, we describe a new dancing semislug from a limestone hill area in northeastern Thailand. *Cryptosemelus niger* **sp. nov.** differs from the three recognized congener species from western and southern Thailand, due to differences in their body and shell lobes coloration, appearance of penial caecum, shape and surface texture of penis and epiphallus, and radula formula and morphology.

Keywords

Genital system, karst topography, limestone hill, mantle extensions, protective behavior, shell lobes

Introduction

Cryptosemelus Collinge, 1902 is a member of family Ariophantidae. Its common characters comprise a shell with reduced number of whorls, body with well-developed mantle extensions, tail without caudal horn and genitalia without flagellum and amatorial organ. This genus differs from other long-tail semislug genera described from the Malay Peninsula. It differs from *Apoparmarion* due to more shell whorls and the absence of a caudal horn, flagellum and dart apparatus; and, it differs from *Paraparmarion* by the presence of both right and left shell lobes, whereas, the latter genus presents only a right shell lobe (Collinge 1902; Pholyotha et al. 2021a) (Table 1).

Cryptosemelus has been referred to as a 'dancing semislug' because of its dance-like movement that it makes when it is disturbed or attacked (Collinge 1902). This protective behavior has also been reported in other species, including *Laocaia simori* Dedov & Schneppat, 2019 in Dedov et al. (2019), *Cryptaustenia altatorial* Wiktor, 2002 and *Cryptaustenia mirabilis* Wiktor, 2002, *Muangnua arborea* Tumpeesuwan & Tumpeesuwan, 2019; *Cryptosemelus gracilis* Collinge, 1902, *C. betarmon* Pholyotha, 2021 and *C. tigrinus* Pholyotha, 2021 in Pholyotha et al. (2021a), *Ibycus* spp. and *Helicarion* spp. (Junn Kitt Foon, pers. comm.)

According to a recent study by Pholyotha et al. (2021a), the type species of the genus, *Cryptosemelus gracilis*, and the recently named species *C. betarmon* and *C. tigrinus* were studied and described from their genital anatomy and radula morphology. These three species are characterized by differences in the anatomical details of their penis, epiphallus and spermatophore. We discovered and examined this lovely semislug from a limestone hill in Loei Province, Thailand, and it possesses distinct characters of external shell morphology, mantle lobes coloration, radula and genital organs. Thus, we describe it here as a new species of *Cryptosemelus*.

Material and methods

Sixty specimens were collected from November to December 2012, June to September 2013, and 12th October 2018 in the Phu Pha Lom limestone area (17°33'62"N, 101°52'31"E), elevation about 380–390 m above mean sea level, in the Mueang Loei District, Loei Province, northeastern Thailand (Fig. 1). The specimens were composed of fifty empty shells and 10 living specimens, which were collected from both leaf litter and the ground surface. The living specimens were photographed in their natural habitat (Figs 2B, 3), and then euthanized and preserved in 70 (v/v) ethanol for morphological and anatomical studies. Specimens were classified and identified from the literature, such as Collinge (1902), Blanford and Godwin-Austen (1908), Solem (1966), Schileyko (2003) and Pholyotha et al. (2021a). For the descriptive study, adult shells were measured for size using a vernier caliper and the number of whorls were counted. Photomicrographs were taken using a scanning electron microscope (JEOL, JSM-6460 LV) housed at the Central Laboratory, Faculty of Science, Mahasarakham University, Thailand. Eight specimens were dissected and examined under a stereoscopic light microscope.

Characters	Cryptosemelus	Apoparmarion	Paraparmarion
Number of shell whorls	3-4	2	3–4
Left shell lobe	Present	Present	Absent
Caudal horn	Absent	Present	Absent
Flagellum	Absent	Present	No information
Dart apparatus	Absent	Present	No information

Table 1. Comparison of morphological characters among three semislug genera, *Cryptosemelus, Apoparmarion* and *Paraparmarion* (data from Collinge 1902; Schileyko 2003; Pholyotha et al. 2021a).

Descriptions of the new species herein are attributed to the first and the third authors, as indicated below. Type specimens and other voucher specimens were deposited in the Natural History Museum of Mahasakham University, Maha Sarakham, Thailand (NHMSU).

The abbreviations used were as defined by Blanford and Godwin-Austen (1908), Solem (1966), Pholyotha et al. (2020) and Pholyotha et al. (2021a, b): **ag**, albumen gland; **at**, atrium; **e1**, portion of epiphallus nearer to penis; **e2**, portion of epiphallus nearer to retractor muscle; **fo**, free oviduct; **gd**, gametolytic duct; **gs**, gametolytic sac; **hd**, hermaphroditic duct; **ldl**, left dorsal lobe; **lsl**, left shell lobe; **ovt**, ovotestes; **p**, penis; **prm**, penial retractor muscle; **pro**, prostate gland; **rsl**, right shell lobe; **v**, vagina; **vd**, vas deferens; **ut**, uterus.

For the description of the genital system; 'proximal' refers to the region closest to the genital opening and 'distal' refers to the region outermost from the genital opening.

Results

Systematic description

Superfamily Helicarionoidea Bourguignat, 1877 Family Ariophantidae Godwin-Austen, 1883 Subfamily Ostracolethinae Simroth, 1901

Genus Cryptosemelus Collinge, 1902

Cryptosemelus Collinge, 1902: 76. Blanford and Godwin-Austen 1908: 180. Thiele 1931: 640. Zilch 1959: 326. Vaught 1989: 97. Schileyko 2003: 1332. Bank 2017: 53. Inkhavilay et al. 2019: 75. Pholyotha et al. 2021a: 43–65.

Type species. *Cryptosemelus gracilis* Collinge, 1902. *Cryptosemelus* has a reduced shell of three to four whorls, well-developed mantle extensions with two dorsal lobes and right shell lobe covering the apex and larger than the left shell lobe. Caudal horn absent. Genital system without flagellum and dart apparatus.



Figure 1. Map of type locality of Cryptosemelus niger S. Tumpeesuwan & C. Tumpeesuwan, sp. nov.

Cryptosemelus niger S. Tumpeesuwan & C. Tumpeesuwan, sp. nov.

https://zoobank.org/FA7C7967-4A62-4A6E-992C-4BE2E6DC9B36 Figs 1–4

Cryptaustenia sp. Tanmuangpak 2016: 109–110. *Cryptaustenia* sp. Chimsaeng 2019: 41–42.

Type material. *Holotype.* NHMSU-00054 (Fig. 3). Phu Pha Lom limestone area, Mueang Loei District, Loei Province, northeastern Thailand, coll. Kitti Tanmuangpak, Nov. 2012. *Paratypes.* NHMSU-00055. Same locality and same date as holotype.

Type locality. Phu Pha Lom limestone area, Mueang Loei District, Loei Province, Thailand.

Diagnosis. Animal with blackish body, shell lobes with blackish reticulated skin (Figs 2, 3). Genitalia with very short cylindrical vagina, smooth elongated cylindrical epiphallus, without penial caecum (Fig. 4). Radula with bicuspid lateral teeth (Fig. 5B, C).

Description. (empty shells = 8, living specimen = 4) **Shell** (Fig. 2A). Shell globose, small size (shell height $6.03 \pm 0.71.00$ mm, shell width 9.72 ± 1.32 mm), shell imperforate, thin, smooth, dark brown color; transparence, aperture large (aperture height 5.28 ± 0.68 mm and aperture width 5.71 ± 0.81 mm).

Genital system (N = 3) (Fig. 4). Atrium (at) short. Penis rather long and cylindrical, with thin penial sheath covering entire penis. Penial retractor muscle (prm) present, short, thin and attached at junction of e1 and e2. Epiphallus (e1+e2) length is slightly equal to penis length, surface smooth, e1 cylindrical and gradually smaller in diameter, e2 cylindrical and larger than e1. Flagellum absent. Vas deferens long. Vagina is shorter than penis, cylindrical. Gametolytic duct (gd) thickened at base, gametolytic sac (gs) swollen gland at distal end. Free oviduct (fo) is shorter than vagina. Uterus and prostate gland long and stout.

Radula (N = 3) (Fig. 5). Teeth arranged in a wide V-shape with half row formula: 1-7-70+teeth. Central teeth symmetric tricuspid. Lateral teeth and marginal teeth gradually changing from broad to narrow bicuspid.

External appearance (Figs 2B, 3). Living semislug with reticulated skin, blackish to dark body marked by conspicuous grooves running downward. Four mantle extensions well developed and same color body. Shell lobes do not cover entire shell. Caudal horn absent.

Etymology. The species name "*niger*" is derived from Latin word, meaning "black" referring to blackish body and mantle extensions.

Distribution, habitat and behavior observations. *Cryptosemelus niger* sp. nov. is a species restricted to the dry evergreen forest that covers the Phu Pha Lom limestone area, Loei Province, Thailand. We searched after rain and found the specimens normally hiding on the ground and in the leaf litter. When the snails were disturbed, they escaped by quickly flipping and waging their tail. Information on its natural predators is unknown, but the carnivorous land snails, *Discartemon* sp., *Oophana* sp. (Streptaxidae), and *Sinoen-nea loeiensis* Tanmuangpak & S. Tumpeesuwan, 2015 (Diapheridae) were found in the same locality (Tanmuangpak et al. 2012; Tanmuangpak et al. 2015; Tanmuangpak 2016).



Α



Figure 2. *Cryptosemelus niger* S. Tumpeesuwan & C. Tumpeesuwan, sp. nov. Photograph by Kitti Tanmuangpak A shell morphology of holotype NHMSU-00054 B living snail.



Figure 3. *Cryptosemelus niger* S. Tumpeesuwan & C. Tumpeesuwan, sp. nov. Living snail in natural habitats. Photograph by Chanidaporn Tumpeesuwan 12 December 2018 **A** *C. niger* crawling on soil in limestone crevice (white circle) **B** close-up view in living position **C**, **D** semislug was moved to green leaf for taking photo **C** left side represents left shell lobe (lsl) **D** right side represents right shell lobe (rsl), left shell lobes (lsl), and left dorsal lobe (ldl).



Figure 4. Genital system of *Cryptosemelus niger* S. Tumpeesuwan & C. Tumpeesuwan, sp. nov. (paratype NHMSU-00055) **A** photograph and **B** drawing by Kitti Tanmuangpak.



Figure 5. Radula morphology of *Cryptosemelus niger* S. Tumpeesuwan & C. Tumpeesuwan, sp. nov. (paratype NHMSU-00055) **A** radula plate, teeth rows arranged in wide V-shape **B** close-up view of middle part of radula **C** close-up view of right side of radula **D** close-up view of right side of radula showing marginal teeth. Central teeth indicated by 'C'; lateral teeth indicated by 'L'; marginal teeth indicated by 'M'.

Remarks. *Cryptosemelus niger* sp. nov. differ from other *Cryptosemelus* species by its black body and mantle lobes. The shell seems to have a more rapidly descending whorl than in *C. gracilis* and *C. betarmon*, but is similar to *C. tigrinus. Cryptosemelus gracilis* also lack a penial caecum but differs in the undulated surface patch on the proximal part of e2. The epiphallus and penis are cylindrical without a caecum, diverticulum, and granulate surface. The radula of the new species differs from all *Cryptosemelus* in having bicuspid lateral teeth, whereas other species have tricuspid lateral teeth (Table 2, Figs 2A, B, 3A–D, 4, 5B–D).

Discussion

The absence of a caudal horn is the unique character shared between *Cryptosemelus* and *Paraparmarion* (Collinge 1902; Blanford and Godwin-Austen 1908; Solem 1966; Schileyko 2002, 2003; Pholyotha et al. 2021a). *Cryptosemelus* differs from *Paraparmarion* in that the left shell lobe is well developed, whereas it is missing in *Paraparmarion* (Collinge 1902; Pholyotha et al. 2021a).

Characters	C. gracilis	C. betarmon	C. tigrinus	C. niger sp. nov.
Shell:		1		
Shape	Less, globose	Depressed, subglobose	Globose	Globose
Shell width	Up to 6.6 mm	Up to 7.4 mm	Up to 10.7 mm	Up to 11.04 mm
Shell height	Up to 4.2 mm	Up to 4.1 mm	Up to 7.6 mm	Up to 6.74 mm
Whorls number	3 1/2 -4	3 1/2 -4	4-4 1/2	3–4
Shell color	Pale golden amber	Pale yellowish with olive	Pale yellowish with olive	Dark brown
	_	tinge	tinge	transparent
Living snails:				
Shell lobes	Monochrome blue-	Monochrome pale to	Pale yellowish-orange	Blackish reticulated
coloration	gray to blackish	dark-grayish	banded	skin
Radula:		·		
Radula formula	1-(19-20)-38	1-(27-28)-37	1-(38-39)-44	1-7-70+
Central tooth	Tricuspid	Tricuspid	Tricuspid	Tricuspid
Lateral teeth	Tricuspid	Tricuspid	Tricuspid	Bicuspid
Marginal teeth	Tricuspid	Bicuspid	Bicuspid	Bicuspid
Genital system:				
Epiphallus e2:	Enlarged with	Enlarged and with	Cylindrical smooth	Long cylindrical with
Proximal part	irregularly undulated	undulated surface	surface	smooth surface
	surface patch			
Epiphallus e2:	Smooth surface	Cylindrical and	Cylindrical with	Long cylindrical with
Distal part		gradually tapering to	prominently granulated	smooth surface
		distal end, smooth	surface	
		surface		
Penial caecum	Absent	Present	Present	Absent
Vagina	Larger and shorter	Smaller and shorter than	Long slender and longer	Smaller and shorter
	than penis length	half of penis length	than half of penis length	than penis length

Table 2. Comparison of shell, genital system and radula of *Cryptosemelus* spp. (data for *C. gracilis, C. betarmon* and *C. tigrinus* based on Pholyotha et al. 2021a).

All previously described species of *Cryptosemelus* show no epiphallic caecum, flagellum, and dart apparatus. Shell lobes coloration, appearance of the penial caecum, shape and surface sculpture of the epiphallus, and radula morphology are considered as taxonomically informative and these can be used to distinguish the new species from all recognized *Cryptosemelus* species.

We have improved the key to the genera of mainland Southeast Asian slug-like semislugs provided by Tumpeesuwan and Tumpeesuwan (2019b) for identifying slug-like semislugs in mainland Southeast Asia and provide a key to species of genus *Cryptosemelus* below.

Key to genera of mainland Southeast Asian slug-like semislugs

1	Finger nail or triangular-shaped shell, always covered by shell lobes2
_	Ear-shape, subglobose, or globose-shaped shell, frequently covered by shell
	lobe
2	Finger nail-shaped shell; gametolytic sac long, cylindrical tube Muangnua
_	Triangular-shaped shell; gametolytic sac stalk, short and stout or moderately
	long and slender

3	Ear-shape shell; caudal horn present; dart apparatus and flag	ellum present4
_	Subglobose; or globose-shaped shell; caudal horn absent; o	lart apparatus and
	flagellum absent or no information	5
4	Penis length shorter than half of dart apparatus length	Parmarion
_	Penis length longer than dart apparatus length	Apoparmarion
5	Left shell lobe present only; dart apparatus no information	Paraparmarion
_	Both shell lobes present, dart apparatus absent	Cryptosemelus

Key to species of genus Cryptosemelus

1	Shell lobes monochrome
_	Shell lobes with black reticulated stripes on pale colour
2	Shell globose; body blue-gray; penial caecum absent; vagina large cylindrical
	C. gracilis
_	Shell depressed subglobose; body grayish, penial caecum present; vagina cylin-
	drical
3	Body color brownish; vagina long slender; penial caecum present; distal part of
	epiphallus with prominently granulated surface
_	Body color dark brown to blackish; vagina short; penial caecum absent;
	epiphallus with smooth surface

Since 2007, an intensive survey on land snail diversity in limestone and non-limestone hills in northeastern Thailand has been continuously conducted and published (Tumpeesuwan 2007; Tumpeesuwan and Tumpeesuwan 2010a, 2010b; Srihata et al. 2010; Tanmuangpak et al. 2012; Jumlong et al. 2013 Tumpeesuwan et al 2014; Tanmuangpak 2016; Sasang 2019; Nahok 2020). In total, 16 species have been described as new to science, comprising 11 species from limestone hills, four species from sandstone hills, and one species from volcanic hills (Tumpeesuwan and Tumpeesuwan 2014, 2017, 2019a, 2019b; Tanmuangpak et al. 2015, 2017; Nahok et al. 2020, 2021a, 2021b; Deeprom et al. 2022; Tanmuangpak and Dumrongrojwattana 2022; Tongkerd et al. 2023). Future studies on the malacofauna of the northeastern part of Thailand require more surveys in overlooked and isolated natural areas.

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RESEARCH ARTICLE



Description of the male of *Erromyrma* Bolton & Fisher, 2016 (Hymenoptera, Formicidae)

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Abstract

The male of the myrmicine genus *Erromyrma* is described for the first time on the basis of two specimens of *Erromyrma latinodis* (Mayr, 1872) collected in northern Madagascar. We used COI barcoding to confirm the identification of the male specimens as conspecific with *Erromyrma latinodis*. We provide an illustrated male-based key to the four Myrmicinae tribes (Attini, Crematogastrini, Solenopsidini, Stenammini) and to the Solenopsidini genera (*Adelomyrmex, Erromyrma, Solenopsis, Syllophopsis* and *Monomorium*) for the Malagasy region.

Keywords

Erromyrma, Madagascar, male ants, morphology, Myrmicinae, Solenopsidini

Introduction

Within the Malagasy region, Myrmicinae is one of the largest and most diverse subfamilies of Formicidae (Hymenoptera), with 30 genera in four tribes (Fisher and Peeters 2019; Fisher 2022). The genus *Erromyrma* Bolton & Fisher, 2016 (Solenopsidini), is represented by one species in the Malagasy region, *Erromyrma latinodis* (Mayr, 1872). The species has been introduced in many countries, including the Malagasy region, and is thought to have originated in India (Sharaf et al. 2018). The global distribution also includes Indomalaya, the Southeastern Palearctic and Oceania bioregions. *Erro-myrma latinodis* was originally placed in *Monomorium* but was shown to be a distinct lineage within the Solenopsidini based on molecular phylogenetic evidence (Ward et al. 2015) and placed in the newly described genus *Erromyrma*. Here we present the first description of the previously unknown male of *Erromyrma* based on *E. latinodis*, collected in northern Madagascar. We provide a male-based key to the Myrmicinae tribes and to genera for the tribe Solenopsidini of the Malagasy region.

Material and methods

This study is based on two male ant specimens (unique specimen identifiers: CASENT0788835 and CASENT0801166) collected in northern Madagascar in the town of Antsohihy (-14.89385, 47.98261) in the Region of Sofia, at c. 11 m above sea level on April 23, 2017, by Brian L. Fisher and the Madagascar Biodiversity Center team (Team Vitsika). Two males along with workers and queens were collected by hand under the bark of a mango tree along a dirt road 1 km outside of the town of Antsohihy (collection code identifiers: BLF40204, BLF40205). The mango tree was 1.5 m in diameter and approximately 5 m tall. The ants were found under bark flakes before the first branch at about 1 m in height.

Terminology for general morphology follows Bolton (1994) and Boudinot (2013, 2015). The terminology of the wing venation follows Yoshimura and Fisher (2007). When referring to the presence or absence of veins in the descriptions, a vein is considered present regardless of whether it is tubular, nebulous, or spectral (Mason 1986).

Imaging

Digital color montage images were created using a JVC KY-F75 digital camera and Syncroscopy Auto-Montage software (ver. 5.0), or a Leica DFC 425 camera in combination with the Leica Application Suite software (ver. 3.8). These images are available online through AntWeb.org (2022) and are accessible using the unique specimen identifier code.

Mapping

The distribution map was generated by importing specimen distribution records into the Diva-GIS program (Hijmans et al. 2011).

Morphological study

Morphological observations and measurements were carried out under Leica stereoscopic microscopes (MZ9.5). All measurements (see Fig. 1) and indices are expressed in millimeters.



Figure 1. Illustration of measurements of *Erromyrma latinodis* (CASENT0788835) **A** head in full-face view **B** segment abdominal in dorsal view **C** segment abdominal in lateral view.

The following characters were recorded:

- **EL:** Maximum eye length measured in full-face view along its maximum vertical diameter.
- **F1:** Maximum length of the pedicel (1st funicular segment, 2nd antennal segment) measured in a straight line.
- **HL:** Maximum head length in full-face view, measured in a straight line, from the anterior clypeal margin to the midpoint of a straight line drawn across the occipital margin.

- **HW1:** Head width at the level of the posterior margin of compound eyes, measured in full-face view.
- **HW2:** Maximum head width including the compound eyes, measured in full-face view.
- **IOD:** Inner ocellar distance. Minimum distance between the inner edges of the two lateral ocelli, measured in full-face view.
- **LOD:** Lateral ocellar distance. Minimum distance between the inner edge of the median and lateral ocelli, measured in full-face view.
- **OOD:** Ocular-ocellar distance. Minimum distance from the outer edge of a lateral ocellus to the compound eyes, measured in full-face view.
- **PL:** Petiole length, measured in profile view from the anterior margin of the peduncle to posterior most point of the petiolar tergite.
- **PW:** Petiolar width. Maximum petiole width, measured in dorsal view.
- **PPW:** Postpetiolar width. Maximum postpetiole width, measured in dorsal view.
- **SL:** Scape length. Maximum length of the antennal scape measured in a straight line, excluding the basal constriction and condylar bulb.

Indices

- **CI:** Cephalic index. HW1/HL × 100.
- **SI:** Scape index. SL/HW1 × 100.
- **EI:** Eye index. $EL/HW1 \times 100$.
- **PI:** Petiolar index. PL/PPL.

DNA sampling

After searching for the males in colonies across Madagascar for six years, we wanted to confirm that these males did represent the first males of *E. latinodis* even though they were collected along with queens and workers. We sequenced 658 base pairs (bp) of mitochondrial cytochrome oxidase I (COI) gene from one of the males to evaluate similarity with CO1 sequenced from 33 workers of *E. latinodis* across the region. The distribution of the specimens sequenced is shown in Fig. 10. DNA extraction and COI sequencing were performed at University of Guelph (Ontario, Canada), following the protocol described in Fisher and Smith (2008).

Abbreviation of depositories:

BMNH	British Museum of Natural History, London, UK;
CASC	California Academy of Sciences, San Francisco, CA, USA;
MCZ	Museum of Comparative Zoology Cambridge, MA, USA;
MHNG	Muséum d'histoire naturelle, Genève, Switzerland;
MSNG	Museo Civico di Storia Naturale 'Giacomo Doria', Genova, Italy;
NHMW	Naturhistorisches Museum, Wien (= Vienna), Austria.

Results

The 34 specimens sequenced (see Table 1) had a within-species sequence divergence of 0.00%. Thus, based on CO1, the male specimen sequenced is conspecific with the workers from throughout the region.

Table 1. *Erromyrma latinodis* Specimens sequenced for mitochondrial cytochrome oxidase I (COI) gene, including Genbank accession number, and caste. All voucher specimens are housed at the California Academy of Sciences.

Specimen Identifier	Collection	BOLD Process	COI-5P	sequence	Country	Caste
	Event identifier	ID	GenBank	length		
CASENT0010900-D01	R.J.1.765	ASANR501-09	HQ925412	590	Mayotte	worker
CASENT0107528-D01	BLF11668	JDWAM495-05	OP442963	654	Madagascar	worker
CASENT0107541-D01	BLF11664	JDWAM503-05	OP442956	654	Madagascar	worker
CASENT0123018-D01	BLF16532	ASANP672-09	GU710443	596	Madagascar	worker
CASENT0123025-D01	BLF16539	ASANP673-09	GU710442	625	Madagascar	worker
CASENT0123498-D01	BLF16507	ASANP676-09	HQ925385	618	Madagascar	worker
CASENT0132440-D01	BLF18832	ASANO176-09	GU709833	658	Mayotte	worker
CASENT0134112-D01	BLF19142	ASANP692-09	GU710444	658	Madagascar	worker
CASENT0134329-D01	BLF19879	ASANO717-09	GU709835	658	Comoros	worker
CASENT0134937	BLF18804	ASIMB817-09	OP442961	654	Mayotte	worker
CASENT0134955	BLF18810	ASIMB824-09	OP442957	654	Mayotte	worker
CASENT0134970	BLF18809	ASIMB832-09	OP442962	654	Mayotte	worker
CASENT0136510-D01	BLF19801	ASANO766-09	GU709838	658	Comoros	worker
CASENT0136519-D01	BLF19811	ASANO769-09	GU709837	658	Comoros	worker
CASENT0136656-D01	BLF19846	ASANO786-09	GU709840	658	Comoros	worker
CASENT0136764-D01	BLF19700	ASANO809-09	GU709839	658	Comoros	worker
CASENT0136784	BLF18809	ASIMB886-09	OP442959	654	Mayotte	worker
CASENT0136900-D01	BLF20364	ASANR766-09	GU711159	658	Madagascar	worker
CASENT0136902-D01	BLF20384	ASANP695-09	GU710446	658	Madagascar	queen
CASENT0136903-D01	BLF20384	ASANP696-09	GU710445	645	Madagascar	worker
CASENT0137058-D01	BLF19947	ASANO840-09	GU709842	658	Comoros	worker
CASENT0137059-D01	BLF19947	ASANO841-09	GU709841	658	Comoros	worker
CASENT0137334-D01	BLF19951	ASANO912-09	GU709844	658	Comoros	worker
CASENT0137487-D01	BLF19767	ASANO967-09	GU709836	658	Comoros	worker
CASENT0145999-D01	BLF21147	ASANQ049-09	GU710903	658	Comoros	worker
CASENT0146463-D01	BLF21164	ASANQ138-09	GU710902	658	Comoros	worker
CASENT0146468-D01	BLF21187	ASANQ140-09	GU710905	658	Comoros	worker
CASENT0146475-D01	BLF21160	ASANQ144-09	GU710904	658	Comoros	worker
CASENT0146479-D01	BLF21176	ASANQ146-09	GU710907	658	Comoros	worker
CASENT0146495-D01	BLF21188	ASANQ150-09	GU710906	658	Comoros	worker
CASENT0147204-D01	BLF20835	ASANQ268-09	GU710909	658	Comoros	worker
CASENT0189653	BLF18804	ASIMB946-09	OP442955	654	Mayotte	worker
CASENT0189654	BLF18810	ASIMB947-09	OP442960	654	Mayotte	worker
CASENT0788835-D01	BLF40204	BFANT381-22	OP442958	658	Madagascar	male

Taxonomic synopsis

Erromyrma latinodis (Mayr, 1872)

- Monomorium latinode Mayr, 1872: 152 (w.). Lectotype worker (designated by Heterick 2006: 108): Malaysia ("Borneo"), Sarawak, 1865–66 (J. Doria & O. Beccari), unique specimen identifier: CASENT0010941, examined [BMNH]. Paralectotype with same data as lectotype, unique specimen identifier: CASENT0905756, examined [MSNG]. [Combination in *Erromyrma*: Fisher and Bolton 2016: 276].
- Monomorium latinode var. bruneum Emery, 1893: 243 (w.). Lectotype worker (designated by Heterick 2006: 108): Sri Lanka ("Ceylon"), Kandy, i.–ii.1892 (E. Simon), unique specimen identifier: CASENT0008632, examined [MSNG]. [Junior synonym of latinode: Heterick 2006: 108].
- Monomorium latinode var. voeltzkowi Forel, 1907: 78 (w.). Lectotype worker (designated by Heterick 2006: 108): Tanzania ("Ostafrika"), Pemba I., Chake-Chake (A. Voeltzkow) [MCZC]. Paralectotype with same data as lectotype, unique specimen identifier: CASENT0101928, examined [MHNG]. [Junior synonym of latinodis: Bolton 1987: 429].
- Monomorium latinodoides Wheeler, 1928: 17 (w.). Syntype worker: China: Hong Kong, Kowloon (F. Silvestri) unique specimen identifier: MCZ-ENT00727982, examined [MCZC]. comb nov., syn. n.

Note. The type series at MCZ was examined. The syntypes series are labeled "Kowloon" (F. Silvestri): one pin with 3 workers (MCZ-ENT00020883) and 2 workers and one dealate queen on a second pin (MCZ-ENT00727982). The workers match the description and diagnosis (see below) of worker of *E. latinodis*. We formally combine the species in *Erromyrma* and synonymize the species with *E. latinodis*. However, we exclude the queen (on MCZ-ENT00727982) from the syntype series; it belongs to the genus *Carebara* (Westwood, 1840).

Diagnosis. *Erromyrma* workers [modified from Heterick (2006) and Fisher and Bolton (2016)]:

- 1. Worker caste polymorphic
- 2. Palp formula 3,3
- 3. Mandible triangular, smooth, and shiny
- 4. Five mandibular teeth
- 5. Antenna with 12 segments, with 3-segmented apical club
- 6. Scape short, failing to reach occipital margin
- 7. Compound eyes present and conspicuous
- 8. Clypeus with a distinct unpaired seta at the midpoint of the anterior margin
- 9. Frontal carinae short and parallel
- 10. Antennal scrobe absent
- 11. Head without raised nuchal (= occipital) carina

- 12. Tibial spurs absent from meso- and metatibia
- 13. Promesonotal suture not distinct in dorsal view
- 14. Metanotal groove present
- 15. Propodeum unarmed
- 16. Propodeal dorsum with strong transverse striolae
- 17. Petiole pedunculated
- 18. Subpetiolar process absent
- 19. Sting developed

Erromyrma latinodis males:

The following combination of characters diagnose males of Erromyrma latinodis.

- 1. Palp formula 5,3
- 2. Mandible triangular with distinct basal and masticatory margins (Fig. 2B)
- 3. Four mandibular teeth (Fig. 2B)
- 4. Antenna short and filiform, with 13 segments; pedicel subglobular (Fig. 2B)
- 5. Scape short (SI < 33, Fig. 2B)
- 6. Compound eyes large (EL/HW1 0.58, Fig. 1A)
- 7. Ocelli present and similar in size (Fig. 1A)
- 8. Clypeus with anterior margin convex. (Fig. 2B)
- 9. Frontal carinae absent (Fig. 2B)
- 10. Antennal scrobe absent (Fig. 2B)
- 11. Head without raised nuchal (= occipital) carina (Fig. 2C)
- 12. Notauli absent (Fig. 2C)
- 13. Single spur present on meso- and metatibia (Fig. 2A)
- 14. Pterostigma present on the forewing (Fig. 3)
- 15. First median-cubital cross-vein (1m-cu) present on the forewing (Fig. 3)
- 16. Cubital vein of the forewing fused with the median vein (M+Cu) and forms an angle higher than 45° with M (Fig. 3)
- 17. Forewing cross-vein 2rs-m absent (Fig. 3)
- 18. Petiole pedunculate (Fig. 2A)
- 19. Postpetiole elongated anteriorly, subglobose in lateral view (Fig. 2A)
- 20. Abdominal segment IV elongate and not shouldered (Fig. 2A)
- 21. Pygostyles present (Fig. 2A)

Male measurements (*N* = 2). HL 0.60–0.62, HW1 0.48–0.5, HW2 0.62–0.65, EL 0.28–0.29, EW 0.21–0.23, IOD 0.20–0.21, LOD 0.06–0.07, OOD 0.16–0.18, SL 0.12–0.14, F1 0.09–0.10, PL 0.51–0.54, PW 0.20–0.21, PPW 0.33–0.34, CI 81–82, SI 28, EI 0.58.

Description. Erromyrma latinodis males:

Structure. In full-face view, the head including compound eyes slightly wider than long. Posterior head margin relatively rounded; head with three large, rounded ocelli of the same size, situated on the frontal face of the head, lateral ocelli directed 45° toward lateral sides. Compound eye large, strongly bulging. Anterior margin of clypeus



Figure 2. *Erromyrma latinodis* (CASENT0788835) **A** body in lateral view **B** head in full-face view **C** body in dorsal view.

convex. Mandible well developed and elongate triangular; masticatory margin with four teeth, the basal and masticatory margins are distinct.

Antennae 13-segmented short and filiform, pedicel subglobular. The mesoscutum is strongly convex and bulging, in the dorsal view much broader than the head at the level of the forewing insertion. In dorsal view, pronotum short in the median portion; notauli absent on the mesoscutum; mesoscutellum broader than long and smaller than mesoscutum. Metapleural gland bulla present with metapleural lobe closed. In profile, propodeal angle rounded, without spines or teeth. Hind femora longer than tibia.

In lateral view, petiole distinctly pedunculated; subpetiolar process absent (Fig. 2A). In dorsal view, abdominal segment III (postpetiole) elongated anteriorly; abdominal segment IV not shoulder and broader than the remaining tergites.



Figure 3. Male forewing veins of *Erromyrma latinodis* (CASENT0788835). Abbreviations: **Pt** pterostigma; **Sc** subcosta; **R**, **r** radius; **Rs**, **rs** radial sector; **M**, **m** media; **Cu** cubitus; **A**, **a**, anal.

Sculpture. Clypeus, dorsum, lateral face, and venter of head weakly smooth and shiny. Pro- and mesothorax extensively smooth or very superficially sculptured and shiny, with posterolateral area of mesoscutum and posterior zone of mesopleuron unsculptured with shiny area. Metanotum and metapleuron unsculptured and matte. Apical area of anterior slope of petiole, coxae, femora, and tibiae of all legs smooth to superficially sculptured and shiny; tarsi entirely microsculptured. Gaster (abdominal segments IV to the apex) entirely smooth to superficially sculptured and shiny.

Color. Body and mandible largely brownish yellow except the ocellar region and the abdominal segments IV to the apex, brown.

Pilosity. Anterior margin of clypeus with a pair of stout setae and without a distinct unpaired seta at its midpoint. Mandible covered with standing hairs. Antennal scape and pedicel with short and decumbent whitish hairs; the flagellomeres densely hairy. Hairs on head and body moderately abundant, erect, short, and stout. Pronotum, mesoscutum, and mesoscutellum with many obliquely standing hairs; hairs on mesopleuron much sparser; metanotum and propodeum with erect hair. Femora and tibiae with appressed hairs; tarsi covered with short appressed hairs. Posterior margins of each abdominal tergite and sternite with long and suberect hairs. Parameres covered with stout hair.

Wings. (Fig. 3) Forewing with four closed cells. Costal vein (C) absent. Pterostigma pigmented, visible on the leading edge of the forewing. Radial vein (R) fused proximally to constitute Sc+R+Rs before reaching the pterostigma.

Radial sector (Rs). Past the separation from Sc+R+Rs, Rs usually short free abscissa down curved and never reaching to the costal margin, the radial sector connects to the pterostigma via the second radial-radial sector cross-vein (2r-rs). Then merging with median vein (M) and continuing fused (Rs+M).

Median vein (M). Further away from the leading wing margin is the median vein, proximally fused with cubital vein (M+Cu), following separation continuing as a free abscissa M before joining with radial sector to form Rs+M. Median vein (M) is fused with radial sector and present in past the junction of the radial sector.

Cubital vein (Cu). Proximally the cubital vein is fused with median vein (M+Cu), the cubital vein (Cu) divided by median-cubital cross-vein (1m-cu) the cubital vein does not connect to the distal wing margin.

Anal vein (A). A longitudinal vein running near the posterior wing margin. Consists of a free abscissa fused to cubital-anal cross-vein (cu-a), and continuing past cu-a.

Comments. The tribe Solenopsidini is separated from other Malagasy myrmicine tribes by the following combination of characters: with the head in full-face view, mandibles with masticatory margin less than five teeth; antennal scrobe reduced to absent; pedicel not more elongated than the remaining segments; ocelli present and same size situated on the frontal face of the head, lateral ocelli directed toward oblique front sides; occipital carina not visible in full-face view; head (including compound eyes) slightly wider than long with occipital margin of head rounded. In lateral view, the anterodorsal margin of mesopleuron lower than the highest point of the wing process, pronotum and mesonotum from a smooth convexity, pronotal furrow less marked; forewing venation: cross-vein 2rs-m absent, costal vein absent, radial sector down curved and never reaching to the costal margin; propodeal spines absent; pygostyle present; abdominal segment III attached anteriorly to abdominal segment IV; peduncle of abdominal segment III is distinctly longer than that of the petiole; single tibial spur present on the front leg. In dorsal view, notauli absent.

Erromyrma can be distinguished from three other genera, *Adelomyrmex* (Emery, 1897), *Monomorium* (Mayr, 1855) and *Syllophopsis* (Santschi, 1915), by its subglobular pedicels. It can be separated from the genus *Solenopsis* (Westwood, 1840) by the number of its antennal segment.

Key to the tribes of subfamily Myrmicinae based on males in the Malagasy region

The subfamily of Myrmicinae is represented by four tribes in the Malagasy region: Attini, Crematogastrini, Solenopsidini, Stenammini.

Attini: Cyphomyrmex (introduced), Eurhopalothrix, Pheidole, Pilotrochus, Strumigenys.

Crematogastrini: Calyptomyrmex, Cardiocondyla, Carebara, Cataulacus, Crematogaster, Dicroaspis, Eutetramorium, Malagidris, Melissotarsus, Meranoplus, Metapone, Nesomyrmex, Pristomyrmex, Royidris, Terataner, Tetramorium, Trichomyrmex, Vitsika, Vollenhovia (introduced?).

Solenopsidini: Adelomyrmex, Erromyrma (introduced), Monomorium, Solenopsis, Syllophopsis.

Stenammini: Aphaenogaster.



Figure 4. In profile view showing occipital carina **A**, **B** *Aphaenogaster bressleri* (CASENT0495103). In dorsal view form mesoscutellum **C**, **D** *Cyphomyrmex minitus* (CASENT0264488).



Figure 5. Head in profile view **A** *Strumigenys chilo* (CASENT0145240) **B** *Tetramorium silvicola* (CASENT0494732).

3	Cross-vein 2rs-m present on forewing (Fig. 6A)(Attini) Pheidole
_	Cross-vein 2rs-m absent on forewing (Fig. 6B)4



Figure 6. Forewing A Pheidole mgs006 (CASENT0135889) B Carebara drm03 (CASENT0143975).


Figure 7. Mandible A Pilotrochus besmerus (CASENT0057183) B Malagidris sofina (CASENT0906626).

- - duced anterodorsally (Fig. 8C)..... Crematogastrinii



Figure 8. In profile view **A** *Monomorium termitobium* (CASENT0135952) **B** *Meranoplus mayri* (CASENT0062813) **C** *Crematogaster hazolava* (CASENT0317643).

Male-based key to genera of the tribe Solenopsidini in the Malagasy region

1	Antennae 12-segmented Solenopsis
_	Antennae 13-segmented
2	In full-face view, pedicel subglobular; posteromedian margin of clypeus ef-
	faced so that clypeus and frons form a continuous surface (Fig. 9A); mandible
	triangular with distinct basal angle, masticatory margin with exactly 4 teeth
	Erromyrma
_	In full-face view, pedicel not globular, more cylindrical; posteromedian mar-
	gin of clypeus visible (Fig. 9B); mandible spatulate to triangular, but its basal
	angle always indistinct, masticatory margin with 1 to 4 teeth



Figure 9. Head in full-face view showing the pedicel, mandible, postero-median margin of clypeus **A** *Erromyrma latinodis* (CASENT0788835) **B** *Syllophopsis cryptobia* (CASENT0103340).



Figure 10. In profile view showing forewing, petiole and post petiole **A**, **C** *Syllophopsis modesta* (CASENT0135642) **B** *Monomorium termitobium* (CASENT0135673) **D** *Monomorium termitobium* (CASENT0135952).



Figure 11. Head in full-face view showing mandible and scape **A** *Monomorium exiguum* (CASENT0135614) **B** *Adelomyrmex* sc01 (CASENT0160764).

Discussion

In the Malagasy region, *Erromyrma latinodis* was collected from Comoros, Madagascar and Mayotte (see Fig. 12). The species inhabits montane rainforest, mangrove, *Uapaca* woodland, dry forest, and anthropogenic habitats from elevations of 2 to 1726 m. Workers were collected from a range of microhabitats and methods including foraging on low vegetation, on the ground, in ground nests, sifted litter, under stones, rotten wood or from dead twigs above ground. The males were collected along with workers and queens under the bark on the main trunk of a mango tree along a village road.

The males for this species were only collected after six expeditions. They are not collected by traditional means for example: malaise traps sampling or UV light samples from the region. Initial expeditions to known localities in northern Madagascar did not find the males. Colonies were kept alive for over a year without the production of males. Two males were finally found at one of the known collection sites.

The C01 data confirms the identification of the males and also shows a pattern of 0% sequence divergence between the samples from Madagascar, Comoros, and Mayotte. The lack of sequence divergence across island systems supports the hypothesis that this species is introduced in the region. Low sequence diversity could also be explained by other factors such as reproductive systems. The difficulty of finding males could be linked to a reproductive system that would reduce sequence divergence.



Figure 12. Distribution of *Erromyrma latinodis* in the Malagasy region. Red indicates localities of sequenced specimens.

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RESEARCH ARTICLE



Tapeworms (Platyhelminthes, Cestoda) from marine chondrichthyans of the Southwestern Atlantic Ocean, and the sub-Antarctic and Antarctic islands: a checklist

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Abstract

A parasite-host list of cestodes parasitizing chondrichthyans in the Southwest Atlantic off Argentina and surrounding waters of Antarctica is compiled based on the available literature. The list is based on published descriptions and redescriptions of species, and newly collected worms during the current study. A total of 57 valid species belonging to 28 genera of the orders Cathetocephalidea, Diphyllidea, Gyrocotylidea, Lecanicephalidea, Onchoproteocephalidea, Phyllobothriidea, Rhinebothriidea, "Tetraphyllidea", and Trypanorhyncha is listed. Information on hosts, localities, specimens in collections and comments on tapeworms are also included. A host-parasite list including chimaeras (1 order, 1 genus), batoids (4 orders, 10 genera), and sharks (3 orders, 5 genera) is provided. Tapeworm diversity, distribution range, and host associations are discussed. The cestodes orders Phyllobothriidea and Rhinebothriidea exhibit the highest species richness, with 13 and 12 species, respectively. Onchoproteocephalideans and rhinebothriideas have the broadest geographic distribution in the study area. Regarding hosts, arhynchobatid skates are the group most frequently associated with cestodes. However, further collecting efforts are necessary to understand whether this data reflect the real diversity and host association of these parasites or is a result of a bias in sampling.

