RESEARCH ARTICLE



A new species of *Tegenaria* Latreille, 1804 (Araneae, Agelenidae) from Turkey

Rahşen S. Kaya^{1,†}, Kadir B. Kunt^{2,‡}, Yuri M. Marusik^{3,§}, İsmail H. Uğurtaş^{1,1}

I Department of Biology, Faculty of Arts and Sciences, Uludağ University, TR-16059, Nilüfer, Bursa, Turkey
 2 Turkish Arachnological Society, Eserköy Sitesi, 9/A Blok, No 7, TR-06530, Ümitköy, Ankara, Turkey
 3 Institute for Biological Problems of the North RAS, Portovaya Str. 18, Magadan, Russia

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Corresponding author: Rahşen S. Kaya (rkaya@uludag.edu.tr)

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Abstract

A new species of the spider genus *Tegenaria* Latreille, 1804 is described, based on newly collected specimens from Turkey. Detailed morphological descriptions, diagnosis and figures of the copulatory organs of both sexes are presented. Finally, a checklist and distribution maps for Turkish *Tegenaria* species are provided.

Keywords

Agelenidae, new species, Tegenaria, Turkey

Introduction

The spider family Agelenidae currently constitutes 514 species in 42 genera and has a global distribution (Platnick 2010). *Tegenaria* Latreille, 1804 is the largest genus of the family, with 101 described species, primarily from the Palaearctic region, but with

some from the Oriental Region and a few from the Nearctic (Roth 1968; Gertsch 1971; Levy 1996; Platnick 2010). To date, 22 *Tegenaria* species have been reported from Turkey, of which 15 are endemic to the country (Bayram et al. 2010; Platnick 2010). Brignoli (1972, 1978 a, b) was the most prominent contributor to the knowledge of Turkish agelenid spiders, having described and/or recorded 16 species from the country. However, most of these species are still poorly understood and remain known only from their original descriptions.

In general, the supraspecific taxonomy of *Tegenaria* and the tribe Tegenariini is poorly resolved. The genus includes species with very different palpal and epigynal conformations. Recently, Guseinov et al. (2005) removed 26 species from *Tegenaria* and transferred them to *Malthonica* Simon, 1898. The taxonomy of *Tegenaria* with respect to the Mediterranean fauna is currently being developed by A. Bolzern (Bolzern 2007; Bolzern et al. 2008, 2009).

During our surveys of the Turkish spider fauna, we found an undescribed species in the southern region of the country. This species possesses copulatory organs different from other Turkish and eastern Mediterranean *Tegenaria* and is described here as a new species.

Material and methods

The specimens were studied using a Leica M205 C stereomicroscope. The description of colour was based on live specimens. The epigyne was macerated in 10% KOH. Measurements were taken with a micrometer eyepiece from the dorsal aspect of the palps and legs. The morphological terminology follows Levy (1996) and Guseinov et al. (2005). Leg spination follows Bolzern et al. (2008, 2009). The taxonomy and world distribution data were derived from Platnick (2010).

Specimens were photographed using an Olympus Camedia E-520 camera attached to an Olympus SZX16 stereomicroscope. Images were produced using "CombineZP" image stacking software. Photographs were taken in dishes of different sizes with paraffin at the bottom. Holes of different sizes were made in the paraffin in order to keep specimens in the required position.

The following abbreviations are used:

AER anterior eye row; **ALE** anterior lateral eyes; **AME** anterior median eyes; **PER** posterior eye row; **PLE** posterior lateral eyes; **PME** posterior median eyes.

All measurements are in millimeters (mm).

Type specimens have been preserved in 70% ethanol and deposited in the Zoological Museum of Uludağ University (ZMUU, Department of Biology, Bursa, Turkey) and the Zoological Museum of the Moscow State University (ZMMU, Moscow, Russia; curator Dr K.G. Mikhailov).

Description

Genus Tegenaria Latreille, 1804

Tegenaria bayrami sp. n.

urn:lsid:zoobank.org:act:705E551F-CD34-4BAE-9757-48B8AC25B970 Figs 1–16, 20

Material. Holotype: male (ZMUU): Turkey: Antalya Province, Manavgat District, Beşkonak Village, Köprülü Canyon, 37°11'N 31°11'E, 243 m a.s.l., 01.VI.2006, R. S. Kaya.

Paratypes. One male, one female and three subadult females (ZMUU), one male (ZMMU): same data as for the holotype, 21.VI.2010.