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Keywords

Batoids, biodiversity, parasites, sharks, tapeworms, taxonomy

Introduction

According to Froese and Pauly (2022), more than 500 species of fishes have been registered along the Southwestern Atlantic off Argentina and the sub-Antarctic and Antarctic islands (including South Georgia, Elephant, and Joinville islands), including 100 chondrichthyan species (Table 1) (Gabbanelli et al. 2018; Concha et al. 2019; Froese and Pauly 2022). Since these cartilaginous fishes are the definitive hosts of a great diversity of adult cestodes (Caira and Jensen 2014), it is not uncommon to find a large variety of taxa of tapeworms along the Southwestern Atlantic and the Southern seas.

Complete and accurate species lists are essential for many biological disciplines such as ecology, conservation, and biogeography. Particularly, comprehensive fish cestodes datasets are necessary if we consider the usefulness of these parasites as biological tags for stock identification of their elasmobranch hosts in the context of overfishing and habitat degradation have profoundly altered the populations of marine elasmobranch (Dulvy et al. 2014; Irigoitia et al. 2017; Irigoitia et al. 2022). To date, cestodes from the Southwestern Atlantic, sub-Antarctic, and Antarctic regions were listed only in a few articles. These included a list of fishes and their tapeworms from South America (Alves et al. 2017), a compilation of marine invertebrates from the Argentine Sea focusing on taxonomic information at the generic level only (Bigatti and Signorelli 2018), and a few works about cestodes of Antarctic fishes (Rocka and Zdzitowiecki 1998; Rocka 2003, 2017). The analysis of the endoparasites in Antarctic fishes showed significantly higher values of diversity indices compared to the sub-Antarctic ichthyofauna (Muñoz and Cartes 2020); it would be interesting to consider the diversity of cestodes in a wider context, especially including the Southwestern Atlantic and southern latitudes off Antarctica in a single study. However, no complete work about cestodes from chondrichthyans, with detailed distributional ranges and host associations in this particular area of the Southern Hemisphere has been compiled so far.

In order to facilitate further studies, the main goal of this work is to elaborate a complete checklist of cestodes in chondrichthyan hosts based on summarizing references. The study area includes the Southwestern Atlantic Ocean off Argentina, Río de la Plata estuary, and the surrounding waters of South Georgia and the Elephant and Joinville islands by surrounding waters of South Georgia, Elephant and Joinville islands. This list includes information on localities, specimens in collections, and comments about the parasites and their hosts reported in previous works. We have also incorporated information about cestodes described in the last years, which included numerous new records and new localities (Menoret et al. 2017; Franzese and Ivanov 2018, 2020a, b, 2021; Menoret and Ivanov 2021; Franzese et al. 2022; this study).

Table 1. Chondrichthyans reported from the Southwestern Atlantic Ocean off Argentina,	Río de la
Plata estuary, and the sub-Antarctic and Antarctic islands (including South Georgia, Elephant	, and Join-
ville islands).	

Subclass	Order	Family	Genera	Species	Sampled chondrichthyan species
Holocephalii	Chimaeriformes	Callorhinchidae	1	1	1
		Chimaeridae	1	1	0
Subtotals	1	2	2	2	1
Batoidea	Myliobatiformes	Dasyatidae	2	3	0
		Mobulidae	1	1	0
		Myliobatidae	1	3	2
	Rajiformes	Arhynchobatidae	5	31	19
		Rajidae	2	8	3
	Rhinopristiformes	Pristidae	1	1	0
		Rhinobatidae	1	1	0
		Trygonorrhinidae	1	1	1
	Torpediniformes	Narcinidae	2	3	1
		Torpedinidae	1	1	0
Subtotals	4	10	17	53	26
Selachii	Carcharhiniformes	Carcharhinidae	2	7	1
		Galeocerdonidae	1	1	0
		Scyliorhinidae	2	2	0
		Sphyrnidae	1	3	0
		Triakidae	2	4	3
	Echinorhiniformes	Echinorhinidae	1	1	0
	Hexanchiformes	Hexanchidae	3	3	1
	Lamniformes	Alopiidae	1	1	0
		Carchariidae	1	1	0
		Cetorhinidae	1	1	0
		Lamnidae	3	3	0
	Squaliformes	Dalatiidae	2	2	0
		Etmopteridae	2	6	0
		Somniosidae	3	4	0
		Squalidae	1	3	0
	Squatiniformes	Squatinidae	1	3	1
Subtotals	6	16	27	45	6
Totals	11	28	46	100	33

Materials and methods

After an exhaustive bibliographical search, an annotated and revised parasite-host checklist was generated for the adult cestodes from marine chondrichthyans reported between 35°S–63°S. The geographical area considered covers the Southwestern Atlantic Ocean off Argentina (from 35°S southward), Río de la Plata estuary, and surrounding waters off South Georgia, Elephant, and Joinville islands. The cestode species are arranged according to taxonomic categories and are presented alphabetically, followed by data on their hosts, including valid species name, order, family, and synonymous species name used in literature (if available) in parentheses. The information for localities includes location, coordinates in degrees and minutes (if available in the literature), province, and country (where applicable) only for the type locality. The type-host and the type locality refer to data included in the original descriptions of cestodes species.

Other hosts and other localities only refer to the records within the study area, including those in the original descriptions as well as those mentioned in redescriptions, other papers and newly collected materials sampled during the present study. Specimens in collections include type material from original descriptions, voucher specimens from redescriptions and new voucher specimens prepared during the present study. Information about the new voucher specimens is in bold.

For the preparation of the figures, estimated coordinates were assigned to those records that lacked such information in the original publication.

Based on the information from the parasite-host checklist, the host-parasite data were subdivided into two inventories, one for batoids and chimaeras and another for sharks. The host species are arranged according to taxonomic categories and presented alphabetically, followed by the data on their parasites.

New vouchers of cestodes were obtained from the spiral intestines of chondrichthyans that had been caught by commercial trawlers between 2009 and 2017. The spiral intestines were fixed in 10% formalin and transferred to 70% ethanol for storage in the Laboratorio de Sistemática y Biología de Parásitos de Organismos Acuáticos (SIBIPOA) of Instituto de Biodiversidad y Biología Experimental y Aplicada (IBBEA, CONICET-UBA). Cestodes were hydrated in a graded ethanol series, stained with Harris' hematoxylin, dehydrated in a graded ethanol series, cleared in methyl salicylate, and mounted in Canada balsam (Menoret and Ivanov 2021; Franzese et al. 2022).

The accession numbers of the available molecular sequences were taken from the Gen-Bank database, considering only those specimens whose identification is not doubtful.

The classification and valid cestodes names follow Caira and Jensen (2017) and Caira et al. (2022). The classification and valid host names follow Menni and Lucifora (2007), Naylor et al. (2012), Weigmann (2016), Gabbanelli et al. (2018), Concha et al. (2019), Stehmann et al. (2021), and Froese and Pauly (2022). Abbreviations of the collection names used are listed in Table 2.

AHC	Australian Helminthological Collection, South Australian Museum, Adelaide, Australia					
CHIOC	Coleção Helmintológica do Instituto Oswaldo Cruz, Rio de Janeiro, Brazil					
BMNH/NHMUK Natural History Museum, London, United Kingdom						
HWML Harold W. Manter Laboratory of Parasitology, University of Nebraska						
	State Museum, Nebraska, United States of America					
IPCAS Institute of Parasitology, Academy of Sciences of the Czech Republic, České Budějovice, Czech F						
LRP	Lawrence R. Penner Parasitology Collection, Department of Ecology and Evolutionary Biology, University					
	Connecticut, Connecticut, United Stated of America					
MACN-Pa	IACN-Pa Museo Argentino de Ciencias Naturales, Colección Parasitológica, Buenos Aires, Argentina					
MLP	Colección de Invertebrados, Museo de La Plata, La Plata, Argentina					
MNHNC	Museo Nacional de Historia Natural de Chile, Santiago, Chile					
MNHNF	Muséum National d'Histoire Naturelle, Paris, France					
MZPW Museum and Institute of Zoology, Polish Academy of Science, Warsaw, Poland						
NMW	Naturhistorisches Museum Wien, Vienna, Austria					
USNM	National Museum of Natural History of the Smithsonian Institution, Washington, United States of America					
USNPC	U. S. National Parasite Collection, Maryland, United States of America, currently incorporated in the UNNM					

Table 2. Museum abbreviations.

Results

Parasite-host checklist

Order Cathetocephalidea Schmidt & Beveridge, 1990 Family Cathetocephalidae Dailey & Overstreet, 1973 Genus *Cathetocephalus* Dailey & Overstreet, 1973

Cathetocephalus australis Schmidt & Beveridge, 1990

Type host. Carcharhinus brachyurus (Günther) (Carcharhiniformes: Carcharhinidae).
Type locality. Goolwa, South Australia.
Other locality. Off Argentina.
Specimens in collections. AHC No. V4123 (holotype); AHC Nos. 17535, 17536 (paratypes).
References. Schmidt and Beveridge (1990), Suriano and Labriola (2001a).

Order Diphyllidea Carus, 1863 Family Echinobothriidae Perrier, 1897 Genus *Coronocestus* Caira, Marques, Jensen, Kutcha & Ivanov, 2013

Coronocestus notoguidoi (Ivanov, 1997)

Echinobothrium notoguidoi Ivanov, 1997. Syn.

Type host. Mustelus schmitti Springer (Carcharhiniformes: Triakidae).

Type locality. Mar del Plata (38°00'S, 57°33'W), Buenos Aires Province, Argentina. Specimens in collections. MLP No. 3893C (holotype); MLP Nos. 3894C (paratypes); USNPC No. 87169 (paratypes).

 $\mathbf{C} = \mathbf{D} + \mathbf{A} + \mathbf{N} = \mathbf{D} - \mathbf{O} + \mathbf{O} +$

GenBank Acc. No. DQ088034.

References. Ivanov (1997), Alarcos et al. (2006), Tyler (2006), Caira et al. (2013b).

Comments. Tyler (2006) modified the original description of Ivanov (1997) and added new morphological information based on type material.

Genus Echinobothrium Van Beneden, 1849

Echinobothrium acanthocolle Wojciechowska, 1991

Type host. Amblyraja georgiana (Norman) (Rajiformes: Rajidae) (Raja georgiana).
Type locality. Shelf near South Georgia, South Atlantic Ocean.
Specimens in collections. No specimens were deposited in a public collection.
References. Wojciechowska (1991a), Rocka (2003).
Comments. Holotype and paratype are in Wojciechowska's personal collection.

Genus Halysioncum Caira, Marques, Jensen, Kutcha & Ivanov, 2013

Halysioncum megacanthum (Ivanov & Campbell, 1998)

Echinobothrium megacanthum Ivanov & Campbell, 1998. Syn.

Type host. Myliobatis goodei Garman (Myliobatiformes: Myliobatidae).

Type locality. San Antonio Oeste, San Matías Gulf (40°44'S, 64°56'W), Río Negro Province, Argentina.

Specimens in collections. MLP No. 3958 (holotype); IPCAS No. C-288 (para-types); USNM No. 1382674 (paratypes).

References. Ivanov and Campbell (1998a), Tyler (2006), Caira et al. (2013b).

Comments. Tyler (2006) modified the original description of Ivanov and Campbell (1998a) and added new morphological information based on type material.

Halysioncum pigmentatum (Ostrowski de Núñez, 1971)

Echinobothrium pigmentatum Ostrowski de Núñez, 1971. Syn.

Type host. *Zapteryx brevirostris* (Müller & Henle) (Rhinopristiformes: Trygonorrhinidae). **Type locality.** Mar del Plata, Buenos Aires Province, Argentina.

Specimens in collections. No specimens were deposited in a public collection. **References.** Ostrowski de Núñez (1971), Tyler (2006), Caira et al. (2013b).

Comments. Holotype and paratypes remain in Ostrowski de Núñez's personal collection. Tyler (2006) modified the original description of Ostrowski de Núñez (1971) and added new morphological information based on material from the author's personal collection.

Order Gyrocotylidea Poche, 1926 Genus *Gyrocotyle* Diesing, 1850

Gyrocotyle maxima Mac Donagh, 1927

Type host. Probably *Callorhinchus callorynchus* (Linnaeus) (Chimaeriformes: Callorhinchidae) (*Mustelus asterias*).

Type locality. Probably off Mar del Plata, Buenos Aires Province, Argentina. Specimens in collections. Instituto Bacteriológico, Buenos Aires. Reference. Mac Donagh (1927).

Gyrocotyle rugosa Diesing, 1850

Type host. Callorhinchus callorynchus (Chimaeriformes: Callorhinchidae).

Type locality. Portum Natalensem, South Africa. Other locality. Necochea, Buenos Aires Province. Specimen in collections. NMW No. 2502 (neotype). GenBank Acc. Nos. MW587267, MW587258, MW581656. References. Mac Donagh (1927), Barčák et al. (2021). Comments. *Gyrocotyle rugosa* has a wide distribution including coastal waters of South America, South Africa, and New Zealand.

Order Lecanicephalidea Hyman, 1951 Family Aberrapecidae Jensen, Caira, Cielocha, Littlewood & Waeschenbach, 2016 Genus *Aberrapex* Jensen, 2001

Aberrapex arrhynchum (Brooks, Mayes & Thorson, 1981)

Discobothrium arrhynchum Brooks, Mayes & Thorson, 1981. Syn.

Type host. *Myliobatis goodei* (Myliobatiformes: Myliobatidae).
Type locality. Río de la Plata estuary near Montevideo, Uruguay.
Specimens in collections. USNPC No. 75722 (holotype); USNPC No. 75723 (paratype); HWML No. 21003 (paratypes).
References. Brooks et al. (1981), Jensen (2001).

Aberrapex ludmilae Menoret, Mutti & Ivanov, 2017

Type host. Myliobatis goodei (Myliobatiformes: Myliobatidae).

Type locality. San Matias Gulf (40°58'S, 64°56'W), Río Negro Province, Argentina.

Specimens in collections. MACN-Pa No 616-1 (holotype); MACN-Pa Nos. 616/2–5 (paratypes); IPCAS No. C-755/1–2 (paratypes); LRP No. 9239 (paratypes).

Reference. Menoret et al. (2017).

Aberrapex sanmartini Menoret, Mutti & Ivanov, 2017

Type host. Myliobatis goodei (Myliobatiformes: Myliobatidae).

Type locality. Off Carmen de Patagones (40°42'S, 62°00'W), Buenos Aires Province, Argentina.

Specimens in collections. MACN-Pa No. 617/1 (holotype); MACN-Pa Nos. 617/2–12 (paratypes); IPCAS Nos. C-756/1–2 (paratypes); LRP Nos. 9242, 9243 (paratypes).

Reference. Menoret et al. (2017).

Aberrapex vitalemuttiorum Menoret, Mutti & Ivanov, 2017

Type host. *Myliobatis ridens* Ruocco, Lucifora, Díaz de Astarloa, Mabragaña & Delpiani (Myliobatiformes: Myliobatidae).

Type locality. Off Villa Gesell (37°29'S, 56°45'W), Buenos Aires Province, Argentina.

Other locality. Punta Negra, Necochea (38°37'S, 58°51'W), Buenos Aires Province.

Specimens in collections. MACN-Pa No 618/1 (holotype); MACN-Pa Nos. 618/2–10 (paratypes); IPCAS Nos. C-757/1–2 (paratypes); LRP Nos. 9240, 9241 (paratypes).

Reference. Menoret et al. (2017).

Family Paraberrapecidae Jensen, Caira, Cielocha, Littlewood & Waeschenbach, 2016 Genus *Paraberrapex* Jensen, 2001

Paraberrapex atlanticus Mutti & Ivanov, 2016

Type host. Squatina guggenheim Marini (Squatiniformes: Squatinidae).

Type locality. Off Puerto Quequén (38°53'S, 58°27'W), Buenos Aires Province, Argentina.

Other localities. Near Río de la Plata estuary (36°21'S, 54°32'W), off Villa Gesell (37°17'S, 56°27'W), off Carmen de Patagones (40°58'S, 62°00'W), Buenos Aires Province. San Matías Gulf (41°03'S, 64°06'W), Río Negro Province.

Specimens in collections. MACN-Pa No 618/1 (holotype); MACN-Pa Nos. 618/2–10 (paratypes); IPCAS Nos. C-757/1–2 (paratypes); LRP Nos. 9240, 9241 (paratypes).

Reference. Mutti and Ivanov (2016).

Order Onchoproteocephalidea Caira, Jensen, Waeschenbach, Olson & Littlewood, 2014 Family Onchobothriidae Braun, 1900

Genus Acanthobothrium Blanchard, 1848

Acanthobothrium carolinae Franzese & Ivanov, 2020

Type host. Bathyraja magellanica (Philippi) (Rajiformes: Arhynchobatidae).

Type locality. Coastal waters off Puerto San Julián (49°29'S, 66°11'W), Santa Cruz Province, Argentina.

Other localities. Coastal waters off Río Grande (54°01'S, 67°06'W), Tierra del Fuego Province. Namuncurá Marine Protected Area/Burdwood Bank (54°32'S, 60°01'W).

Specimens in collections. MACN-Pa No. 716 (holotype); MACN-Pa Nos. 717/1–4, 718/1–3, 719/1–2 (paratypes); IPCAS No. C-838 (paratypes); LRP Nos. 10179–10184 (paratypes).

Reference. Franzese and Ivanov (2020a).

Taxon	Host	Capture coordinates	New locality
Onchoproteocephalidea			
Onchobothriidae			
Acanthobothrium			
A. domingae	Dipturus brevicaudatus	38°00'S, 56°04'W	Mar del Plata, Buenos Aires
A. marplatensis	Atlantoraja castelnaui	38°46'S, 57°56'W	Puerto Quequén, Buenos Aires
A. stefaniae	Discopyge tschudii	38°46'S, 57°56'W	Puerto Quequén, Buenos Aires
Rhinebothriidea			
Echeneibothriidae			
Echeneibothrium			
E. williamsi	Dipturus brevicaudatus	38°46'S, 57°56'W	Puerto Quequén, Buenos Aires
Notomegarhynchus			
N. navonae	Atlantoraja castelnaui	38°46'S, 57°56'W	Puerto Quequén, Buenos Aires

Table 3. Cestodes and their respective hosts collected for this study.

Acanthobothrium domingae Franzese & Ivanov, 2020

Type host. Dipturus brevicaudatus (Marini) (Rajiformes: Rajidae).

Type locality. Coastal waters off Santa Teresita (36°35'S, 54°54'W), Buenos Aires Province, Argentina.

Other localities. Coastal waters off Río Grande (53°35'S, 66°37'W), Tierra del Fuego Province. Coastal waters off Mar del Plata (38°00'S, 56°04'W), Buenos Aires Province (Table 3).

Specimens in collections. MACN-Pa No. 720 (holotype); MACN-Pa Nos. 721/1–3, 722/1–9, 723(paratypes); IPCAS No. C-839 (paratypes); LRP Nos. 10185–10195 (paratypes); **MACN-Pa No. 770 (voucher)**.

Reference. Franzese and Ivanov (2020a).

Acanthobothrium marplatensis Ivanov & Campbell, 1998

Type host. *Atlantoraja castelnaui* (Miranda Ribeiro) (Rajiformes: Arhynchobatidae) (*Rioraja castelnaui*).

Type locality. Mar del Plata (38°00'S, 57°33'W), Buenos Aires Province, Argentina. Other locality. Puerto Quequén (38°46'S, 57°56'W), Buenos Aires Province (Table 3).

Specimens in collections. MLP No. 4025 (holotype); MLP No 4026 (paratype); USNM No. 1382675 (paratypes); BMNH No 1998.2.10.1–2 (paratypes); **MACN-Pa No. 771 (voucher)**.

Reference. Ivanov and Campbell (1998b).

Acanthobothrium stefaniae Franzese & Ivanov, 2018

Type host. Discopyge tschudii Heckel (Torpediniformes: Narcinidae).

Type locality. Coastal waters off Mar Chiquita City (37°46'S, 56°56'W), Buenos Aires Province, Argentina.

Other localities. Coastal waters off Villa Gesell (37°29'S, 56°45'W), off San Clemente del Tuyú (35°50'S, 56°18'W), **off Puerto Quequén (38°46'S, 57°56'W)** (Table 3), Buenos Aires Province. Coastal waters off Camarones (45°08'S, 65°19'W), Chubut Province.

Specimens in collections. MACN-Pa No 624 (holotype); MACN-Pa Nos. 625/1–6, 626/1–3, 627/1, 628/1–2 (paratypes); IPCAS No. C-786 (paratypes); LRP Nos. 9403–9410 (paratypes); **MACN-Pa No. 772 (voucher)**.

Reference. Franzese and Ivanov (2018).

Acanthobothrium zapterycum Ostrowski de Núñez, 1971

Type host. *Zapteryx brevirostris* (Rhinopristiformes: Trygonorrhinidae).

Type locality. Mar del Plata, Buenos Aires Province, Argentina.

Other localities. Coastal waters off Villa Gessel (37°29'S, 56°45'W), La Lucila del Mar (36°38'S, 56°15'W), Puerto Quequén (38°46'S, 57°56'W), Buenos Aires Province. Puerto Pirámides (42°05'S, 62°50'W), Chubut Province.

Specimens in collections. MACN-Pa No. 214/1(holotype); MACN-Pa No. 214/1–5 (paratypes); MACN-Pa Nos. 629/1, 630/1–3, 631/1–4, 632/1–4 (vouchers); IPCAS No. C-787 (vouchers); LRP Nos. 9411–9417 (vouchers).

Reference. Ostrowski de Núñez (1971), Franzese and Ivanov (2018).

Acanthobothrium sp.

Hosts. Bathyraja cousseauae Díaz de Astarloa & Mabragaña, Bathyraja magellanica (Rajiformes: Arhynchobatidae); Myliobatis goodei (Myliobatiformes: Myliobatidae); Zapteryx brevirostris (Rhinopristiformes: Trygonorrhinidae).

Localities. Río de La Plata estuary, Uruguay; Mar del Plata, Buenos Aires Province, Argentina; Malvinas Islands, Southwestern Atlantic Ocean.

Specimens in collections. HWML Nos. 20999, 21000.

References. Ostrowski de Núñez (1971), Brooks et al. (1981), Beer et al. (2019).

Comments. Ostrowski de Núñez (1971) registered *Acanthobothrium* sp. from *Z. brevirostris* in Mar del Plata. Brooks et al. (1981) reported two specimens of *Acanthobothrium* sp. from *M. goodei* at Río de la Plata, which could be a different species. They pointed out that one of these specimens could correspond to the same species reported by Ostrowski de Núñez (1971) in *Z. brevirostris*. Beer et al. (2019) reported *Acanthobothrium* sp. from *B. cousseauae* and *B. magellanica* off Malvinas Islands. The deposited material only corresponds to the specimens studied by Brooks et al. (1981).

Genus Onchobothrium de Blainville, 1828

Onchobothrium antarcticum Wojciechowska, 1990

Type host. *Bathyraja eatonii* (Günther) (Rajiformes: Arhynchobatidae).
Type locality. shelf around Joinville Island in Bransfield's Strait, Antarctica.
Specimens in collections. MZPW No. 1805 (holotype); MZPW No. 1806 (paratype); BMNH 1989.4.19.1 (paratype).
References. Wojciechowska (1990a), Rocka (2003, 2017).

Order Phyllobothriidea Caira, Jensen, Waeschenbach, Olson & Littlewood, 2014 Family Phyllobothriidae Braun, 1900 Genus *Crossobothrium* Linton, 1889

Crossobothrium antonioi Ivanov, 2009

Type host. Notorynchus cepedianus (Péron) (Hexanchiformes: Hexanchidae).

Type locality. Puerto Quequén (38°32'S, 58°42'W), Buenos Aires Province, Argentina.

Specimens in collections. MACN-Pa No. 493/1 (holotype); MACN-Pa Nos. 493/2–6 (paratypes).

Reference. Ivanov (2009).

Crossobothrium pequeae Ivanov, 2009

Type host. *Notorynchus cepedianus* (Hexanchiformes: Hexanchidae).

Type locality. Puerto Quequén (38°32'S, 58°42'W), Buenos Aires Province, Argentina.

Specimens in collections. MACN-Pa No. 494/1 (holotype); MACN-Pa Nos. 494/2–6 (paratypes).

Reference. Ivanov (2009).

Genus Guidus Ivanov, 2006

Guidus antarcticus (Wojciechowska, 1991)

Marsupiotbothrium antarcticum Wojciechowska, 1991. Syn.

Type host. *Bathyraja maccaini* Springer (Rajiformes: Arhynchobatidae). **Other host.** *Bathyraja eatonii* (Rajiformes: Arhynchobatidae). Type locality. Shelf around Joinville Island, Antarctica.

Specimens in collections. MZPW No. 1817 (holotype); BMNH No. 1992.1.6.31 (paratype).

References. Wojciechowska (1991a), Rocka (2003), Ivanov (2006).

Guidus argentinense Ivanov, 2006

Type host. Bathyraja brachyurops (Fowler) (Rajiformes: Arhynchobatidae).

Type locality. Coastal waters off Buenos Aires Province (37°06'S, 54°20'W), Argentina.

Other localities. Off Bahía Blanca (39°34'S, 56°16'W), Buenos Aires Province. Namuncurá Marine Protected Area/Burdwood Bank (54°44'S, 59°56'W).

Specimens in collections. MACN-Pa No. 432/1 (holotype); MACN-Pa Nos. 432/2–7 (paratypes); USNM No. 1393041 (paratypes); MACN-Pa Nos. 750–751 (vouchers).

References. Ivanov (2006), Menoret and Ivanov (2021).

Guidus francoi Menoret & Ivanov, 2021

Type host. *Bathyraja magellanica* (Rajiformes: Arhynchobatidae).

Type locality. Off Río Grande (53°56'S, 66°04'W), Tierra del Fuego Province, Argentina.

Other localities. Off Puerto San Julián (49°29'S, 66°11'W), Santa Cruz Province. Off Río Grande (54°30'S, 65°13'W; 54°24'S, 63°57'W; 54°01'S, 67°06'W; 53°55'S, 67°05'W; 53°36'S, 67°39'W), Tierra del Fuego Province.

Specimens in collections. MACN-Pa No. 739 (holotype); MACN-Pa Nos. 740/1–3, 741/1, 744, 745, 746/1–2, 740/4, 741/2–3, 742/1–3, 743, 746/3–7 (paratypes); IPCAS No. C-887 (paratypes).

Reference. Menoret and Ivanov (2021).

Guidus magellanicus Menoret & Ivanov, 2021

Type host. *Bathyraja magellanica* (Rajiformes: Arhynchobatidae).

Type locality. Off Río Grande (54°01'S, 67°06'W), Tierra del Fuego Province, Argentina.

Other localities. Off Puerto San Julian (49°29'S, 66°11'W), Santa Cruz Province. **Specimens in collections.** MACN-Pa No. 747 (holotype); MACN-Pa Nos.

748/1-2, 749/1-2 (paratypes); IPCAS No. C-888 (paratypes).

Reference. Menoret and Ivanov (2021).

Guidus sp.

Host. *Bathyraja multispinis* (Norman) (Rajiformes: Arhynchobatidae). Locality. Malvinas Islands Shelf, Southwestern Atlantic Ocean. Reference. Beer et al. (2019).

Comments. These specimens were studied by Beer et al. (2019) at a molecular rather than morphological level, without reaching an identification at the specific level.

Genus Orygmatobothrium Diesing, 1863

Orygmatobothrium juani Ivanov, 2008

Type host. Mustelus fasciatus (Garman) (Carcharhiniformes: Triakidae).

Typelocality. Puerto Quequén (38°32'S, 58°42'W), Buenos Aires Province, Argentina. **Specimens in collections.** MACN-Pa No. 445/1 (holotype); MACN-Pa Nos.

445/2–6 (paratypes).

Reference. Ivanov (2008).

Orygmatobothrium schmitti Suriano & Labriola, 2001

Type host. Mustelus schmitti (Carcharhiniformes: Triakidae).

Type locality. Mar del Plata (38°00'S, 57°33'W), Buenos Aires Province, Argentina. **Other locality.** Puerto Quequén (38°32'S, 58°42'W), Buenos Aires Province.

Specimens in collections. MACN-Pa Nos. 382/1–2 (holotype and paratype); MNHN 20HG:158 CIX, MNHN 20HG:159 CIX (paratypes); MACN-Pa Nos. 444/1–5 (vouchers).

References. Ostrowski de Núñez (1973), Suriano and Labriola (2001b), Alarcos et al. (2006), Ivanov (2008).

Comments. Ostrowski de Núñez (1973) redescribed *O. velamentum* based on material collected in Mar del Plata. Later, Ivanov (2008) reassigned these specimens to *O. schmitti*.

Genus Phyllobothrium Van Beneden, 1850

Phyllobothrium sp.

Hosts. Sympterygia bonapartii Müller & Henle (Rajiformes: Rajidae) (as Psammobatis microps in Ostrowski de Núñez [1971]), Myliobatis goodei (Myliobatiformes: Myliobatidae), Zapteryx brevirostris (Rhinopristiformes: Trygonorrhinidae).

Localities. Mar del Plata, Argentina. Río de la Plata estuary near Montevideo, Uruguay. **Specimen in collections.** HWML 21001.

References. Ostrowski de Núñez (1971), Brooks et al. (1981).

Comments. Ostrowski de Núñez (1971) registered *Phyllobothrium* sp. from *S. bonapartii* and *Z. brevirostris* in Mar del Plata. Brooks et al. (1981) reported ten specimens of *Phyllobothrium* sp. from *M. goodei* at the Río de la Plata estuary. The deposited material only corresponds to the specimens studied by Brooks et al. (1981).

Genus Rockacestus Caira, Bueno & Jensen, 2021

Rockacestus arctowskii (Wojciechowska, 1991)

Phyllobothrium arctowskii Wojciechowska, 1991, *Anthocephalum arctowskii* Rocka & Zdzitowiecki, 1998. Syns.

Type host. Bathyraja arctowskii (Dollo) (Rajiformes: Arhynchobatidae) (Bathyraja sp. 2).
 Type locality. Admiralty Bay, environs of the South Shetlands, Antarctica.
 Other locality. Shelf near Elephant Island, Antarctica.

Specimens in collections. MZPW No. 1814 (holotype); BMNH No. 1992.1.6.30 (paratypes).

References. Wojciechowska (1991b), Rocka (2003, 2017), Caira et al. (2021).

Comments. Rocka (2017) established the name *Rajicestus* Rocka & Laskowski, 2017 for cestodes from Antarctic and sub-Antarctic skates described originally in Wojciechowska (1991b) as members of *Phyllobothrium*. Unfortunately, no generic diagnosis or type species was designated; therefore, the name *Rajicestus* is unavailable. Regarding host identification, Stehmann et al. (2021) assigned specimens of *Bathyraja* sp. 2 to *Bathyraja arctowskii*, a wide-ranging, circum-Antarctic species locally common in the Atlantic sector of the Southern Ocean.

Rockacestus conchai Caira, Bueno & Jensen, 2021

Type host. Bathyraja albomaculata (Norman) (Rajiformes: Arhynchobatidae).

Type locality. Malvinas Islands (48°39'S, 60°44'W), Southwestern Atlantic Ocean. **Other locality.** Malvinas Islands (49°38'S, 59°50'W).

Specimens in collections. NHMUK No. 2020.12.17.1 (holotype); USNM Nos. 1638654, 1638655 (paratypes); LRP Nos. 10293, 10294 (paratypes); LRP Nos. 10279–10281 (SEM vouchers).

GenBank Acc. No. MW419959. **Reference.** Caira et al. (2021).

Rockacestus georgiensis (Wojciechowska, 1991)

Phyllobothrium georgiense Wojciechowska, 1991, *Anthocephalum georgiense* Rocka & Zdzitowiecki, 1998. Syns.

Type host. *Amblyraja georgiana* (Rajiformes: Rajidae) (*Raja georgiana*).

Type locality. Shelf around South Georgia, South Atlantic Ocean.

Specimens in collections. MZPW No. 1812 (holotype); No. BMNH No. 1992.1.6.27 (paratype).

References. Wojciechowska (1991b), Rocka (2003, 2017), Caira et al. (2021).

Comments. Rocka (2017) established the name *Rajicestus* for cestodes from Antarctic and sub-Antarctic skates described originally in Wojciechowska (1991b) as members of *Phyllobothrium*. Unfortunately, no generic diagnosis or type species was designated; therefore, the name *Rajicestus* is unavailable.

Rockacestus rakusai (Wojciechowska, 1991)

Phyllobothrium rakusai Wojciechowska, 1991, *Anthocephalum rakusai* Rocka & Zdzi-towiecki, 1998. Syns.

Type host. Bathyraja maccaini (Rajiformes: Arhynchobatidae).

Type locality. Shelf around Elephant Island and Joinville Island in Bransfield Strait, Antarctica.

Specimens in collections. MZPW No. 1816 (holotype); BMNH No. 1992.1.6.28 (paratype).

References. Wojciechowska (1991b), Rocka (2003, 2017), Caira et al. (2021).

Comments. Rocka (2017) established the name *Rajicestus* for cestodes from Antarctic and sub-Antarctic skates described originally in Wojciechowska (1991b) as members of *Phyllobothrium*. Unfortunately, no generic diagnosis or type species was designated; therefore, the name *Rajicestus* is unavailable.

Rockacestus siedleckii (Wojciechowska, 1991)

Phyllobothrium siedleckii Wojciechowska, 1991, *Anthocephalum siedleckii* Rocka & Zdzitowiecki, 1998. Syns.

Type host. Bathyraja eatonii (Rajiformes: Arhynchobatidae).

Type locality. Shelf around Elephant Island and Joinville Island in Bransfield Strait, Antarctica.

Specimens in collections. MZPW No. 1815 (holotype); BMNH No. 1992.1.6.29 (paratype).

References. Wojciechowska (1991b), Rocka (2003, 2017), Caira et al. (2021).

Comments. Rocka (2017) established the name *Rajicestus* for cestodes from Antarctic and sub-Antarctic skates described originally in Wojciechowska (1991b) as members of *Phyllobothrium*. Unfortunately, no generic diagnosis or type species was designated; therefore, the name *Rajicestus* is unavailable.

Phyllobothriidea gen. sp.

Hosts. Amblyraja doellojuradoi (Pozzi), Bathyraja albomaculata, B. brachyurops, B. cousseauae, B. macloviana (Norman), B. magellanica, B. multispinis, B. scaphiops (Norman), Dipturus chilensis (Guichenot), Psammobatis sp. 3, Psammobatis sp. 2.

Locality. Malvinas Islands Shelf, Southwestern Atlantic Ocean.

Reference. Beer et al. (2019).

Comments. Beer et al. (2019) studied these specimens at the molecular rather than the morphological level, without reaching generic or specific identification. Caira et al. (2021) noted that the specimens of Phyllobothriidea gen. sp. found by Beer et al. (2019) could correspond to the genus *Rockacestus*; however, further molecular and morphological studies are necessary to identify them at the specific level. Beer et al. (2019) also pointed out the presence of Phyllobothriidea gen. sp. parasitizing *D. chilensis*. Nevertheless, the distribution of *D. chilesis* is restricted to the Pacific Ocean; therefore, this record is based on a misidentification of the host (Concha et al. 2019).

Order Rhinebothriidea Healy, Caira, Jensen, Webster & Littlewood, 2009 Family Echeneibothriidae de Beauchamp, 1905 Genus *Echeneibothrium* van Beneden, 1850

Echeneibothrium cristinae Franzese, 2022

Type host. Bathyraja cousseauae (Rajiformes: Arhynchobatidae).

Type locality. Isla de los Estados (54°25'S, 65°18'W), Tierra del Fuego Province, Argentina.

Specimens in collections. MACN-Pa No. 734 (holotype); MACN-Pa Nos. 735/1–5, 736/1–23 (paratypes).

Reference. Franzese et al. (2022).

Echeneibothrium multiloculatum Carvajal & Dailey, 1975

Type host. Dipturus chilensis (Rajiformes: Rajidae) (Raja chilensis).

Other host. Dipturus brevicaudatus (Rajiformes: Rajidae).

Type locality. Between Papudo and Talcahuano (between 32°28'S and 37°15'S), Chile.

Other localities. Mar de Ajó (36°34'S, 54°39'W), Mar del Plata (38°05'S, 56°58'W), Quequén (38°35'S, 58°39'W), Buenos Aires Province. San Jorge Gulf (46°13'S, 66°26'W), Santa Cruz Province. Tolhuin (54°29'S, 65°59'W), Río Grande (53°31'S, 67°48'W), Tierra del Fuego Province.

Specimens in collections. USNM No. 1368523 (holotype); USNM No. 1368524 (paratypes); MACN-Pa Nos. 737/1–10, 738, 739, 740/1–8 (vouchers).

GenBank Acc. Nos. MZ594651, MH688748, KY569546, KY569547, KY569548, KY569549.

References. Carvajal and Dailey (1975), Franzese et al. (2022).

Echeneibothrium williamsi Carvajal & Dailey, 1975

Type host. Dipturus chilensis (Rajiformes: Rajidae) (Raja chilensis).
Other host. Dipturus brevicaudatus (Rajiformes: Rajidae).
Type locality. Between Papudo and Talcahuano (between 32°28'S and 37°15'S), Chile.

Other localities. San Jorge Gulf (46°13'S, 66°26'W), Santa Cruz Province. Tolhuin (54°29'S, 65°59'W), Río Grande (53°31'S, 67°48'W), Tierra del Fuego Province.

Puerto Quequén (38°46'S, 57°56'W), Buenos Aires Province (Table 3).

Specimens in collections. USNM No. 1368521 (holotype); USNM No. 1368522 (paratypes); MACN-Pa Nos. 741/1–14, 742/1–4, 743, **773** (vouchers).

GenBank Acc. Nos. MZ594641, MH688742, KY569542, KY569543, KY569544, KY569545.

References. Carvajal and Dailey (1975), Franzese et al. (2022).

Echeneibothrium sp.

Hosts. Bathyraja albomaculata, B. brachyurops, B. cousseauae, B. griseocauda (Norman), B. macloviana, B. multispinis, B. scaphiops (Rajiformes: Arhynchobatidae).

Locality. Malvinas Islands, Southwestern Atlantic Ocean.

Reference. Beer et al. (2019).

Comments. These specimens were studied by Beer et al. (2019) at a molecular rather than morphological level and did not manage to reach an identification at a specific level. Franzese et al. (2022) noted that the specimens of *Echeneibothrium* sp. found in *B. cousseauae* by Beer et al. (2019) at Malvinas Islands could correspond to *E. cristinae*. Considering that the remaining species of *Bathyraja* have not been recorded as hosts for *Echeneibothrium* and that most marine rhinebothriideans show a high degree of specificity to their definitive hosts, Franzese et al. (2022) supposed that some *Echeneibothrium* specimens reported by Beer et al. (2019) could be new species. However, further morphological studies are necessary to identify them at a specific level. Beer et al. (2019) also pointed out the presence of *Echeneibothrium* and *Echeneibothrium* sp. 2 parasitizing *D. chilensis* at Malvinas Islands; however, the distribution of *D. chilesis* is restricted to the Pacific Ocean, i. e. this record has been based on a host misidentification.

Genus Notomegarhynchus Ivanov & Campbell, 2002

Notomegarhynchus navonae Ivanov & Campbell, 2002

Type host. Atlantoraja castelnaui (Rajiformes: Arhynchobatidae).

Type locality. Mar del Plata (38°00'S, 57°33'W), Buenos Aires Province, Argentina.

Other locality. Puerto Quequén (38°46'S, 57°56'W), Buenos Aires Province (Table 3).

Specimens in collections. MACN-Pa No. 404/1 (holotype); MACN-Pa Nos. 404/2–3 (paratypes); USNM No.1387025 (paratypes); MACN-Pa No. 774 (voucher). Reference. Ivanov and Campbell (2002).

Notomegarhynchus shetlandicum (Wojciechowska, 1990)

Pseudanthobothrium shetlandicum Wojciechowska, 1990. Syn.

Type host. Bathyraja eatonii (Rajiformes: Arhynchobatidae). Other host. Bathyraja maccaini (Rajiformes: Arhynchobatidae). Specimens in collections. MZPW No. 1810 (holotype); MZPW No. 1811 (paratypes); BMNH No. 1989.4.19.3 (paratypes).

Type locality. South Shetlands region, Joinville shelf, Elephant Island Shelf, and Admiralty Bay, Antarctica.

References. Wojciechowska (1990b), Ivanov and Campbell (2002), Rocka (2003, 2017).

Genus Pseudanthobothrium Baer, 1956

Pseudanthobothrium notogeorgianum Wojciechowska, 1990

Type host. Amblyraja georgiana (Rajiformes: Rajidae) (Raja georgiana).
Type locality. South Georgia area, South Atlantic Ocean.
Specimens in collections. MZPW No. 1807 (holotype); MZPW Nos. 1808–1809 (paratypes); BMNH No. 1989.4.19.2 (paratypes).
References. Wojciechowska (1990b), Rocka (2003, 2017).

Pseudanthobothrium minutum Wojciechowska, 1991

Type host. Bathyraja eatonii (Rajiformes: Arhynchobatidae).
Type locality. Elephant Island, Antarctica.
Specimens in collections. No specimens were deposited in a public collection.
References. Wojciechowska (1991a), Rocka (2003, 2017).
Comments. Type specimens are in Wojciechowska's personal collection.

Pseudanthobothrium sp.

Host. Amblyraja doellojuradoi (Rajiformes: Rajidae).

Locality. Malvinas Islands, South Atlantic Ocean. **Reference.** Beer et al. (2019).

Comments. Beer et al. (2019) indicated the presence of *Pseudanthobothrium* sp. and *Pseudanthobothrium* sp. 2 parasitizing *A. doellojuradoi* at Malvinas Islands.

Family Rhinebothriidae Euzet, 1953 Genus *Rhinebothrium* Linton, 1890

Rhinebothrium chilensis Euzet & Carvajal, 1973

Type host. Sympterygia lima (Poeppig) (Rajiformes: Arhynchobatidae) (Psammobatis lima).

Other host. Sympterygia bonapartii (Rajiformes: Arhynchobatidae).

Type locality. North coast of Chile.

Other localities. Estuary of Bahía Blanca (38°45'S, 62°15'W), Villa Gesell, Necochea, El Rincón, Buenos Aires Province, Argentina. San Matías Gulf, Río Negro Province, Argentina. San Jorge Gulf, Santa Cruz Province, Argentina. Río de La Plata estuary, Uruguay.

Specimens in collections. MNHNC No. 20005 (holotype); MNHNF Nos. Sb 267, Sb 268 (paratypes).

References. Euzet and Carvajal (1973), Tanzola et al. (1998), Irigoitia et al. (2017).

Genus Scalithrium Ball, Neifar & Euzet, 2003

Scalithrium ivanovae Franzese, 2021

Type host. Atlantoraja platana (Günther) (Rajiformes: Arhynchobatidae).

Type locality. San Matías Gulf (41°11'S, 64°03'W), Río Negro Province, Argentina. **Specimens in collections.** MACN-Pa No. 762 (holotype); MACN-Pa Nos. 763/1–4, 764/1–7, 765/1–3 (paratypes); IPCAS No. C-897 (paratypes).

Reference. Franzese and Ivanov (2021).

Scalithrium kirchneri Franzese & Ivanov, 2021

Type host. Rioraja agassizii (Müller & Henle) (Rajiformes: Arhynchobatidae).

Type locality. Continental shelf waters off San Clemente del Tuyú (36°12'S, 55°20'W), Buenos Aires Province, Argentina.

Other locality. Continental shelf waters off Quequén (39°56'S, 58°20'W), Buenos Aires Province.

Specimens in collections. MACN-Pa No. 757 (holotype); MACN-Pa Nos. 758/1–13, 759, 760/1–3, 761(paratypes); IPCAS No. C-896 (paratypes).

Reference. Franzese and Ivanov (2021).

Genus incertae sedis and other forms with uncertain family allocations

Genus Semiorbiseptum Franzese & Ivanov, 2020

Semiorbiseptum alfredoi Franzese & Ivanov, 2020

Type host. Psammobatis normani McEachran (Rajiformes: Arhynchobatidae).

Type locality. Coastal waters off Mar de Ajó (36°34'S, 54°39'W), Buenos Aires Province, Argentina.

Other localities. Coastal waters off Pinamar (37°12'S, 54°53'W), Buenos Aires Province. Caleta Olivia (46°23'S, 64°20'W), Santa Cruz Province.

Specimens in collections. MACN-Pa No. 706 (holotype); MACN-Pa Nos. 707/1–5, 708/1–3, 709, 710, 711/1–2 (paratypes); IPCAS No. C-837/1 (paratypes). **Reference.** Franzese and Ivanov (2020b).

Semiorbiseptum mariae Franzese & Ivanov, 2020

Type host. Psammobatis rudis Günther (Rajiformes: Arhynchobatidae).

Other host. Psammobatis normani (Rajiformes: Arhynchobatidae).

Type locality. Coastal waters off Isla de los Estados (54°30'S, 65°13'W), Tierra del Fuego Province, Argentina.

Other localities. Coastal waters off Río Grande (53°34'S, 66°32'W), Tierra del Fuego Province. Coastal waters off Miramar (39°34'S, 56°16'W), Buenos Aires Province.

Specimens in collections. MACN-Pa No. 701 (holotype); MACN-Pa Nos. 702/1–4, 703, 704/1–13, 705 (paratypes); IPCAS No. C-836/1 (paratypes).

Reference. Franzese and Ivanov (2020b).

Rhinebothriidea gen. sp.

Hosts. *Psammobatis* sp. 1, *Psammobatis* sp. 2, *Psammobatis* sp. 3 (Rajiformes: Arhynchobatidae).

Locality. Malvinas Islands, Southwestern Atlantic Ocean.

References. Beer et al. (2019).

Comments. These cestode specimens were studied by Beer et al. (2019) at a molecular rather than morphological level.

Order "Tetraphyllidea" van Beneden, 1850 Clade 2 Genus *Anthobothrium* van Beneden, 1850

Anthobothrium galeorhini Suriano, 2002

Type host. *Galeorhinus galeus* (Linnaeus) (Carcharhiniformes: Triakidae).
Type locality. Puerto Madryn (42°43'S, 65°00'W), Chubut Province, Argentina.
Specimens in collections. MLP No. 4942 (holotype); MNHN No. 37G (paratype).
Reference. Suriano (2002).

Anthobothrium sp.

Host. Bathyraja arctowskii (Rajiformes: Arhynchobatidae) (Bathyraja sp. 2).

Locality. Drake Strait near King George Island and environs of Elephant Island, Antarctica.

Reference. Wojciechowska (1991a, b).

Comments. Specimens remain in Wojciechowska's personal collection. Regarding host identification, Stehmann et al. (2021) assigned specimens of *Bathyraja* sp. 2 to *Bathyraja arctowskii*, a wide-ranging, circum-Antarctic species locally common in the Atlantic sector of the Southern Ocean.

Family Calliobothriidae Perrier, 1897 Genus *Calliobothrium* van Beneden, 1850

Calliobothrium australis Ostrowski de Núñez, 1973

Type host. Mustelus schmitti (Carcharhiniformes: Triakidae).

Type locality. Mar del Plata, Buenos Aires Province, Argentina.

Other locality. Puerto Quequén (38°32'S, 58°42'W), Provincia de Buenos Aires.

Specimens in collections. MACN No. 409/1 (holotype); MACN Nos. 405/1–4 (vouchers); USNPC No. 92398 (voucher).

GenBank Acc. Nos. KP128030, KP128031.

References. Ostrowski de Núñez (1973), Ivanov and Brooks (2002), Alarcos et al. (2006).

Comments. Ivanov and Brooks (2002) redescribed *C. australis* based on the material studied originally by Ostrowski de Núñez (1973), who considered this species a subspecies of *C. verticillatum*.

Genus Symcallio Bernot, Caira & Pickering, 2015

Symcallio barbarae (Ivanov & Brooks, 2002)

Calliobothrium barbarae Ivanov & Brooks, 2002. Syn.

Type host. Mustelus schmitti (Carcharhiniformes: Triakidae).

Type locality. Puerto Quequén (38°32'S, 58°42'W), Buenos Aires Province, Argentina.

Other locality. Mar del Plata (38°00'S, 57°33'W), Buenos Aires Province.

Specimens in collections. MACN No. 410/1 (holotype); MACN No. 410/2 (paratypes); USNPC No. 92399 (paratypes).

GenBank Acc. Nos. KP128023.

References. Ivanov and Brooks (2002), Alarcos et al. (2006), Bernot et al. (2015). Comments. Specimens of *Calliobothrium eschrichti* van Beneden, 1850, identified by Ostrowski de Núñez (1973), were considered by Ivanov and Brooks (2002) as *C. barbarae*. Later, Bernot et al. (2015) transferred *C. barbarae* to the new genus *Symcallio*.

Symcallio lunae (Ivanov & Brooks, 2002)

Calliobothrium lintoni Euzet, 1954, Calliobothrium lunae Ivanov & Brooks, 2002. Syns.

Type host. Mustelus schmitti (Carcharhiniformes: Triakidae).
Type locality. La Paloma (34°40'S, 54°10'W), Rocha, Uruguay.
Other locality. Mar del Plata (38°00'S, 57°33'W), Buenos Aires Province.
Specimens in collections. MACN No. 411/1 (holotype); MACN Nos. 411/2–5 (paratypes); USNPC No. 92400 (paratypes).
References. Ivanov and Brooks (2002), Alarcos et al. (2006), Bernot et al. (2015).

Clade 4 Genus *Caulobothrium* Baer, 1948

Caulobothrium ostrowskiae Brooks, Mayes & Thorson, 1981

Type host. *Myliobatis goodei* (Myliobatiformes: Myliobatidae).

Type locality. Río de La Plata estuary, near Montevideo, Uruguay.

Specimens in collections. USNM No. 75726 (holotype); USNM No. 75727

(paratype), Univ. Nebraska State Museum No. 21004 (paratype).

Reference. Brooks et al. (1981).

Caulobothrium uruguayense Brooks, Mayes & Thorson, 1981

Type host. Probably *Myliobatis goodei* (Myliobatiformes: Myliobatidae) (*Mylioba-tis uruguayensis*).

Type locality. Río de la Plata estuary, Uruguay.

Specimens in collections. USNM No. 75724 (holotype); USNM No. 75725 (paratype); Univ. Nebraska State Museum No. 21002.

Reference. Brooks et al. (1981).

Comments. *Caulobothrium uruguayense* was originally described by Brooks et al. (1981) from *Myliobatis uruguayensis*. However, this batoid's name is invalid. Considering original article's title, the type host of this cestode species is probably *M. goodei*.

Order Trypanoryncha Diesing, 1863 Suborder Trypanobatoida Olson, Caira, Jensen, Overstreet, Palm & Beveridge, 2010 Superfamily Eutetrarhynchoidea Guiart, 1927 Genus *Dollfusiella* Campbell & Beveridge, 1994

Dollfusiella acuta Menoret & Ivanov, 2015

Type host. Sympterygia acuta Garman (Rajiformes: Arhynchobatidae).

Other hosts. *Atlantoraja castelnaui*, *Atlantoraja platana*, *Sympterygia bonapartii* (Rajiformes: Arhynchobatidae).

Type locality. Off Punta Mejillón (41°11'S, 64°03'W), Río Negro Province, Argentina. **Other localities.** off Puerto Quequén (38°37'S, 58°53'W), off Río Colorado

(39°55'S, 62°03'W), Bahía Blanca, Buenos Aires Province. San Matías Gulf, Río Negro/Chubut Provinces.

Specimens in collections. MACN-Pa No. 575/1 (holotype); MACN-Pa Nos. 575/2–4 (paratypes); IPCAS No. C-700 (paratypes).

References. Menoret and Ivanov (2015), Irigoitia et al. (2017).

Dollfusiella taminii Menoret & Ivanov, 2014

Type host. Psammobatis bergi Marini (Rajiformes: Arhynchobatidae).

Type locality. Puerto Quequén (38°37'S, 58°53'W), Buenos Aires Province, Argentina.

Other locality. off Necochea (38°46'S, 57°56'W), Buenos Aires Province.

Specimens in collections. MACN-Pa No. 544/1 (holotype); MACN-Pa Nos. 544/2–4 (paratypes); IPCAS No. C-661 (paratypes).

Reference. Menoret and Ivanov (2014).

Dollfusiella vooremi (São Clemente & Gomes, 1989)

Eutetranychus vooremi São Clemente & Gomes, 1989. Syn.

Type host. *Mustelus canis* (Mitchill) (Carcharhiniformes: Triakidae).
Other hosts. *Mustelus schmitti* (Carcharhiniformes: Triakidae).
Type locality. Southern Brazilian coast (30°40'S, 53°20'W–50°40'W).
Other localities. Off San Antonio Oeste (40°50'S, 64°58'W), Río Negro Prov-

ince. Off Mar del Plata (38°00'S, 57°33'W), Buenos Aires Province.

Specimens in collections. CHIOC No. 32.566e (holotype); CHIOC Nos. 32.566a-d (paratypes); MACN-Pa Nos. 543/1–2 (vouchers).

References. São Clemente and Gomes (1989), Tanzola et al. (1998), Alarcos et al. (2006), Menoret and Ivanov (2014).

Genus Mecistobothrium Heinz & Dailey, 1974

Mecistobothrium oblongum Menoret & Ivanov, 2015

Type host. Myliobatis goodei (Myliobatiformes: Myliobatidae).

Typelocality. OffPunta Mejillón (41°11'S, 64°03'W), Río Negro Province, Argentina. **Specimens in collections.** MACN-Pa No. 576/1 (holotype); MACN-Pa Nos. 576/2–3 (paratypes).

Reference. Menoret and Ivanov (2015).

Genus Parachristianella Dollfus, 1946

Parachristianella damiani Menoret & Ivanov, 2014

Type host. *Myliobatis goodei* (Myliobatiformes: Myliobatidae).

Type locality. Playa Punta Negra (38°36'S, 58°48'W), Necochea, Buenos Aires Province, Argentina.

Specimens in collections. MACN-Pa No. 545/1 (holotype); MACN-Pa No. 545/2 (paratypes), IPCAS No. C-660 (paratypes).

Reference. Menoret and Ivanov (2014).

Superfamily Tentacularoidea Poche, 1926 Genus *Heteronybelinia* Palm, 1999

Heteronybelinia mattisi Menoret & Ivanov, 2012

Type host. Sympterygia bonapartii (Rajiformes: Arhynchobatidae).

Typelocality. Puerto Quequén (38°37'S, 58°53'W), Buenos Aires Province, Argentina. **Specimens in collections.** MACN-Pa No. 537/1 (holotype); MACN-Pa Nos. 537/2–4 (paratypes); NHMUK Nos. 2012.9.11.1–2 (paratypes).

Reference. Menoret and Ivanov (2012a).

Comments. Larval stages (plerocercoids) of *H. mattisi* were reported from teleosts from coastal waters off Buenos Aires Province (Menoret and Ivanov 2012a).

Suborder Trypanoselachoida Olson, Caira, Jensen, Overstreet, Palm & Beveridge, 2010 Superfamily Lacistorhynchoidea Guiart, 1927 Genus *Grillotia* Guiart, 1927

Grillotia (Christianella) carvajalregorum Menoret & Ivanov, 2009

Progrillotia dollfusi Carvajal & Rego, 1983, Grillotia (Progrillotia) dollfusi (Carvajal & Rego, 1983) Palm 2004, Grillotia carvajalregorum Menoret & Ivanov, 2009. Syns.

Type host. Cynoscion striatus (Cuvier) (Perciformes: Sciaenidae).

Other host. Squatina guggenheim (Squatiniformes: Squatinidae).

Type locality. Coast of Brazil.

Other locality. Puerto Quequén (38°37'S, 58°53'W), Buenos Aires Province.

Specimens in collections. CHIOC No. 32.018a (holotype); CHIOC Nos. 32.018b–d (paratypes); MACN-Pa Nos. 487/1–2 (vouchers).

References. Carvajal and Rego (1983), Menoret and Ivanov (2009, 2012b), Beveridge and Campbell (2010).

Comments. Grillotia (C.) carvajalregorum was originally described from plerocercoids from C. striatus at coasts off Brazil (Carvajal and Rego 1983). Later, Menoret and Ivanov (2009) described adults of G. (C.) carvajalregorum from S. guggenheim at coasts of Argentina. This species was found in a wide range of teleost fishes (Menoret and Ivanov 2009, 2012b).

Grillotia (Grillotia) patagonica Menoret & Ivanov, 2012

Type host. Psammobatis rudis (Rajiformes: Arhynchobatidae).

Other host. Sympterygia bonapartii (Rajiformes: Arhynchobatidae).

Type locality. Off Puerto San Julián (48°59'S, 65°15'W), Santa Cruz Province, Argentina.

Other locality. San Jorge Gulf, Santa Cruz Province.

Specimens in collections. MACN-Pa No. 534/1 (holotype); MACN-Pa Nos. 534/2–4 (paratypes).

References. Menoret and Ivanov (2012b), Irigoitia et al. (2017).

Comments. *Grillotia* (*G.*) *patagonica* was originally described from adults and plerocercoids caught at different localities along the Patagonian Shelf of Argentina (Menoret and Ivanov 2012b). Other reports in the area include this cestode in *S. bonapartii* at San Jorge Gulf (Irigoitia et al. 2017).

Grillotia sp.

Hosts. Amblyraja doellojuradoi, Bathyraja brachyurops, B. cousseauae, B. griseocauda, Bathyraja magellanica, Dipturus chilensis, Psammobatis sp. 2, Psammobatis sp. 3.

Locality. Malvinas Islands Shelf, Southwestern Atlantic Ocean.

Reference. Beer et al. (2019).

Comments. These specimens were studied by Beer et al. (2019) at a molecular rather than a morphological level, without reaching a specific identification. Beer et al. (2019) noted the presence of *Grillotia* sp. parasitizing *D. chilensis*. However, the distribution of *D. chilesis* is restricted to the Pacific Ocean. Therefore, this record was based on a misidentified host (Concha et al. 2019).

Species incertae sedis (at the ordinal level)

Phyllobothrium myliobatidis Brooks, Mayes & Thorson, 1981

Type host. Myliobatis goodei (Myliobatiformes: Myliobatidae).

Type locality. Río de la Plata estuary, Uruguay.

Specimens in collections. USNM No. 1371266 (holotype); USNM No. 1371267 (paratype).

Reference. Brooks et al. (1981).

Comments. Ruhnke (2011) considers *P. myliobatidis* as a possible member of the order Rhinebothriidea.

Host-parasite checklist: chimaeras and batoids

Order Chimaeriformes

Family Callorhinchidae Callorhinchus callorynchus Gyrocotyle maxima (Gyrocotylidea) Gyrocotyle rugosa (Gyrocotylidea)

Order Myliobatiformes

Family Myliobatidae

Myliobatis goodei

Aberrapex arrhynchum (Lecanicephalidea) Aberrapex ludmilae (Lecanicephalidea) Aberrapex sanmartini (Lecanicephalidea) Acanthobothrium sp. (Onchoproteocephalidea) Caulobothrium ostrowskiae ("Tetraphyllidea") Caulobothrium uruguayense ("Tetraphyllidea") Halysioncum megacanthum (Diphyllidea) Mecistobothrium oblongum (Trypanorhyncha)

Parachristianella damiani (Trypanorhyncha) Phyllobothrium myliobatidis (Incertae sedis) *Phyllobothrium* sp. (Phyllobothriidea) Myliobatis ridens Aberrapex vitalemuttiorum (Lecanicephalidea) **Order Rajiformes** Family Arhynchobatidae Atlantoraja castelnaui Acanthobothrium marplatensis (Onchoproteocephalidea) Dollfusiella acuta (Trypanorhyncha) Notomegarhynchus navonae (Rhinebothriidea) Atlantoraja platana Dollfusiella acuta (Trypanorhyncha) Scalithrium ivanovae (Rhinebothriidea) Bathyraja albomaculata *Echeneibothrium* sp. (Rhinebothriidea) Rockacestus conchai (Phyllobothriidea) Phyllobothriidea gen. sp. (Phyllobothriidea) Bathyraja arctowskii Anthobothrium sp. ("Tetraphyllidea") Rockacestus arctowskii (Phyllobothriidea) Bathyraja brachyurops *Echeneibothrium* sp. (Rhinebothriidea) Grillotia sp. (Trypanorhyncha) Guidus argentinense (Phyllobothriidea) Phyllobothriidea gen. sp. (Phyllobothriidea) Bathyraja cousseauae Acanthobothrium sp. (Onchoproteocephalidea) Echeneibothrium cristinae (Rhinebothriidea) *Echeneibothrium* sp. (Rhinebothriidea) Grillotia sp. (Trypanorhyncha) Phyllobothriidea gen. sp. (Phyllobothriidea) Bathyraja eatonii Guidus antarcticus (Phyllobothriidea) Notomegarhynchus shetlandicum (Rhinebothriidea) *Onchobothrium antarcticum* (Onchoproteocephalidea) *Pseudanthobothrium minutum* (Rhinebothriidea) Rockacestus siedleckii (Phyllobothriidea) Bathyraja griseocauda *Echeneibothrium* sp. (Rhinebothriidea) Grillotia sp. (Trypanorhyncha) Bathyraja maccaini Guidus antarcticus (Phyllobothriidea)

Notomegarhynchus shetlandicum (Rhinebothriidea) Rockacestus rakusai (Phyllobothriidea) Bathyraja macloviana *Echeneibothrium* sp. (Rhinebothriidea) Phyllobothriidea gen. sp. (Phyllobothriidea) Bathyraja magellanica Acanthobothrium carolinae (Onchoproteocephalidea) Acanthobothrium sp. (Onchoproteocephalidea) Grillotia sp. (Trypanorhyncha) Guidus francoi (Phyllobothriidea) Guidus magellanicus (Phyllobothriidea) Phyllobothriidea gen. sp. (Phyllobothriidea) Bathyraja multispinis *Echeneibothrium* sp. (Rhinebothriidea) *Guidus* sp. (Phyllobothriidea) Phyllobothriidea gen. sp. (Phyllobothriidea) Bathyraja scaphiops Echeneibothrium sp. (Rhinebothriidea) Phyllobothriidea gen. sp. (Phyllobothriidea) Psammobatis bergi Dollfusiella taminii (Trypanorhyncha) Psammobatis normani Semiorbiseptum alfredoi (Rhinebothriidea) Semiorbiseptum mariae (Rhinebothriidea) Psammobatis rudis Grillotia (G.) patagonica (Trypanorhyncha) Semiorbiseptum mariae (Rhinebothriidea) Psammobatis sp. 1 Rhinebothriidea gen. sp. (Rhinebothriidea) Psammobatis sp. 2 Grillotia sp. (Trypanorhyncha) Phyllobothriidea gen. sp. (Phyllobothriidea) Rhinebothriidea gen. sp. (Rhinebothriidea) Psammobatis sp. 3 Grillotia sp. (Trypanorhyncha) Phyllobothriidea gen. sp. (Phyllobothriidea) Rhinebothriidea gen. sp. (Rhinebothriidea) Rioraja agassizii Scalithrium kirchneri (Rhinebothriidea) Sympterygia acuta Dollfusiella acuta (Trypanorhyncha) Sympterygia bonapartii Dollfusiella acuta (Trypanorhyncha) Grillotia (G.) patagonica (Trypanorhyncha)

Heteronybelinia mattisi (Trypanorhyncha) *Phyllobothrium* sp. (Phyllobothriidea) *Rhinebothrium chilensis* (Rhinebothriidea)

Family Rajidae

Amblyraja doellojuradoi

Grillotia sp. (Trypanorhyncha) Phyllobothriidea gen. sp. (Phyllobothriidea) *Pseudanthobothrium* sp. (Rhinebothriidea)

Amblyraja georgiana

Echinobothrium acanthocolle (Diphyllidea) *Pseudanthobothrium notogeorgianum* (Rhinebothriidea) *Rockacestus georgiensis* (Phyllobothriidea)

Dipturus brevicaudatus

Acanthobothrium domingae (Onchoproteocephalidea) Echeneibothrium multiloculatum (Rhinebothriidea) Echeneibothrium williamsi (Rhinebothriidea)

Order Rhinopristiformes

Family Trygonorrhinidae

Zapteryx brevirostris

Acanthobothrium zapterycum (Onchoproteocephalidea) Acanthobothrium sp. (Onchoproteocephalidea) Halysioncum pigmentatum (Diphyllidea) Phyllobothrium sp. (Phyllobothriidea)

Order Torpediniformes

Family Narcinidae

Discopyge tschudii

Acanthobothrium stefaniae (Onchoproteocephalidea)

Host-parasite checklist: sharks

Order Carcharhiniformes Family Carcharhinidae *Carcharhinus brachyurus Cathetocephalus australis* (Cathetocephalidea) Family Triakidae *Galeorhinus galeus Anthobothrium galeorhini* ("Tetraphyllidea") *Mustelus fasciatus Orygmatobothrium juani* (Phyllobothriidea) *Mustelus schmitti Calliobothrium australis* ("Tetraphyllidea") *Coronocestus notoguidoi* (Diphyllidea) *Dollfusiella vooremi* (Trypanorhyncha) Orygmatobothrium schmitti (Phyllobothriidea) Symcallio barbarae ("Tetraphyllidea") Symcallio lunae ("Tetraphyllidea") Order Hexanchiformes Family Hexanchidae Notorynchus cepedianus Crossobothrium antonioi (Phyllobothriidea) Crossobothrium pequeae (Phyllobothriidea) Order Squatiniformes Family Squatinidae Squatina guggenheim Grillotia (C.) carvajalregorum (Trypanorhyncha) Paraberrapex atlanticus (Lecanicephalidea)

Geographical distribution of the cestode orders

The tapeworm orders reviewed in this study show different geographical ranges. These distributions are represented in Fig. 1A for the Phyllobothriidea, Fig. 1B for the Onchoproteocephalidea, Fig. 2A for the Rhinebothriidea, Fig. 2B for "Tetraphyllidea" and Gyrocotylidea, Fig. 3A for the Diphyllidea and Lecanicephalidea, and Fig. 3B for Trypanorhyncha. Geographical sites of the order Cathetocephalidea could not be rep-



Figure 1. Distribution of representatives of the orders Phyllobothriidea and Onchoproteocephalidea **A** order Phyllobothriidea **B** order Onchoproteocephalidea. Insets show records in the sub-Antarctic and Antarctic regions.


Figure 2. Distribution of representatives of the orders Rhinebothriidea, "Tetraphyllidea" and Gyrocotylidea **A** order Rhinebothriidea **B** red dot Orders "Tetraphyllidea" and black star Gyrocotylidea. Insets show records in the sub-Antarctic and Antarctic regions.

resented since the only existing record reports *Cathetocephalus australis* in Argentina, without specifying the locality or coordinate.

The orders with the broadest geographic distributions are Onchoproteocephalidea (Fig. 1B) and Rhinebothriidea (Fig. 2A), with representatives in the Río de la Plata estuary, along the Argentine Sea, and the southern islands. In addition, the phyllobo-thriideans (Fig. 1A) show a similar distribution, although without records between the 40°S–47°S latitudes, in the central region of the Argentine Sea. On the other hand, the cestodes with the narrowest distribution are those of the order Gyrocotylidea (Fig. 2B), being recorded only in two locations in the Buenos Aires Province.

Discussion

Cestode diversity

Cestodes as parasites of chondrichthyans have been mostly recorded in the Northern Hemisphere (Caira et al. 2022). However, reports in southern latitudes have remarkably increased in the last decades due to focused sampling efforts in the area (Menoret and Ivanov 2012a, b, 2014, 2015, 2021; Pickering and Caira 2012; Caira et al. 2013a; Abbott and Caira 2014; Mutti and Ivanov 2016; Menoret et al. 2017; Franzese and



Figure 3. Distribution of the orders Diphyllidea, Lecanicephalidea and Trypanorhyncha **A** black star Diphyllidea and red dot Lecanicephalidea **B** order Trypanorhyncha. Inset shows records in the sub-Antarctic region.

Ivanov 2018, 2020a, b, 2021; Palm et al. 2019; Oosthuizen et al. 2021; Franzese et al. 2022; Van Der Spuy et al. 2022). The present annotated checklist comprises 57 valid cestode species of 28 genera in nine orders, registered in the Río de la Plata estuary, Southwestern Atlantic off Argentina and the surrounding waters off Antarctica. The orders Phyllobothriidea and Rhinebothriidea show the highest richness at the specific level, with 13 and 12 valid species, respectively; they are followed by the order Trypanorhyncha, with a total of eight species. In addition, the list includes cestodes without an identification up to the generic or the specific level, as in the case of the Onchoproteocephalidea (i.e., *Acanthobothrium* sp.), Phyllobothriidea (i.e., Genus sp., *Guidus* sp., *Phyllobothrium* sp.), Rhinebothriidea (i.e., *Genus* sp., *Echeneibothrium* sp., *Pseudanthobothrium* sp.) and Trypanorhyncha (i.e., *Grillotia* sp.) (Ostrowski de Núñez 1971; Brooks et al. 1981; Beer et al. 2019). Several of the comments made in this work are intended to aid in future morphological and molecular studies addressing the lower taxonomic resolution of these entities.

In view of the high degree of specificity of adult cestodes to their marine hosts (Reyda and Marques 2011; Caira and Jensen 2017) and that only 33% (33/100) of marine chondrichthyans in the study area have been sampled for cestodes (Table 1),

this fauna is probably underestimated. We can speculate that more than 60 species of cestodes have not yet been discovered in this area. Future taxonomic surveys will be essential to increase the knowledge of the diversity of these parasites in the region.

Taxonomic resolution

The poor taxonomic resolution of several taxa listed in the present study is probably a consequence of the lack of use of multiple tools to develop an integrative taxonomy, such as morphological and molecular studies used as evidence to delineate species boundaries. Some of the previous works cited here lacked modern morphological tools, e.g., scanning (SEM) and transmission electron microscopy (TEM) and the molecular tools necessary for the development of an integrative approach (Ostrowski de Núñez 1971; Brooks et al. 1981). In contrast, the recent work by Beer et al. (2019) recorded in the Argentine Sea numerous specimens of cestodes belonging to different orders but without achieving a specific identification for many of them, using molecular sequences as the only identification tool. The development and use of molecular tools have allowed the detection of cryptic species in some cestode groups (Scholz et al. 2014; Choudhury and Scholz 2020). Of the 57 valid species recorded in this work, only seven have been sequenced, so it is still unknown whether cryptic species will be discovered in this particular region. In addition to molecular sequences, the use of modern morphological tools, such as SEM and TEM, might be helpful in discovering new characters that complement traditional morphological studies, which could contribute to solve species identification problems (Franzese et al. 2023; Mutti et al. 2023). The development of the integrative taxonomy, including the use of all available tools, will allow resolving the poor taxonomic resolution observed in several taxa registered in our study area.

Host association

Rajiform batoids represent the most frequent hosts for adult cestodes in the study area. In particular, the family Arhynchobatidae has been found parasitized by 42% (24/57) of the recorded cestode species (Ivanov and Campbell 1998b, 2002; Rocka 2003; Menoret and Ivanov 2012a, 2014, 2021; Irigoitia et al. 2017; Franzese and Ivanov 2020a, b; Caira et al. 2021; Franzese et al. 2022). This percentage could be higher since many species of arhynchobatids of the region, such as *Atlantoraja cyclophora* (Regan), *Bathyraja meridionalis* Stehmann, *Bathyraja papilionifera* Stehmann, *Bathyraja schroederi* (Krefft), *Psammobatis extenta* (Garman), *Psammobatis lentiginosa* McEachran, *Psammobatis parvacauda* McEachran, *Psammobatis rutrum* Jordan, and *Psammobatis scobina* (Philippi), have not yet been sampled for cestodes. The association between tapeworms and this host family is not surprising if we consider that arhynchobatids have the highest species number, with 31% (31/100) of the chondrichthyan fauna recorded in the area (Table 1) (Menni and Lucifora 2007; Froese and Pauly 2022). Upcoming studies should focus on sampling arhyncobatids that have not yet been reported as hosts for tapeworms.

Considering that the major number of cestode species from this checklist are hosted by the myliobatiform *Myliobatis goodei* (Brooks et al. 1981; Ivanov and Campbell 1998a; Menoret and Ivanov 2014, 2015; Menoret et al. 2017), it would be interesting to sample *M. freminvillei* Lesueur, the only species of myliobatid that has not been yet examined for cestodes in the region. On the other hand, only 13% (6/45) of the species of sharks have been reported as hosts in this area (Table 1). Host species with a relatively low occurrence or a particular bathymetric distribution are likely to host an undiscovered and exciting cestode fauna.

More collecting efforts are necessary to conclude if this data reflects the actual biodiversity of cestodes in the different groups of chondrichthyans or is a result of a bias in sampling. Although this list shows the substantial advances in taxonomical surveys in the last decades, expanding the number of sampled hosts is essential to increase the knowledge of the current cestode fauna of chondrichthyans in the region.

Studied area and newly collected material

Five species of cestodes have been recorded in new localities of the Southwestern Atlantic Ocean (Table 3). New material (voucher) identified, processed, and deposited in the MACN parasitological collection corresponds to three onchoproteocephalideans (i.e., *Acanthobothrium domingae*, *A. marplatensis*, *A. stefaniae*) and two rhinebotriideans (i.e., *Echeneibothrium williamsi*, *Notomegarhynchus navonae*). One of these records has extended until the Buenos Aires Province the northern limit of the known geographic distribution in the Argentine Sea of *E. Williamsi*, which, prior to this work, ranged from Santa Cruz Province to Tierra del Fuego Province (Franzese et al. 2022). The remaining new records have added new localities within the province of Buenos Aires for *A. domingae*, *A. marplatensis*, *A. stefaniae*, and *N. navonae*. Previously, these four species had been reported off Buenos Aires, although in different locations (Ivanov and Campbell 1998b, 2002; Franzese and Ivanov 2018, 2020a).

Several of the original descriptions of cestode species are based on material collected from a single locality. However, this probably reflects the absence of a more exhaustive sampling. The present checklist shows that about half of the species included in this region have additional localities. Among these, *Rhinebothrium chilensis* and *Echeneibothrium williamsi* show the highest number with 7 and 6 localities, respectively (Tanzola et al. 1998; Irigoitia et al. 2017). It is likely that as the intensity of sampling increases, new localities will be discovered for several known cestode species.

The localities with the most significant number of cestodes species are Puerto Quequén and Mar del Plata, with 17 and 11 species reported to date, respectively. A strong sampling effort could explain these numbers since both sites are commercial ports from the Buenos Aires Province close to the facilities of the main Argentinean research taxonomic cestodes groups (Luque and Poulin 2007; Randhawa and Poulin 2019).

Conclusions

Some difficulties concerning the understanding of chondrichthyan cestode diversity are:

1) many works have a poor taxonomic resolution or are outdated, with incomplete drawings and without the use of modern tools such as transmission electron microscopy, scanning electron microscopy and molecular approaches;

2) the existence of cryptic species underestimates the actual number of cestodes;

3) less than half of the marine chondrichthyans have been examined for cestodes in the area covered in this work.

A modern taxonomic approach for future characterizations should be made by combining descriptive tools (e.g., TEM and SEM, molecular data, histological sections, and histochemical techniques). It would also be desirable that all the voucher material could be available in public parasitological collections to facilitate its study to the entire community of taxonomists. Regarding sampling effort, it is likely that the higher the number of chondrichthyans examined in parasitological surveys, the higher the number of parasite-host associations will be identified. We have critically compiled as much detailed information as possible including valuable comments, providing a complete list of references and information from the deposited material. We hope this list may help future studies and contributes to correctly estimating the cestode biodiversity that inhabits this underexplored region of the Southern Hemisphere.

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REVIEW ARTICLE



A zoogeographical analysis of true bugs (Insecta, Heteroptera) from Uzbekistan

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Abstract

The purpose of this study is to perform a zoogeographic analysis of terrestrial true bugs (Heteroptera) in the Lower Amudarya Territory, Uzbekistan. According to the findings of a literature review, there are 149 species of terrestrial hemipterans in the Territory. All hemipteran species, with the possible exception of five, have most likely been misidentified. Until now, reliable information on the zoogeography of true bug species in Uzbekistan's north-western region has not been published. The composition of species, diversity, and the proportion of endemism vary greatly across the country's zoogeographic regions. The Heteroptera fauna of the Khorezm and Karakalpakstan can be divided into four groups: most species belonging to the Palaearctic region, with 125 species constituting 83.89% of the fauna; the second group of Holarctic origin is characterized by no more than ten species, which constitutes 6.71%; the third consists of endemics, 13 species or 8.72%; and one species (0.67%) is cosmopolitan. Much more research is needed to investigate distributions in a more northern climate. The introduction of invasive Heteroptera to the north-western part of Uzbekistan will increase and deserves further consideration.

Keywords

Abundance, distribution, faunistics, geography range, Karakalpakstan, Khorezm, Lower Amudarya, occurrence

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Introduction

Heteroptera or true bugs are a large group with more than 40,000 species in approximately 50 families distributed across the world (Weirauch and Schuh 2011; Henry 2017a). In Russia, 760 species in 285 genera, and 35 families, are recorded (Vinokurov et al. 2010), however, more than 1250 species are distributed in Central Asia (Esenbekova 2013), and 700 species of true bugs are distributed in Uzbekistan (Animal World of Uzbekistan 2023).

The study of the fauna of true bugs by Central Asia region has been occurring for more than 170 years (Saprykin 2013). Many individuals have studied regional true bugs from 1995–2013 using the large, published Catalogue of Palaearctic Heteroptera (Catalogue of Palaearctic true bugs 2013).

The geographical distribution of Heteroptera from around the world has always been of interest to researchers (Latreille 1810; Leach 1815; Panizzi and Grazia 2015; Schuh and Weirauch 2020). Many research papers have been published recently, including Chandra and Kushwaha (2013); Samra et al. (2015); Vinokurov et al. (2015); Yasunaga (2016); Drapolyuk (2017); Henry (2017b); Oh et al. (2017); Kim and Jung (2018); Kuzhuget and Vinokurov (2018); Gapon (2019); Yazici (2020); Gandjaeva (2011, 2012a, b, 2020); Gandjaeva and Abdullaeva (2022a, b); Gandjaeva and Allabergenova (2022); Gandjaeva et al. (2019, 2020a, b, c, d, e, 2021, 2022a, b, c); Abdullaeva (2022); Yusupova et al. (2022); Iskandarov et al. (2022).

Since the second half of the 19th century, new descriptions of Central Asian species have been published regularly in the works of Yakovlev (1890); Oshanin (1891) and others. These researchers conducted route surveys in the Fergana Valley, Turkestan Ridge, Alay Range, and Alay Valley, as well as in Samarkand and Djizzakh. Approximately 384 species of true bugs were identified during expeditions, and their zoogeography was studied in Central Asia by prominent zoologists such as Oshanin (1891), who was the first scientist to investigate Heteropteran zoogeography and listed more than 530 species. In the 21st century, many American scientists studied regional Heteroptera including Rider (2006, 2016); Hoebeke and Carter (2003); Bundy and McPherson (2018); Schuh and Weirauch (2020).

The literature on the fauna of terrestrial true bugs in different habitats of the Republic of Uzbekistan is meager. This lack of study also includes true bugs of Central Asia, mainly in the southern regions, which cover the territories of Samarkand, Bukhara, Tashkent, Andijan, Fergana, Kashkadarya, and Surkhandarya.

The purpose of the current paper is to explain database entries for the Lower Amudarya Heteroptera species, including brief geographic histories and original references. Every database should be a living document, with the ability to track changes regularly. Additional information on newly studied species is being added continuously (Gandjaeva 2011, 2012a, b, 2020; Gandjaeva et al. 2019, 2020a, b, c, d, e, 2021, 2022a, b, c; Abdullaev et al. 2020a, b; Allabergenova and Gandzhaeva 2022; Gandjaeva and Abdullaeva 2022a, b; Gandjaeva and Allabergenova 2022; Iskandarov et al. 2022; Yusupova and Gandjaeva 2022; Yusupova et al. 2022). The goals of this study include classifying species ranges and conducting a zoogeographical analysis of the nation's actual true bug fauna, as well as determining species compositions and distributions in various belts of the Khorezm region and Karakalpakstan Republic.

Materials and methods

The study was conducted in a lowland area in the northwestern part of Uzbekistan along the lower sections of the Amudarya River: between 60' and 61' longitude and 41' and 42' latitude, at an altitude of 113–138 m above sea level. The vegetative cycle of plants lasts 200–210 days. The climate is continental, with an average annual precipitation of 80–90 mm, and average temperature ranges from -5 °C in January to 40 °C in July. The climate has been changing, and the temperature has risen in summer, reaching 50 °C in July (Gandjaeva 2019; Abdullaev et al. 2022; Ruzmetov et al. 2022). The usual alkali soils are meadow, meadow–marsh, and marsh–sandy. The area is located in the steppe zone, as well as in the southern portion of the Aral Sea and the western part of the Khorezm oasis. The historic Amudarya delta is made up of river sediments. Sand can be found on the sections connecting with Karakum in the west and southwest. Minerals include limestone, sand, clay, and other building materials (Khamraev 2003).

For the analysis, we used zoogeographical categories of the heteropteran species that had been recorded earlier. Approximately 180 specimens of Heteroptera indexed in the territory of the Lower Amudarya River and were identified to 149 species in 89 genera, and two infraorders. These species were deposited in the Zoological collections of the Zoology Institute (**ZIN**) of the Academy of Sciences of the Republic of Uzbekistan.

The study was carried out between 2007 and 2020 (see Gandjaeva 2011, 2012a, b, 2020; Gandjaeva et al. 2019, 2020a, b, c, d, e, 2021, 2022a, b, c; Abdullaev et al. 2020a, b; Allabergenova and Gandzhaeva 2022; Gandjaeva and Abdullaeva 2022a, b; Gandjaeva and Allabergenova 2022). Terrestrial Heteroptera were collected from various fields, including the agricultural farms "Odilbek," "Amir Temur," "Gulrukhbe-gim," and "Oltin Kal'a" located in the Urgench district, "Dildora Bojimon" and "Buz Os Yep" agricultural farms, as well as the educational-experimental station of UrSU named "Uchkhoz" in Yangibazar district, "Ziroat-21" agricultural farm of Kushkupir district, "Raximbergan Xoji Anbar" in Khiva district, "Otabek garchak" and "Gulkand Istikbolli bog'i" in Khanka district and natural landscapes in the Khorezm region, as well as "Zaripboy," "Kilchinok," and "Badai Tugai Nature Reserve," Karatau mountain in the Beruniy district of the Republic of Karakalpakstan (Gandjaeva et al. 2021). The geographical locations of the sites are shown in Fig. 1.

The zoogeographic analysis of identified species in the Lower Amudarya was based on zoogeographical nomenclature by Emelyanov (1974). In brief, geographic longitude was used to establish the zone along its meridional boundaries.



Figure 1. Geographical locations of the collection sites of terrestrial Heteroptera specimens in the Lower Amudarya Territory.

The descriptive area nomenclature utilized in this work uses the concepts of physical geography and applies two axis coordinates: the latitudinal axis runs from north to south and is critical because it is used to determine climatic conditions of the distributed species, especially temperature; the longitudinal axis runs from west to east. In some species, the range coincides with the boundaries of the landscape zone and is labeled as Arctic (polar deserts, tundra), boreal (taiga), subboreal (broad-leaved forests), subtropical and tropical (evergreen forests) (Lopatin and Meleshko 2016).

We used the basic data on the geographic distribution of these species from the Catalogue "Heteroptera of the Palaearctic" Volumes I–VI, published by the Netherlands Entomological Society, Amsterdam (NES) (1995–2013) (Catalogue of Palaearctic true bugs 2013) to describe the analysis of the zoogeographic areas of terrestrial Heteroptera (Aukema et al. 2013) the database is continually updated.

An analysis of the occurrence and abundance of species on cultivated and wild plants were carried out by observing 50–100 plant specimens every day along the diagonal of the fields. The number of adult bugs, larvae of all ages, and egg clutches was recorded (Gandjaeva et al. 2021).