Etymology. The species is named in honor of Prof. Dr. Abdullah Bayram, who has made an important contribution to Turkish arachnology.

Diagnosis. *Tegenaria bayrami* sp. n. is closely related to *T. longimana* Simon, 1898, *T. vignai* Brignoli, 1978 and *T. halidi* Guseinov, Marusik & Koponen, 2005. Males of the new species can be easily distinguished from the mentioned species by the shape of the large and curved median apophysis and the pointed tip of the conductor (Figs 4, 6). The female of *T. bayrami* sp. n. can be separated from all other *Tegenaria* species by the square-shaped epigynal plate (Fig. 11), short ducts and round spermathecae (Figs 14–16).

Description. Male (holotype). Total length 9.00. Prosoma: carapace 4.60 long, 3.50 wide. Carapace brownish yellow, with two longitudinal darkened bands (Fig. 1), margins not darkened, scarce plumose hairs present. Cephalic region: 1.80 wide, darker and separated from the thoracic region by a distinct, darkened line. PER: 0.9 wide. Diameter of PME: 0.20; PLE: 0.22; AME: 0.10; ALE: 0.22. Distance of PME-PME: 0.10; PME-AME: 0.07. Eye formula: ALE=PLE>PME>AME. Clypeus height (measured from bottom of AME): 0.35, clypeus height (measured from bottom of ALE): 0.30. Clypeus deep reddish brown. Eve rows: AER slightly recurved, PER straight in dorsal view. Eye region darker. Chelicerae: 1.17 long; 0.90 wide. Chelicerae red-brown. Gnathocoxae: 1.32 long; 0.65 wide. Labium: 0.77 long; 0.70 wide. Gnathocoxae and labium brown. Sternum: 2.25 long; 2.22 wide. Sternum heart-shaped, pointed backwards, brown, with a light median band and three pairs of sublateral round spots. Legs light brown, with dark annulations, densely covered with plumose hairs; legs I and II are darker than legs III and IV (Fig. 1). Number of dorsal tarsal trichobothria on tarsi I and III: 10, tarsi II and IV: 9. Leg measurements are given in Table 1, and spine formulae in Table 2. Abdomen: 4.4 long, 2.6 wide; dorsum appears yellowish brown, with a reticulate patter of a series of transverse black lines along the dorsal mid-line and sides. Venter pale brown, with many short hairs and longitudinal black bars between the epigastric furrow and spinnerets.

Male palp as in Figs 4–10; very long (femur 5.10, patella 1.00, tibia 2.70, tarsus 2.20, (total 11.00), longer than body. Femur approximately 1.8 times longer than tibia,



Figures 1–5. The general appearance and male palp of *Tegenaria bayrami* sp. n. **I** male, dorsal view **2** female, dorsal view **3** female prosoma, lateral view, showing long legs **4–5** male palp, ventral and retrolateral views respectively.

tibia 1.2 times longer than cymbium. Retrolateral tibial apophysis with two branches: lateral branch in dorsal view elongated and more or less rectangular, in retrolateral view triangular and tapering off towards the tip; broad and rounded latero-ventral branch with a small protuberance close to lateral branch in retrolateral view. Median apophysis

		femur	patella	tibia	metatarsus	tarsus	total
male	palp	5.1	1.0	2.7	-	2.2	11.0
	Leg I	11.1	2.1	11.6	13.6	4.2	42.6
	Leg II	9.7	1.9	9.6	12.0	3.6	36.8
	Leg III	8.2	1.8	7.8	10.5	3.0	31.3
	Leg IV	9.6	1.8	9.4	13.4	3.4	37.6
female	palp	3.3	1.2	2.2	-	2.7	9.4
	Leg I	9.7	2.1	8.8	11.4	3.7	35.7
	Leg II	8.8	2.0	7.9	9.6	3.2	31.5
	Leg III	7.2	1.6	6.6	8.5	3.0	26.9
	Leg IV	9.4	2.0	8.2	11.1	3.2	33.9

Table 1. Leg and palp measurements of the holotype male and paratype female of Tegenaria bayrami sp. n.



Figures 6–10. The male palp of *Tegenaria bayrami* sp. n. 6 ventral view 7 lateral view 8 dorsal view 9 entire palp, retrolateral view 10 tibia and tarsus, retrolateral view.

long, in ventral view its base is large and broad, tip is claw-like. Conductor long, beakshaped in ventral view; embolus thick and short in ventral view.