The number of species and their occurrence was calculated using the formula devised by Dajoz (2000):

$$F(\%) = 100 \times (Pi/P)$$

where Pi refers to the species that was found; P is an absolute number.

Species are divided into four groups based on their frequency of occurrence:

Constantly occurring species: F ≥ 50% Often occurring species: 25% < F < 50% Additional occurring species: 5% ≤ F < 25% Rarely occurring species: F < 5%

The dynamics of the abundance of species was calculated using the formula of Zaime and Gautier (1989):

$$Ar(\%) = 100 \times (Ni/N)$$

where Ni is the coefficient of special observable species; N is the absolute number of all observable species.

The analyses of the dynamics of the numbers of species are also divided into four groups:

Abundant:
$$Ar \ge 10$$

Frequent: $5 \le Ar < 10$
Some: $1 \le Ar < 5$
Few: $Ar < 1$

Results and discussion

Checklists of Heteroptera for the Khorezm region and Karakalpakstan Republic were published more than 20 years ago. Khamraev (2003) and Kulumbetova (1998a, b, c, 1999) listed several species found to the north of Uzbekistan and, respectively, but some species have yet to be discovered while others are rare or migratory.

We carried out a comparative analysis of the lists of regional faunas using the data from Khamraev (2003) in the Khorezm Region and Kulumbetova (1998a, b, c, 1999) in the Republic of Karakalpakstan, which allowed us to determine regional features of the fauna in the Lower Amudarya (Table 1). Based on taxonomic distribution, this method enables the collection of data about species complexes with various zoogeographical characteristics (Table 1; Fig. 2). To classify the areas of the Lower Amudarya, information from Gandjaeva et al. (2021) was used (Fig. 2).

Entomologists (Kulumbetova 1998a, b, c, 1999; Khamraev 2003) discovered five new species: *Tarajala brevicornis* (Reuter, 1879), *Emblethis dilaticollis* (Jakovlev, 1874), *Aethus nigronervosus* (Melichar, 1906), *Microporus virgata* (Fabricius, 1974), and *Sciocoris helferi* (Fieber, 1851), which were indexed between 1998–2003 (Kulumbetova 1998a, b, c, 1999; Khamraev 2003) for the Lower Amudarya. These could be rare or migratory species, or are probably misidentified. These five species, shaded in Table 1, have not yet been verified and these records are not used in the distributional and zoogeographical analyses of the group; they are only mentioned in the checklist of the heteropterans found in the Khorezm region and Karakalpakstan.



Khorezm region
Republic of Karakalpakstan

Figure 2. Numbers of terrestrial Heteroptera recorded in the regions of the northern part of Uzbekistan.

	Taxon	Family	Occurrence	Abundance	Distribution	Zoogeographic	References
						categories	
1	Anthocoris pilosus		+	F	***	SA	Khamraev (2003);
	(Jakovlev, 1877)						Gandjaeva et al. (2021)
2	Orius niger (Wolff, 1811)		++	FR	0	TP	Khamraev (2003);
		Anthogonidae					Kulumbetova (1999);
		Fieber 1837					Gandjaeva et al. (2021)
3	Orius ribauti	Fiebel, 1657	+	F	***	Р	Khamraev (2003);
	(Wagner, 1952)						Gandjaeva et al. (2021)
4	Orius albidipennis		+	S	**	TP	Kulumbetova (1999);
	(Reuter, 1884)						Gandjaeva et al. (2021)
5	Nabis ferus		++	FR	0	TP	Khamraev (2003);
	(Linnaeus, 1758)						Kulumbetova (1999);
							Gandjaeva et al. (2021)
6	Nabis palifer		+	F	***	TS	Khamraev (2003);
	(Seidenstücker, 1954)						Gandjaeva et al. (2021)
7	Nabis viridis		+	F	***	SA	Khamraev (2003);
	(Brullé, 1839)	NLL: L.					Gandjaeva et al. (2021)
8	Nabis rugosus	Costo 1852	++	FR	***	SA	Khamraev (2003);
	(Linnaeus, 1758)	Costa, 16 <i>5</i> 2					Gandjaeva et al. (2021)
9	Nabis remanei		+	F	**	ChCA	Kulumbetova (1999);
	(Kerzhner, 1962)						Gandjaeva et al. (2021)
10	Nabis sareptanus		+	F	***	TP	Khamraev (2003);
	(Dohrn, 1862)						Gandjaeva et al. (2021)
11	Prostemma sanguineum		+	F	**	PA	Kulumbetova (1999);
	(Rossi, 1790)						Gandjaeva et al. (2021)

Table 1. Checklist of the terrestrial Heteroptera from the Lower Amudarya (2007–2020).

	Taxon	Family	Occurrence	Abundance	Distribution	Zoogeographic	References
						categories	
12	Deraeocoris punctulatus		++	FR	0	Р	Khamraev (2003);
	(Fallén, 1807)						Kulumbetova (1999);
							Gandjaeva et al. (2021)
13	Deraeocoris serenus (Douglas & Scott, 1868)		++	FR	** **	W	Gandjaeva et al. (2021)
14	Adelphocoris lineolatus		+++	А	0	ТР	Khamraev (2003);
	(Coeze, 1778)						Kulumbetova (1999);
							Gandjaeva et al. (2021)
15	Adelphocoris seticornis (Fabricius, 1775)		+++	A	** **	W	Gandjaeva et al. (2021)
16	Agnocoris rubicundus (Fallen, 1807)		++	FR	***	TP	Khamraev (2003); Gandjaeva et al. (2021)
17	Brachycoleus decolor		++	FR	***	W	Khamraev (2003);
	(Reuter, 1887)						Gandjaeva et al. (2021)
18	Lygus pratensis		+++	А	0	SA	Khamraev (2003);
	(Linnaeus, 1758)						Kulumbetova (1999);
							Gandjaeva et al. (2021)
19	Lygus gemellatus (Herrich-		++++	А	0	TP	Khamraev (2003);
	Schäffer, 1835)						Kulumbetova (1999);
							Gandjaeva et al. (2021)
20	Lygus pachycnemis		+++	А	***	TNT	Khamraev (2003);
	(Reuter, 1879)						Gandjaeva et al. (2021)
21	Lygus rugulipennis		+++	A	** **	TP	Gandjaeva et al. (2021)
	(Poppius, 1911)						
22	Lygus punctatus		+++	A	** **	ТР	Gandjaeva et al. (2021)
	(Zetterstedt, 1838)						
23	Megacoelum brevirostre		++	FR	***	TS	Khamraev (2003);
	(Reuter, 1879)						Gandjaeva et al. (2021)
24	Orthops basalis	Miridae	++	FR	***	SA	Khamraev (2003);
	(Costa, 1853)	Hahn, 1833					Gandjaeva et al. (2021)
25	Orthops kalmi		++	FR	0	SA	Khamraev (2003);
	(Linnaeus, 1758)						Kulumbetova (1999);
							Gandjaeva et al. (2021)
26	Polymerus vulneratus		+++	A	0	TP	Khamraev (2003);
	(Panzer, 1806)						Kulumbetova (1999);
							Gandjaeva et al. (2021)
27	Polymerus cognatus		+++	A	**	TP	Kulumbetova (1999);
	(Fieber, 1858)						Gandjaeva et al. (2021)
28	Notostira elongata (Geoffroy, 1785)		++	FR	** **	SA	Gandjaeva et al. (2021)
29	Megaloceroea recticornis		++	FR	** **	W	Gandiaeva et al.
	(Geoffroy, 1785)						(2021)
30	Stenodema calcaratum		+++	A	0	ТР	Khamraev (2003):
5.0	(Fallen, 1807)				-		Gandiaeva et al. (2021)
31	Stenodema tripsinosa		+++	A	***	ТР	Khamraev (2003):
	(Reuter, 1904)						Gandjaeva et al. (2021)
32	Stenodema laevigata		+++	A	***	PA	Khamraev (2003);
	(Linnaeus, 1758)						Gandjaeva et al. (2021)
33	Stenodema turanica		++	FR	0	NC	Khamraev (2003);
	(Reuter, 1904)						Kulumbetova (1999);
							Gandjaeva et al. (2021)
34	Trigonotylus ruficornis		++	FR	0	PA	Khamraev (2003);
	(Geoffroy, 1785)						Kulumbetova (1999);
							Gandjaeva et al. (2021)
35	Trigonotylus pulchellus		++	FR	** **	Р	Gandjaeva et al. (2021)
	(Hahn, 1834)						
36	Orthotylus eleagni		++	FR	***	TS	Khamraev (2003);
	(Jakovlev, 1881)						Gandjaeva et al. (2021)

37 Orbioplan flamogamu (Sahlberg, 1841) ** FR *** TP Khamnev (2003); Gandjaeve et al. (2021) 38 Campjomma annilizome (Biguoter, 1878) *** FR *** PG Kulumberov (1999); Gandjaeve et al. (2021) 40 Campopinum a teristici (Meuser, 1879) *** A *** PA Kulumberov (2003); Gandjaeve et al. (2021) 41 Campopinum a teristici (Reuser, 1879) Kiridae *** FR *** PA Kulumberov (2003); Gandjaeve et al. (2021) 42 Campopindia albin (Reuser, 1879) Miridae ** FR *** TP Khamnaev (2003); Gandjaeve et al. (2021) 44 Herrospila laphin (Reuser, 1873) * F * SA Gandjaeve et al. (2021) 45 Macrophy berrichi (Reuser, 1873) * F * SA Gandjaeve et al. (2021) 47 Taponia digmin (Boovlew, 1867) * FR *** SA Khamnaev (2003); Gandjaeve et al. (2021) 49 Taponia digmin (Boovlew, 1883) * F o SA Khamnaev (2003); Gandja		Taxon	Family	Occurrence	Abundance	Distribution	Zoogeographic categories	References
Solbberg, 1841) Gandjaeva et al. (2021) 38 Gampfomma anunilerrie (Signoret, 1865) FR ** P Kulumbeova (1999); Gandjaeva et al. (2021) 40 Gampfomma direvisionitii (Reuret, 1873) FR ** FR ** NS Khamraev (2003); Gandjaeva et al. (2021) 40 Campfomma verboxic (Meyer-Dut, 1873) H++ A *** PA Kulumbeova (1999); Gandjaeva et al. (2021) 41 Gampfolden albin (Reuret, 1873) Hiridae +++ FR *** PA Kulumbeova (1999); Gandjaeva et al. (2021) 42 Campipolita ingripe (Reuret, 1873) Hahn, 1833 ++ FR *** TP Gandjaeva et al. (2021) 44 Herosopillus ingripe (Reuret, 1873) Hahn, 1833 + F * SA Gandjaeva et al. (2021) 45 Marropluk herrichi (Reuret, 1873) H FR *** FR * FA SA Gandjaeva et al. (2021) 47 Tippinia robejeminis (Reuret, 1879) * F * F * F ChCAA Khamraev (2003	37	Orthotylus flavosparsus		++	FR	***	TP	Khamraev (2003);
38 Campylomma annulicorne (Signoret, 1865) *** FR *** P Kulumberova (1999); (Campioration directional (Reuter, 1875) 40 Campylomma directional (Meyter, Dur, 1843) Campioration directional (Reuter, 1875) *** A *** PA Kulumberova (1999); (Campioration erefroits) 41 Campioration directional (Reuter, 1875) Hiridae (Reuter, 1875) *** FR *** PA Kulumberova (1999); (Campioration erefroits) 42 Campioration erefroits) (Reuter, 1875) Hiridae Hahn, 1833 * FR *** FR Kalamace (2003); (Campioration erefroits) 45 Maronylua herrichi (Reuter, 1873) Hiridae Hahn, 1833 * F * SA Gandjaeva et al. (2021) 47 Tiponita legrons (Idavolev, 1867) Hiridae Hahn, 1833 * F * SA Gandjaeva et al. (2021) 48 Tiponita legrons (Idavolev, 1867) Hiridae Hahn, 1833 * F SA Gandjaeva et al. (2021) 47 Tiponita legrons (Idavolev, 1883) Tiponita legrons (Idavolev, 1867) Khamarev (2003); (Idavolev, 1867) Khamarev (2003); (Idavolev, 1867)		(Sahlberg, 1841)						Gandjaeva et al. (2021)
(Signore, 1865) Gandjæva er al. (2021) 39 Gampjomma diveriarnin (Reuer, 1875) +++ A **** NS Khamrae (2003); Gandjæva er al. (2021) 40 Campjomma verbaci (Meyer-Dur, 1843) +++ A **** NS Khamrae (2003); Gandjæva er al. (2021) 41 Campopfidea alba (Reuer, 1875) +++ FR **** NS Khamrae (2003); Gandjæva er al. (2021) 42 Campopfidea alba (Reuer, 1875) ++ FR ***** TP Gandjæva er al. (2021) 44 Herroopfillon igrips (Reuer, 1873) ++ FR ***** TP Gandjæva er al. (2021) 45 Macrophillon berricht (Reuer, 1873) + F * SA Gandjæva er al. (2021) 46 Tiponic aclepsmi (Jakovlev, 1867) ++ FR ***** SA Khamrae (2003); Gandjæva er al. (2021) 47 Tiponia pallida (Reuer, 1879) - - - - Khamrae (2003); Gandjæva er al. (2021) 50 Monoterin diaxolditis (Jakovlev, 1883) * F o SA Khamrae (200	38	Campylomma annulicorne		++	FR	**	Р	Kulumbetova (1999);
39 Campplomma diversionnin (Reurer, 1878) +++ A *** NS Khamraev (2003); Gandjaeva et al. (2021) 40 Camppionna werbasi (Meyer-Dar, 1843) +++ A *** PA Kulumbeevon (1999); Gandjaeva et al. (2021) 41 Camptoplian meeri (Prey- Gesner, 1875) Gandjaeva et al. (2021) +++ FR **** TNT Khamraev (2003); Gandjaeva et al. (2021) 42 Camptoplian meeri (Prey- Gesner, 1875) Hiridae ++ FR **** TP Gandjaeva et al. (2021) 44 Hetercopling Hiridae ++ FR ***** SA Gandjaeva et al. (2021) 45 Macroplu berrichin (Reuter, 1873) Hiridae ++ FR *** SA Gandjaeva et al. (2021) 47 Tiponia rokigomi (Bevier, 1875) Gandjaeva et al. (2021) ++ FR *** FR ChCA Khamraev (2003); Gandjaeva et al. (2021) 48 Tiponia rokigomini (Revier, 1879) Tingidae ++ FR *** F o SA Khamraev (2003); Gandjaeva et al. (2021)		(Signoret, 1865)						Gandjaeva et al. (2021)
Image: Instance (Rever, 1878) Image: Im	39	Campylomma diversicornis		+++	А	***	NS	Khamraev (2003);
40 Campylamma verbasci (Meyer-Dur, 1843) *** PA Kulumbetova (1999); Candjaeva et al. (2021) 41 Campioglida alba (Reuter, 1879) *** FR *** PA Kulumbetova (1999); Candjaeva et al. (2021) 42 Campioglida alba (Reuter, 1879) Hahn, 1833 ** FR *** NS Khammaev (2003); Candjaeva et al. (2021) 43 Izupriella alpina (Reuter, 1875) Miridae (Hahn, 1833) ** FR *** TP Gandjaeva et al. (2021) 44 Hercoglilla tigripe (Meyer & Dur, 1852) Hahn, 1833 * F SA Gandjaeva et al. (2021) 45 Macroglub herrichi (Reuter, 1873) Hahn, 1833 * F SA Gandjaeva et al. (2021) 46 Tipponia pullida (Jakovlev, 1867) * FR *** SA Khammaev (2003); Candjaeva et al. (2021) 49 Tingi dab metiornib (Reuter, 1879) Tingi dab (Reuter, 1879) * F o SA Khammaev (2003); Candjaeva et al. (2021) 50 Mamorin alsonidili (Jakovlev, 1889) Tingidae Laporte, 1832 * F o <td></td> <td>(Reuter, 1878)</td> <td></td> <td></td> <td></td> <td></td> <td></td> <td>Gandjaeva et al. (2021)</td>		(Reuter, 1878)						Gandjaeva et al. (2021)
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1 Image: Application of the second of th	54	Coranus aegyptius		++	FR	***	SA	Khamraev (2003):
55 Coranus subapterus (De Geer, 1773) 56 Rhynocoris monticola (Oshanin, 1870) 57 Rhynocoris monticola (Oshanin, 1870) 57 Rhinocoris nigronitens Reuter, 1881 58 Vachiria deserta (Becker, 1867) 59 Ectomocoris ululans (Rossi, 1807) 60 Reduviidae (Herrich-Schäffer, 1845) 60 Reduvius testaceus (Herrich-Schäffer, 1845)	-	(Fabricius, 1775)						Gandjaeva et al. (2021)
59 Gendineva et al. (2021) 56 Rhynocoris monitcola (Oshanin, 1870) Gandjaeva et al. (2021) 57 Rhinocoris nigronitens Reuter, 1881 ++ 58 Vachiria deserta (Becker, 1867) Reduviidae 59 Ectomocoris ululans (Rossi, 1807) Reduviidae 60 Reduvius testaceus (Herrich-Schäffer, 1845) + 60 Reduvius testaceus (Herrich-Schäffer, 1845) +	55	Coranus subapterus		++	FR	**	NS	Kulumbetova (1999):
56 Rbynocoris monitcola (Oshanin, 1870) 57 Rbinocoris monitcola (Oshanin, 1870) 57 Rbinocoris nigronitens Reuter, 1881 58 Vachiria deserta (Becker, 1867) 59 Ectomocoris ululans (Rossi, 1807) 60 Reduvius testaceus (Herrich-Schäffer, 1845) 60 Reduvius testaceus (Herrich-Schäffer, 1845)		(De Geer, 1773)						Gandiaeva et al. (2021)
(Oshanin, 1870) Gandjaeva et al. (2021) 57 Rbinocoris nigronitens Reuter, 1881 ++ FR *** TS Khamraev (2003); Gandjaeva et al. (2021) 58 Vachiria deserta (Becker, 1867) Reduviidae + F **** ITCA Gandjaeva et al. (2021) 59 Ectomocoris ululans (Rossi, 1807) Reduviidae + F **** ETPE Khamraev (2003); Gandjaeva et al. (2021) 60 Reduvius testaceus (Herrich-Schäffer, 1845) + S **** TS Gandjaeva et al. (2021)	56	Rhynocoris monticola		++	FR	***	TS	Khamraev (2003):
57 Rbinocoris nigronitens Returer, 1881 58 Vachiria deserta (Becker, 1867) 59 Ectomocoris ululans (Rossi, 1807) 60 Reduviidae (Herrich-Schäffer, 1845)	20	(Oshanin, 1870)					10	Gandiaeva et al. (2021)
7) Formetric Reduvition Returer, 1881 Gandjaeva et al. (2021) 58 Vachiria deserta (Becker, 1867) 59 Ectomocoris ululans (Rossi, 1807) 60 Reduviidae 4 F 4 F 59 Ectomocoris ululans (Rossi, 1807) 60 Reduvius testaceus (Herrich-Schäffer, 1845) 60 Reduvius testaceus (Herrich-Schäffer, 1845)	57	Rhinocoris nigronitens		++	FR	***	TS	Khamraev (2003):
58 Vachiria deserta (Becker, 1867) Reduviidae + F ** ** ITCA Gandjaeva et al. (2021) 59 Ectomocoris ululans (Rossi, 1807) Latreille, 1807 + F **** ETPE Khamraev (2003); Gandjaeva et al. (2021) 60 Reduvius testaceus (Herrich-Schäffer, 1845) + S **** TS Gandjaeva et al. (2021)	21	Reuter, 1881					10	Gandiaeva et al. (2021)
50 Hability and Call (Becker, 1867) Reduviidae 59 Ectomocoris ululans (Rossi, 1807) 60 Reduvius testaceus (Herrich-schäffer, 1845)	58	Vachiria deserta		+	F	** **	ITCA	Gandiaeva et al. (2021)
59 Ectomocoris ululans (Rossi, 1807) Latreille, 1807 + F *** ETPE Khamraev (2003); Gandjaeva et al. (2021) 60 Reduvius testaccus (Herrich-Schäffer, 1845) + S *** TS Gandjaeva et al. (2021)	20	(Becker, 1867)	Reduviidae				11011	
(Rossi, 1807) Gandjaeva et al. (2021) 60 Reduvius testaceus (Herrich-Schäffer, 1845)	59	Ectomocoris ululans	Latreille, 1807	+	F	***	ETPE	Khamraev (2003):
60 Reduvius testaceus (Herrich-Schäffer, 1845)		(Rossi, 1807)			-			Gandiaeva et al. (2021)
(Herrich-Schäffer, 1845)	60	Reduvius testaceus		+	S	***	Т	Gandiaeva et al. (2021)
	00	(Herrich-Schäffer, 1845)					10	
6] Reduvius disciger + F **** TS Khamraev (2003)	61	Reduvius disciger		+	F	***	TS	Khamraev (2003).
(Horváth, 1896) Gandiaeva et al. (2021)	01	(Horváth, 1896)		'				Gandiaeva et al. (2021)
62 Redunius christophi	62	Redunius christophi			S	0	Т	Khamraev (2003).
(Iakovlev, 1874)	02	(Jakovley, 1874)		- T			1.5	Kulumbetova (1999).
Gandiaeva et al. (2021)		0						Gandiaeva et al. (2021)
63 Redunius fedtschenkianus + F o TNT Khammay (2003).	63	Reduvius fedtschenbianus		+	F	0	TNT	Khamraev (2003).
(Oshanin, 1871)	00	(Oshanin, 1871)		'				Kulumbetova (1999).
Gandiaeva et al. (2021)								Gandjaeva et al. (2021)

	Taxon	Family	Occurrence	Abundance	Distribution	Zoogeographic categories	References
64	<i>Reduvius semenovi</i> (Jakovlev, 1885)		+	F	***	TNT	Khamraev (2003); Gandjaeva et al. (2021)
65	<i>Reduvius elegans</i> (Jakovley, 1885)	Reduviidae	++	FR	***	TNT	Khamraev (2003); Gandiaeva et al. (2021)
66	Oncocephalus brachymerus	Latreille, 1807	++	FR	***	TS	Khamraev (2003); Candiaeva et al. (2021)
67	Oncocephalus termezanus		++	FR	**	ITCA	Kulumbetova (1999); Candiagun et al. (2021)
68	<i>Camptopus lateralis</i> (German, 1817)	Alydidae Amyot	+	F	0	SA	Khamraev (2003); Kulumbetova (1999); Gandjaeva et al. (2021)
69	Megalotomus ornaticeps (Stål, 1858)	& Serville, 1843	+	F	**	NS	Kulumbetova (1999); Gandjaeva et al. (2021)
70	Centrocoris volxemi (Puton, 1878)		+	F	***	TS	Khamraev (2003); Gandjaeva et al. (2021)
71	Coreus marginatus (Linnaeus, 1758)		+	S	***	TP	Khamraev (2003); Gandjaeva et al. (2021)
72	Enoplops eversmanni (Jakovlev, 1881)		+	F	***	Т	Khamraev (2003); Gandjaeva et al. (2021)
73	<i>Bathysolen nubilus</i> (Fallen, 1807)	Leach, 1815	+	F	**	TS	Kulumbetova (1999); Gandjaeva et al. (2021)
74	Bothrostethus annulipes (Herrich-Schäffer, 1835)		+	S	**	TS	Kulumbetova (1999); Gandjaeva et al. (2021)
75	Coriomeris vitticollis (Reuter, 1900)		+	F	0	TS	Khamraev (2003); Kulumbetova (1999); Gandjaeva et al. (2021)
76	Brachycarenus tigrinus (Schilling, 1829)		++	FR	0	TP	Khamraev (2003); Kulumbetova (1999); Gandjaeva et al. (2021)
77	<i>Chorosoma schillingi</i> (Schilling, 1829)		++	FR	***	SA	Khamraev (2003); Gandjaeva et al. (2021)
78	Corizus limbatus (Rey, 1887)		+++	А	0	SA	Khamraev (2003); Kulumbetova (1999); Gandjaeva et al. (2021)
79	Corizus tetraspilus (Horvath, 1917)		+++	A	**	NS	Khamraev (2003); Kulumbetova (1999); Gandiaeva et al. (2021)
80	<i>Corizus hyoscyami</i> (Linnaeus, 1758)	Rhopalidae Amyot & Serville,	+++	A	***	TP	Khamraev (2003); Gandiaeva et al. (2021)
81	Maccevethus persicus (Jakovley, 1882)	1843	++	FR	***	TS	Khamraev (2003); Gandjaeva et al. (2021)
82	<i>Liorhyssus hyalinus</i> (Fabricius, 1794)		++	FR	0	С	Khamraev (2003); Kulumbetova (1999); Gandjaeva et al. (2021)
83	<i>Rhopalus parumpunctatus</i> (Schilling, 1829)		++	FR	***	TP	Khamraev (2003); Gandjaeva et al. (2021)
84	Rhopalus distinctus (Signoret, 1859)		++	FR	***	TS	Khamraev (2003); Gandjaeva et al. (2021)
85	Stictopleurus unicolor (Jakovlev, 1873)		++	FR	***	W	Khamraev (2003); Gandjaeva et al. (2021)
86	Dicranocephalus marginatus (Ferrari, 1874)	Stenocephalidae	+	F	0	TS	Khamraev (2003); Kulumbetova (1999); Gandjaeva et al. (2021)
87	Dicranocephalus ferghanensis (Horváth, 1887)	Dallas, 1852	+	F	0	TS	Khamraev (2003); Kulumbetova (1999); Gandjaeva et al. (2021)

	Taxon	Family	Occurrence	Abundance	Distribution	Zoogeographic categories	References
88	Artheneis alutacea	Artheneidae	+	S	***	W	Khamraev (2003);
	(Fieber, 1861)	Stål, 1872					Gandjaeva et al. (2021)
89	Geocoris ater		++	FR	**	ТР	Kulumbetova (1999);
	(Fabricius, 1787)						Gandjaeva et al. (2021)
90	Geocoris arenarius		+	F	**	NS	Kulumbetova (1999);
	(Jakovlev, 1867)						Gandjaeva et al. (2021)
91	Geocoris dispar		++	FR	**	W	Kulumbetova (1999);
	(Waga, 1839)						Gandjaeva et al. (2021)
92	<i>Geocoris lapponicus</i> (Zetterstedt, 1838)		+	F	** **	Р	Gandjaeva et al. (2021)
93	Geocoris fedtschenkoi (Reuter, 1885)	Baerensprung,	+	F	***	NS	Khamraev (2003); Gandjaeva et al. (2021)
94	Geocoris scutellatus	1860	+	F	***	KNTIT	Khamraev (2003);
	(Montandon, 1907)						Gandjaeva et al. (2021)
95	Engistus salinus		+	F	***	TS	Khamraev (2003);
	(Jakovlev, 1874)			-			Gandjaeva et al. (2021)
96	Engistus exsanguis	-	++	FR	***	TS	Khamraev (2003);
, .	(Stál, 1872)						Gandjaeva et al. (2021)
97	Henestaris halophilus		+	F	***	W	Khamraev (2003):
,,	(Burmeister, 1835)						Gandiaeva et al. (2021)
98	Lygaeus equestris		++	FR	0	ТР	Khamraev (2003):
,0	(Linnaeus, 1758)				Ū		Kulumbetova (1999);
	(, _ , _ , _ , _ , _ , _ , _ ,						Gandiaeva et al. (2021)
99	Spilostethus rubriceps		+	F	0	TS	Khamraev (2003):
//	(Horvath, 1899)				Ū	10	Kulumbetova (1999);
	(,,,,,,,,,,,,,						Gandiaeva et al. (2021)
100	Spilostethus pandurus	Lvœeidae	+	F	**	TS	Kulumbetova (1999):
100	(Scopoli, 1763)	Schilling 1829				10	Gandiaeva et al. (2021)
101	Nusius graminicola	5cming, 102)	++	FR	***	SA	Khamraev (2003):
101	(Kolenati, FA, 1845)			110		011	Gandiaeva et al. (2021)
102	Oxycarenus pallens	-	+	S	***	SA	Khamraev (2003):
102	(Herrich-Schäffer, 1850)					011	Gandiaeva et al. (2021)
103	Ortholomus punctipennis		++	FR	***	р	Khamraev (2003):
105	(Herrich-Schäffer, 1850)					-	Gandiaeva et al. (2021)
104	Reasus auadritumctatus		++	FR	**	SA	Kulumbetova (1999):
104	(Muller, 1766)			110		571	Gandiaeva et al. (2021)
105	Rletenanus heckeri (Frev-		+	F	**	Т	Kulumbetova (1999).
109	Gessner, 1863)			1		10	Gandiaeva et al. (2021)
106	Emplethis griseus		+	F	0	SA	Khamraev (2003):
100	(Wolff 1802)			1	Ŭ	011	Kulumbetova (1999)
	(1002)						Gandiaeva et al. (2021)
107	Emhlethis verhasci	-	+	F	0	SA	Khamraev (2003):
107	(Fabricius, 1803)			1	Ŭ	011	Kulumbetova (1999):
	(Gandiaeva et al. (2021)
108	Emblethis ciliatus	Rhyparochromidae	+	F	0	SA	Khamraev (2003):
	(Horváth, 1875)	Amyot & Serville,		-	-		Kulumbetova (1999);
		1843					Gandjaeva et al. (2021)
109	Emblethis denticollis		+	F	***	Р	Khamraev (2003);
	(Horváth, 1878)						Gandjaeva et al. (2021)
110	Emblethis dilaticollis		_	_	_	_	Kulumbetova (1999)
	(Jakovlev, 1874)						
111	Hyalocoris pilicornis	1	+	S	0	TS	Khamraev (2003):
	(Jakovlev, 1874)					_	Kulumbetova (1999);
							Gandjaeva et al. (2021)
112	Lamprodema maura	1	++	FR	0	W	Khamraev (2003):
	(Fabricius, 1803)						Kulumbetova (1999);
							Gandjaeva et al. (2021)

	Taxon	Family	Occurrence	Abundance	Distribution	Zoogeographic categories	References
113	Aethus pilosulus (Klug. 1845)		+	F	0	TS	Khamraev (2003); Kulumbetova (1999):
	(1002, 101))						Gandiaeva et al.
							(2021)
114	Aethus nigronervosus (Melichar, 1906)		-	-	-	-	Khamraev (2003)
115	Byrsinus fossor		+	F	0	TP	Khamraev (2003);
	(Mulsant & Rey, 1866)						Kulumbetova (1999);
		Cardarida					Gandjaeva et al. (2021)
116	<i>Microporus virgata</i> (Fabricius, 1794)	Billberg, 1820	-	-	_	_	Khamraev (2003)
117	<i>Microporus nigrita</i> (Fabricius, 1794)		+	F	**	ETPE	Gandjaeva et al. (2021)
118	<i>Stibaropus hohlbecki</i> (Kiritshenko, 1912)		+	F	**	TNT	Kulumbetova (1999); Gandjaeva et al. (2021)
119	Sehirus morio		+	F	***	W	Khamraev (2003);
	(Linnaeus, 1761)						Gandjaeva et al. (2021)
120	Amaurocoris candidus		+	F	***	TS	Khamraev (2003);
	(Horváth, 1889)						Gandjaeva et al. (2021)
121	Aelia acuminata		+++	A	**	W	Kulumbetova (1999);
	(Linnaeus, 1758)						Gandjaeva et al. (2021)
122	<i>Aelia furcula</i> (Fieber, 1868)		+++	A	***	TS	Khamraev (2003); Gandjaeva et al. (2021)
123	<i>Aelia melanota</i> (Fieber, 1868)		+++	A	**	TS	Kulumbetova (1999); Gandjaeva et al. (2021)
124	Brachynema germari		++	FR	0	ТР	Khamraev (2003);
	(Kalenati, 1846)						Kulumbetova (1999);
							Gandjaeva et al.
	a				datat		(2021)
125	Carpocoris pudicus		++	FR	***	P	Khamraev (2003);
126	(roua, 1701)			ED	0	W/	Khamraev (2003):
120	(Boheman, 1851)		++	I'K	0	~~	Kulumbetova (1999);
							Gandjaeva et al.
							(2021)
127	Palomena prasina		+++	A	** **	SA	Gandjaeva et al. (2021)
	(Linnaeus, 1761)	Pentatomidae					
128	Dolycoris penicillatus	Leach, 1815	+++	A	о	TS	Khamraev (2003);
	(Horváth, 1904)						Kulumbetova (1999); Candiagua et al. (2021)
120	Dauntamanida			Δ	***	NIS	Khammaay (2003).
129	auadrimaculata		+++	Л		113	Gandiaeva et al. (2003);
	(Horváth, 1892)						
130	Desertomenida albula		+++	A	***	TS	Khamraev (2003);
	(Kiritshenko, 1914)						Gandjaeva et al. (2021)
131	Derula longipennis		+	F	** **	TP	Gandjaeva et al. (2021)
	(Oshanin, 1871)						
132	Apodiphus integriceps		+++	A	0	TS	Khamraev (2003);
	(Horváth, 1888)						Kulumbetova (1999); Candiaeva et al. (2021)
122	Cellobius abdominalic			ED	***	NS	Khamraev (2003).
100	(Jakovley, 1885)		+ ⁺⁺	IR		113	Gandjaeva et al. (2021)
134	Codophila varia		++	FR	***	SA	Khamraev (2003):
	(Fabricius, 1787)						Gandjaeva et al. (2021)
135	Holcostethus nitidus		++	FR	***	TNT	Khamraev (2003);
	(Kiritshenko, 1914)						Gandjaeva et al. (2021)

	Taxon	Family	Occurrence	Abundance	Distribution	Zoogeographic	References
						categories	
136	Holcostethus strictus		++	FR	**	Р	Kulumbetova (1999);
	vernalis (Wolff, 1804)						Gandjaeva et al. (2021)
137	Menaccarus deserticola		++	FR	***	TS	Khamraev (2003);
	(Jakovlev, 1900)						Gandjaeva et al. (2021)
138	Eurydema ornata		+++	A	***	SA	Khamraev (2003);
	(Linnaeus, 1758)						Gandjaeva et al. (2021)
139	Eurydema oleracae		+++	A	** **	SA	Gandjaeva et al. (2021)
	(Linnaeus, 1758)						
140	Eurydema wilkinsi		+++	A	*	NS	Gandjaeva et al. (2021)
	(Distant, 1879)						
141	Eurydema ventralis		+++	A	** **	SA	Gandjaeva et al. (2021)
	(Kolenati, 1846)						
142	Eurydema maracandica		+++	A	**	NS	Kulumbetova (1999);
	(Oshanin, 1871)	Pentatomidae					Gandjaeva et al. (2021)
143	Graphosoma lineatum	Leach, 1815	++	FR	***	SA	Khamraev (2003);
	(Linnaeus, 1758)						Gandjaeva et al. (2021)
144	Graphosoma consimile		++	FR	***	TS	Khamraev (2003);
	(Horvath, 1903)						Gandjaeva et al. (2021)
145	Tarisa elevata		++	FR	***	TS	Khamraev (2003);
	(Reuter, 1901)						Gandjaeva et al. (2021)
146	Tarisa subspinosa		++	FR	***	TP	Khamraev (2003);
	(Germar, 1839)						Gandjaeva et al. (2021)
147	Tarisa virescens (Herrich-		++	FR	***	NS	Khamraev (2003);
	Schäffer, 1851)						Gandjaeva et al. (2021)
148	Tarisa pallescens		++	FR	***	TS	Khamraev (2003);
	(Jakovlev, 1871)						Gandjaeva et al. (2021)
149	Sciocoris helferi		-	_	_	_	Kulumbetova (1999)
	(Fieber, 1851)						
150	Eurygaster integriceps		++	FR	0	Р	Khamraev (2003);
	(Puton, 1881)						Kulumbetova (1999);
							Gandjaeva et al. (2021)
151	Odontotarsus impictus	Scutelleridae	+	F	0	TS	Khamraev (2003);
	(Jakovlev, 1886)	Leach, 1815					Kulumbetova (1999);
							Gandjaeva et al. (2021)
152	Odontotarsus angustatus		+	F	***	TS	Khamraev (2003);
	(Jakovlev 1883)						Gandjaeva et al. (2021)
153	Scantius aegyptius		+	F	0	NS	Khamraev (2003);
	(Linnaeus, 1758)	D 1 11					Kulumbetova (1999);
		Pyrrhocoridae					Gandjaeva et al. (2021)
154	Pyrrhocoris apterus	Amyot & Serville,	++	FR	o	W	Khamraev (2003);
	(Linnaeus, 1758)	1843					Kulumbetova (1999);
							Gandjaeva et al. (2021)
Tota	l number of species: 154						

Symbols and abbreviations used in the table

Occurrence: constantly occurring species (CO): ++++; often occurring species (OO): +++; additional occurring species (AO): ++; Rarely occurring species (RO): +.

Abundance: Abundant: A; frequent: FR; some: S; few: F.

Distribution: 0 - species presence;

- species presence not confirmed

* - previously unregistered species for Uzbekistan;

** - previously unregistered species for the Khorezm region;

*** - previously unregistered species for the Republic of Karakalpakstan;

** ** – previously unregistered species for the Khorezm region and the Republic of Karakalpakstan.

Zoogeographical categories

C – Cosmopolitan; **TP** – Trans-Palaearctic; **P** – Pancontinental; **ETPE** – Ethiopia – Trans-Palaearctic – Eastern; **SA** – Super-Atlantic; **W** – The Western; **PA** – Pan-Atlantic; **NC** – Narrow continental; **NS** – The North Seitan; **TS** – Tethyan-Siberian; **ChCA** – Chinese-Central Asian endemics; **TNT** – Turkestanian-Northern Turanian endemics; **ITCA** – Irano-Turanian-Central Asian endemics; **KNTIT** – Kazakh-Northern Turanian, Irano-Turanian; **T** – Turanian endemics. Khamraev (2003) identified 110 species for the Khorezm, and Kulumbetova (1998a, b, c, 1999) 62 species for the Republic of Karakalpakstan.

The analysis of terrestrial Heteroptera in the Lower Amudarya by Gandjaeva (2007–2020) represented 39 species, which were first studied for the fauna of the Khorezm region and 87 species for the Republic of Karakalpakstan. According to the data, there are currently 149 species of terrestrial Heteroptera recorded in the Lower Amudarya (Fig. 2).

During 2007–2020, 149 species of terrestrial heteropterans were recorded in the Lower Amudarya territory as represented in Table 1.

From the surveys, it has been established that approximately 30 species are abundant and numerous. Sixty-two species are frequent, eight are sometimes encountered, and 49 were recorded as few. They belong to 17 families, 89 genera and the most numerous are Miridae – 37 species and Pentatomidae – 28 species, followed by Reduviidae – 15; Rhopalidae – 10; Geocoridae – 9; Rhyparochromidae – 8; Nabidae – 7; Coreidae, Lygaeidae, Cydnidae – 6, Anthocoridae – 4. Other families are represented by not more than two or three species (Table 2).

Recorded species belong to 11 types according to sector ranges, and 28 groups of areas according to belt ranges (Table 3). The Lower Amudarya's hemipteran species were divided into four large groups: Wide Areas, Holarctic Areas, Palaearctic Areas, and Endemic Areas (Fig. 3).

Broad areas – extend beyond the Holarctic;

Cosmopolitan areas – occur on at least three continents;

Holarctic areas – cover the Palaearctic and the Nearctic region;

Palaearctic areas – cover parts of Europe, Asia, and North Africa;

- Nearctic areas - cover North America, Mexico, and Greenland;

 The Ethiopia – Trans-Palaearctic – Eastern areas – this complex combines the Palaearctic, Ethiopia and Eastern regions;

Trans-Palaearctic areas – cover the entire Palaearctic;

 Super-Atlantic areas – cover from the Atlantic sectors to the Eastern transitional sectors;

- The Western areas – cover the part of the Palaearctic Realm from the Eastern Atlantic to the Western Eucontinental sectors;

- Pan-Atlantic areas – encompass the Atlantic sector as well as the western subcontinental subsectors;

Pancontinental areas – located from the sub-Atlantic to the eastern continental sectors inclusive;

– Narrow Continental areas – cover the Sahara-Gobi Desert area, the Mediterranean and the Irano-Turanian sub-areas.

 The North-Setian areas – cover the Trans-Scythian, the Western-Scythian, and the Eastern-Scythian sub-regions;

 Tethyan-Siberial areas – cover the Tethyan Subkingdom, Scythian, Setian, and European, Mediterranean, and Irano-Turanian subregions;

– Endemic areas – occur only in a certain area and nowhere else.

Family	Number of genera	%	Number of species	%
Anthocoridae	2	2.27	4	2.68
Nabidae	2	2.27	7	4.70
Miridae	20	21.59	37	24.16
Tingidae	3	3.41	3	2.01
Reduviidae	7	7.95	15	10.07
Alydidae	2	2.27	2	1.34
Coreidae	6	6.82	6	4.03
Rhopalidae	7	7.95	10	6.71
Stenocephalidae	1	1.14	2	1.34
Artheneidae	1	1.14	1	0.67
Geocoridae	3	3.41	9	6.04
Lygaeidae	5	5.68	6	4.70
Rhyparochromidae	5	5.68	8	5.37
Cydnidae	6	6.82	6	4.03
Pentatomidae	15	17.05	28	18.79
Scutelleridae	2	2.27	3	2.01
Pyrrhocoridae	2	2.27	2	1.34
Total:	89	100	149	100

Table 2. Distribution of the number of genera, species within families, as well as their percentage (%) in the fauna of terrestrial heteropterans.



Figure 3. Species numbers of true bugs by area grouping.

In the northern part of Uzbekistan, only one species (0.67%) is cosmopolitan. The group of the Holarctic range is characterized by no more than ten species, which constitutes 6.71% of the total, and most species belong to the Palaearctic group, which is most diverse. The group contains 125 species (83.89%), with 38 from the Tethyan-Siberian type constituting 25.50%. Approximately 15 species account for 10.07% of the Irano-Turanian range, while ten species constitute 6.71% of the Euro-Mediterranean-Turanian range. In the Super-Atlantic range, 28 species account for 18.79%, with eight

Type area	The sector and belt	Number	Species	Percentage
~1	range	of species	*	U
I. Groups of wide areas	I.1. Cosmopolitan	1	Liorhyssus hyalinus;	0.67
II. Holarctic	II.1. Trans-Palaearctic	9		6.04
Type area I. Groups of wide areas II. Holarctic III. Palaearctic	a) Extratropical, Nearctic	3	Lygus rugulipennis, Orius albidipennis, Derula longipennis;	2.01
	b) Boreal-subtropical, Nearctic	3	Agnocoris rubicundus, Lygus punctatus, Polymerus cognatus;	2.01
	c) Boreal-subtropical	2	Polymerus vulneratus, Orthotylus flavosparsus;	1.34
	d) Boreal – subboreal	1	Stenodema tripsinosa;	0.67
	II.2. Pancontinental	1	1	0.67
	a) Extratropical	1	Deraeocoris punctulatus;	0.67
III. Palaearctic	III.1. Ethiopia – Trans-	2	I	1.34
	Palaearctic – Eastern			
	a) Southern	2	Ectomocoris ululans, Microporus nigrita;	1.34
	III.2. Trans-Palaearctic	16		10.74
	a) Extratropical	1	Europiella alpina;	0.67
	b) Arctic	3	Brachynema germari, Byrsinus fossor, Tarisa fraudatrix;	2.01
	c) Boreal	2	Nabis ferus, Nabis sareptanus;	1.34
	d) Boreal-subtropical	9	Orius niger, Adelphocoris lineolatus, Lygus gemellatus	6.04
	*		gemellatus, Stenodema calcaratum, Geocoris ater, Coreus	
			marginatus, Brachycarenus tigrinus, Corizus hyoscyami	
			hyoscyami, Rhopalus parumpunctatus;	
	e) Boreal-subboreal	1	Lygaeus equestris;	0.67
	III.3. Super-Atlantic	28		18.79
	a) Arcto-Subboreal	7	Tuponia elegans, Tuponia pallida, Coranus aegyptius,	4.70
			Nysius graminicola graminicola, Emblethis griseus,	
			Emblethis verbasci, Corizus limbatus;	
	b) Boreal-subboreal	1	Orthops basalis;	0.67
	c) Boreal-subtropical	7	Lygus pratensis, Notostira elongata, Eurydema ornata,	4.70
			Eurydema oleracae, Palomena prasina, Orthops kalmi, Chorocom a cohillingi	
	d) Subbaral	0	Nahia mugana Nahia nini dia Duallá	5 27
	u) Subboleai	0	Ivadis rugosus, Ivadis viriais Druue, Heterocapillus tiaripes Macrotylus herrichi	5.57
			Monosteira discoidalis, Beosus quadripunctatus,	
			Codophila varia, Camptopus lateralis;	
	e) Subboreal-subtropical	2	Eurydema ventralis, Graphosoma lineatum;	1.34
	f) Southern	3	Anthocoris pilosus, Oxycarenus pallens, Emblethis ciliatus;	2.01
	III. 4. The Western	13		8.72
	a) Boreal	2	Deraeocoris serenus, Adelphocoris seticornis;	1.34
	b) Boreal-subtropical	5	Lamprodema maura, Stictopleurus unicolor, Sehirus morio,	3.36
	1		Aelia acuminata, Carpocoris fuscispinus;	
	c) Boreal-subboreal	2	Pyrrhocoris apterus, Megaloceroea recticornis;	1.34
	d) Subboreal	3	Artheneis alutacea, Brachycoleus decolor, Geocoris dispar;	2.01
	e) Southern	1	Henestaris halophilus;	0.67
	III. 5. Pan-Atlantic	4		2.68
	a) Boreal-subtropical	2	Stenodema laevigata, Campylomma verbasci;	1.34
	b) Boreal-subboreal	1	Trigonotylus ruficornis;	0.67
	c) Subboreal-subtropical	1	Prostemma sanguineum;	0.67
	III. 6. Pancontinental	10		6.71
	a) Northern	1	Geocoris lapponicus;	0.67
	b) Boreal-subtropical	5	Ortholomus punctipennis, Emblethis denticollis,	3.36
			Holcostethus strictus vernalis, Carpocoris pudicus,	
			Trigonotylus pulchellus;	
	c) Subboreal	1	Orius ribauti;	0.67
	d) Subboreal-subtropical	1	Eurygaster integriceps;	0.67
	e) Southern	2	Campylomma annulicorne, Stephanitis pyri;	1.34

Table 3. Percentage of the terrestrial Heteroptera by area grouping.

Type area	The sector and belt	Number	Species	Percentage
	range	of species		
	III. 7. Narrow	2		1.34
	Continental			
	a) Eastern	1	Stenodema turanica;	0.67
	Mediterranean Gobian			
	b) Mediterranean-Irano-	1	Geocoris fedtschenkoi;	0.67
	Turanian			
	III. 8. The North	12		8.05
	Setian			
	a) Trans-Scythian	1	Geocoris arenarius;	0.67
	b) Western Scythian	3	Coranus subapterus, Campylomma diversicorne,	2.01
			Camptotylus meyeri;	
	c) Eastern Scythian	8	Corizus tetraspilus, Megalotomus ornaticeps,	5.37
			Desertomenida quadrimaculata, Cellobius abdominalis,	
			Eurydema wilkinsi, Eurydema maracandica, Tarisa	
			virescens, Scantius aegyptius;	
	III. 9. Tethyan-Siberian	38		25.50
	a) Western-Scythian- Saharo-Gobian	1	Stenolemus bogdanovi;	0.67
	b) Euro-Mediterranean	10	Spilostethus pandurus Tarisa pallescens	671
	– Turanian	10	Reduvius testaceus, Centrocoris volxemi, Bathysolen	01/1
			nubilus, Coriomeris vitticollis, Rhopalus distinctus, Engistus	
			exsanguis, Aelia furcula, Graphosoma consimile;	
	c) Irano-Turanian-	4	Megacoelum brevirostre, Orthotylus eleagni,	2.68
	Gobian		Oncocephalus brachymerus, Bothrostethus annulipes;	
	d) Irano-Turanian	15	Reduvius disciger, Reduvius christophi, Engistus salinus,	10.07
			Tarisa elevata, Desertomenida albula, Odontotarsus impictus,	
			Odontotarsus angustatus, Amaurocoris candidus,	
			Aelia melanota, Dolycoris penicillatus, Apodiphus integriceps,	
			Menaccarus deserticola, Maccevethus corsicus persicus,	
			Dicranomerus marginatus, Dicranomerus ferghanensis;	
	e) Kazakh-Northern	6	Nabis palifer, Rhynocoris monticola monticola,	4.03
	Turanian, Irano-		Rhynocoris nigronitens, Spilostethus rubriceps,	
	Turanian		Bleteogonus beckeri, Geocoris scutellatus;	
	f) Tethys-Ethiopian	2	Hyalocoris pilicornis, Aethus pilosulus;	1.34
IV. Endemics	IV. Endemics	13		8.72
	a) Chinese-Central	2	Nabis remanei, Tuponia roseipennis;	1.34
	Asian			
	b) Chinese-Irano-	1	Reduvius fedtschenkianus;	0.67
	Central Asian			
	c) Turkestanian-	6	Stibaropus hohlbecki, Holcostethus nitidus, Lygus pachycnemis,	4.03
	Northern Turanian		Camptotylidea alba, Reduvius semenovi, Reduvius elegans;	
	d) Irano-Turanian-	3	Vachiria deserta, Tingis leptochila, Oncocephalus termezanus;	2.01
	Central Asian		•	
	e) Turanian	1	Enoplops eversmanni;	0.67
Total:		149		100

species making up 5.37% of subboreal and seven species accounting for 4.70% of boreal-subtropical species recorded. Sixteen Trans-Palaearctic species (10.74%) have been recorded, followed by 13 Western (8.72%), 12 North Setian (8.05%), ten Pancontinental (6.71%), and four Pan-Atlantic (2.68%) species. The number of species with Ethiopia-Trans-Palaearctic-Eastern distributions and Narrow Continental is only two for each area or 1.34%. It can be seen that the prevailing part of the group,125 species (83.89%), were found in wider areas of the Holarctic, and 13 are endemic species (8.72%). The endemics are divided into Chinese-Central Asian, Chinese-Irano-Central Asian, Turkestanian-Northern Turanian, Irano-Turanian-Central Asian, and Turanian (found in Central Asia only). For the assessment of any territory, endemics have a high conservation value since they indicate the distinctive nature of the fauna.

Conclusions

In this study, we collected new 39 species for the Khorezm region and 87 species for the Republic of Karakalpakstan during 2007–2020. In addition, we compare our collections with reports of Khamraev (2003) and Kulumbetova (1998a, b, c, 1999) and a total of 154 species (17 families) of terrestrial Heteroptera (Fig. 2, Table 1) were analyzed.

Khamraev (2003) identified 110 species for the Khorezm, and Kulumbetova (1998a, b, c, 1999) 62 species for the Republic of Karakalpakstan. There are currently 149 species of terrestrial Heteroptera in the Lower Amudarya. The results show that 62 species are highly abundant at the site, divided into 17 families and 89 genera, with the Miridae and Pentatomidae having most species (37 and 28, respectively), followed by Reduviidae (15), Rhopalidae (10), Geocoridae (9), Rhyparochromidae (8), Nabidae (7), Coreidae, Lygaeidae, Cydnidae (6 each) (Table 2).

The Heteroptera fauna of Khorezm and Karakalpakstan can be divided into four groups: Cosmopolitan with one species (0.67%); Holarctic, with no more than ten species, or 6.71%; Palaearctic, with most of species (125 species, or 83.89%); and endemic with 13 species, or 8.72%.

An understanding of the fauna is important, as the productivity of crops is currently being negatively impacted by invasive species from neighboring countries. For example, recently we recorded (Gandjaeva et al. 2022b) the brown marmorated stink bug *Halyomorpha halys* (Stål, 1855) (Heteroptera: Pentatomidae) from Uzbekistan for the first time. Several adults and immatures were found in the Khorezm and Ferghana provinces. This species is native to East Asia (China, Korea, Japan, and Taiwan) (Rider et al. 2002; Hoebeke and Carter 2003; Rider 2006, 2016) and is a dangerous pest of many agricultural plants. Therefore, more study is required to examine the impacts of dispersion in a northern environment. In the north-western region of Uzbekistan, an increase in the number of invasive Heteroptera is expected, which will require careful monitoring.

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Two new species of *Dixonius* from Vietnam and Laos with a discussion of the taxonomy of *Dixonius* (Squamata, Gekkonidae)

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Abstract

Integrated analyses using maximum likelihood (ML), Bayesian inference (BI), principal component analysis (PCA), discriminate analysis of principal components (DAPC), multiple factor analysis (MFA), and analysis of variance (ANOVA) recovered two new diagnosable species of gekkonid lizards in the genus *Dixonius*, one from the Central Highlands, Gia Lai Province, Vietnam and another from the Vientiane Province, Laos. Phylogenetic analyses based on the mitochondrial NADH dehydrogenase subunit 2 gene (ND2) and adjacent tRNAs showed that *Dixonius gialaiensis* **sp. nov.** is the sister species of *D. minhlei* from Dong Nai Province, Vietnam and is nested within a clade that also includes the sister species *D. siamensis* and *D. somchanhae. Dixonius muangfuangensis* **sp. nov.** is the sister species to *D. lao* from Khammouane Province, Laos and is embedded in a clade with *D. vietnamensis*, *D. taoi*, and undescribed species from Thailand. Multivariate (PCA, DAPC, and MFA) and univariate (ANOVA) analyses using combinations of 15 meristic (scale counts), six morphometric (measurements), and five categorical (color pattern and morphology) characters from 44 specimens encompassing all eight species of *Dixonius* from Vietnam and Laos clearly illustrate *Dixonius gialaiensis* **sp. nov.** and *Dixonius muangfuangensis* **sp. nov.** are statistically different and discretely diagnosable from all closely related species of *Dixonius*. These integrative analyses also highlight additional taxonomic issues that remain unresolved within *Dixonius* and the need for additional studies. The discovery of these new species further emphasizes the underappreciated herpetological diversity of the genus *Dixonius* and illustrates the continued need for field work in these regions.

Keywords

Gekkota, Indochina, integrative taxonomy, molecular phylogeny, morphology, new species, Southeast Asia

Introduction

The genus Dixonius was established by Bauer et al. (1997) to contain two species, D. melanostictus (Taylor, 1962) and D. siamensis (Boulenger, 1898), with a distribution range through Myanmar, Thailand, Laos, Vietnam, and Cambodia. Currently, thirteen species have been recognized worldwide (Nguyen et al. 2020, 2021; Pauwels et al. 2021; Uetz et al. 2022). In Vietnam, six species of Dixonius have been documented, including four originally described from the country, i.e., D. vietnamensis (Das 2004) from Khanh Hoa and Binh Thuan provinces, D. aaronbaueri (Ngo and Ziegler 2009) from Ninh Thuan and Binh Thuan provinces, D. taoi (Botov, Phung, Nguyen, Bauer, Brennan & Ziegler, 2015) from Binh Thuan Province, D. minhlei (Ziegler, Botov, Nguyen, Bauer, Brennan, Ngo & Nguyen, 2016) from Dong Nai Province, and two from outside Vietnam, D. siamensis from Thailand and Cambodia and D. melanostictus from Thailand (Uetz et al. 2022). Lastly, in Laos, there are three species (D. siamensis, D. lao (Nguyen, Sitthivong, Ngo, Luu, Nguyen, Le & Ziegler, 2020), D. somchanhae (Nguyen, Luu, Sitthivong, Ngo, Nguyen, Le & Ziegler, 2021)) two of which, D. lao from Vientiane Capital and D. somchanhae from Khammouane Province, were described within the last five years (Fig. 1).

During a recent herpetofaunal surveys in Chu Se Mountain Pass, Hbong Commune, Gia Lai Province in Vietnam and Vientiane Province in Laos, new populations of *Dixonius* were found at each location (Fig. 1). Based on phylogenetic evidence from the mitochondrial NADH dehydrogenase subunit 2 (ND2) gene and adjacent tRNAs, morphometric, meristic, and color pattern data, neither can be ascribed to any known species and as such they are described below as new species.

Materials and methods

A total of six *Dixonius* specimens were caught by hand from Gia Lai Province, Vietnam and Vientiane Province, Laos. The specimens were fixed in approximately 80% ethanol and then transferred to 70% ethanol for permanent storage. Tissue samples taken before the specimens were preserved were stored separately in 95% ethanol.


Figure 1. Location of the type localities of all known species of *Dixonius*. The inset delimits the study area. 1 *Dixonius aaronbaueri* from Ninh Thuan Province, Vietnam; 2 *D. dulayaphitakorum* from Ranong Province, Thailand; 3 *D. mekongensis* from Ubon Ratchathani Province, Thailand; 4 *D. hangseesom* from Kanchanaburi Province, Thailand; 5 *D. kaweesaki* from Prachuap Khiri Khan Province, Thailand; 6 *D. pawangkhananti* from Phetchaburi Province, Thailand; 7 *D. lao* from Khammouane Province, Laos; 8 *D. melanostictus* from Nakhon Ratchasima Province, Thailand; 9 *D. minhlei* from Dong Nai Province, Vietnam; 10 *D. siamensis* from SaraBuri and Nakhon Ratchasima province, Vietnam; 13 *D. vietnamensis* from Khanh Hoa Province, Vietnam; 14 *D. muangfuangensis* sp. nov. from Vientiane Province, Laos; 15 *D. gialaiensis* sp. nov. from Gia Lai Province, Vietnam.

The specimens have been deposited in the collection of the Vietnam National University of Forestry (**VNUF**), Hanoi, Vietnam and the National University of Laos (**NUOL**), Vientiane, Laos.

Species delimitation

The general lineage concept (GLC: de Queiroz 2007) adopted herein proposes that a species constitutes a population of organisms evolving independently from other such populations owing to a lack of, or limited gene flow. By "independently," it is meant that new mutations arising in one species cannot spread readily into another species (Barraclough et al. 2003; de Queiroz 2007). Molecular phylogenies recovered multiple monophyletic mitochondrial lineages of individuals (populations) that were used to develop initial species-level hypotheses, the grouping stage of Hillis (2019). Discrete color pattern data and univariate and multivariate analyses of morphological data were then used to search for characters and morphospatial patterns consistent with the tree-designated species-level hypotheses, the construction of boundaries representing the hypothesistesting step of Hillis (2019), thus providing independent diagnoses to complement the molecular analyses. In this way, delimiting (phylogeny) and diagnosing (taxonomy) species are not conflated (Frost and Hillis 1990; Frost and Kluge 1994; Hillis 2019).

Molecular data and phylogenetic analyses

Four samples of the newly collected specimens were analyzed, two from Gia Lai Province, Vietnam (VNUF R.2020.22 - field number GL.02, VNUF R.2020.33 - field number GL.03) and two from Vientiane Province, Laos (VNUF R.2022.42 - field number MF.02, VNUF R.2022.52 - field number MF.03). We used the protocols of Nguyen et al. (2021) for DNA extraction, amplification, and sequencing. The complete NADH dehydrogenase subunit 2 (ND2) gene with six partial or complete adjacent tRNAs, approximately 1200 bp long, respectively, were amplified and sequenced using the primer pair, MetF1(5'-AAGCTTTCGGGCCCATACC-3') and COIR1(5'-AGRGTGCCAATGTCTTTGTGRTT-3') (Macey et al. 1997). Genomic DNA was extracted from all liver tissues stored in ethanol following the standard protocols of DNeasy blood and tissue kit, Qiagen (California, USA). The PCR volume consisted of 20 μ l (1 μ l each primer, 7 μ l water, 10 μ l of Taq mastermix and 1 μ l DNA template). PCR conditions were: 95 °C for 5 min, followed by 42 cycles: 95 °C for 30 s, 50 °C for 45 s and 72 °C for 60 s with a final elongation step for 6 min at 72 °C. PCR products were visualized using electrophoresis through a 1.2% agarose gel, marker 100 bp, 1X TAE and stained with RedSafe Nucleic Acid Staining Solution and photographed under UV light of Geldoc system (Quantum CX5, Villber, France). Successful amplifications were purified using innuPREP Gel Extraction Kit (Analytik Jena, Germany). Cleaned PCR products were sent to 1st Base (Malaysia) for sequencing in both directions.

We obtained 1,444 base pairs of NADH dehydrogenase subunit 2 gene (ND2) sequence data and the flanking tRNAs from 29 ingroup individuals of *Dixonius*

representing 13 nominal species including the new samples from Vietnam and Laos. *Heteronotia spelea* was used as an outgroup to root the tree based on the phylogenetic results generated by Gamble et al. (2015). Sequence data for other species were acquired from GenBank. Newly generated sequences were deposited in GenBank (Table 1).

Maximum likelihood (ML) and Bayesian inference (BI) were used to estimate phylogenetic trees. Best-fit models of evolution determined in IQ-TREE (Nguyen et al. 2015) using the Bayesian information criterion (BIC) implemented in ModelFinder (Kalyaanamoorthy et al. 2017) indicated that F81+F was the best-fit model of evolution for the tRNAMET and K2P+I, and HKY+F+G4 were the best models of evolution for tRNAs2 and ND2, respectively. The ML analysis was performed using the IQ-TREE webserver (Trifinopoulos et al. 2016) with 1000 bootstrap pseudoreplicates using the ultrafast bootstrap (UFB) analysis (Minh et al. 2013; Hoang et al. 2018). The BI analysis was performed on CIPRES Science Gateway (Miller et al. 2010) using MrBayes v. 3.2.4 (Ronquist et al. 2012). Two independent runs were performed using Metropolis-coupled Markov Chain Monte Carlo (MCMCMC), each with four chains: three hot and one cold. The MCMCMC chains were run for 80,000,000 generations with the cold chain sampled every 8000 generations and the first 10% of each run being discarded as burn-in. The posterior distribution of trees from each run was summarized using the sumt function in MrBayes v. 3.2.4 (Ronquist et al. 2012). Stationarity was checked with Tracer v. 1.6 (Rambaut et al. 2014) to ensure effective sample sizes (ESS) for all parameters were well above 200. We considered Bayesian posterior probabilities (BPP) of 0.95 and above and ultrafast bootstrap support values (UFB) of 95 and above as an indication of strong nodal support (Huelsenbeck et al. 2001; Minh et al. 2013). Uncorrected pairwise sequence divergences (p-distance) were calculated in MEGA 11 (Kumar et al. 2016) using the complete deletion option to remove gaps and missing data from the alignment prior to analysis.

A time-calibrated Bayesian phylogenetic tree was estimated using BEAST 2 (Bayesian Evolutionary Analysis by Sampling Trees) v. 2.7.3 (Drummond et al. 2012) implemented in CIPRES (Cyberinfrastructure for Phylogenetic Research; Miller et al. 2010) where the ingroup node subtending the split between Dixonius aaronbaueri and the remaining species was given a 24.04 mya prior with an offset range of 20.23–27.68 mya following Gamble et al. (2015). The split between Heteronotia and Dixonius was set at 45.0 mya with an offset range of 33.3–56.8 mya (Gamble et al. 2015). An input file was constructed in BEAUti (Bayesian Evolutionary Analysis Utility) v. 2.7.3. An optimized relaxed clock with unlinked site models, linked clock models and linked trees, and a calibrated Yule prior were employed for the species level. BEAST Model Test (Bouckaert and Drummond 2017), implemented in BEAST, was used to numerically integrate over the uncertainty of substitution models while simultaneously estimating phylogeny using Markov chain Monte Carlo (MCMC). MCMC chains were run for 80 million generations and logged every 8,000 generations. The BEAST log file was visualized in Tracer v. 1.7.2 (Rambaut et al. 2014) to ensure effective sample sizes (ESS) were above 200 for all parameters. A maximum clade credibility tree using mean heights at the nodes was generated using TreeAnnotator v. 2.7.3 (Rambaut and

Species	Catalog no.	Location	GenBank no.
Dixonius aaronbaueri	ZFMK87274	Nui Chua NP, Ninh Thuan Province, southern Vietnam	HM997152
Dixonius gialaiensis sp. nov.	VNUF R.2020.22	Chu Se District, Gia Lai Province, Vietnam	OQ819041
	(Field no. GL.02)		
	VNUF R.2020.33	Chu Se District, Gia Lai Province, Vietnam	OQ8190412
	(Field no. GL.03)		
Dixonius lao	VNUF R.2016.2	Khammouane Province, Laos	MT024681
	IEBR A.2019.5	Khammouane Province, Laos	MT024683
	IEBR A.2019.6	Khammouane Province, Laos	MT024682
Dixonius melanostictus	VU 022	Captive, Thailand	HM997153
Dixonius minhlei	ZFMK 97745	Vinh Cuu, Dong Nai Province, Vietnam	KX379194
Dixonius muangfuangensis sp. nov.	VNUF R.2020.42	Muangfuang District, Vientiane Province, Central Laos	OQ818586
	(Field no. MF02)		
	VNUF R.2020.52	Muangfuang District, Vientiane Province, Central Laos	OQ818587
	(Field no. MF03)		
Dixonius cf. siamensis	VU 023	Captive, Thailand	KX379195
Dixonius siamensis	LSUHC 7328	Phnom Aural, Purset Province, Cambodia	EU054299
	FMNH 263003	Keo Seima District, Mondolkiri- Province, Cambodia	EU054298
	LSUHC 7378	Phnom Aural, Purset Province, Cambodia	KP979732
Dixonius somchanhae	VNUF R.2020.2	Nasaithong District, Vientiane Capital, Laos	MW605166
	VNUF R.2020.1	Nasaithong District, Vientiane Capital, Laos	MW605165
	VNUF R.2020.3	Nasaithong District, Vientiane Capital, Laos	MW605167
	VNUF R.2020.55	Vientiane Capital, Laos	OQ818589
	(Field no. VT05)		
	VNUF R.2020.54	Vientiane Capital, Laos	OQ818588
	(Field no. VT04)		
	VNUF R.2020.59	Vientiane Capital, Laos	OQ818591
	(Field no.VT09)		
	VNUF R.2020.56	Vientiane Capital, Laos	OQ818590
	(Field no. VT0T06)		
Dixonius sp.	LSUHC 9466	Sai Yok, Kanchanaburi Province, Thailand	KX379196
Dixonius taoi	ZFMK 96680	Phu Quy Island, Binh Thuan Province, Vietnam	KP979733
	CAS 257300	Phu Quy Island, Binh Thuan Province, Vietnam	KP979734
	IEBR A 2014-26	Phu Quy Island, Binh Thuan Province, Vietnam	KP979735
	IEBR A 2014-27	Phu Quy Island, Binh Thuan Province, Vietnam	KP979736
Dixonius cf. vietnamensis	ZFMK 87273	Nui Chua, Ninh Thuan Province, Vietnam	KX379201
Dixonius vietnamensis	IEBR R.20163	Nha Trang, Khánh Hòa Province, Vietnam	KX379198

Table 1. List of specimens used for the phylogenetic analyses.

Drummond 2013) with a burn-in of the first 10% of each run. Nodes with Bayesian posterior probabilities (BPP) of 0.95 and above were considered strongly supported (Huelsenbeck et al. 2001; Wilcox et al. 2002).

Morphological data and analysis

The morphological data set comprised six closely related species including six type specimens of *Dixonius minhlei* from Dong Nai Province, Vietnam (IEBR A.0801-02, VNMN R.2016.1-2, ZFMK 97745-46), three type specimens of *D. lao* from Khammouane Province, Laos (VNUF R.2016.2, IEBR A.2016.5-6), eight specimens of *D. siamensis* from Pursat Province, Cambodia (LSUHC 07328, 07378, 08420, 08487,

08491, 08522, 09284, 09289), five type specimens of *D. somchanhae* from Vientiane Capital, Laos (VNUF R.2020.1-5), four specimens of *D.* sp. from Gia Lai Province, Vietnam, and 12 specimens of *D. vietnamensis* from Nha Trang Province, Vietnam (ZRC 2.6024-27, IEBR R.2016.1, 2016.3, 2016.4, VNMN R.2016.3-4, ZFMK 97747-49).

Morphological data included both meristic and morphometric characters. Morphological characters were taken from the 44 specimens following Bauer et al. (2004) and Ngo and Ziegler (2009). Morphometric characters were taken after preservation with a digital caliper to the nearest 0.1 mm under a zoom stereomicroscope on the right/left of the body. Recorded data included: SVL: snout-vent length (taken from the tip of the snout to the vent), **TaL**: tail length (taken from the vent to the tip of the tail, original or partially regenerated), TW: tail width (taken at the base of the tail immediately posterior to the postcloacal swelling), BW: body width (greatest width of torso, taken at the level of midbody), HL: head length (the distance from the posterior margin of the retroarticular process of the lower jaw to the tip of the snout), HW: head width (the distance from the posterior margin of the retroarticular process of the lower jaw to the tip of the snout), HD: head depth (the maximum height of head measured from the occiput to base of the lower jaw), EL: ear length (greatest oblique length across the auditory meatus), TBL: Tibia length (taken on the ventral surface from the posterior surface of the knee while flexed 90° to the base of the heel), AG: axilla to groin length (taken from the posterior margin of the forelimb at its insertion point on the body to the anterior margin of the hind limb at its insertion point on the body), FA: forearm length (taken on the ventral surface from the posterior margin of the elbow while flexed 90° to the inflection of the flexed wrist), ED: eye diameter (the greatest horizontal diameter of the eye-ball), EN: eye nostril distance (measured from the anterior margin of the bony orbit to the posterior margin of the external nares), ES: eye snout distance (measured from anteriormost margin of the bony orbit to the tip of snout), **EE**: eye ear distance (measured from the anterior edge of the ear opening to the posterior edge of the bony orbit), IN: internarial distance (measured between the external nares across the rostrum), **IO**: interorbital distance (measured between the dorsal-most edges of the bony orbits).

Meristic data taken were: V: ventral scales (counted transversely across the abdomen midway between limb insertions from one ventrolateral fold to the other), **DTR**: longitudinal rows of dorsal tubercles (counted transversely across the body midway between the limb insertions from one ventrolateral body fold to the other), **PV**: paravertebral scales (counted in a paravertebral row from first scale posterior to parietal scale to last scale at the level of vent opening), **PV**': paravertebral scales (counted in a row between limb insertions), **T4**: lamellae under fourth toe (counted from the distal scale containing claw to basal scale that broadly contacts adjacent fragmented scales), **IOS**: Interorbital scales (counted at narrowest point between orbits), **ICS**: interciliary scales (counted between supraciliaries at midpoint of orbit), **SPL**: supralabials (counted from the largest scale at the corner of the mouth to the rostral scale), **IFL**: infralabials (counted from termination of enlarged scales at the corner of the mouth to the mental scale), **MO**: number of supralabial at midorbital position, **PP**: precloacal pores in males. Color pattern on dorsum including the presence or absence of canthal stripes (**CanthStrp**), the presence or absence of strong darkly barred lips (**LipBar**), the presence or absence of dark-colored round blotches on the top of the head (**RdHdBlch**) and dorsum (**RdBodBlch**), and the presence or absence of two regularly arranged whitish tubercles on flanks (**Tub**). The raw morphological data for all characters and specimens are presented in Tables 2, 3.

All statistical analyses were performed using R v. 4.2.1 (R Core Team, 2021). Morphometric characters used in the statistical analyses were SVL, BW, HL, HW, HD, EL, ED, EN, ES, EE, IN, IO, FAr, TBLr, and AGr. Tail metrics were not used due to the high degree incomplete sampling (i.e., regenerated, broken, or missing). To remove potential effects of allometry on morphometric traits (sec. Chan and Grismer 2022), we used the following equation: $Xadj = log(X) - \beta[log(SVL) - log(SVLmean)]$, where Xadj = adjusted value; X = measured value; β = unstandardized regression coefficient for each population; and SVLmean = overall average SVL of all populations (Thorpe 1975, 1983; Turan 1999; Lleonart et al. 2000, accessible in the R package GroupStruct (available at https://github.com/chankinonn/ GroupStruct). The morphometrics of each species were normalized separately and then concatenated into a single data set so as not to conflate potential intra- with interspecific variation (Reist 1986; McCoy et al. 2006). All data were scaled to their standard deviation to ensure they were analyzed on the basis of correlation and not covariance. Meristic characters (scale counts) used in statistical analyses were SPLr/l, IFLr/l, MO, IOS, ICS, V, DTR, and T4r/l. Precloacal and femoral pores were omitted from the analyses due to their absence in females. Categorical characters analyzed were CanthStrp, LipBar, RdHdBlch, RdBodBlch, and Tub.

A Levene's test for normalized morphometric and meristic characters was conducted to test for equal variances across all groups. Analyses of variance (ANOVA) were conducted on meristic and normalized morphometric characters (see below) with statistically similar variances to search for the presence of statistically significant mean differences (p < 0.05) among species across the data set. Characters bearing statistical differences were subjected to a TukeyHSD test to ascertain which species pairs differed significantly from each other for those particular characters. Boxplots were generated for discrete meristic characters in order to visualize the range, mean, median, and degree of differences between pairs of species bearing statistically different mean values and violin plots were generated for continuous morphometric characters to visualize the same.

Morphospatial positions were visualized using principal component analysis (PCA) from the ADEGENET package in R (Jombart et al. 2010) to determine if their positioning was consistent with the putative species boundaries delimited by the molecular phylogenetic analyses and defined by the univariate analyses (see above). PCA, implemented using the "prcomp()" command in R, is an indiscriminate analysis plotting the overall variation among individuals (i.e., data points) while treating each individual independently (i.e., not coercing data points into pre-defined groups). Subsequent to the PCA, a discriminant analysis of principle components (DAPC) was used to test

Species	Museum no.	Sex	1	N	Aeristi	ic data	ι				Categori	ical data	
			SPL	IFL	MO	IOS	V	T4	Canthal	Lips	Blotches	Blotches	Two regularly
			r/l	r/1				r/l	stripe	strong	on the head	on dorsum	disposed
										barred	round	round	whitish
													tubercles on
													each side of the
	1EBD 4 0902		0	6	6	10	22	1.4					папкя
minmei	7EMK 07746	m	0	65	6	10	22	14	present	no	yes	yes	absent
	LEBD A 0801	f f	0	0.5	6	10	25	14.)	present	110	yes	yes	absent
	7EMK 07745	ſ	0.)	6	55	10	22	12	present	110	yes	yes	absent
	VNIMN P 2016 1	L L	/.)	6	5.5	0	23	15	present	110	yes	yes	absent
	VINIMIN R.2010.1	f I	0	65	5.5	0	20	13	present	no	yes	yes	absent
aialaiancic	VNUE P 2020 22	m	75	6	6	7	20	1/	present	TIO	yes	yes	precent
sp. nov	VNUE R 2020.22	f	7.5	6	6	7	10	14	present	yes	yes	yes	present
op: 110 11	VNUE R 2020.33	1 mi	2	7	6	7	21	14	present	yes	yes	yes	present
nietnamencic	7RC 2 6024	m	5	6	5	10	20	14.)	present	905	yes	yes	present
vicinamensis	ZRC 2.6024	m	5	6	5	9	20	13	present	10	110	110	present
	ZRC 2.6025	:	5	6	6	9	20	13	present	no	110	110	present
	ZRC 2.6020) i	6	7	6	8	20	13	present	110	110	110	present
	IEBR R 2016 3)	8	6	55	10	19	13.5	present	no	110	110	present
	VNMN R 2016 3	m	75	6	5.5	9	19	13.5	present	no	10	10	present
	IFBR R 2016 1	f	7.5	6	5.5	8	18	13.5	present	no	no	no	present
	VNMN R 2016 4	f	75	7	6	9	20	13.5	present	no	10	10	present
	ZEMK 97748	f	7.5	6	6	8	20	14	present	no	no	no	present
	ZEMK 97747	mi	7.5	6	55	10	15	13.5	present	no	no	no	present
	IEBR R 2016 4	fi	8	7	6	7	21	12.5	present	no	no	no	present
	ZEMK 97749	fi	7	65	55	8	19	13.5	present	no	no	no	present
sp.	VNUF R.2022.81	m	8	6.5	6	9	24	14	present	no	no	ves	present
.1	VNUF R.2022.82	f	7.5	5.5	6	8	23	14.5	present	no	no	ves	present
	VNUF R.2022.83	fi	8	7	6	8	23	14	present	no	no	ves	present
	VNUF R.2022.84	fi	8.5	6	6	8	22	13.5	present	no	no	ves	present
somchanhae	VNUF R.2020.3	m	7	5	6	8	24	14	present	ves	no	no	present
	VNUF R.2020.2	m	8	6	6	8	23	15	present	ves	no	no	present
	VNUF R 2020 1	m	8	55	6	8	23	15	present	ves	no	no	present
	VNUF R 2020 4	f	8	5.5	6	8	23	15	present	ves	no	no	present
	VNUF R.2020.5	f	8	6	6	7	26	13	present	ves	no	no	present
siamensis	LSUHC09284	f	8	7	6	9	19	14	absent	ves	no	ves	present
	LSUHC08522	f	8	65	6	10	22	14.5	absent	ves	no	ves	present
	LSUHC08487	f	8	7	6	10	20	14.5	absent	ves	no	ves	present
	LSUHC08420	m	85	7	6	10	21	13	absent	ves	no	ves	present
	LSUHC08491	f	8	7	6	9	20	14.5	absent	ves	no	ves	present
	LSUHC07328	i	75	6	55	9	20	14	absent	ves	no	ves	present
	LSUHC07378)	8	6	6	10	20	14 5	absent	ves	110	yes	present
	LSUHC09289	m	75	6	6	10	20	14.5	absent	Vec	10	yes	present
maranafu anamaic	NUOL R 2022 01	m	7.5	6.5	6	7	21	15	absent	yes	110	ycs	present
sp. nov.	VNLIF R 2020 42	m	/	7	6	7	20	15	absent	yes	110	110	present
-r.	VNILIE R 2020.42	f	8	65	6	7	20	15	absent	yes	10		present
100	VNILIE P 2016 2	m	95	8	75	0	21	15	absent	yes	10		abcont
uw	IFRR A 2010.5	f III	9.5	0	7.5	9	23	15	absent	yes	110	110	absent
	IEBR A 2010 (1 £	0.7	0	0	0	23	15	absent	yes	110	110	absent
	1EDIC A.2019.0	1	2	1.1	0	0	24t	1)	ausent	yes	110	10	ausein

Table 2. Sex and raw meristic and categorical data used in the analyses from specimens of *Dixonius* from Vietnam and Laos. m = male; f = female; j = juvenile; r/l = right/left.

Table 3. Sex and raw	v morphometric o	lata use	d in the	analyse	s from s	pecimer	1s of <i>Di</i>	<i>conius</i> fr	om Viet	nam an	d Laos.	m = ma	le; f = fe	:male; j	= juveni	le.	
Species	Museum no.	Sex	SVL	BW	HL	ΜH	ЦIJ	EL	ED	EN	ES	EE	ZI	OI	FAr	TBLr	AGr
minhlei	IEBR A.0802	ш	43.9	9.4	7.3	7.7	4.7	1.5	2.7	3.7	5	3.5	1.6	4	6.2	7.7	18.7
	ZFMK 97746	ш	40.6	8.5	6.7	6	4.3	1.3	2.2	3.2	4.4	3.6	1.3	3.5	6.7	7	18.2
	IEBR A.0801	f	45.9	9.7	7.2	6.6	5.2	1.2	3.3	3.4	4.4	3.4	1.5	3.7	5.9	7.2	21.2
	ZFMK 97745	f	47.5	9.6	7.6	6.8	4.7	1.5	3.1	3.5	4.9	3.9	1.5	3.7	9	7.3	21.5
	VNMN R.2016.1	f	43.3	9.3	7.1	6.5	4.4	1.3	2.5	3.5	4.6	3.8	1.5	3.8	6.1	7.5	20.6
	VNMN R.2016.2	f	46.7	9.2	7.7	6.2	4.6	1.2	3.1	3.8	5.2	3.6	1.5	3.4	6.6	7	30.3
gialaiensis sp. nov.	VNUF R.2020.22	ш	41.2	8.6	11.7	7.7	5.2	1.1	2.9	3.1	4.3	3.3	1.3	1.2	6.1	6.9	15.8
	VNUF R.2020.33	f	47.4	8.4	12.3	8.8	6.1	1.3	3.3	3.5	4.8	3.5	1.5	1.4	6.3	7.7	21.8
	VNUF R.2020.44	mj	35.9	8.3	10.9	6.8	4.7	0.9	2.6	2.9	3.8	3	1.3	1.3	4.5	5.6	14
vietnamensis	ZRC 2.6024	ш	40.8	∞	7.5	7.9	5.5	-	2.9	3.2	4.3	3.8	2.1	3.6	5.6	7.7	21
	ZRC 2.6025	ш	42.4	9.1	7.5	7.6	9	1.1	2.9	3.7	4.6	4	1.6	3.6	6.2	7.2	21
	ZRC 2.6026		26.6	5.4	5.4	5.2	4	0.6	2.1	2.2	3	2.5	1.1	2.7	4.4	4.4	13
	ZRC 2.6027	:	25.9	4	5.2	5.1	3.3	0.6	1.8	2.3	3.5	2.2	0.9	2.1	4	4.6	11.8
	IEBR R.2016.3	ш	39	6.5	6.9	6.8	4.2	1.1	2.8	2.9	3.9	3.1	1.1	1.6	4.7	6.5	14.8
	VNMN R.2016.3	ш	39.9	7.8	7.2	7	4.7	0.8	2.5	3.4	4.6	3.3	1.3	1.7	5.2	6.5	16.6
	IEBR R.2016.1	f	43.5	7.6	7.6	6.9	4.7	1	2.7	3.1	4.5	2.7	1.3	1.6	Ś	6.2	19.2
	VNMN R.2016.4	f	43.7	8.6	7.7	7.7	4.7	1.1	2.8	3.4	4.7	3.6	1.3	1.8	5.5	6.3	18.2
	ZFMK 97748	f	45.2	10.3	8.5	8.2	5.7	1.3	2.9	3.8	5.4	4.3	1.5	2.7	5.5	9.9	19.2
	ZFMK 97747	mj	34.1	4.7	6.2	5.7	4.1	0.9	2.3	2.7	3.6	2.5	1.2	1.3	4.2	5.9	12.3
	IEBR R.2016.4	fj	31.2	5.2	5.7	5.8	3.7	0.9	2.4	2.4	3.4	2.4	1	1.2	3.1	4.8	11.9
	ZFMK 97749	ţ)	29.2	4.8	5.2	4.8	3.1	0.9	2.5	2.1	2.9	2.3	1	1.2	3.1	4.9	11.1
sp.	VNUF R.2022.81	ш	46	10.7	13.7	7.8	5.7	1.4	2.2	3.4	4.8	3.7	1.7	1.9	5.5	6.8	20.2
	VNUF R.2022.82	f	35.2	7.5	10.9	6.9	3.3	1.1	2.1	2.9	4.1	3.2	1.3	1.6	4.7	6.2	14.2
	VNUF R.2022.83	ý	31.1	5.1	9.2	5.1	2.4	1.2	2.2	2.3	2.3	2.5	1.1	1.4	4.5	5.1	12.5
	VNUF R.2022.84	ť j	30.3	5.6	6.3	5.8	3	8.0	2	2.7	3.4	2.9	1.1	1.5	3.7	4.6	13.3
somchanhae	VNUF R.2020.3	ш	43.8	9.4	12.2	8.5	5.6	1.6	3.4	ĉ	5.1	3.4	1.3	1.7	6.2	7.3	20.5
	VNUF R.2020.2	ш	47.1	11.1	12.9	9.7	5.9	1.9	3.3	3.4	5	3.5	1.6	1.8	5.6	8	19.5
	VNUF R.2020.1	ш	39.8	8.9	11.6	7.9	5.2	1.2	2.9	2.9	4.2	3.1	1.7	1.3	4.8	9.9	17.4
	VNUF R.2020.4	f	35.5	9.4	9.7	6.9	4.2	1.2	2.2	2.8	3.7	2.5	1.2	1.4	4.3	5.5	15.5
	VNUF R.2020.5	f	39.9	8.9	11.4	7.6	4.4	1.5	3.1	2.6	4	3.1	1.5	1.3	4.9	9	19.7
siamensis	LSUHC09284	f	45.4	8.6	12.8	8.7	5.2	1.6	3	3.7	5.1	4	2	3.6	6.7	7.3	19
	LSUHC08522	f	44.1	9.4	12.5	8.1	5.7	1.4	2.4	4.4	5.2	4.5	1.8	3.7	6.7	6.9	21.2
	LSUHC08487	f	48.6	10.7	14.3	8.7	5.4	1.6	3.2	3.4	5.4	4.2	1.7	3.5	7.1	8	21.8

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		-		1.10	1414		11111	-			TAT	0		TAT.	4		TUT	4
opectes	I MIUSCUIII I		3CX	JVL	PW		N LI		3			3			2	Ŀ	IDLI	IDN
siamensis	LSUHC08-	420	в	46.9	8.8	13.1	9.1	5.3	1.3	2.7	3.7	5.3 .	3.9	1.5	3.7	6.7	7.3	20.7
	LSUHC08-	491	f	45.2	10.2	13	8.2	5.7	1.4	2.8	3.3	4.7	4.2	2	3.7	6.2	6.9	19
	LSUHC07.	328		28.6	5.8	8.4	5.5	3	0.7	2.1	2.4	3.3	2.8	1.5	2.8	3.8	2	12
	LSUHC07	378	н	36.7	6.5	10.9	7.3	4.5	1.3	2.6	3.1	4.6	3.4	1.6	3.4	9	6.6	16.1
	LSUHC09.	289	в	45.3	9.1	12.7	8.6	5.1	1.6	2.6	3.7	5	3.6	2	3.5	7	7.3	18.9
muangfuangensis sp. nov.	NUOL R.20:	22.01	в	38.3	7.83	10.5	7.2	4.3	0.8	2.4	2.8	3	3.4	1.3	1.7	4.3	4.9	16.5
	VNUF R.202	20.42	Е	55.6	11.93	15.2	10.8	6.9	2.3	3	3.8	5.9	5.1	1.6	2.3	6.8	7.2	23.1
	VNUF R.202	20.52	f	56.7	12.23	16.7	10.7	6.9	2.1	3.5	3.8	5.8	5.1	1.7	2.4	7.1	7.3	27.4
lao	VNUF R.20	016.2	н	50.1	9.7	14.1	9.2	5.3	1.4	3.6	4.4	5.6 4	4.1	1.7	1.7	6.9	7.6	20.6
	IEBR A.201	19.5	f	55.4	11.5	14.3	9.7	6.2	1.7	3.6	4	5.5	4.4	1.8	1.5	7.1	8.5	22.2
	IEBR A.201	19.6	f	35.8	7.2	9.6	7	4	1.1	2.7	2.8	3.6	2.6	1.1	1.1	4.6	5.9	15.2
	Dixonius sp. c	cf. siamen.	sis aaroı	nbaueri	taoi	vietnamen	nsis cf. m	ietnamensi	is muang	fuangensis nov.	i lao	minblei	gialaie sp. nu	ensis sia ov.	mensis s	omchanha	te melan	ostictus
Dixonius sp.	n/a																	
cf. siamensis	6.33	n/a																
aaronbaueri	18.52	18.37	T	n/a														
taoi	11.49	13.16	16	6.07	0.01													
vietnamensis	12.12	13.67	15	8.84	6.58.	n/a												
cf. vietnamensis	12.12	12.43	15	8.31	7.36	2.57		n/a										
muangfuangensis sp. nov.	10.78	8.17	16	8.17	11.36	12.79		12.50	9	00.0								
lao	8.46	9.26	16	6.66	10.90	11.90		11.39	(1)	3.10	0.00							
minhlei	13.97	15.33	17	7.56.	13.35	14.13		13.92	1.	3.23	13.24	n/a						
gialaiensis sp. nov.	13.51	14.27	15	5.73	11.78	13.40		13.18	1.	3.11	10.90	3.60	0.0	0				
siamensis	13.71	14.83	16	6.14	11.74	12.33		12.22	1.	2.70	11.96	12.54	10.5	99	00.0			
somchanhae	13.31	12.66	17	7.73	12.90	12.57		12.40	1.	2.40	12.27	12.24	10.6	53 5	.07	0.00		
melanostictus	13.30	13.04	15	5.16	11.23	13.12		13.01	1	1.99	10.70	14.09	11.5	i3 1	2.10	11.09	I	u/a

for corroboration and further discrimination of morphospatial differences among the putative species. DAPC a priori groups the individuals of each predefined population inferred from the phylogeny into separate clusters (i.e., plots of points) bearing the smallest within-group variance that produce linear combinations of centroids having the greatest between-group variance (i.e., linear distance; Jombart et al. 2010). DAPC relies on standardized data from its own PCA as a prior step to ensure that variables analyzed are not correlated and number fewer than the sample size. Principal components with eigenvalues accounting for 90–95% of the variation in the data set were retained for the DAPC analysis according to the criterion of Jombart et al. (2010).