Female. Total length 11.40. Prosoma: carapace 5.40 long, 4.00 wide. Carapace light yellow, with two longitudinal darkened bands (Figs 2–3), margins not darkened, scarce hairs present. Cephalic region: 2.40 wide, darker and separated from the thoracic region by a distinct, darkened line. PER: 1.17 wide. Diameter of PME: 0.20; PLE: 0.22; AME: 0.12; ALE: 0.22. Distance of PME–PME: 0.20; PME–AME: 0.25. Eye formula: ALE=PLE>PME>AME. Clypeus height (measured from bottom of AME): 0.42, clypeus height (measured from bottom of ALE): 0.40. Clypeus dark brown. Eye rows: AER slightly recurved, PER straight in dorsal view. Chelicerae: 2.50 long; 1.30 wide. Chelicerae brown. Gnathocoxae: 1.50 long; 0.90 wide. Labium: 0.90 long; 0.80 wide. Gnathocoxae and labium brown, labium slightly longer than wide. Sternum: 2.60 long; 2.40 wide. Sternum heart-shaped, pointed towards rear end, brown, with light median band and three pairs of sublateral round spots. Legs light brown, with dark annulations, densely covered by long hairs, plumose hairs present. Number of dorsal tarsal trichobothria on tarsi I and IV: 11, tarsi II and III: 10. Leg measurements are given in Table 1, and spine formulae in Table 2. Abdomen:

Table 2. Spination of legs and palps of *Tegenaria bayrami* sp. n. The formula gives the number of spines in the following order: dorsal – prolateral – retrolateral – ventral. The letter 'p' indicates a pair of spines that occur at this position.

		femur	patella	tibia	metatarsus	tarsus
palp	Paratype (female)	2-1-1-0	2-0-0-0	2-2-0-0	-	many
leg I	Holotype (male)	1-2-3-0	1-0-0-0	0-1-1-1	0-1-0-1p+1+1p	0-0-0-0
	Paratype (female)	2-3-2-0	2-0-0-0	1-1-1-1	1-1-1-1p+1p+1p	0-0-0-0
leg II	Holotype (male)	2-3-2-0	1-0-0-0	1-2-1-1+1p	0-2-1-1p+1+1p	0-0-0-0
	Paratype (female)	2-3-2-0	1-0-0-0	1-2-0-1p+1p	0-2-1-1p+1p+1p	0-0-0-0
leg III	Holotype (male)	2-2-2-0	1-0-0-0	1-2-1-1p+1p+1p	1-3-3-1p+1+1+1p	0-0-0-0
	Paratype (female)	4-5-4-0	1-0-0-0	1-2-1-1p+1p+1p	1-4-4-1p+1+1+1p+1p	0-0-0-0
leg IV	Holotype (male)	2-2-3-0	1-0-0-0	1-2-2+1p+1p	2-3-4-1+1+1+1p	0-0-0-0
	Paratype (female)	2-2-3-0	2-0-0-0	2-3-2-1p+1+1+1p	2-3-4-1p+1p+1p	0-0-0-0



Figures 11–16. The epigyne and spermathecae of *Tegenaria bayrami* sp. n. **11** before maceration, ventral view **12** ditto, caudal view **13–14** after maceration, ventral and dorsal views **15** ditto, latero-dorsal view **16** ditto, dorsal view.

6.00 long, 4.10 wide; dorsum yellowish brown, with a reticulate patter of a series of transverse, thick black lines along the dorsal mid-line and sides (Fig. 2). Venter pale brown, with many short hairs and longitudinal black bars between the epigastric furrow and spinnerets.

Epigyne and spermathecae as in Figs 11–16. Fovea absent, median plate squareshaped; copulatory openings almost invisible on intact epigyne, but readily visible following hair removal. Insemination duct short, spermathecae almost round.

Habitat. The new species was collected from damp places of rocky areas along the River Köprüçay (Köprülü Canyon, Antalya). The canyon is located on the lower slopes of the West Taurus Mountain ranges. Samples were collected from their big funnel webs during the day. The collection of a male in copula with a female clearly suggests that both sexes described here are conspecific.

Distribution. Turkey, known only from the type locality (Fig. 20).

Checklist of Tegenaria species known from Turkey

Figs 17-20

1. Tegenaria agnolettii Brignoli, 1978

Fig. 20

Tegenaria agnolettii Brignoli, 1978a: 44, fig. 7 (known from female only).

General distribution: Turkey.