To test and further corroborate the PCA and DAPC analyses, we conducted a multiple factor analysis (MFA) on the above-mentioned morphological characters plus the categorical color pattern differences for a near total evidence data set (see Tables 5, 6). The MFA was implemented using the *mfa()* command in the R package FactorMineR (Husson et al. 2017) and visualized using the Factoextra package (Kassambara and Mundt 2017). MFA is a global, unsupervised, multivariate analysis that incorporates qualitative and quantitative data (Pagès 2015), making it possible to analyze different data types simultaneously in a nearly total evidence environment. In an MFA, each individual is described by a different set of variables (i.e., characters) which are structured into different data groups in a global data frame, in this case, quantitative data (i.e., meristics and normalized morphometrics) and categorical data (i.e., color pattern). In the first phase of the analysis, separate multivariate analyses are carried out for each set of variables, principal component analyses (PCA) for the quantitative data sets and multiple correspondence analysis (MCA) for categorical data. The data sets are then normalized separately by dividing all their elements by the square root of their first eigenvalues. For the second phase of the analysis, the normalized data sets are concatenated into a single matrix for a global PCA of the data. Standardizing the data in this manner prevents one data type from overleveraging another. In other words, the normalization of the data in the first phase prevents data types with the highest number of characters or the greatest amount of variation from outweighing other data types in the second phase. This way, the contribution of each data type to the overall variation in the data set is scaled to define the morphospatial distance between individuals as well as calculating each data type's and each character's contributions to the overall variation in the data set (Pagès 2015; Kassambara and Mundt 2017).

Results

Molecular results

The results of ML, BI, and BEAST analyses produced trees with identical topologies and strong support at nearly every node (Figs 2, 3). The molecular analyses suggest that *Dixonius aaronbaueri* is the sister species to a clade containing all other species of *Dixonius*. Additionally, all analyses recovered the newly discovered population from

	PC1	PC2	PC3	PC4	PC5	PC6	PC7
Standard deviation	3.01003227	1.685877698	1.23949927	1.189032683	1.136318219	0.950656207	0.922402779
Proportion of Variance	0.43144	0.13534	0.07316	0.06732	0.06149	0.04304	0.04052
Cumulative Proportion	0.43144	0.56678	0.63994	0.70727	0.76875	0.81179	0.85231
eigen	9.060294267	2.842183612	1.53635844	1.413798721	1.291219096	0.903747223	0.850826887
SVL	-0.183137642	0.011423135	-0.069418522	0.076025214	-0.119546371	0.451176774	-0.589642945
BW	-0.287276767	0.064974951	0.187163981	-0.199453201	0.019777911	-0.133068566	-0.114357041
HL	-0.222534372	0.251387029	0.23514022	0.300194841	0.119329084	-0.056134295	0.150350725
HW	-0.264923454	0.100856053	0.274888978	0.257153297	-0.193697896	-0.025433828	0.20364848
HD	-0.239223187	-0.126312635	0.224210506	-0.024761051	-0.413575793	0.029259717	0.233903564
EL	-0.2480955	0.169750915	0.178082873	0.002208353	0.210266124	0.137233441	-0.232577889
ED	-0.202876478	0.122593123	0.079950567	-0.239727042	-0.47584928	0.235373894	-0.048044975
EN	-0.265593548	-0.130857091	-0.293077474	0.03772842	0.029146276	-0.105240363	0.142115916
ES	-0.267303156	-0.128737264	-0.102433066	-0.036514974	-0.068578553	-0.009743264	0.195931987
EE	-0.276238196	-0.150072094	-0.016576264	0.149081788	0.006956725	-0.271219422	-0.084638951
IN	-0.239210846	-0.181935095	0.070874242	0.114696597	0.170327297	0.022503069	0.138746934
Ю	-0.131045671	-0.460675273	-0.164479294	-0.032535496	0.242758327	-0.169473493	-0.152061581
FAr	-0.279019143	-0.171574811	-0.122828868	-0.090763378	0.096076353	-0.023168457	0.04857391
TBLr	-0.256167278	-0.099347048	-0.096744886	-0.219547386	0.043230096	0.332696024	0.101539921
AGr	-0.262180808	-0.1304743	0.000207287	-0.261650023	-0.044763987	-0.216118201	-0.26353247
SPLr.1	-0.138456955	0.383331303	-0.225322477	0.206591458	0.113507526	0.110869199	-0.176892801
IFLr.l	-0.089464182	0.168661032	-0.585083828	0.180041929	-0.237863864	-0.199925005	-0.127174583
МО	-0.156905954	0.393579439	-0.305813247	0.010226561	-0.089299256	-0.164453012	0.254918394
IOS	-0.068091843	-0.230600144	0.078301763	0.673617186	0.047911701	0.164434462	-0.062199104
V	-0.140473075	0.310134826	0.27924011	-0.11493361	0.255279707	-0.405751544	-0.23957707
T4r.l	-0.152382721	0.157971329	-0.130436885	-0.183960387	0.490226326	0.396201891	0.316382072
	DC8	DCO	DC10	DOI1	DC10	DC12	DO1 /
	100	PC9	PCI0	PCII	PC12	PC13	PC14
Standard deviation	0.843138943	0.710443326	PC10 0.614017867	0.525772586	0.515133085	PC13 0.463343505	PC14 0.418149629
Standard deviation Proportion of Variance	0.843138943 0.03385	0.710443326 0.02403	0.614017867 0.01795	0.525772586 0.01316	0.515133085 0.01264	0.463343505 0.01022	PC14 0.418149629 0.00833
Standard deviation Proportion of Variance Cumulative Proportion	0.843138943 0.03385 0.88616	0.710443326 0.02403 0.91019	0.614017867 0.01795 0.92815	0.525772586 0.01316 0.94131	0.515133085 0.01264 0.95395	0.463343505 0.01022 0.96417	PC14 0.418149629 0.00833 0.97249
Standard deviation Proportion of Variance Cumulative Proportion eigen	0.843138943 0.03385 0.88616 0.7108832777	PC9 0.710443326 0.02403 0.91019 0.50472972	PC10 0.614017867 0.01795 0.92815 0.37701794	PCI1 0.525772586 0.01316 0.94131 0.276436812	PC12 0.515133085 0.01264 0.95395 0.265362095	PC13 0.463343505 0.01022 0.96417 0.214687204	PC14 0.418149629 0.00833 0.97249 0.174849113
Standard deviation Proportion of Variance Cumulative Proportion eigen SVL	0.843138943 0.03385 0.88616 0.710883277 0.265288193	PC9 0.710443326 0.02403 0.91019 0.50472972 -0.446853384	PC10 0.614017867 0.01795 0.92815 0.37701794 0.196416397	PC11 0.525772586 0.01316 0.94131 0.276436812 -0.110376596	PC12 0.515133085 0.01264 0.95395 0.265362095 0.139472173	PC13 0.463343505 0.01022 0.96417 0.214687204 -0.13673416	PC14 0.418149629 0.00833 0.97249 0.174849113 0.085656549
Standard deviation Proportion of Variance Cumulative Proportion eigen SVL BW	0.843138943 0.03385 0.88616 0.710883277 0.265288193 0.09057594	PC9 0.710443326 0.02403 0.91019 0.50472972 -0.446853384 -0.129906618	PC10 0.614017867 0.01795 0.92815 0.37701794 0.196416397 -0.173199899	PC11 0.525772586 0.01316 0.94131 0.276436812 -0.110376596 0.177854897	PC12 0.515133085 0.01264 0.95395 0.265362095 0.139472173 0.108703018	PC13 0.463343505 0.01022 0.96417 0.214687204 -0.13673416 -0.085524495	PC14 0.418149629 0.00833 0.97249 0.174849113 0.085656549 -0.103253386
Standard deviation Proportion of Variance Cumulative Proportion eigen SVL BW HL	0.843138943 0.03385 0.88616 0.710883277 0.265288193 0.09057594 -0.070645969	PC9 0.710443326 0.02403 0.91019 0.50472972 -0.446853384 -0.129906618 -0.213980283	PC10 0.614017867 0.01795 0.92815 0.37701794 0.196416397 -0.173199899 -0.087846741	PC11 0.525772586 0.01316 0.94131 0.276436812 -0.110376596 0.177854897 -0.389903504	PC12 0.515133085 0.01264 0.95395 0.265362095 0.139472173 0.108703018 -0.321747003	PC13 0.463343505 0.01022 0.96417 0.214687204 -0.13673416 -0.085524495 -0.17842853	PC14 0.418149629 0.00833 0.97249 0.174849113 0.085656549 -0.103253386 -0.021701889
Standard deviation Proportion of Variance Cumulative Proportion eigen SVL BW HL HW	0.843138943 0.03385 0.88616 0.710883277 0.265288193 0.09057594 -0.070645969 0.039378469	PC9 0.710443326 0.02403 0.91019 0.50472972 -0.446853384 -0.129906618 -0.213980283 -0.022086396	PC10 0.614017867 0.01795 0.92815 0.37701794 0.196416397 -0.173199899 -0.087846741 0.070374143	PC11 0.525772586 0.01316 0.94131 0.276436812 -0.110376596 0.177854897 -0.389903504 0.022285485	PC12 0.515133085 0.01264 0.95395 0.265362095 0.139472173 0.108703018 -0.321747003 0.134276418	PC13 0.463343505 0.01022 0.96417 0.214687204 -0.13673416 -0.085524495 -0.17842853 -0.209651757	PC14 0.418149629 0.00833 0.97249 0.174849113 0.085656549 -0.103253386 -0.021701889 0.058151643
Standard deviation Proportion of Variance Cumulative Proportion eigen SVL BW HL HW HD	0.843138943 0.03385 0.88616 0.710883277 0.265288193 0.09057594 -0.070645969 0.039378469 0.139854316	IC(3) 0.710443326 0.02403 0.91019 0.50472972 -0.446853384 -0.129906618 -0.213980283 -0.022086396 -0.180680891	PC10 0.614017867 0.01795 0.92815 0.37701794 0.196416397 -0.0173199899 -0.087846741 0.070374133 -0.127550531	PC11 0.525772586 0.01316 0.94131 0.276436812 -0.110376596 0.177854897 -0.389903504 0.022285485 0.157737189	PC12 0.515133085 0.01264 0.95395 0.265362095 0.139472173 0.108703018 -0.321747003 0.134276418 -0.027411952	PC13 0.463343505 0.01022 0.96417 0.214687204 -0.13673416 -0.085524495 -0.17842853 -0.209651757 0.137530567	PC14 0.418149629 0.00833 0.97249 0.174849113 0.085656549 -0.103253386 -0.021701889 0.058151643 -0.134451774
Standard deviation Proportion of Variance Cumulative Proportion eigen SVL BW HL HW HD EL	0.843138943 0.03385 0.88616 0.710883277 0.265288193 0.09057594 -0.070645969 0.339378469 0.139854316 -0.203202698	IC(3) 0.710443326 0.02403 0.91019 0.50472972 -0.446853384 -0.129906618 -0.213980283 -0.022086396 -0.180680891 0.278604397	PC10 0.614017867 0.01795 0.92815 0.37701794 0.196416397 -0.087846741 0.070374143 -0.127550531 -0.198153958	PC11 0.525772586 0.01316 0.94131 0.276436812 -0.110376596 0.177854897 -0.389903504 0.022285485 0.157737189 0.402630535	PC12 0.515133085 0.01264 0.95395 0.265362095 0.139472173 0.108703018 -0.321747003 0.134276418 -0.027411952 -0.109054652	PC13 0.463343505 0.01022 0.96417 0.214687204 -0.13673416 -0.085524495 -0.17842853 -0.209651757 0.137530567 -0.264792874	PC14 0.418149629 0.00833 0.97249 0.174849113 0.085656549 -0.103253386 -0.021701889 0.058151643 -0.134451774 0.164044114
Standard deviation Proportion of Variance Cumulative Proportion eigen SVL BW HL HW EL ED	0.843138943 0.03385 0.88616 0.710883277 0.265288193 0.09057594 -0.070645969 0.339378469 0.139854316 -0.203202698 -0.319474696	IC(3) 0.710443326 0.02403 0.91019 0.50472972 -0.446853384 -0.129906618 -0.213980283 -0.022086396 -0.180680891 0.278604397 0.251272882	PC10 0.614017867 0.01795 0.92815 0.37701794 0.196416397 -0.087846741 0.070374143 -0.127550531 -0.198153958 -0.008164379	PC11 0.525772586 0.01316 0.94131 0.276436812 -0.110376596 0.177854897 -0.389903504 0.022285485 0.157737189 0.402630535 0.059050615	PC12 0.515133085 0.01264 0.95395 0.265362095 0.139472173 0.108703018 -0.321747003 0.134276418 -0.027411952 -0.109054652 -0.034208937	PC13 0.463343505 0.01022 0.96417 0.214687204 -0.13673416 -0.085524495 -0.17842853 -0.209651757 0.137530567 -0.264792874 0.225488518	PC14 0.418149629 0.00833 0.97249 0.174849113 0.085656549 -0.103253386 -0.021701889 0.058151643 -0.134451774 0.164044114 0.158104491
Standard deviation Proportion of Variance Cumulative Proportion eigen SVL BW HL HW EL ED EN	0.843138943 0.03385 0.88616 0.710883277 0.265288193 0.09057594 -0.070645969 0.039378469 0.139854316 -0.203202698 -0.319474696 0.295981088	IC(3) 0.710443326 0.02403 0.91019 0.50472972 -0.446853384 -0.129906618 -0.213980283 -0.022086396 -0.180680891 0.278604397 0.251272882 0.09576584	PC10 0.614017867 0.01795 0.92815 0.37701794 0.196416397 -0.173199899 -0.087846741 0.070374143 -0.127550531 -0.0198153958 -0.008164379 0.048312128	PC11 0.525772586 0.01316 0.94131 0.276436812 -0.110376596 0.177854897 -0.389903504 0.022285485 0.157737189 0.402630535 0.059050615 0.019723407	PC12 0.515133085 0.01264 0.95395 0.265362095 0.139472173 0.108703018 -0.321747003 0.134276418 -0.027411952 -0.109054652 -0.034208937 0.172978909	PC13 0.463343505 0.01022 0.96417 0.214687204 -0.13673416 -0.085524495 -0.17842853 -0.209651757 0.137530567 -0.264792874 0.225488518 0.06220716	PC14 0.418149629 0.00833 0.97249 0.174849113 0.085656549 -0.103253386 -0.021701889 0.058151643 -0.134451774 0.164044114 0.158104491 -0.41905017
Standard deviation Proportion of Variance Cumulative Proportion eigen SVL BW HL HW EL ED EN ES	0.843138943 0.03385 0.88616 0.710883277 0.265288193 0.09057594 -0.070645969 0.039378469 0.139854316 -0.203202698 -0.319474696 0.295981088 0.426919556	ICS 0.710443326 0.02403 0.91019 0.50472972 -0.446853384 -0.129906618 -0.213980283 -0.022086396 -0.180680891 0.278604397 0.251272882 0.09576584 0.259878689	PC10 0.614017867 0.01795 0.92815 0.37701794 0.196416397 -0.173199899 -0.87846741 0.070374143 -0.127550531 -0.0198153958 -0.008164379 0.048312128 -0.007215665	PC11 0.525772586 0.01316 0.94131 0.276436812 -0.110376596 0.177854897 -0.389903504 0.022285485 0.157737189 0.402630535 0.059050615 0.019723407 -0.131144367	PC12 0.515133085 0.01264 0.95395 0.265362095 0.139472173 0.108703018 -0.321747003 0.134276418 -0.027411952 -0.034208937 0.172978909 0.25121175	PC13 0.463343505 0.01022 0.96417 0.214687204 -0.13673416 -0.085524495 -0.17842853 -0.209651757 0.137530567 -0.264792874 0.0225488518 0.06220716 -0.129629771	PC14 0.418149629 0.00833 0.97249 0.174849113 0.085656549 -0.103253386 -0.021701889 0.058151643 -0.134451774 0.164044114 0.158104491 -0.41905017 0.403591724
Standard deviation Proportion of Variance Cumulative Proportion eigen SVL BW HL HW EL ED EN ES EE	0.843138943 0.03385 0.88616 0.710883277 0.265288193 0.09057594 -0.070645969 0.039378469 0.139854316 -0.203202698 -0.319474696 0.295981088 0.426919556 0.038959782	Inclusion 0.710443326 0.02403 0.91019 0.50472972 -0.446853384 -0.129906618 -0.213980283 -0.022086396 -0.180680891 0.278604397 0.251272882 0.09576584 0.259878689 -0.113710926	PC10 0.614017867 0.01795 0.92815 0.37701794 0.196416397 -0.087846741 0.070374143 -0.127550531 -0.08164379 0.048312128 -0.007215665 -0.227904855	PC11 0.525772586 0.01316 0.94131 0.276436812 -0.110376596 0.177854897 -0.389903504 0.022285485 0.157737189 0.402630535 0.059050615 0.019723407 -0.131144367 0.339050813	PC12 0.515133085 0.01264 0.95395 0.265362095 0.139472173 0.108703018 -0.321747003 0.134276418 -0.027411952 -0.034208937 0.172978909 0.25121175 -0.133303008	PC13 0.463343505 0.01022 0.96417 0.214687204 -0.13673416 -0.085524495 -0.17842853 -0.209651757 0.137330567 -0.264792874 0.0225488518 0.06220716 -0.129629771 -0.064748891	PC14 0.418149629 0.00833 0.97249 0.174849113 0.085656549 -0.103253386 -0.021701889 0.058151643 -0.134451774 0.164044114 0.158104491 -0.419050172 0.403591724 -0.201696035
Standard deviation Proportion of Variance Cumulative Proportion eigen SVL BW HL HW EL ED EN ES EE IN	0.843138943 0.03385 0.88616 0.710883277 0.265288193 0.09057594 -0.070645969 0.03378469 0.139854316 -0.203202698 -0.319474696 0.295981088 0.426919556 0.03895782 -0.469863359	IC(3) 0.710443326 0.02403 0.91019 0.50472972 -0.446853384 -0.129906618 -0.213980283 -0.022086396 -0.180680891 0.278604397 0.251272882 0.09576584 0.259878689 -0.113710926 -0.267676841	PC10 0.614017867 0.01795 0.92815 0.37701794 0.196416397 -0.173199899 -0.087846741 0.070374143 -0.127550531 -0.08164379 0.048312128 -0.007215665 -0.227904855 -0.188020288	PC11 0.525772586 0.01316 0.94131 0.276436812 -0.110376596 0.177854897 -0.389903504 0.022285485 0.157737189 0.402630535 0.059050615 0.019723407 -0.131144367 0.339050813 -0.317994993	PC12 0.515133085 0.01264 0.95395 0.265362095 0.139472173 0.108703018 -0.321747003 0.134276418 -0.027411952 -0.034208937 0.172978909 0.25121175 -0.13303008 0.412756086	PC13 0.463343505 0.01022 0.96417 0.214687204 -0.13673416 -0.085524495 -0.17842853 -0.209651757 0.137530567 -0.264792874 0.06220716 -0.129629771 -0.064748891 0.253021631	PC14 0.418149629 0.00833 0.97249 0.174849113 0.085656549 -0.103253386 -0.021701889 0.058151643 -0.134451774 0.164044114 0.158104491 -0.41905017 0.403591724 -0.201696035 0.111955286
Standard deviation Proportion of Variance Cumulative Proportion eigen SVL BW HL HW EL ED EN ES EE IN IO	0.843138943 0.03385 0.88616 0.710883277 0.265288193 0.09057594 -0.070645969 0.03378469 0.139854316 -0.203202698 -0.319474696 0.295981088 0.426919556 0.038959782 -0.469863359 -0.122814373	IC(3) 0.710443326 0.02403 0.91019 0.50472972 -0.446853384 -0.129906618 -0.213980283 -0.022086396 -0.180680891 0.278604397 0.251272882 0.09576584 0.259878689 -0.113710926 -0.267676841 0.056652546	PC10 0.614017867 0.01795 0.92815 0.37701794 0.196416397 -0.173199899 -0.087846741 0.070374143 -0.127550531 -0.198153958 -0.008164379 0.048312128 -0.027904855 -0.125361847	PC11 0.525772586 0.01316 0.94131 0.276436812 -0.110376596 0.177854897 -0.389903504 0.022285485 0.157737189 0.402630535 0.059050615 0.019723407 -0.131144367 0.339050813 -0.317994993 0.03792394	PC12 0.515133085 0.01264 0.95395 0.265362095 0.139472173 0.108703018 -0.321747003 0.134276418 -0.027411952 -0.034208937 0.172978909 0.25121175 -0.13303008 0.412756086 0.095742055	PC13 0.463343505 0.01022 0.96417 0.214687204 -0.13673416 -0.085524495 -0.17842853 -0.209651757 0.137530567 -0.264792874 0.06220716 -0.129629771 -0.064748891 0.253021631 -0.182302581	PC14 0.418149629 0.00833 0.97249 0.174849113 0.085656549 -0.103253386 -0.021701889 0.058151643 -0.134451774 0.164044114 0.158104491 -0.41905017 0.403591724 -0.201696035 0.111955286 0.359575483
Standard deviation Proportion of Variance Cumulative Proportion eigen SVL BW HL HW EL ED EN ES EE IN IO FAr	0.843138943 0.03385 0.88616 0.710883277 0.265288193 0.09057594 -0.070645969 0.039378469 0.139854316 -0.203202698 -0.319474696 0.295981088 0.426919556 0.038959782 -0.469863359 -0.122814373 -0.057154891	IC(3) 0.710443326 0.02403 0.91019 0.50472972 -0.446853384 -0.129906618 -0.213980283 -0.022086396 -0.180680891 0.278604397 0.251272882 0.09576584 0.259878689 -0.113710926 -0.267676841 0.056652546 0.014271255	PC10 0.614017867 0.01795 0.92815 0.37701794 0.196416397 -0.087846741 0.070374143 -0.127550531 -0.198153958 -0.008164379 0.048312128 -0.027904855 -0.188020288 -0.125361847 0.303625758	PC11 0.525772586 0.01316 0.94131 0.276436812 -0.110376596 0.177854897 -0.389903504 0.022285485 0.157737189 0.402630535 0.059050615 0.019723407 -0.131144367 0.339050813 -0.317994993 0.03792394 -0.210415667	PC12 0.515133085 0.01264 0.95395 0.139472173 0.108703018 -0.321747003 0.134276418 -0.027411952 -0.109054652 -0.34208937 0.172978909 0.25121175 -0.133303008 0.412756086 0.095742055 -0.567849769	PC13 0.463343505 0.01022 0.96417 0.214687204 -0.13673416 -0.085524495 -0.17842853 -0.209651757 0.137530567 -0.264792874 0.0225488518 0.06220716 -0.129629771 -0.064748891 0.253021631 -0.182302581 -0.191700829	PC14 0.418149629 0.00833 0.97249 0.174849113 0.085656549 -0.103253386 -0.021701889 0.058151643 -0.134451774 0.164044114 0.158104491 -0.41905017 0.403591724 -0.201696035 0.111955286 0.359575483 -0.00332367
Standard deviation Proportion of Variance Cumulative Proportion eigen SVL BW HL HW EL ED EN ES EE IN IO FAr TBLr	0.843138943 0.03385 0.88616 0.710883277 0.265288193 0.09057594 -0.070645969 0.039378469 0.139854316 -0.203202698 -0.319474696 0.295981088 0.426919556 0.038959782 -0.469863359 -0.122814373 -0.057154891 -0.266800377	IC(3) 0.710443326 0.02403 0.91019 0.50472972 -0.446853384 -0.129906618 -0.213980283 -0.22086396 -0.180680891 0.278604397 0.251272882 0.09576584 0.259878689 -0.113710926 -0.267676841 0.056652546 0.014271255 0.27997707	PC10 0.614017867 0.01795 0.92815 0.37701794 0.196416397 -0.087846741 0.070374143 -0.127550531 -0.18153958 -0.008164379 0.048312128 -0.027904855 -0.125361847 0.303625758 0.303625758 0.228807449	PC11 0.525772586 0.01316 0.94131 0.276436812 -0.110376596 0.177854897 -0.389903504 0.022285485 0.157737189 0.402630535 0.059050615 0.019723407 -0.131144367 0.339050813 -0.37994993 0.03792394 -0.210415667 -0.14978157	PC12 0.515133085 0.01264 0.95395 0.139472173 0.108703018 -0.321747003 0.134276418 -0.027411952 -0.109054652 -0.34208937 0.172978909 0.25121175 -0.133303008 0.412756086 0.095742055 -0.567849769 0.145371473	PC13 0.463343505 0.01022 0.96417 0.214687204 -0.13673416 -0.085524495 -0.17842853 -0.209651757 0.137530567 -0.264792874 0.0225488518 0.06220716 -0.064748891 0.253021631 -0.182302581 -0.191700829 -0.238209022	PC14 0.418149629 0.00833 0.97249 0.174849113 0.085656549 -0.103253386 -0.021701889 0.058151643 -0.134451774 0.164044114 0.158104491 -0.41905017 0.403591724 -0.201696035 0.111955286 0.359575483 -0.00332367 -0.413156342
Standard deviation Proportion of Variance Cumulative Proportion eigen SVL BW HL HW EL ED EN ES EE IN IO FAr TBLr AGr	0.843138943 0.03385 0.88616 0.710883277 0.265288193 0.09057594 -0.070645969 0.039378469 0.139854316 -0.203202698 -0.319474696 0.295981088 0.426919556 0.038959782 -0.469863359 -0.12814373 -0.057154891 -0.266800377 0.069118103	ICS 0.710443326 0.02403 0.91019 0.50472972 -0.446853384 -0.129906618 -0.213980283 -0.022086396 -0.180680891 0.278604397 0.251272882 0.09576584 0.259878689 -0.113710926 -0.66652546 0.014271255 0.27997070 0.008227511	PC10 0.614017867 0.01795 0.92815 0.37701794 0.196416397 -0.087846741 0.070374143 -0.127550531 -0.18153958 -0.004812128 -0.07215665 -0.227904855 -0.18020288 -0.125361847 0.303625758 0.228807449 -0.004079106	PC11 0.525772586 0.01316 0.94131 0.276436812 -0.110376596 0.177854897 -0.389903504 0.022285485 0.157737189 0.402630535 0.059050615 0.019723407 -0.131144367 0.339050813 -0.37994993 0.03792394 -0.210415667 -0.14978157 -0.18336757	PC12 0.515133085 0.01264 0.95395 0.265362095 0.139472173 0.108703018 -0.321747003 0.134276418 -0.027411952 -0.034208937 0.172978909 0.25121175 -0.133303008 0.412756086 0.095742055 -0.567849769 0.145371473 -0.303043068	PC13 0.463343505 0.01022 0.96417 0.214687204 -0.13673416 -0.085524495 -0.17842853 -0.209651757 0.137530567 -0.264792874 0.06220716 -0.129629771 -0.064748891 0.253021631 -0.191700829 -0.238209022 0.52714368	PC14 0.418149629 0.00833 0.97249 0.174849113 0.085656549 -0.103253386 -0.021701889 0.058151643 -0.134451774 0.164044114 0.158104491 -0.41905017 0.403591724 -0.201696035 0.111955286 0.359575483 -0.00332367 -0.413156342 0.990386865
Standard deviation Proportion of Variance Cumulative Proportion eigen SVL BW HL HW HD EL EN ES EE IN IO FAr TBLr AGr SPLr.I	0.843138943 0.8385 0.88616 0.710883277 0.265288193 0.09057594 -0.070645969 0.03378469 0.139854316 -0.203202698 -0.319474696 0.295981088 0.426919556 0.038959782 -0.469863359 -0.12814373 -0.057154891 -0.266800377 0.069118103 0.178898959	IC(3) 0.710443326 0.02403 0.91019 0.50472972 -0.446853384 -0.129906618 -0.213980283 -0.022086396 -0.180680891 0.278604397 0.251272882 0.09576584 0.259878689 -0.113710926 -0.267676841 0.056652546 0.014271255 0.27997707 0.008227511 0.359957261	PC10 0.614017867 0.01795 0.92815 0.37701794 0.196416397 -0.087846741 0.070374143 -0.127550531 -0.18153958 -0.0048312128 -0.07215665 -0.227904855 -0.188020288 -0.123361847 0.303625758 0.228807449 -0.004079106 -0.0462995625	PC11 0.525772586 0.01316 0.94131 0.276436812 -0.110376596 0.177854897 -0.389903504 0.022285485 0.157737189 0.402630535 0.059050615 0.019723407 -0.131144367 0.339050813 -0.37994993 0.03792394 -0.14978157 -0.18336757 -0.293841774	PC12 0.515133085 0.01264 0.95395 0.265362095 0.139472173 0.108703018 -0.321747003 0.134276418 -0.027411952 -0.034208937 0.172978909 0.25121175 -0.13303008 0.412756086 0.095742055 -0.567849769 0.145371473 -0.303043068 0.004054536	PC13 0.463343505 0.01022 0.96417 0.214687204 -0.13673416 -0.085524495 -0.17842853 -0.209651757 0.137530567 -0.264792874 0.06220716 -0.129629771 -0.064748891 0.253021631 -0.191700829 -0.238209022 0.52714368 0.173258047	PC14 0.418149629 0.00833 0.97249 0.174849113 0.085656549 -0.103253386 -0.021701889 0.058151643 -0.134451774 0.164044114 0.158104491 -0.41905017 0.403591724 -0.201696035 0.111955286 0.359575483 -0.00332367 -0.413156342 0.990386865 -0.103413131
Standard deviation Proportion of Variance Cumulative Proportion eigen SVL BW HL HW HD EL EN ES EE IN IO FAr TBLr AGr SPLr.I IFLr.I	0.843138943 0.03385 0.88616 0.710883277 0.26528193 0.09057594 -0.070645969 0.039378469 0.139854316 -0.203202698 -0.319474696 0.295981088 0.426919556 0.038959782 -0.469863359 -0.122814373 -0.057154891 -0.266800377 0.069118103 0.178898959 -0.352501894	IC(3) 0.710443326 0.02403 0.91019 0.50472972 -0.446853384 -0.129906618 -0.213980283 -0.022086396 -0.180680891 0.278604397 0.251272882 0.09576584 0.259878689 -0.113710926 -0.267676841 0.056652546 0.014271255 0.27997707 0.008227511 0.359957261 -0.193922056	PC10 0.614017867 0.01795 0.92815 0.37701794 0.196416397 -0.087846741 0.070374143 -0.127550531 -0.18153958 -0.0048312128 -0.07215665 -0.227904855 -0.188020288 -0.123361847 0.303625758 0.228807449 -0.004079106 -0.462995625 0.002786908	PC11 0.525772586 0.01316 0.94131 0.276436812 -0.110376596 0.177854897 -0.389903504 0.022285485 0.157737189 0.402630535 0.059050615 0.019723407 -0.131144367 0.339050813 -0.3729394 -0.210415667 -0.14978157 -0.18336757 -0.293841774 0.157568267	PC12 0.515133085 0.01264 0.95395 0.265362095 0.139472173 0.108703018 -0.321747003 0.134276418 -0.027411952 -0.034208937 0.172978909 0.25121175 -0.13303008 0.412756086 0.095742055 -0.567849769 0.145371473 -0.303043068 0.004054536 0.04772871	PC13 0.463343505 0.01022 0.96417 0.214687204 -0.13673416 -0.085524495 -0.17842853 -0.209651757 0.137530567 -0.264792874 0.06220716 -0.129629771 -0.064748891 0.253021631 -0.191700829 -0.2714368 0.173258047 -0.46397338	PC14 0.418149629 0.00833 0.97249 0.174849113 0.085656549 -0.103253386 -0.021701889 0.058151643 -0.134451774 0.164044114 0.158104491 -0.41905017 0.403591724 -0.201696035 0.111955286 0.359575483 -0.00332367 -0.413156342 0.990386865 -0.103413131 -0.113553524
Standard deviation Proportion of Variance Cumulative Proportion eigen SVL BW HL HW HD EL EN ES EE IN IO FAr TBLr AGr SPLr.I IFLc.I MO	0.843138943 0.03385 0.88616 0.710883277 0.265288193 0.09057594 -0.070645969 0.039378469 0.139854316 -0.203202698 -0.23202698 -0.239281088 0.426919556 0.038959782 -0.469863359 -0.122814373 -0.057154891 -0.266800377 0.069118103 0.178898959 -0.352501894 -0.000619521	IC(3) 0.710443326 0.02403 0.91019 0.50472972 -0.446853384 -0.129906618 -0.213980283 -0.022086396 -0.180680891 0.278604397 0.251272882 0.09576584 0.259878689 -0.113710926 -0.267676841 0.05652546 0.014271255 0.27997707 0.008227511 0.359957261 -0.193922056 -0.057816313	PC10 0.614017867 0.01795 0.92815 0.37701794 0.196416397 -0.087846741 0.070374143 -0.127550531 -0.18153958 -0.008164379 0.048312128 -0.027904855 -0.123361847 0.303625758 0.228807449 -0.004079106 -0.462995625 0.002786908 0.271775541	PC11 0.525772586 0.01316 0.94131 0.276436812 -0.110376596 0.177854897 -0.389903504 0.022285485 0.157737189 0.402630535 0.059050615 0.019723407 -0.131144367 0.339050813 -0.317994993 0.03792394 -0.14978157 -0.18336757 -0.293841774 0.157568267 0.090085724	PC12 0.515133085 0.01264 0.95395 0.139472173 0.108703018 -0.321747003 0.134276418 -0.027411952 -0.034208937 0.172978909 0.25121175 -0.133303008 0.412756086 0.095742055 -0.567849769 0.145371473 -0.303043068 0.04054536 0.04772871 0.002030737	PC13 0.463343505 0.01022 0.96417 0.214687204 -0.13673416 -0.085524495 -0.17842853 -0.209651757 0.137530567 -0.264792874 0.06220716 -0.129629771 -0.064748891 0.253021631 -0.191700829 -0.2714368 0.173258047 -0.046397338 -0.03433238	PC14 0.418149629 0.00833 0.97249 0.174849113 0.085656549 -0.103253386 -0.021701889 0.058151643 -0.134451774 0.164044114 0.158104491 -0.41905017 0.403591724 -0.201696035 0.111955286 0.359575483 -0.00332367 -0.413156342 0.990386865 -0.103413131 -0.113553524 0.40989474
Standard deviation Proportion of Variance Cumulative Proportion eigen SVL BW HL HW HD EL EN ES EE IN IO FAr TBLr AGr SPLr.I IFLr.I MO IOS	0.843138943 0.03385 0.88616 0.710883277 0.265288193 0.09057594 -0.070645969 0.039378469 0.139854316 -0.203202698 -0.23202698 -0.239281088 0.426919556 0.038959782 -0.469863359 -0.122814373 -0.057154891 -0.266800377 0.069118103 0.178898959 -0.352501894 -0.002790961	ICS 0.710443326 0.02403 0.031019 0.50472972 -0.466853384 -0.129906618 -0.22086396 -0.18060891 0.278604397 0.251272882 0.09576584 0.259878689 -0.113710926 -0.267676841 0.056652546 0.014271255 0.27979707 0.08227511 0.359957261 -0.193922056 -0.057816313 0.257813239	PC10 0.614017867 0.01795 0.92815 0.37701794 0.196416397 -0.087846741 0.070374143 -0.127550531 -0.18153958 -0.008164379 0.048312128 -0.027904855 -0.12361847 0.303625758 0.228807449 -0.004079106 -0.462995625 0.002786908 0.271775541 0.336314946	PC11 0.525772586 0.01316 0.94131 0.276436812 -0.110376596 0.177854897 -0.389903504 0.022285485 0.157737189 0.402630535 0.059050615 0.019723407 -0.131144367 0.339050813 -0.317994993 0.03792394 -0.14978157 -0.18336757 -0.293841774 0.157568267 0.90085724 0.2104137021	PC12 0.515133085 0.01264 0.95395 0.139472173 0.108703018 -0.321747003 0.134276418 -0.027411952 -0.034208937 0.172978909 0.25121175 -0.133303008 0.412756086 0.095742055 -0.567849769 0.145371473 -0.303043068 0.04054536 0.04772871 0.002030737 -0.064780745	PC13 0.463343505 0.01022 0.96417 0.214687204 -0.13673416 -0.085524495 -0.17842853 -0.209651757 0.137530567 -0.264792874 0.06220716 -0.129629771 -0.064748891 0.253021631 -0.191700829 -0.2714368 0.173258047 -0.046397338 -0.03433238 -0.03433238 -0.352986111	PC14 0.418149629 0.00833 0.97249 0.174849113 0.085656549 -0.103253386 -0.021701889 0.058151643 -0.134451774 0.164044114 0.158104491 -0.41905017 0.403591724 -0.201696035 0.111955286 0.359575483 -0.00332367 -0.413156342 0.990386865 -0.103413131 -0.113553524 0.40989474 0.03220845
Standard deviation Proportion of Variance Cumulative Proportion eigen SVL BW HL HW HD EL EN ES EE IN IO FAr TBLr AGr SPLr.I IFLr.I MO IOS V	0.843138943 0.03385 0.88616 0.710883277 0.265288193 0.09057594 0.039378469 0.039378469 0.139854316 -0.203202698 -0.203202698 -0.2039281088 0.426919556 0.038959782 -0.469863359 -0.122814373 -0.057154891 -0.266800377 0.069118103 0.178898959 -0.352501894 -0.02790961 -0.02790961 -0.02790961 -0.02790961	ICS 0.710443326 0.02403 0.031019 0.50472972 -0.46853384 -0.129906618 -0.22086396 -0.18060891 0.278604397 0.251272882 0.09576584 0.259878689 -0.113710926 -0.267676841 0.05652546 0.014271255 0.27997070 0.080520511 0.359957261 -0.139922056 -0.057816313 0.257813239 0.086524979	PC10 0.614017867 0.01795 0.92815 0.37701794 0.196416397 -0.173199899 -0.087846741 0.070374143 -0.127550531 -0.198153958 -0.008164379 0.048312128 -0.07215665 -0.227904855 -0.125361847 0.303625758 0.0228807449 -0.004079106 -0.462995625 0.027175541 0.336314946 0.460243812	PC11 0.525772586 0.01316 0.94131 0.276436812 -0.110376596 0.177854897 -0.389903504 0.022285485 0.157737189 0.402630535 0.059050615 0.019723407 -0.131144367 0.339050813 -0.317994993 0.03722394 -0.14978157 -0.18336757 -0.293841774 0.157568267 0.90085724 0.217437021 -0.02655612	PC12 0.515133085 0.01264 0.95395 0.139472173 0.108703018 -0.321747003 0.134276418 -0.027411952 -0.109054652 -0.34208937 0.172978909 0.25121175 -0.13303008 0.412756086 0.095742055 -0.567849769 0.145371473 -0.303043068 0.04054536 0.04772871 0.002030737 -0.064780745 0.309267431	PC13 0.463343505 0.01022 0.96417 0.214687204 -0.13673416 -0.085524495 -0.17842853 -0.209651757 0.137530567 -0.264792874 0.06220716 -0.129629771 -0.064748891 0.253021631 -0.191700829 -0.2714368 0.173258047 -0.046397338 -0.03433238 0.352986111 0.129809552	PC14 0.418149629 0.00833 0.97249 0.174849113 0.085656549 -0.103253386 -0.021701889 0.058151643 -0.134451774 0.164044114 0.158104491 -0.41905017 0.403591724 -0.201696035 0.111955286 0.359575483 -0.00332367 -0.413156342 0.990386865 -0.103413131 -0.113553524 0.40989474 0.03220845 -0.119165889

Table 5. Summary statistics of the principal component analysis of *Dixonius* species. Abbreviations are listed in the Materials and methods.