Distribution in Turkey: Antalya Province: Döşemealtı District, Mustanini Cave (Brignoli 1978a).

2. Tegenaria agrestis (Walckenaer, 1802)

Fig. 17

For a complete list of references see Platnick (2010).

General distribution: Europe to Central Asia, USA and Canada.

Distribution in Turkey: Anatolia, no exact locality. It was reported from Turkey by Caporiacco (1935) only. It is likely that this record is the result of a misidentification.

3. Tegenaria atrica C.L. Koch, 1843

Fig. 18

For a complete list of references see Platnick (2010).

General distribution: Europe, introduced to North America.

Distribution in Turkey: İstanbul Province: Şile District; Kayseri Province: Yeşilhisar District, Harmankaya Cave (Roewer 1959). It is likely that this species was misidentified from Turkish specimens and probably does not occur in the country.



Figure 17. The distribution of *Tegenaria agrestis* (? = no exact locality in Anatolia; see, Caporiacco, 1935), *T. domestica* (1) and *T. parietina* (2) in Turkey.

4. Tegenaria averni Brignoli, 1978

Fig. 20

Tegenaria averni Brignoli, 1978a: 50, fig. 10 (known from female only).

General distribution: Turkey.

Distribution in Turkey: Mersin Province: Silifke District, Cennet Cave (Brignoli 1978a).

5. *Tegenaria bayrami* sp. n. Fig. 20

General distribution: Turkey only.

Distribution in Turkey: Antalya Province: Manavgat District, Beşkonak Village, Köprülü Canyon.

6. Tegenaria bithyniae Brignoli, 1978

Fig. 19

Tegenaria bithyniae Brignoli, 1978b: 515, fig. 97 (known from female only).

General distribution: Bulgaria and Turkey.

Distribution in Turkey: Bolu Province: Abant (Brignoli 1978b).



Figure 18. The distribution of *Tegenaria atrica* (1) in Turkey.

7. Tegenaria comnena Brignoli, 1978

Fig. 20

Tegenaria comnena Brignoli, 1978b: 520, fig. 108 (known from female only).

General distribution: Turkey.

Distribution in Turkey: Trabzon Province: Maçka District, Sümela Monastery (Brignoli 1978b).

8. Tegenaria cottarellii Brignoli, 1978

Fig. 20

Tegenaria cottarellii Brignoli, 1978b: 523, fig. 106 (known from female only).

General distribution: Turkey.

Distribution in Turkey: Rize Province: Kalkandere District; Artvin Province: Borçka District (Brignoli 1978b).

9. Tegenaria domestica (Clerck, 1757)

Fig. 17

For a complete list of references see Platnick (2010).

General distribution: Cosmopolitan, synanthropic in most places.

Distribution in Turkey: Hatay Province: Narlıca Town, Narlıca Cave; Urfa Province; Mardin Province: Midyat District, a hill near Derömer Area (Roewer 1959); Kırıkkale Province (Bayram et al. 2005).



Figure 19. The distribution of Tegenaria bithyniae (1), T. longimana (2) and T. rhodiensis (3) in Turkey.

10. Tegenaria elysii Brignoli, 1978

Fig. 20

Tegenaria elysii Brignoli, 1978a: 49, fig. 9 (known from female only).

General distribution: Turkey.

Distribution in Turkey: Mersin Province: Silifke District, Dilek Cave and Cennet Cave (Brignoli 1978a).

11. Tegenaria faniapollinis Brignoli, 1978

Fig. 20

Tegenaria faniapollinis Brignoli, 1978a: 50, fig. 13 (known from female only).

General distribution: Turkey.

Distribution in Turkey: Hatay Province: Harbiye Town, Harbiye Cave (Brignoli 1978a).

12. Tegenaria forestieroi Brignoli, 1978

Fig. 20

Tegenaria forestieroi Brignoli, 1978a: 45, fig.12 (known from female only)

General distribution: Turkey.

Distribution in Turkey: Konya Province: Beyşehir District, Kurucuova Village (Asarini Cave and İnönüini Cave); Seydişehir District (Ferzene Cave and fossile sink-



Figure 20. The distribution of *Tegenaria agnolettii* (1), *T. averni* (2), *T. comnena* (3), *T. cottarellii* (4), *T. elysii* (5), *T. faniapollinis* (6), *T. forestieroi* (7), *T. hamid* (8), *T. karaman* (9), *T. mamikonian* (10), *T. melbae* (11), *T. percuriosa* (12), *T. tekke* (13), *T. vignai* (14), *T. xenophontis* (15) and *T. bayrami* sp. n. (star) in Turkey.

hole of Tınaztepe Cave); Çamlık District (Körükini Cave); Hadım District (Suçıktığı Cave); Antalya Province: Akseki District (Demirci Dükkanları Cave, a cave in Dikmen Village and from a well) (Brignoli 1978a).