	PC15	PC16	PC17	PC18	PC19	PC20	PC21
Standard deviation	0.376199721	0.365477475	0.339179752	0.282916626	0.236187037	0.171149685	0.149480188
Proportion of Variance	0.00674	0.00636	0.00548	0.00381	0.00266	0.00139	0.00106
Cumulative Proportion	0.97923	0.98559	0.99107	0.99488	0.99754	0.99894	1
eigen	0.14152623	0.133573785	0.115042904	0.080041817	0.055784316	0.029292215	0.022344327
SVL	-0.083499418	0.052323475	-0.106015238	0.003344968	-0.031996278	0.03916795	-0.019457555
BW	-0.178247777	-0.058497317	0.597846907	-0.255954135	0.379366422	-0.199217481	0.221418054
HL	0.08265144	-0.13083192	-0.024132742	0.014837636	0.131660321	0.479388229	0.2891919
HW	0.244724903	-0.059011694	0.113956101	-0.074931386	0.04577337	-0.069612504	-0.732492773
HD	0.050630806	0.316234183	0.16660119	0.299515683	-0.49781424	0.046244883	0.219619924
EL	0.296740909	0.376559691	-0.260809485	-0.089676204	-0.027290387	-0.071210438	0.140852117
ED	-0.231235089	-0.168155577	-0.115371244	0.284151752	0.361474786	0.202917841	-0.049017145
EN	0.022603597	0.420837275	-0.236893263	0.02900181	0.436157574	0.238920063	-0.045962367
ES	0.248024801	-0.355459446	-0.140327076	0.068202164	0.014098586	-0.168841736	0.325882917
EE	-0.393037351	-0.425564191	-0.418495874	-0.066368342	-0.173649977	-0.04666024	-0.080329
IN	-0.081626216	0.152259274	-0.192312604	-0.041856001	0.036286384	-0.306664296	0.054524547
IO	-0.115305892	0.069986307	0.310505175	0.23842857	-0.096262685	0.459593261	-0.180632462
FAr	-0.116757716	0.126720851	0.055407627	0.30600813	0.081267972	-0.470097472	-0.064137815
TBLr	-0.021197578	-0.178071358	0.100589652	-0.310374261	-0.331807871	0.142300685	0.047913831
AGr	0.334353255	-0.016725971	-0.026314358	-0.397995653	-0.105887039	0.100382932	-0.137085205
SPLr.1	-0.184269598	0.036899566	0.194841372	0.163667167	-0.204455175	-0.121267207	-0.156153276
IFLr.l	0.428551026	-0.165166993	0.155004291	0.142458525	0.008969802	-0.065554124	0.111490515
МО	-0.391157106	0.255079755	-0.004834981	-0.342258191	-0.175496507	0.081476947	0.028734251
IOS	-0.059743664	-0.04851249	0.20733712	-0.095515858	0.057436279	-0.015186946	0.173384569
V	0.002458015	-0.062420243	-0.039680685	0.361422477	-0.145522506	0.02608135	0.040083497
T4r.l	0.117972701	-0.206198025	0.0622901	0.17118706	0.012651195	0.069479213	-0.122746338

Chu Se District, Gia Lai Province, Vietnam as the strongly supported (1.00/100) sister species of *D. minhlei* and the newly discovered population from Muangfuang District, Vientiane Province, Laos as the strongly supported (1.00/100) sister species of *D. lao* (Figs 2, 3). Uncorrected pairwise sequence divergences among *Dixonius* species ranged from 2.57–18.84% (Table 4). Ranges for the new species described (see below) are as follows: new species from Vietnam 3.60–15.73%, being most similar to *D. minhlei* and most distant to *D. aaronbaueri* and new species from Laos 3.10–18.17%, being most similar to *D. lao* and most distant to *D. aaronbaueri*.

The time-calibrated BEAST analysis places the divergence between *Dixonius aar-onbaueri* and the remaining species of *Dixonius* at approximately 24.04 mya (20.23–27.68 highest posterior density [HPD]). Within the Vietnam's lineages, *D. gialaiensis* sp. nov. and *D. minhlei* diverged from each other at approximately 3.19 mya (0.79–5.78 HPD) and within the Lao lineages, *D. muangfuangensis* sp. nov. and *D. lao* diverged approximately 3.47 mya (1.37–6.16 HPD) (Fig. 3).

Statistical analyses

The first two principal components (PC1 and PC2) of the PCA analysis recovered 56.6% of the variation in the morphometric and meristic data set (Fig. 4A) and loaded most heavily for body width (BW), head width (HW), eye nostril distance (EN), eye snout distance (ES), and eye ear distance (EE) along PC1 and interorbital dis-



Figure 2. Maximum likelihood topology of the *Dixonius* species from Vietnam and Laos with ultrafast bootstrap values (UFB) and Bayesian posterior probabilities (BPP) at the nodes, respectively.



Figure 3. BEAST chronogram of the *Dixonius* species from Vietnam and Laos. Numbers at the nodes are mean ages in millions of years. Bars represent 95% highest posterior densities.

tance (IO), supralabials (SPLr/l), number of supralabial at midorbital position (MO), and ventral scales (V) along PC2 (Table 5). The PCA recovered *D. gialaiensis* sp. nov. and *D. muangfuangensis* sp. nov. to be widely separated from most other species with *D. muangfuangensis* sp. nov. only overlapping with the distantly related *D. siamensis*. The two distantly related new species are well-separated from most other species in the DAPC but each overlaps with one other species in their 67% inertia ellipses (Fig. 4B).

The MFA analysis recovered all species to be separated from one another including *Dixonius muangfuangensis* sp. nov. and *D. siamensis* (Fig. 5A). The morphometric data

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Table 6	. Sumn	nary stai	tistics o	f morp	hometr	ic and r	neristic	charact	ers amo	ng the I	Dixoniu	s specie	s.								
Species	SVL	BW	HL	ΜH	HD	EL	ED	EN	ES	EE	N	IO	FAr	TBLr	AGr	SPLr.1	IFLr.1	MO	IOS	v	T4r.l
Dixonius	<i>vialaiens.</i>	is sp. nov.	(n = 3)																		
Mean	1.62	0.93	1.07	0.89	0.73	0.04	0.47	0.50	0.63	0.51	0.14	0.11	0.75	0.83	1.23	7.5	6.33	9	4	20.33	14.17
SD	0.060	0.007	0.003	0.001	0.007	0.005	0.002	0.007	0.002	0.005	0.018	0.029	0.034	0.013	0.025	0.5	0.577	0	0	1.155	0.289
Lower	1.56	0.92	1.06	0.89	0.72	0.04	0.47	0.49	0.63	0.51	0.12	0.08	0.73	0.82	1.20	~	9	9	4	19	14
Upper	1.68	0.93	1.07	0.89	0.73	0.05	0.47	0.50	0.64	0.52	0.15	0.13	0.79	0.84	1.25	8	7	9	7	21	14.5
D. lao (n =	: 3)																				
Mean	1.67	0.98	1.11	0.94	0.71	0.15	0.52	0.57	0.69	0.57	0.18	0.16	0.79	0.87	1.29	6	7.83	7.5	8.33	23.33	15
SD	0.099	0.014	0.017	0.005	0.013	0.022	0.016	0.042	0.028	0.012	0.013	0.047	0.017	0.007	0.003	0.5	0.289	0.5	0.577	0.577	0
Lower	1.55	0.96	1.09	0.93	0.70	0.12	0.51	0.54	0.67	0.56	0.17	0.12	0.78	0.86	1.29	8.5	7.5	7	8	23	15
Upper	1.74	0.99	1.13	0.94	0.72	0.17	0.54	0.62	0.72	0.58	0.20	0.21	0.81	0.87	1.29	9.5	8	8	6	24	15
D. minhle	i(n = 6)																				
Mean	1.65	70.07	0.86	0.82	0.67	0.12	0.45	0.55	0.68	0.56	0.17	0.57	0.80	0.86	1.33	7.75	6.42	5.83	7.67	21.33	14.33
SD	0.025	0.012	0.008	0.037	0.022	0.044	0.022	0.021	0.025	0.022	0.023	0.025	0.020	0.017	0.060	0.418	0.376	0.258	1.211	1.366	1.033
Lower	1.61	0.95	0.85	0.79	0.65	0.08	0.42	0.52	0.64	0.53	0.14	0.53	0.78	0.85	1.28	4	9	5.5	7	20	13
Upper	1.68	0.98	0.87	0.89	0.71	0.18	0.49	0.57	0.70	0.59	0.21	0.60	0.83	0.89	1.44	8	7	9	10	23	15
Dixonius	muangfu	uangensis	sp. nov. (n = 3																	
Mean	1.69	1.03	1.15	0.99	0.78	0.21	0.47	0.54	0.68	0.66	0.19	0.33	0.78	0.81	1.35	8.17	6.5	9	10	22.33	13.5
SD	0.096	0.001	0.016	0.006	0.005	0.031	0.030	0.003	0.011	0.005	0.011	0.006	0.004	0.001	0.032	0.289	0.5	0	0	0.577	1.323
Lower	1.58	1.03	1.13	0.97	0.77	0.18	0.44	0.54	0.67	0.65	0.18	0.32	0.78	0.81	1.31	8	9	9	10	22	12
Upper	1.75	1.03	1.16	0.99	0.78	0.25	0.50	0.54	0.69	0.66	0.20	0.34	0.78	0.81	1.38	8.5	7	9	10	23	14.5
D. siamen	sis $(n = $	8)																			
Mean	1.62	0.93	1.09	0.90	0.70	0.13	0.43	0.54	0.68	0.58	0.25	0.54	0.80	0.84	1.27	7.94	6.56	5.94	9.63	20.63	14.38
SD	0.077	0.0357	0.009	0.014	0.029	0.048	0.034	0.044	0.021	0.031	0.046	0.016	0.028	0.017	0.021	0.320	0.496	0.177	0.518	1.061	0.835
Lower	1.61	0.95	0.85	0.79	0.65	0.08	0.42	0.52	0.64	0.53	0.14	0.53	0.78	0.85	1.23	\sim	9	5.5	4	20	13
Upper	1.68	0.987	0.87	0.89	0.71	0.18	0.49	0.57	0.70	0.59	0.21	0.60	0.83	0.89	1.44	8	~	9	10	23	15
D. somcha	nbae (n	= (9)																			
Mean	1.62	0.97	1.07	0.91	0.70	0.17	0.46	0.48	0.65	0.50	0.18	0.23	0.73	0.83	1.26	7.75	5.67	9	8.17	23.33	14.67
SD	0.045	0.033	0.013	0.009	0.026	0.034	0.043	0.041	0.024	0.023	0.073	0.150	0.050	0.016	0.027	0.418	0.408	0	0.983	1.633	1.033
Lower	1.55	0.93	1.05	06.0	0.66	0.10	0.40	0.42	0.62	0.47	0.098	0.13	0.68	0.80	1.24	7	2	9	7	21	13
Upper	1.67	1.01	1.08	0.92	0.74	0.20	0.51	0.55	0.68	0.54	0.29	0.53	0.82	0.84	1.31	8	9	9	10	26	16

Species	SVL	BW	HL	ΜH	Π	EL	ED	EN	ES	EE	Z	IO	FAr	TBLr	AGr	SPLr.1	IFLel	MO	IOS	>	T4r.l
D. sp. (n =	= (1)																				
Mean	1.55	0.85	1.03	0.81	0.54	0.05	0.33	0.45	0.55	0.49	0.11	0.21	0.66	0.75	1.18	8	6.25	9	8.25	23	14
SD	0.083	0.033	0.009	0.037	0.049	0.068	0.017	0.033	0.087	0.033	0.007	0.015	0.032	0.032	0.020	0.408	0.645	0	0.5	0.816	0.408
Lower	1.48	0.81	1.02	0.76	0.49	-0.03	0.31	0.41	0.44	0.44	0.11	0.19	0.62	0.72	1.16	7.5	5.5	9	8	22	13.5
Upper	1.66	0.88	1.04	0.84	0.61	0.13	0.35	0.48	0.62	0.52	0.12	0.22	0.70	0.80	1.20	8.5	7	9	6	24	14.5
D. vietna	nensis (n	= 12)																			
Mean	1.56	0.83	0.83	0.82	0.65	-0.03	0.41	0.47	0.61	0.48	0.10	0.29	0.67	0.78	1.20	6.75	6.29	5.63	8.67	19.25	13.25
SD	0.088	0.055	0.016	0.028	0.049	0.054	0.030	0.031	0.035	0.055	0.070	0.165	0.063	0.035	0.051	1.177	0.450	0.377	0.985	1.545	0.399
Lower	1.41	0.72	0.80	0.77	0.58	-0.13	0.35	0.42	0.55	0.36	0.02	0.12	0.55	0.73	1.12	2	9	2	~	15	12.5
Upper	1.66	0.92	0.85	0.86	0.72	0.05	0.46	0.51	0.68	0.55	0.28	0.53	0.76	0.85	1.27	8	7	9	10	21	14

contributed to approximately 40% of the variation along Dim-1 followed by the categorical and meristic data. For Dim-2, the categorical data contributed 80% of the variation followed by morphometric and meristic data. Dim-3 showed that meristic data contributed 70% of the variation followed by morphometric and categorical data (Fig. 5B).

The ANOVAs and subsequent TukeyHDS tests demonstrated that *Dixonius gialaiensis* sp. nov. bears statistically different mean values between it and all other species in various combinations of characters (Tables 6, 7) and differs significantly from its sister species *D. minhlei* in head length (HL mean = 1.07 vs. 0.86, p = 0.000, respectively), in head width (HW mean = 0.89 vs. 0.82, p = 0.005, respectively), and in axilla to groin length, (AGr mean = 1.23 vs 1.32 p = 0.022) (Fig. 5; Tables 6, 7). *Dixonius muangfuangensis* sp. nov. also differed significantly from all other species in various combinations of characters and from its sister species *D. lao* it differs in head length (HL mean = 1.15 vs. 1.11, p = 0.004, respectively) and numbers of infralabials (IFL mean = 6.50 vs. 7.83, p = 0.026, respectively), and in numbers of supralabial at midorbital position (MO mean = 6.00 vs. 7.50, p = 0.00001, respectively) (Fig. 5, Tables 6, 7).

Taxonomy

Dixonius gialaiensis sp. nov.

https://zoobank.org/10BF67E1-8059-47CE-891C-B219BD7AA9C1 Fig. 8 Gialai leaf-toed gecko

Material examined. *Holotype.* Adult male, VNUF R.2020.22 (Field no. GL02) in Chu Se Mountain Pass, H'Bong Commune, Chu Se District, Gia Lai Province (13°34'44.3"N, 108°13'55.7"E; 330 m a.s.l.), collected by Oanh Van Lo and Khanh Quoc Nguyen on 15 February 2020. *Paratypes.* VNUF R.2020.44 (Field No. GL04), juvenile male, and VNUF R.2020.33 (Field No. GL03), adult female; the same data as the holotype.

Diagnosis. *Dixonius gialaiensis* sp. nov. can be separated from all other species of *Dixonius* by possessing the unique combination of having a maximum SVL of 47.4 mm; 19 longitudinal rows of dorsal tubercles at midbody; 19–21 longitudinal rows of ventrals across the abdomen; 7 or 8 supralabials, sixth in at midorbital position; 6 or 7 infralabials; 7 interorbital scales; 7 or 8 precloacal pores in males, femoral pores lacking; precloacal and femoral pores absent in female; 13–15 lamellae on fourth toe; dorsum olive grey color with more round brown blotches; canthal stripe continues behind orbit to back of head; lips with dark bars; two regularly disposed whitish tubercles along the sides near the flanks to tail tip. These characters are scored across all *Dixonius* species from Vietnam and Laos in Tables 6, 7.

Description of the holotype. Adult male, SVL 41.2 mm; head moderate in length (HL/SVL 0.28), wide (HW/HL 0.66), depressed (HD/HL 0.44), distinct from

Table 7. Significant *p*-values from the results of the ANOVA and TukeyHDS analyses comparing all combinations of species pairs. Character abbreviations are listed in the Materials and methods.

Morphometric characters	BW	HL	HW	HD	EL	ED	EN	ES	FAr	TBLr	AGr
lao vs. gialaiensis sp. nov.		0.007									
minhlei vs. gialaiensis sp. nov.		0.00	0.005								0.022
muangfuangensis sp. nov. vs. gialaiensis	0.040	< 0.001	0.001		0.001						0.023
sp. nov.											
<i>siamensis</i> vs. <i>gialaiensis</i> sp. nov.											
<i>somchanhae</i> vs. <i>gialaiensis</i> sp. nov.					0.016						
sp. vs. gialaiensis sp. nov.		0.021	0.001	< 0.001		< 0.001				0.006	
<i>vietnamensis</i> vs. <i>gialaiensis</i> sp. nov.	0.005	0.00	< 0.001	0.030		0.040				0.036	
minhlei vs. lao		0.00	< 0.001			0.017					
<i>muangfuangensis</i> sp. nov. vs. <i>lao</i>		0.003									
siamensis vs. lao						< 0.001					
somchanhae vs. lao		< 0.001					0.002				
sp. vs. lao	0.002	< 0.001	< 0.001	< 0.001		< 0.001	< 0.001	< 0.001	0.005	< 0.001	0.018
vietnamensis vs. lao	< 0.001	0.00	< 0.001		< 0.001	< 0.001	< 0.001	0.017	0.001	< 0.001	0.023
<i>muangfuangensis</i> sp. nov. vs. <i>minhlei</i>		0.00	< 0.001	0.002							
siamensis vs. minhlei		0.00	< 0.001								
somchanhae vs. minhlei		0.00	< 0.001				0.006		0.035		
sp. vs. <i>minhlei</i>	< 0.001	0.00		< 0.001		< 0.001	0.001	< 0.001	< 0.001	< 0.001	< 0.001
vietnamensis vs. minhlei	< 0.001	< 0.001			< 0.001		< 0.001	0.007	< 0.001	< 0.001	< 0.001
siamensis vs. muangfuangensis sp. nov.	0.016	< 0.001	0.001	0.030							
somchanhae vs. muangfuangensis sp.		< 0.001	0.006								
nov.											
sp. vs. <i>muangfuangensis</i> sp. nov.	< 0.001	< 0.001	< 0.001	< 0.001	0.001	< 0.001	0.016	0.001	0.013		< 0.001
<i>vietnamensis</i> vs. <i>muangfuangensis</i> sp.	< 0.001	0.00	< 0.001	< 0.001	< 0.001	0.021	0.019	0.038	0.004		< 0.001
somehanhaevs siamencis		0.031					0.010		0.018		
sp vs siamensis	0.016	< 0.001	< 0.001	< 0.001		< 0.001	0.002	< 0.001	< 0.010	< 0.001	0.012
vietnamensis vs. siamensis	< 0.001	0.00	< 0.001	0.0001	< 0.001	0.0001	< 0.001	< 0.001	< 0.001	< 0.001	0.007
sp vs somehanhae	< 0.001	0.017	< 0.001	< 0.001	0.013	< 0.001	. 0.001	0.017	0.0001	0.003	0.032
vietnamensis vs. somchanhae	< 0.001	0.00	< 0.001	0.0001	< 0.001	0.003		0.017		0.013	0.038
vietnamensis vs. sp.	01001	0.00	0.0001	< 0.001	01001	< 0.001				01019	0.050
Morphometric characters	SPLr.1	IFLr.l	MO	IOS	v	T4r.1					
lao ys. gialaiensis sp. nov.		0.008	< 0.001								
minhlei vs. gialaiensis sp. nov.											
muanofuangensis sp. nov. vs. gialaiensis				< 0.001							
sp. nov.											
siamensis vs. gialaiensis sp. nov.				< 0.001							
somchanhae vs. gialaiensis sp. nov.					0.011						
sp. vs. gialaiensis sp. nov.											
vietnamensis vs. gialaiensis sp. nov.				0.041							
minhlei vs. lao		0.003	< 0.001								
muangfuangensis sp. nov. vs. lao		0.026	< 0.001								
siamensis vs. lao		0.007	< 0.001								
somchanhae vs. lao		< 0.001	< 0.001								
sp. vs. lao		0.002	< 0.001								
vietnamensis vs. lao	< 0.001	< 0.001	< 0.001		< 0.001	0.015					
muangfuangensis sp. nov. vs. minhlei				0.004							
siamensis vs. minhlei				0.001							
somchanhae vs. minhlei					0.045						
sp. vs. minhlei											
vietnamensis vs. minhlei					0.038						
siamensis vs. muangfuangensis sp. nov.											

Morphometric characters	SPLr.1	IFLr.l	MO	IOS	v	T4r.
somchanhae vs. muangfuangensis				0.010		
sp. nov.						
sp. vs. <i>muangfuangensis</i> sp. nov.						
vietnamensis vs. muangfuangensis					0.011	
sp. nov.						
somchanhae vs. siamensis		0.019			0.002	
sp. vs. <i>siamensis</i>					0.065	
vietnamensis vs. siamensis	0.022					0.035
sp. vs. somchanhae						
vietnamensis vs. somchanhae					< 0.001	
vietnamensis vs. sp.					< 0.001	



Figure 4. A principal component analysis (PCA) of *Dixonius* species showing their morphospatial relationships along the first two components based on normalized morphometric and meristic characters **B** discriminant analysis of principal components (DAPC) based on retention of the first five PCs with 67% inertia ellipsoids.



Figure 5. A MFA scatter plot showing the morphospatial relationships among the *Dixonius* species based on normalized morphometric, meristic, and color pattern characters **B** bar graphs showing the percent contribution of each data type to the overall variation in the data dimensions 1–4. The dashed red line in the bar graphs indicates the expected average value if the contributions of each data type were equal.

neck; prefrontal region concave; canthus rostralis rounded; snout elongate (ES/HL 0.37), rounded in dorsal profile; eye moderate size (ED/HL 0.25); ear opening oval, obliquely oriented, moderate in size; diameter of eye slightly smaller than eye to ear distance (ED/EE 0.88); rostral rectangular, partially divided dorsally by straight rostral groove, bordered posteriorly by large left and right supranasals, bordered laterally by first supralabials; external nares bordered anteriorly by rostral, dorsally by large supranasal, posteriorly by two smaller postnasals, bordered ventrally by first supralabial; 8,7 (R,L) rectangular supralabials extending to below and slightly past posterior margin of



Figure 6. Boxplot comparisons of meristic characters among the *Dixonius* species where interspecific statistical differences were recovered (see Table 7). Pale blue circles are means and the black horizontal bars are medians.

eye, sixth in midorbital position; 6,6 (R,L), infralabials tapering smoothly to just below midpoint of eye, decreasing gradually in size; scales of rostrum and lores flat to domed, larger than granular scales on top of head and occiput; scales of occiput intermixed with distinct, small, conical tubercles; superciliaries elongate, largest anteriorly; mental triangular, bordered laterally by first infralabials and posteriorly by large left and right trapezoidal postmentals contacting medially for 60% of their length posterior to mental; gular and throat scales small, granular, grading anteriorly into slightly larger, flatter, smooth, imbricate, pectoral and ventral scales.

Body relatively short (AG/SVL 0.38); dorsal scales small, granular interspersed with larger, conical, regularly arranged, keeled tubercles; tubercles extend from top



Figure 7. Violin plots of the normalized morphometric characters overlain with box plots showing the range, frequency, mean (white dot), and 50% quartile (black rectangle) of characters where interspecific statistical differences were recovered (see Table 7). New species in bold italics.



Figure 8. Dorsal views of *Dixonius gialaiensis* sp. nov. **A** adult male holotype VNUF R.2020.22 (Field no. GL02) **B** adult female paratype VNUF R.2020.33 (Field No. GL03) **C** juvenile male paratype VNUF R.2020.44 (Field No. GL04) in Chu Se Mountain Pass, Hbong Commune, Chu Se District, Gia Lai Province.

of head onto posterior haft of tail forming longitudinal rows, terminating at last portion of tail; smaller tubercles extend anteriorly onto nape and occiput, diminishing in size and distinction on top of head; 19 longitudinal rows of tubercles at midbody; 33 paravertebral scales, number of scales in a paravertebral row from first scale posterior to parietal scale to last scale at the level of vent opening; 23 paravertebral scales in a row between limb insertions; 21 flat, imbricate, ventral scales much larger than dorsal scales; 7 enlarge, pore-bearing, precloacal scales in an angular series; and no deep precloacal groove or depression.

Forelimbs moderate in stature, relatively short (FA/SVL 0.15); granular scales of forearm slightly larger than those on body, interspersed with small tubercles; hind limbs more robust than forelimbs, moderate in length (TBL/SVL 0.17), covered dorsally by granular scales interspersed with large, and small conical tubercles; ventral scales of thigh flat, imbricate, larger than dorsals; subtibial scales flat, imbricate; proximal femoral scales smaller than distal femorals; femoral pores absent; digits relatively long with 14 lamellae on fourth toe; and claws well developed.

Tail 108.4 mm in length, 4.5 mm in width at base, tapering to a point; dorsal scales of flat, square with conical, keeled tubercles in anterior part; median row of transversely expanded subcaudal scales, significantly larger than dorsal caudal scales on original portion; base of tail bearing hemipenal swellings; and postcloacal scales flat, imbricate.

Coloration in life (Fig. 8). Ground color of dorsal head and dorsum grey brown with rounded black-brown blotches, decreasing gradually in size from head to body; canthal stripe continues behind orbit to back of head; dark bars on the lips; uneven light spots running from postorbital along the flanks to tip tail; upper surface of foreand hindlimbs uniformly light grey with black-brown spots; dorsum of tail covered with some small rounded black-brown blotches; ventral surface beige uniformly as the belly and the throat.

Variation (Fig. 8). The female paratype (VNUF R.2020.33) generally has more dark brown blotches on head and dorsum, and uniformly black on the new regenerated tail. The dorsum of the of head and body of the juvenile male paratype (VNUF R.2020.44) pale brown with pale-colored blotches on granulose skin arranged along its sides extending from the flanks to the tail tip. Further measurements are summarized in Tables 2–4, Suppl. material 1: table S1.

Distribution. *Dixonius gialaiensis* sp. nov. currently is only known from the type locality of Chu Se Mountain Pass, H'Bong Commune, Chu Se District, Gia Lai Province, Central Highlands, Vietnam (Fig. 1).

Natural history. The specimens were found at night, between 19:45 and 21:00 h, on the ground in an area along the National Highway 25. The surrounding habitat was secondary montane forest with woody trees. The temperature and humidity were approximately 32.6 °C and 57% (Fig. 9).

Etymology. The new species is named after the type locality of Gia Lai Province, Central Highlands, Vietnam.

Comparisons. *Dixonius gialaiensis* sp. nov. is the sister species to *D. minhlei* (Fig. 2) from which it differs by an uncorrected pairwise sequence divergence of 3.60% (Table 4). It is differentiated from it morphologically by having a significantly higher



Figure 9. Habitat of *Dixonius gialaiensis* sp. nov. HBong Commune, Chu Se District, Gia Lai Province, Central Highlands, Vietnam.

mean number of head length (HL), head width (HW), and axilla to groin length (AG). In addition, it differs from *D. minhlei* in color pattern (grey-brown dorsum with more round black-brown blotches versus olive gray dorsum with round brownish olive blotches). Statistically significant and discrete categorical differences between *Dixonius gialaiensis* sp. nov. and all other species and populations are presented in Tables 5–7.

Dixonius muangfuangensis sp. nov.

https://zoobank.org/A447EC01-F653-4FE5-A616-5FBD25F027C6 Fig. 10 Muangfuang leaf-toed gecko

Material examined. *Holotype.* Adult male, VNUF R.2020.42 (Field no. MF.02) in Sinxay Temple, Nadan Village, Muangfuang District, Vientiane Province, Central Laos (18°32'52"N, 101°58'31"E; 276 m a.s.l.), collected by Saly Sitthivong and Thuong Huyen Nguyen on 05 December 2020. *Paratypes.* NUOL R.2022.01 (Field no. MF. 01), juvenile male, and VNUF R.2020.52 (Field no. MF. 03), adult female; the same data as given for the holotype.

Diagnosis. *Dixonius muangfuangensis* sp. nov. can be separated from all other species of *Dixonius* by possessing the unique combination of having a maximum SVL of 56.7 mm; 21–23 longitudinal rows of dorsal tubercles at midbody; 20 or 21 longitudinal rows of ventrals across the abdomen; 7 or 8 supralabials, sixth in at midorbital position; 6 or 7 infralabials; 7 interorbital scales; 7 or 8 precloacal pores in males, femoral pores lacking; precloacal and femoral pores absent in female; 15 lamellae on fourth toe;

dorsum olive grey color with numerous small and irregular black blotches; head with brown spots; light spots irregularly arranged from the back of the head to base of tail; lips with dark bars; two regularly disposed whitish tubercles on each side on each side. These characters are scored across all *Dixonius* species from Vietnam and Laos in Tables 6, 7.

Description of the holotype. Adult male, SVL 55.6 mm; head moderate in length (HL/SVL 0.28), wide (HW/HL 0.71), depressed (HD/HL 0.45), distinct from neck; prefrontal region concave; canthus rostralis rounded; snout elongate (ES/HL 0.39), rounded in dorsal profile; eye moderate size (ED/HL 0.20); ear opening oval, obliquely oriented, moderate in size; diameter of eye much smaller than eye to ear distance (ED/EE 0.59); rostral rectangular, partially divided dorsally by straight rostral groove, bordered posteriorly by large left and right supranasals, bordered laterally by first supralabials; external nares bordered anteriorly by rostral, dorsally by large supranasal, posteriorly by two smaller postnasals, bordered ventrally by first supralabial; 8,8 (R,L) rectangular supralabials extending to below midpoint of eye, sixth in midorbital position; 7,7 (R,L), infralabials tapering smoothly to be just slightly past posterior below midpoint of eye, decreasing gradually in size; scales of rostrum and lores flat to domed, larger than granular scales on top of head and occiput; scales of occiput intermixed with distinct, small, conical tubercles; superciliaries elongate, largest anteriorly; mental triangular, bordered laterally by first infralabials and posteriorly by large left and right parallelogram postmentals contacting medially for 60% of their length posterior to mental; gular and throat scales small, granular, grading anteriorly into slightly smaller, flatter, smooth, imbricate, pectoral and ventral scales.

Body relatively short (AG/SVL 0.42) with well-defined ventrolateral folds; dorsal scales small, granular interspersed with moderate, conical, regularly arranged, keeled tubercles; tubercles extend from top of head onto interior haft of tail forming longitudinal rows, terminating at regenerated portion of tail; smaller tubercles extend anteriorly onto nape and occiput, diminishing in size and distinction on top of head; 23 longitudinal rows of tubercles at midbody; 45 paravertebral scales, number of scales in a paravertebral row from first scale posterior to parietal scale to last scale at the level of vent opening; 24 paravertebral scales in a row between limb insertions; 20 flat, imbricate, ventral scales much larger than dorsal scales; 8 enlarge, pore-bearing, precloacal scales in an angular series; and no deep precloacal groove or depression.

Forelimbs moderate in stature, relatively short (FA/SVL 0.12); granular scales of forearm slightly larger than those on body, interspersed with small tubercles; hind limbs more robust than forelimbs, moderate in length (TBL/SVL 0.13), covered dorsally by granular scales interspersed with large, and small conical tubercles; ventral scales of thigh flat, imbricate, larger than dorsals; subtibial scales flat, imbricate; proximal femoral scales smaller than distal femorals; femoral pores absent; digits relatively long with 15 lamellae on fourth toe; and claws well developed.

Tail 37.8 mm in length, first 17.1 mm original, 6.1 mm in width at base, tapering to a point; dorsal scales of flat, square with conical, keeled tubercles, regenerated portion covered with small, smooth subcircular scales; median row of transversely expanded subcaudal scales, significantly larger than dorsal caudal scales on original portion; base of tail bearing hemipenal swellings; and postcloacal scales flat, imbricate.



Figure 10. View of *Dixonius muangfuangensis* sp. nov. **A** adult male holotype VNUF R.2020.42 (Field no. MF.02) **B** adult female paratype VNUF R.2020.52 (Field no. MF. 03) **C** juvenile male paratype NUOL R.2022.01 (Field no. MF. 01) in Nadan Village, Muangfuang District, Vientiane Province, Central Laos.



Figure 11. Habitat of *Dixonius muangfuangensis* sp. nov. Nadan Village, Muangfuang District, Vientiane Province, Central Laos.

Coloration in life (Fig. 10). Ground color of dorsal head and dorsum dark grey with numerous small and irregular black blotches; lips with dark bars; two regularly disposed whitish tubercles on each side on each side running from postorbital along the flanks to tail, terminating at regenerated portion of tail; upper surface of fore and hind limbs uniformly dark brown with round black-brown spots; dorsum of tail covered with some large black-brown blotches; ventral surface beige uniformly as the belly and the throat.

Variation (Fig. 10). The female paratype (VNUF R.2020.52) generally matches that of the holotype in all characteristics. The juvenile male paratype (NUOL R.2022.01) has fewer black blotches on head and dorsum and two regularly disposed whitish tubercles on each side on each side of the head extending from the postorbital region, along the flanks, to the tail tip. Further measurements are summarized in Tables 2–4 and Suppl. material 1: table S2.

Distribution. *Disonius muangfuangensis* sp. nov. currently is only known from the type locality of Nadan Village, Muangfuang District, Vientiane Province, Central Laos (Fig. 1).

Etymology. The specific epithet of the new species refers to the type locality of the new species in Muangfuang District, Vientiane Province, Central Laos.

Natural history. The type series was collected between 19:10 and 19:30 h, on the ground inside Sinxay Temple, at an elevation of 276 m a.s.l. The surrounding habitat was disturbed lowland karst forest (Fig. 11).

Comparisons. *Dixonius muangfuangensis* sp. nov. is the sister species to *D. lao* (Fig. 2) from which it differs by an uncorrected pairwise sequence divergence of 3.10% (Table 4). It is differentiated morphologically by having a significantly higher mean number of head length (HL), infralabials (IFL), and numbers of supralabial at midorbital position (MO). In addition, it differs from *D. lao* in dorsal pattern (dorsal pebble brown versus dorsal dark gray with black blotches). Statistically significant and discrete categorical differences between *Dixonius muangfuangensis* sp. nov. and all other species and populations are presented in Tables 5–7.

Discussion

Morphological comparisons indicated that *Dixonius gialaiensis* sp. nov. is most similar to its sister species *D. minhlei*, but can be differentiated from the latter species by the number of dorsal tubercle scale rows and differences in color pattern. The results of the molecular analysis show the uncorrected pairwise sequence divergence between the two taxa is 3.60%. Additionally, the two species are widely separated geographically being in different mountain systems and separated by the Dong Nai River system (Fig. 1). Collectively, these data suggest these are separate and distinct species.

Dixonius gialaiensis sp. nov. was discovered in a protected forest near the National Highway 25. The construction of new infrastructure at this site strongly impacts the habitat of *D. gialaiensis* sp. nov., including range fragmentation and forest degradation. Further investigations on conservation status is urgently required to develop effective conservation measures.

Dixonius muangfuangensis sp. nov. is most closely related to *D. lao*, but can be distinguished from it by head shape and color pattern differences. The molecular analysis indicated these two species differ by a 3.1% uncorrected pairwise genetic distance. In addition, the two species evolved separately in geographically isolated regions. The type locality of *D. muangfuangensis* sp. nov. is approximately 500 km south of the type locality of *D. lao* and the type localities are separated by the Nam Ngiap and Xebangfai river network systems (Fig. 1).

The BEAST analysis indicates that the divergence between *Dixonius gialaiensis* sp. nov. and *D. minhlei* and that between *D. muangfuangensis* sp. nov. and *D. lao* may have been the result of cyclical climatic events during the recent interglacial periods of the Pliocene as noted for several other Indochinese species (see Grismer and Grismer 2017 and references therein). *D. muangfuangensis* sp. nov. and *D. lao* diverged from one another at approximately 3.47 mya. Relatively soon after, at approximately 3.19 mya, *Dixonius gialaiensis* sp. nov. and *D. minhlei* separated from one another, thus allowing sufficient time for them to evolve significant differences between them in a number of characteristics. During this time period, the formation of separate karstic habitats and granitic mountains and hills may have prevented gene flow between these populations, placing each species on separate evolutionary trajectories (Grismer and Grismer 2017).

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Supplementary material I

Measurements and morphological characters of the type series of *Dixonius* gialaiensis sp. nov.

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Data type: tables (Excel spreadsheet)

- Explanation note: table S1: Measurements (in mm) and morphological characters of the type series of *Dixonius gialaiensis* sp. nov. (for abbreviations see Material and methods). Measurements taken on right side; FA is given in the left side; SPL/IFL/ T4 given in right/ left order; -absence; * tail regenerated; table S2: Measurements (in mm) and morphological characters of the type series of *Dixonius muangfuan-gensis* sp. nov. (for abbreviations see material and methods). Measurements taken on right side; FA and T4 are given in the left side; SPL/IFL given in right/ left order; -absence, * tail regenerated; ** tail lost.
- Copyright notice: This dataset is made available under the Open Database License (http://opendatacommons.org/licenses/odbl/1.0/). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this Dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.

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REVIEW ARTICLE



Review of the pill millipede genus Hyperglomeris Silvestri, 1917 (Diplopoda, Glomerida, Glomeridae) with description of two new species from Laos

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Abstract

The pill millipede genus *Hyperglomeris* Silvestri, 1917 is reported from Laos for the first time. Two new species, namely *H. bicaudata* Likhitrakarn, **sp. nov.** and *H. inkhavilayi* Likhitrakarn, **sp. nov.**, from Houaphanh and Khammouane provinces, northern Laos, are described and illustrated based on morphological characters and molecular analyses. Sequences of COI gene were used as DNA barcoding markers, and successfully supported the accurate identification of other Glomeridae species. Interspecific divergence of the COI uncorrected p-distance between these new species and other *Hyperglomeris* species ranged from 7.84–13.07%, while the intraspecific divergence was 0.45% in *H. inkhavilayi* **sp. nov.** and 5.3% in *H. bicaudata* **sp. nov.** The updated status of *Hyperglomeris*, a map of its distribution, and identification keys for all species are given.

Keywords

Distribution map, key, Laos, morphology, molecular phylogeny, new species

Introduction

The pill millipede genus *Hyperglomeris* Silvestri, 1917 belongs to the family Glomeridae, order Glomerida. Members of this family and others in the order are capable of complete volvation, where the head and collum are tucked within the rolled-up body segments or ball-like shape when threatened. For this reason they are commonly referred to as 'pill millipedes'. Prior to this study, the genus *Hyperglomeris* consisted of only seven species, all narrowly endemic to northern Vietnam (Nguyen et al. 2019). Species of this genus are relatively small, ranging in length from 5.5 to 24 millimeters, and have a distinct body color. However, there is one colorless species, *H. depigmentata* Golovatch et al., 2013, which was found to inhabit a cave (Golovatch et al. 2013).

Hyperglomeris is classified within the subfamily Haploglomerinae, which has nine genera, the majority of which have only one or two species. The classification of these genera is still complicated due to few distinctive morphological characteristics, such as the presence of trichosteles on the prefemur or femur of the telopods, the number of apical cones on the antennae, and the number of striae on the thoracic shield (Wesener 2015a), and it is uncertain whether these characteristics represent species-level or genus-level distinctions. Therefore, it is essential to incorporate genetic information (as in our case, DNA barcoding based on COI gene sequences) in order to delineate species boundaries within this group. It can also be used as a foundation for further classification of the family.

Laos (or the Lao PDR) is a Southeast Asian country that shares borders with Myanmar and China to the north, Vietnam to the east, Cambodia to the south, and Thailand to the west. Laos is well-known for its beautiful mountains and forests, as well as its diverse ecosystems, which include tropical rainforests, dry lowlands, and hilly regions (ADB 2000). Previously, a total of 34 species of millipedes from 20 genera, 13 families, and seven orders have been recorded from Laos (Likhitrakarn et al. 2014). Among these, the Glomerida has remained represented by only four species of the genus *Hyleoglomeris* Verhoeff, 1910.

In this study, we were fortunate to discover two new species of the genus *Hyperglomeris* from Laos. These two new species are investigated using an approach of integrative taxonomy, combining both morphological characters and a common DNA barcoding fragment of the COI gene. In addition, we have revised the scope of the genus, also providing its distribution map and an identification key to all nine species.

Materials and methods

Morphological studies

Specimens were collected from Laos under the Animal Care and Use Protocol Review No. 1723018. Locations of collecting sites were recorded by GPS using a Garmin GPSMAP 60 CSx based on the WGS 84 datum, and all coordinates and elevations

were double-checked with Google Earth. Photographs of live animals were taken using a Nikon 700D digital camera with a Nikon AF-S VR 105 mm macro lens. The specimens collected were euthanized by a two-step method following AVMA Guidelines for the Euthanasia of Animals (AVMA 2013). Specimens were then preserved in 90% ethanol for morphological and molecular studies. After 24 hr, ethanol was replaced with new 95% ethanol to prevent their defensive chemicals from interfering with future DNA extraction.

The holotype and all paratypes are housed in the Chulalongkorn University Museum of Zoology (**CUMZ**), Bangkok, Thailand. The specimens were examined, measured, and photographed under a Nikon SMZ 745T trinocular stereo microscope equipped with a Canon EOS 5DS R digital SLR camera. The acquired digital photos were processed and modified with Adobe Photoshop CS5. Line drawings were based on photographs taken under the stereo microscope equipped with a digital SLR camera.

The terminology used to describe morphological structures is consistent with the most recent publications (Golovatch et al. 2006; Golovatch 2017; Nguyen et al. 2019). In the catalogue sections, **D** stands for the original description; **K** for appearance in a key; **L** for appearance in a species list; **M** for a mere mention; and **MI** for molecular information. The following abbreviations listed below are used in the figures:

сх	coxa;
cxl	coxal lobe;
fe	femur;
fp	femoral process;
ŇР	national park;
pf	prefemur;
pfc	prefemoral cone of telopod;
pft	prefemoral trichostele of telopod;
sh	syncoxital horn of telopod;
sl	syncoxital lobe of telopod;
sn	syncoxite notch;
SX	syncoxite;
ta	tarsus;
tc	tibial cone;
ti	tibia;
tp	tibial process.

DNA extraction, PCR amplification, and sequencing

Total genomic DNA was extracted from the legs and part of thoracic tissue of the paratype using the DNA extraction kit for animal tissue (NucleoSpin Tissue extraction kit, Macherey-Nagel, Germany), following the standard procedure of the manual. Fragments with size of 660 bp of the mitochondrial cytochrome *c* oxidase subunit I gene (COI) were amplified using LCO1490 (5'-GGTCAACAAATCATAAAGATATTGG-3'; Folmer et al. 1994) and HCOoutout (5'-GTAAATATATGRTGDGCTC; Schulmeister et al. 2002) or Nancy (5'-CCCGGTAAAATTAAAATATAAACTTC-3'; Bogdanowicz et al. 1993).

The PCR amplification was performed using a T100 thermal cycler (BIO-RAD) with a final reaction volume of 20 μ L (15 μ L of EmeraldAmp GT PCR Master Mix, 1.5 μ L of each primer, 10 ng of template DNA and distilled water up to 20 μ L total volume). Thermal cycling was performed at 94 °C for 3 min, followed by 35 cycles of 94 °C for 30 s, annealing at 42–56 °C (depending on samples and the primer pair) for 60 s, extension at 72 °C for 90 s, and a final extension at 72 °C for 5 min. Amplification of PCR products was confirmed through 1.5% (w/v) agarose gel electrophoresis before purification by MEGAquick-spinTM plus (Fragment DNA purification kit) and sequencing in both directions (forward and reverse) using an automated sequencer (ABI prism 3730XL).

All nucleotide sequences obtained in this study were deposited in the GenBank Nucleotide sequences database under accession numbers OQ661871–OQ661874. The collecting localities and GenBank accession numbers of each nominal species are listed in Table 1.

Phylogenetic analyses

The sequences were aligned using MEGA7 (Kumar et al. 2016). The final aligned dataset included 660 bp of 23 COI sequences. All species of *Hyperglomeris* for which sequences are available in Genbank were included, along with members of some other genera of Glomeridae (i.e., *Peplomeris* Silvestri, 1917, *Tonkinomeris* Nguyen, Sierwald & Marek, 2019, *Rhopalomeris* Verhoeff, 1906, *Hyleoglomeris, Glomeris* Latreille, 1802, and *Trachysphaera* Heller, 1857); the genera *Sphaerobelum* and *Zephronia* were used as outgroups (Table 1).

Two phylogenetic methods were used in this study. Firstly, the maximum likelihood (ML) method was performed using RAxML v. 8.2.10 (Stamatakis, 2014), with GTRGAMMA as the nucleotide substitution model and 1,000 ML bootstrap replicates to assess topology bootstrap support (bp). Secondly, Bayesian Inference (BI) analysis was performed by MrBayes 3.2.6 (Ronquist et al. 2012) using the Markov chain Monte Carlo technique (MCMC), and with the best-fit model of nucleotide substitution as suggested by PartitionFinder2 v. 2.3.4 (Lanfear et al. 2016). The selected best-fit models for the three COI codon positions were SYM+G, F81+I, and GTR+G, respectively. The BI trees were run for ten million generations with a random starting tree. The resultant trees were sampled every 1,000 generations and the values were used to estimate consensus tree topology; bipartition posterior probability (bpp), and branch lengths, after the first 25% of obtained trees were discarded as burn-in. All average effective sample size (ESS) values sampled from the MCMC analysis were greater than 2,000 in all parameters. Both phylogenetic analyses were implemented through the on-line CIPRES Science Gateway (Miller et al. 2010). The obtained tree was drawn by FigTree v. 1.4.3 (http://tree.bio.ed.ac.uk/software/ figtree/, accessed on 28 February 2023). In addition, genetic divergence based on
	1			1	1	
Voucher number	Species	Locality	Geographical coordinates	GenBank accession number COI	Reference	
CUMZ-GLO004*	<i>Hyperglomeris bicaudata</i> Likhitrakarn, sp. nov.	Ban Tham Na Tan, Houaphanh, Laos	20°27'28"N, 104°08'43"E	OQ661871	This study	
CUMZ-GLO007*	<i>Hyperglomeris bicaudata</i> Likhitrakarn, sp. nov.	Limestone mountain area near vocational-technical school, Houaphanh, Laos	20°24'15"N, 104°15'4"E	OQ661872	This study	
CUMZ-GLO095/1*	<i>Hyperglomeris inkhavilayi</i> Likhitrakarn, sp. nov.	Orchard, Ban Phawong, Khammouane, Laos	17°32'24"N, 105°25'18"E	OQ661873	This study	
CUMZ-GLO095/2*	<i>Hyperglomeris inkhavilayi</i> Likhitrakarn, sp. nov.	Orchard, Ban Phawong, Khammouane, Laos	17°32'24"N, 105°25'18"E	OQ661874	This study	
FMNH-SVE102	<i>Hyperglomeris simplex</i> Nguyen et al., 2019	Tam Dao NP, Vinh Phuc, Vietnam		MT749410	Nguyen et al. 2021	
IEBR-Myr 605	<i>Hyperglomeris simplex</i> Nguyen et al., 2019	Tam Dao NP, Vinh Phuc, Vietnam		MT749403	Nguyen et al. 2021	
IEBR-Myr 674	Hyperglomeris sp. 1	Pu Mat NP, Nghe An, Vietnam		MT749409	Nguyen et al. 2021	
FMNH-SVE176	Peplomeris magna Golovatch, 1983	Cuc Phuong NP, Ninh Binh, Vietnam		MT749407	Nguyen et al. 2021	
IEBR-Myr 677	Peplomeris magna Golovatch, 1983	Cuc Phuong NP, Ninh Binh, Vietnam		MT749405	Nguyen et al. 2021	
IEBR-Myr 656	Peplomeris magna Golovatch, 1983	Cuc Phuong NP, Ninh Binh, Vietnam		MT749408	Nguyen et al. 2021	
FMNH-SVE204	<i>Hyleoglomeris lobus</i> Nguyen et al., 2019	Cuc Phuong NP, Ninh Binh, Vietnam		MT749391	Nguyen et al. 2021	
IEBR-Myr 653	<i>Hyleoglomeris lobus</i> Nguyen et al., 2019	Cuc Phuong NP, Ninh Binh, Vietnam		MT749402	Nguyen et al. 2021	
IEBR-Myr 678	<i>Hyleoglomeris lobus</i> Nguyen et al., 2019	Cuc Phuong NP, Ninh Binh, Vietnam		MT749406	Nguyen et al. 2021	
IEBR-Myr 533	<i>Rhopalomeris sauda</i> Nguyen et al., 2019	Ba Be NP, Bac Kan, Vietnam		MT749404	Nguyen et al. 2021	
IEBR-Myr 654	<i>Rhopalomeris sauda</i> Nguyen et al., 2019	Me Linh District, Vinh Phuc, Vietnam		MT749401	Nguyen et al. 2021	
IEBR-Myr 706	<i>Rhopalomeris sauda</i> Nguyen et al., 2019	Khao Ca NR, Ha Giang, Vietnam		MT749400	Nguyen et al. 2021	
IEBR-Myr 801	<i>Rhopalomeris sauda</i> Nguyen et al., 2019	Cham Chu NR, Tuyen Giang, Vietnam		MT749398	Nguyen et al. 2021	
IEBR-Myr 804a	<i>Tonkinomeris napoensis</i> Nguyen et al., 2019	Bac Me NR, Ha Giang, Vietnam		MT749397	Nguyen et al. 2021	
IEBR-Myr 804b	<i>Tonkinomeris napoensis</i> Nguyen et al., 2019	Bac Me NR, Ha Giang, Vietnam		MT749396	Nguyen et al. 2021	
Tcost8-MK	Trachysphaera costata (Waga, 1857)	Slovakia		KX467622	Mock et al. 2016	
GBOL33714	<i>Glomeris marginata</i> (Villers, 1789)	Königshütte, Wernigerode, Sachsen- Anhalt, Germany	51.743°N, 10.767°E	MG892112	Reip and Wesener 2018	
ZFMK1634	Glomeris marginata (Villers, 1789)	Bockswiese Goslar, Niedersachsen, Germany	51.841°N, 10.326°E	MG892119	Reip and Wesener 2018	
Outgroup Sphaeroth	eriida: Zephroniidae					
FMNH-INS 0000 072 674)	Sphaerobelum truncatum Wongthamwanich, 2012	Pang Hi Village, Nan, Thailand	19°23'46.3"N, 100°41'42.4"E	JN885184	Wongthamwanich et al. 2012	
ZFMK Myr3502	Zephronia laotica Wesener, 2019	Garden of Erawan Riverside Hotel, Champasak, Laos	15°6'27.0"N, 105°49'14.3"E	MK330977	Wesener 2019	

 Table 1. List of species used for molecular phylogenetic analyses and relevant information. * = paratype.

the COI sequence was evaluated using uncorrected p-distances as implemented in MEGA7 (Kumar et al. 2016). The missing data in pairwise comparison were treated with pairwise deletion method.

Taxonomy

Family Glomeridae Leach, 1815

Genus Hyperglomeris Silvestri, 1917

Hyperglomeris Silvestri, 1917: 145 (D, K).

Hyperglomeris-Golovatch, 1983a: 110 (M); 2017: 196 (M); Golovatch et al. 2013:

202 (M); Nguyen et al. 2019: 274 (M, K); 2021: 257 (M); Kuroda et al. 2022a: 162 (M); 2022b: 117 (M).

Dinoglomeris Silvestri, 1917: 147 (D, K), synonymized by Golovatch (1983b: 180).

Diagnosis. Pill millipedes with four apical cones on the antennae; the caudal margins of the pygidium are sometimes modified into small paramedian lobes, but are mostly emarginate or slightly concave medially; leg-pair 18 devoid of any evident mesal outgrowths on the femur or tibia; the posterior telopods are rather stout, with prefemoral trichosteles reduced or only present as a small cone; and the femoral trichosteles are strongly reduced or absent.

Type species. Hyperglomeris lamellosa Silvestri, 1917, by original designation.

Species included. Hyperglomeris lamellosa Silvestri, 1917, H. dirupta (Silvestri, 1917), H. conspicua Golovatch, 1983, H. maxima Golovatch, 1983, H. depigmentata Golovatch, Geoffroy & VandenSpiegel, 2013, H. nigra Golovatch, 2017, H. simplex Nguyen, Sierwald & Marek, 2019, H. bicaudata Likhitrakarn, sp. nov., H. inkhavilayi Likhitrakarn, sp. nov.

Remarks. The genus *Hyperglomeris* was established by Silvestri (1917), who designated *H. lamellosa* Silvestri, 1917 as the type species and provided a detailed description and excellent illustrations. At the same time, he created a new genus and species, *Dinoglomeris dirupta*, which only superficially differed from *Hyperglomeris*. Both species were discovered on Mount Mẫu Sơn, Vietnam, but at different altitudes. Subsequently, Golovatch (1983b) investigated the scope of the genus using his material from Vietnam and proposed that the two genera be combined into one. Afterwards, Golovatch published two new species, synonymizing the name *Dinoglomeris* with *Hyperglomeris*.

Hyperglomeris lamellosa Silvestri, 1917

Hyperglomeris lamellosa Silvestri, 1917: 147 (D); Golovatch 1983a: 110 (M, K); 1983b: 180 (L); 2017: 196 (M, K); Golovatch et al. 2013: 201 (M); Enghoff et al. 2004: 31 (L); Nguyen et al. 2019: 263 (L, M).

Remarks. This species was described from Mount Mẫu Sơn, 2000–3000 feet a.s.l., Langson Province, Vietnam (Silvestri 1917). Endemic to Vietnam.

Hyperglomeris dirupta (Silvestri, 1917)

Dinoglomeris dirupta Silvestri, 1917: 147 (D). *Hyperglomeris dirupta*–Golovatch, 1983a: 110 (M, K); 1983b: 180 (L); 2017: 196 (M, K); Golovatch et al. 2013: 201 (M); Enghoff et al. 2004: 31 (L); Nguyen et al. 2019: 263 (L, M).

Remarks. This species was described from Mount Mẫu Sơn, 200–300 feet a.s.l., Langson Province, Vietnam (Silvestri 1917). Endemic to Vietnam.

Hyperglomeris conspicua Golovatch, 1983

Hyperglomeris conspicua Golovatch, 1983a: 110 (D, K); Golovatch 1983b: 180 (L); 2017: 197 (M, K); Golovatch et al. 2013: 201 (M); Enghoff et al. 2004: 31 (L); Nguyen et al. 2019: 262 (L, M).

Remarks. This species was described from Van Mai, Mai Châu District, Hòa Bình Province, Vietnam (Golovatch 1983a). Endemic to Vietnam.

Hyperglomeris maxima Golovatch, 1983

Hyperglomeris maxima Golovatch, 1983a: 108 (D, K); Golovatch, 1983b: 180 (L); 2017: 197 (M, K); Golovatch et al. 2013: 201 (M); Enghoff et al. 2004: 31 (L); Nguyen et al. 2019: 263 (L, M).

Remarks. This species was described from Van Mai, Mai Châu District, Hòa Bình Province, Vietnam (Golovatch 1983a). Endemic to Vietnam.

Hyperglomeris depigmentata Golovatch, Geoffroy & VandenSpiegel, 2013

Hyperglomeris depigmentata Golovatch et al., 2013: 206 (D); Golovatch 2017: 197 (M, K); Nguyen et al. 2019: 262 (L, M); Kuroda et al. 2022a: 162 (M, K).

Remarks. This species was described from Cave Hang Doi, 20.496176°N, 105.137465°E, Lang Kho Muong, Than Son, Thanh Hoa Province, Vietnam (Golovatch et al. 2013). Endemic to Vietnam.

Hyperglomeris nigra Golovatch, 2017

Hyperglomeris nigra Golovatch, 2017: 195 (D, K); Nguyen et al. 2019: 263 (L, M).

Remark. This species was described from Xuan Son National Park, 21°07'52"N, 104°57'07"E, 400–470 m a.s.l., ca. 90 km northwest of Hanoi, Phu Tho Province, Vietnam (Golovatch 2017).

Hyperglomeris simplex Nguyen, Sierwald & Marek, 2019

Hyperglomeris simplex Nguyen et al., 2019: 276 (D). *Hyperglomeris simplis* (sic!)–Nguyen et al. 2021: 258 (MI, M).

Remark. This species was described from Me Linh Station for Biodiversity, 21.3850°N, 105.7119°E, Ngoc Thanh Commune, Phuc Yen Town, Vinh Phuc Province, Vietnam (Nguyen et al. 2019).

Hyperglomeris bicaudata Likhitrakarn, sp. nov.

https://zoobank.org/FB13C74A-496A-45F0-BB73-C710A6C5123D Figs 1–3A, B

Material examined. *Holotype*: LAOS – Houaphanh • \Im (CUMZ-GLO006); Viengxay District, Limestone mountain area near Kaysone Phomvihane Cave; elev. 890 m a.s.l.; 20°20'24"N, 104°13'44"E; 6 Jul. 2014; R. Srisonchai, C. Sutcharit, K. Inkhavilay leg.; CUMZ; *Paratypes*: LAOS – Houaphanh • 1 \Im ; same collection data as holotype; • 3 $\Im \Im$ (CUMZ-GLO004); Viengxay District, Ban Tham Na Tan, Limestone mountain area; elev. 860 m a.s.l.; 20°27'28"N, 104°08'43"E; 5 Jul. 2014; R. Srisonchai, C. Sutcharit, K. Inkhavilay leg.; CUMZ; OQ661871 • 1 \Im , 2 $\Im \Im$ (CUMZ-GLO007); Viengxay District, Limestone mountain area near vocational-technical school around kilometre 31; elev. 840 m a.s.l.; 20°24'15"N, 104°15'4"E; 6 Jul. 2014; R. Srisonchai, C. Sutcharit, K. Inkhavilay leg.; CUMZ; OQ661872.

Name. To emphasize the caudal margin of the anal shield being more (\mathcal{O}) or less (\mathcal{Q}) strongly bisinuate medially; adjective in feminine gender.

Diagnosis. Its unique color pattern is similar to that of *H. nigra* Golovatch, 2017, from Vietnam (Golovatch, 2017), but the two species differ by the thickness of the contrasting paler bands at the lateral and caudal edges of all tergites (ca. 1/3 vs. $1/5 \times$ as high as tergite height), the number of striae at the lateral edge of midbody tergites (2 vs. 3), the number of ommatidia (10+1(2) vs. 8+1), coupled with two tibial processes (one large process and one small cone vs. two small tibial cones), and the caudal edge of the anal shield (two strongly bisinuate medially vs. slightly emarginate medially).



Figure 1. *Hyperglomeris bicaudata* sp. nov. **A–D** ♂ paratype (CUMZ-GLO006), habitus, live coloration **E–G** ♂ holotype (CUMZ-GLO006) habitus in dorsal, ventral, and lateral views **A**, **C** unrolled, sublateral views **B**, **D** rolled, sublateral and subdorsal views, respectively. **A–D** not to scale.

Description. *Body length* of stretched holotype 13.2 mm, width 8.3 mm. Body length of stretched paratypes 13.5 mm (\Im), 13.5–15.5 mm (\Im), width 9.5 (\Im), 8.5–9.5 mm (\Im).

Coloration of live animals (Fig. 1A–D): body blackish, with contrasting pale yellow to orange yellow, rather broad bands at the lateral and caudal edges of all tergites, ca. $1/3 \times$ as high as each tergite height, including collum, thoracic and anal shields.



Figure 2. *Hyperglomeris bicaudata* sp. nov. **A**, **C**, **E**, **F** \mathcal{S} holotype (CUMZ-GLO006) **B** \mathcal{Q} paratype (CUMZ-GLO006) **D** \mathcal{S} paratype (CUMZ-GLO007) **A**, **B** anal shield edge in venter view, male and female, respectively **C** leg 17, anterior view **D** leg 18, anterior view **E**, **F** telopod, posterior and anterior views, respectively **G** tip of syncoxital lobes (not to scale). Scale bars: 1 mm (**A**–**F**). Abbreviations: **cx** coxa, **cxl** coxal lobe, **fe** femur, **fp** femoral process, **pf** prefemur, **pfc** prefemoral cone of telopod, **sh** syncoxital horn of telopod, **sl** syncoxital lobe of telopod, **sn** syncoxite notch, **sx** syncoxite, **ta** tarsus, **tc** tibial cone, **ti** tibia, **tp** tibial process.

Head and antennae black, only labrum and Tömösváry's organ yellowish. Venter and legs dark brown to brown with a pale yellowish claw and the posterior part of each tarsus; coloration in alcohol faded after eight years of preservation (Fig. 1E–G), body pale black to charcoal, with contrasting pale yellow to whitish bands. Head and antennae grey to blackish. Venter and legs pale brown to brownish.

Labrum sparsely setose (Fig. 1F). Gnathochilarium with 2+2 palps of subequal length. Ocular fields whitish, 10+1(2) ommatidia, cornea convex, oval in shape, translucent. Antennae with four evident apical cones, segment 6 ca. 2.1–2.4× as long as high. Organ of Tömösváry typical, horseshoe-shaped, oblong-oval, elongate, ca. 1.5–1.8× as long as broad (Fig. 1F).

Collum as usual, with two transverse striae (Fig. 1F). Thoracic shield with a small hyposchism field not projecting caudad past tergal margin. Striae 4–6, mostly



Figure 3. Leg 18 **A**, **B** *Hyperglomeris bicaudata* sp. nov., \Im paratype (CUMZ-GLO007), left, anterior and posterior views, respectively **C**, **D** *Hyperglomeris inkhavilayi* sp. nov., \Im paratype, right, anterior, and posterior views, respectively. Scale bars: 1 mm.

superficial, only lower 3 or 4 lying above schism, one level with schism, remaining 1 or 2 below schism, with 4 and 5 complete, crossing the dorsum (Fig. 1G). Terga 3 and 4 rather broadly rounded laterally (Fig. 1G). Following terga in front of pygidium faintly concave medially at caudal edge and with two striae starting above lateral edge, sometimes first stria fading away towards midway. Caudal edge of anal shield more (\mathcal{J} , Figs 1C, E, F, G, 2A) or less (\mathcal{Q} , Fig. 2B)) strongly bisinuate medially.

Male legs 17 (Fig. 2C) strongly reduced, with a rather high, often irregularly rounded coxal lobe (cxl) and a 4-segmented telopodite.

Male legs 18 (Figs 2D, 3A, B) simple, rather strongly reduced, without any evident outgrowths; syncoxite membranous, on either side with a simple, small, and narrowly ogival syncoxite notch (sn) and a 4-segmented telopodite.

Telopods (= male legs 19) (Fig. 2E–G) with a very large, broad and roundly subtrapeziform syncoxital lobe (sl) flanked by two short, spiniform, obliquely truncate, setose syncoxital horns (sh), level with syncoxital lobe (Fig. 2F). Telopodite 4-segmented, with a spine apically. Prefemur subellipsoid, with an evident, rather small, distad tapering, tuberculiform, distomesal prefemoral cone (pc) (a reduced trichostele), ca. $1/4-1/5 \times as$ long as femur. The latter in caudal view with a prominent, stout, fingershaped, distomesal femoral process (fp) devoid of a trichostele, produced apically to ca. 3/4 tibia. Tibia elongate, gently tapering distad and curved apically basad towards process on femur, with an evident, caudad curved, distolateral tibial process (tp) and a small, short and pointed distomesal tibial cone (tc). Tarsus smallest, subcylindrical, moderately sigmoid, strongly curved, narrowly rounded apically.

Remarks. Unique to this species is that the caudal margin of the anal shield shows two more (\mathcal{O} , Figs 1C, E, F, G, 2A) or less (\mathcal{Q} , Fig. 2A) pronounced paramedian knobs. That the male is equipped with such modifications is quite usual in various lineages of Glomerida (e.g., Liu and Golovatch 2020), but their presence in the female, albeit not as strongly as in the male, is really striking.

This distinguishing character can be hypothesized as possibly playing an important role in a courtship process or being associated with courtship behavior. Certain male structures dedicated to interactions with females during courtship have often diverged relatively quickly during evolution, causing these features to change into species-specific differences (Eberhard 2004). Noteworthy examples of such characters are antennae, legs and heads in springtails (Collembola: Bourletiellidae) (Kozlowski and Aoxiang 2006) and stridulation organs in giant pill millipedes (Sphaerotheria) (Wesener et al. 2011) that may not be involved directly in sperm transfer but are associated with mating behavior. In order to understand the relationship between these types of traits and their function in the glomerids, it is essential to examine the mating behavior of this species.

Hyperglomeris inkhavilayi Likhitrakarn, sp. nov.

https://zoobank.org/60149C6A-59F8-4AD9-82EC-7A8A1CCBD7EA Figs 3C, D, 4, 5

Material examined. *Holotype*: LAOS – Khammouane • \mathcal{O} (CUMZ-GLO095); Nhommalath District, Ban Phawong, orchard; elev. 190 m a.s.l.; 17°32'24"N, 105°25'18"E; 25 Aug. 2014; R. Srisonchai, C. Sutcharit, K. Inkhavilay leg.; CUMZ; *Paratypes*: LAOS – Khammouane • 2 $\mathcal{O}\mathcal{O}$, 3 $\mathcal{Q}\mathcal{Q}$; same collection data as holotype; OQ661873, OQ661874.

Name. To honor Dr. Khamla Inkhavilay, the director of the Center of Excellence in Biodiversity at National University of Laos, Vientiane, Laos, who participated in collecting the type series.

Diagnosis. Although its color pattern seems to be similar to that of *H. simplex* Nguyen, Sierwald & Marek, 2019 (Nguyen et al. 2019), it differs by the coloration of the collum, thoracic and anal shields (mostly pale yellowish to brownish vs. dark brown to blackish), leg-pair 18 (with a simple, subtriangular syncoxital notch (sn) vs. an evident pronounced syncoxital tubercles), coupled with a longer prefemoral trichostele (pt) (more than 2/3 vs. 1/2 of femur).

Description. Body length of stretched holotype 10.7 mm, width 6.9 mm. Body length of stretched paratypes 9.3 mm (\Im), 13.5–15.5 mm (\Im), width 5.6 (\Im), 5.2–8.5 mm (\Im).

Coloration in alcohol faded after eight years of preservation (Fig. 4), body mostly yellowish, with contrasting black paramedian spots flanking the midline. Mid-dorsal spots on each of tergites 3–11 usually subtriangular (Fig. 4A, D), or parallel-sided



Figure 4. *Hyperglomeris inkhavilayi* sp. nov., habitus in dorsal, ventral, and lateral views **A–C** \bigcirc paratype (CUMZ-GLO095) **D** male paratype (CUMZ-P085) **E, F** \bigcirc holotype (CUMZ-P085). Scale bars: 2 mm.

(Fig. 4E), with smaller and detached patches at caudal edge of tergite 2 and at anterior edge of tergite 12. Lateral sides of each of tergites 2–11 also with a pair of large, sublateral, yellow to marbled blackish spots beside the triangles, normally not reaching the translucent caudal and lateral edges (Fig. 4A, C–E). Head and collum pale yellowish to dark brownish with darker color laterally. Antennae black to dark brown, only tip of antennae yellowish. Legs and venter pale yellowish to pale brown (Fig. 4B).

Labrum sparsely setose (Fig. 4B). Gnathochilarium with 2+2 palps of subequal length. Ocular fields blackish, 8(7)+1 ommatidia, cornea very convex, translucent. Antennae with four evident apical cones, segment 6 ca. $2.1-2.4\times$ as long as high



Figure 5. *Hyperglomeris inkhavilayi* sp. nov. **A** \circlearrowleft paratype (CUMZ-GLO095) **B–F** \circlearrowright holotype (CUMZ-P085) **A, B** leg 17, anterior views **C** leg 18, anterior view **D, E** telopod, posterior and anterior views **F** tip of syncoxital lobes (not to scale). Scale bars: 1 mm (**A–E**). Abbreviations: **cx** coxa, **cxl** coxal lobe, **fe** femur, **fp** femoral process, **pf** prefemur, **pft** prefemoral trichostele of telopod, **sh** syncoxital horn of telopod, **sl** syncoxital lobe of telopod, **sn** syncoxite notch, **sx** syncoxite, **ta** tarsus, **tc** tibial cone, **ti** tibial process.

(Fig. 4B). Organ of Tömösváry typical, horseshoe-shaped, oblong-oval, elongate, ca. 1.3–1.5× as long as broad (Fig. 4B).

Collum as usual, with two transverse striae. Thoracic shield with a small hyposchism field not projecting caudad to nearly reaching the tergal margin. Striae 5–7, mostly superficial, only lower 2 or 3 lying above schism, one level with schism, remaining 3 or 4 below schism, with 5 or 6 complete, crossing the dorsum. Terga 3 and 4 broadly rounded laterally (Fig. 4C, F). Following terga in front of anal shield rather clearly concave medially at caudal edge and with 2–4 striae starting above lateral edge. Male anal shield slightly concave medially at caudal edge (Fig. 4D, E).

Male legs 17 (Fig. 5A, B) strongly reduced, with a rather large, often irregularly rounded coxal lobe (cxl) and a 4-segmented telopodite.

Male legs 18 (Figs 3C, D, 5C) simple, rather strongly reduced, without any evident outgrowths; syncoxite membranous, on either side with a broad, subtriangular syncoxital notch (sn) and a 4-segmented telopodite.

Telopods (= male legs 19) (Fig. 5D–F) with a large, rather roundly subtrapeziform syncoxital lobe (sl) with a small notch medially (Fig. 5E), flanked by two very long, spiniform, obliquely truncate, setose syncoxital horns (sh), two × as high as syncoxital lobe (Fig. 5D, E). Telopodite 4-segmented, with a spine apically. Prefemur subquadrangular, with a long, rather stout, distad tapering, slightly curved prefemoral trichostele (pt) carrying a short seta, ca. $2/3 \times$ as long as femur. The latter on caudal face with a prominent, stout, finger-shaped, gently tapering distad, distomesal femoral process (fp) devoid of a trichostele, produced apically to ca. 3/4 tibia. Tibia elongate, gently tapering distad and curved apically basad towards process on femur, with an evident, caudad curved, caudal tibial process (tp). Tarsus smallest, subcylindrical, moderately sigmoid, strongly curved, narrowly rounded apically.

Remarks. Unfortunately, the claw on the male legs 18 tarsus could not be observed, being broken off in both available male specimens, of which only one leg is available for examining the entire tarsus. Consequently, additional specimens are required to determine tarsal claws.

Key to the known species of *Hyperglomeris* based on adults, modified after Golovatch (2017)

1	Body completely unpigmented, pallidH. depigmentata
_	Body at least partly pigmented (Figs 1, 4)2
2	Dorsum entirely blackish (except for narrow pale lateral and caudal margins
	of tergites) (Fig. 1)
_	Dorsum with evident pale markings (Fig. 4)4
3	Caudal margins 1/3 as high as tergite height; caudal edge of anal shield evi-
	dently bisinuate medially (Figs 1C, F, 2A, B). 10+1(2) ommatidia. Tibia of
	telopod with a large process and a small tibial cone (tc) (Fig. 2E)
	H. bicaudata sp. nov.
_	Caudal margins 1/5 as high as tergite height. Caudal edge of anal shield
	slightly emarginate medially. 8+1 ommatidia. Tibia of telopod with two small
	tibial cones
4	Anal shield entirely, tergum 2 partly or entirely unpigmented; tergum 2 with-
	out fine striae, but with a conspicuous sulcus anterodorsad of schism
	H. conspicua
_	Both anal shield and tergum 2 at least partly with dark pigment
5	Dorsum without a dark axial line, background coloration either black or red-
2	vellow
_	Dorsum with a contrasting and brighter axial line against a darker side back-
	ground (Fig. 4) 7
6	Telopod syncovital lobe trapeziform and truncate its ventral margin
0	straight H diruta
_	Telopod syncovital lobe semi-circular, its ventral margin rounded
	H lamallosa

7	Prefemoral cone very short, less than 1/5 femur. Syncoxital horns (sh) as long
	as syncoxital lobe (sl)
_	Prefemoral trichostele (pt) longer than 1/2 femur. Syncoxital horns (sh) high-
	er than syncoxital lobe (sl)
8	Collum, thoracic and anal shields mostly dark brown to blackish. Male leg-
	pair 18 with an evidently pronounced tubercles on syncoxite. Prefemoral tri-
	chostele (pt) of telopod longer than 1/2 femur
_	Collum, thoracic and anal shields mostly pale yellowish to brownish (Fig. 4).
	Leg-pair 18 with a simple, subtriangular syncoxital notch (sn) (Figs 3C, D,
	5C). Prefemoral trichostele (pt) of telopod longer than 2/3 femur (Fig. 5E)

Phylogenetic analysis

The COI alignment (Table 1) was 660 bp in length and contained 23 individuals, including 21 taxa from the Glomeridae as ingroup and two taxa from the Zephroniidae as outgroup. All ten pill millipede species from seven genera of the family Glomeridae in this study were retrieved as monophyletic with strong support values (Fig. 7) (77– 100% bp for ML and 0.96–1 bpp for BI). However, most relationships among these species were still unresolved (< 80% bootstrap values and < 0.95 bpp for BI).

The COI tree demonstrated that the genus *Hyperglomeris* is at least paraphyletic, because of the inclusion of *Peplomeris magna* in the same clade with *H. bicaudata* sp. nov., *Hyperglomeris* sp. 1, and *H. inkhavilayi* sp. nov., although with moderate nodal support; and the exclusion of *H. simplex*, which was placed distantly at the basal position to all Glomeridae. Each of the three *Hyperglomeris* species in this study (*H. bicaudata* sp. nov., *H. inkhavilayi* sp. nov., and *H. simplex*) was retrieved as a distinct clade/species with significant support (99–100% for ML; and 0.99 bpp for BI, except 0.58 in *H. simplex*).

The interspecific divergence based on COI uncorrected p-distance among the glomerid species in this study ranged from 8.81 to 16.45%, with an average of 13.07% (Table 2), and among *Hyperglomeris* species ranged from 8.81 to 12.48%, with an average of 11.23%. This analysis also demonstrated that the intraspecific divergence for *H. bicaudata* sp. nov. was 5.30% and for *H. inkhavilayi* sp. nov. was 0.45%.

Discussion and conclusion

This study has revealed two new species of *Hyperglomeris*, a genus new to the fauna of Laos. In addition, we have also refined the scope of the genus and the species distributions. These new records have increased the number of species of the order Glomerida in Laos from four (all in *Hyleoglomeris*) to a total of six. At present, the genus *Hyperglomeris* comprises nine species, mostly recorded from Vietnam (seven species), now also from Laos (two species) (Fig. 6). All *Hyperglomeris* species appear to be highly localized and

Taxa	1.	2.	3.	4.	5.	6.	7.	8.	9.	10.	11.	12.
 Hyperglomeris bicaudata sp. nov. 	5.30 ± 0.85											
 Hyperglomeris inkhavilayi sp. nov. 	10.76 ± 1.14	0.45 ± 0.27										
3. Hyperglomeris sp. 1	11.93 ± 1.21	8.81 ± 1.10	n/a									
4. Hyperglomeris simplex	12.48 ± 1.15	11.40 ± 1.20	11.96 ± 1.24	$\begin{array}{c} \textbf{4.86} \pm \\ \textbf{0.84} \end{array}$								
5. Peplomeris magna	10.87 ± 1.16	10.17 ± 1.16	10.01 ± 4.21	12.47 ± 1.25	$\begin{array}{c}\textbf{0.47} \pm \\ \textbf{0.28} \end{array}$							
6. Hyleoglomeris lobus	12.89 ± 1.22	11.65 ± 1.21	13.85 ± 1.31	11.98 ± 1.17	12.73 ± 1.27	3.24 ± 0.55						
7. Tonkinomeris napoensis	12.76 ± 1.17	12.00 ± 1.22	14.25 ± 1.36	13.43 ± 1.24	12.91 ± 1.30	13.58 ± 1.27	2.16± 0.57					
8. Rhopalomeris sauda	13.84 ± 1.22	11.99 ± 1.15	13.53 ± 1.23	12.15 ± 1.11	12.52 ± 1.15	12.25 ± 1.12	13.16± 1.17	6.84± 0.69				
9. Trachysphaera costata	14.46 ± 1.45	13.35 ± 1.41	14.46 ± 1.51	13.44 ± 1.36	13.86 ± 1.45	13.10 ± 1.35	14.29 ± 1.45	14.16± 1.30	n/a			
10. Glomeris marginata	16.45 ± 1.40	14.17 ± 1.42	16.28 ± 1.48	15.50 ± 1.41	14.84 ± 1.40	15.22 ± 1.40	14.23 ± 1.33	15.06± 1.31	12.93 ± 1.41	3.04 ± 0.69		
11. Sphaerobelum truncatum	28.79 ± 1.68	28.64 ± 1.72	29.50 ± 1.82	28.43 ± 1.70	28.36 ± 1.72	29.02 ± 1.70	28.96 ± 1.73	28.64 ± 1.65	28.57 ± 1.87	29.80 ± 1.72	n/a	
12. Zephronia laotica	30.42 ± 1.77	28.91 ± 1.74	28.75 ±1.79	28.54 ± 1.77	29.63 ± 1.77	30.58 ± 1.74	31.91 ± 1.76	29.55 ± 1.72	29.13 ± 1.85	31.35 ± 1.76	22.39 ± 1.65	n/a

Table 2. Matrix of the average uncorrected p-distance (%) based on 660-bp COI barcoding region between *Hyperglomeris* species and some related glomerid and sphaerotheriid taxa. Interspecific divergence is below diagonal and intraspecific divergence is in bold.

endemic, with *H. depigmentata* probably a troglobiont, found exclusively in Hang Doi Cave. At two of these localities (Mount Mẫu Sơn and Vạn Mai), a coexistence of two species has been documented (Fig. 6). In addition to reporting these two new species, this study presents the southernmost record of *Hyperglomeris* in southern Laos. The distribution patterns (Fig. 6) clearly indicate that further new species of the genus can be expected from Laos, southern China and northern and/or eastern Thailand in the future.

The interspecific COI uncorrected p-distances among *Hyperglomeris* species in this study (8.81–16.45%) are comparable to those of European *Glomeris* species (11.5–17.1%; Wesener 2015b) and among the Vietnamese glomeridan genera (*Peplomeris*, *Hyperglomeris*, *Hyleoglomeris*, and *Tonkinomeris*) (13–15.8%; Nguyen et al. 2021). The smallest difference was retrieved between *H. inkhavilayi* sp. nov. and *Hyperglomeris* sp. 1 (8.81%), and the distance between these two species' localities is around 180 kilometers. Thus, it is reasonable to believe that they are highly close congeners. Likewise, this result is consistent with the re-calculated interspecific distances between European *Glomeris* species, which ranged from 6.7% to 15.9%, and where the least distance (6.7–9.0%) was between *G. primordialis* and *G. klugii* (Wesener and Conrad 2016).

The intraspecific distance within the new species ranged from 0.45 to 5.3%. This is comparable to the range of the Vietnamese glomerid species, *Peplomeris magna* (0.2%) and *Rhopalomeris sauda* (7.7%) (Nguyen et al. 2021). The mean intraspecific distance of *R. sauda* was rather high (6.84%) because of its extensive distribution (Nguyen et al. 2021), and the fact that the analyzed samples were gathered from multiple localities,



Figure 6. Distribution of nine *Hyperglomeris* species. Crossed square *H. lamellosa* Silvestri, 1917 and *H. dirupta* (Silvestri, 1917) Crossed circle *H. simplex* Nguyen, Sierwald & Marek, 2019 Open diamond *H. nigra* Golovatch, 2017 Inverted triangle *H. conspicua* Golovatch, 1983 and *H. maxima* Golovatch, 1983 Circle *H. depigmentata* Golovatch, Geoffroy & VandenSpiegel, 2013 Triangle *H. bicaudata* Likhi-trakarn, sp. nov. Square *H. inkhavilayi* Likhitrakarn, sp. nov.

whereas for the other species, a single locale was selected. Similarly, the relatively high value of *H. bicaudata* sp. nov. (5.3%) was obtained from samples collected from two sites for analysis; thus, there are greater differences between the two population groups compared to *H. inkhavilayi* sp. nov., which had a low value (0.45%) due to the selection of study specimens from a single population.

The COI tree clustered both new species with *Hyperglomeris* sp. 1 and *Peplomeris magna* with a supported clade (Fig. 7). *Peplomeris* Silvestri, 1917 and *Hyperglomeris* are closely related genera found in the same country and classified in the same subfamily Haploglomerinae. Morphological characteristics of the genus *Peplomeris* are extremely similar to those of the genus *Hyperglomeris*, including the basic structure of posterior



Figure 7. Maximum likelihood tree (ML) of pill millipedes in the family Glomeridae based on 660 bp of COI gene. Clades of new species in this study are highlighted in blue. Numbers on nodes are bootstrap values (bs) from ML analysis and bipartition posterior probability (bpp) from Bayesian inference analysis (BI), and are shown as ML/BI.

telopods with reduced or eliminated prefemoral and femoral trichosteles. However, *Hyperglomeris* has only four apical cones on their antennae, whereas *Peplomeris* has numerous apical cones (Wesener 2015a; Nguyen et al 2019). Consequently, it is not surprising that the genetic relationship between the members in these two genera is very close. Despite this, it is premature to make conclusions about the relationships among the two genera based on the results of this study; additional persuasive evidence (i.e., more taxa and genetic markers) is needed to clarify the taxonomic status of both genera.

DNA sequence analysis was previously introduced and has provided a more reliable identification of glomerid species (Nguyen et al. 2019, 2021; Liu and Golovatch 2020). The present paper provides a phylogenetic analysis of ten members of seven genera within the family Glomeridae, including three new sequences from two recently discovered species. Unfortunately, the phylogenetic relationships among these genera is still not supported, which is consistent with studies by Liu and Golovatch (2020) and Nguyen et al. (2021). Hence, data from the COI gene alone are not sufficient to confirm the relationship between genera within this millipede family. We recommend including more genes such as 16S, 28S ribosomal RNA or other advanced molecular techniques (i.e., transcriptomic and phylogenomic data) in future studies to clarify phylogenetic relationships (Means et al. 2021; Benavides et al. 2023). Nonetheless, our findings regarding *Hyperglomeris* demonstrate that the sequencing of the COI gene is still beneficial for species delimitation and facilitates accurate identification among glomerid species.

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