13. Tegenaria hamid Brignoli, 1978

Fig. 20

Tegenaria hamid Brignoli 1978b: 515, fig. 96 (known from female only).

General distribution: Turkey.

Distribution in Turkey: Isparta Province: Eğirdir District (Brignoli 1978b).

14. Tegenaria karaman Brignoli, 1978

Fig. 20

Tegenaria karaman Brignoli, 1978a: 48, fig. 8, (known from female only).

General distribution: Turkey.

Distribution in Turkey: Konya Province: Seydişehir District, Ferzene Cave (Brignoli 1978a).

15. Tegenaria longimana Simon, 1898

Fig. 19

For a complete list of references see Platnick (2010).

General distribution: Turkey, Georgia and Russia.

Distribution in Turkey: Rize Province: Fındıklı District (50 km NE of Rize, towards Hopa); Artvin Province: Hopa District; Trabzon Province: Maçka District, Altındere Village, Sümela Monastery (Brignoli, 1978b).

16. Tegenaria mamikonian Brignoli, 1978

Fig. 20

Tegenaria mamikonian Brignoli, 1978b: 520, fig. 104 (known from female only).

General distribution: Turkey.

Distribution in Turkey: Artvin Province: Yalnızçam Pass (Brignoli 1978b).

17. Tegenaria melbae Brignoli, 1972

Fig. 20

Tegenaria melbae Brignoli, 1972: 171, Figs 19–20 (known from female only).

General distribution: Turkey.

Distribution in Turkey: Diyarbakır Province: Lice Province, Korkha Cave (Brignoli 1972).

18. Tegenaria parietina (Fourcroy, 1785)

Fig. 17

For a complete list of references see Platnick (2010).

General distribution: Europe, North Africa to Central Asia, Uruguay and Argentina.
Distribution in Turkey: İstanbul Province (Pavesi 1876; Karol 1966); Ankara
Province (Karol 1966); Mersin Province: Tarsus District, Gülek Town (Topçu et al. 2006), Bursa Province: Görükle Campus (Kaya and Uğurtaş 2007)

19. Tegenaria percuriosa Brignoli, 1972

Fig. 20

For a complete list of references see Platnick (2010).

General distribution: Turkey.

Distribution in Turkey: Isparta Province: Aksu District, Anamas Plateau, Zindan Cave (Brignoli 1972, 1978a; Gasparo 2007) and Barla (Brignoli, 1978a); Konya Province: Beyşehir, Hacı Akif Cave (Brignoli, 1978a); Bolu Province: Abant (Brignoli 1978b); Sivas Province: Çamlıbel Pass (Brignoli, 1978b); Ankara Province: Kızılcahamam District (Brignoli, 1978b) and Antalya Province: Alanya District, Dim Cave (Kunt et al. 2008)

20. Tegenaria rhodiensis Caporiacco, 1948

Fig. 19

Tegenaria rhodiensis Brignoli, 1978b: 513, Figs 90-93.

General distribution: Rhodes and Turkey.

Distribution in Turkey: Konya Province: Beyşehir District, Beyşehir Lake, Island of Hacı Akif; Isparta Province: Eğirdir District (Brignoli 1978b).

21. Tegenaria tekke Brignoli, 1978

Fig. 20

Tegenaria tekke Brignoli, 1978b: 516, fig. 98 (known from female only).

General distribution: Turkey.

Distribution in Turkey: Antalya Province: Around Kaş District (Brignoli 1978b).

22. Tegenaria vignai Brignoli, 1978

Fig. 20

Tegenaria vignai Brignoli 1978b: 524, Figs 110-112, 114.

General distribution: Turkey.

Distribution in Turkey: Artvin Province: Borçka District (Brignoli 1978b).

23. Tegenaria xenophontis Brignoli, 1978

Fig. 20

Tegenaria xenophontis Brignoli, 1978b: 522, Figs 103, 105 (known from female only).

General distribution: Turkey.

Distribution in Turkey: Trabzon Province: Maçka District (Sümela Monastery) and Zigana Pass (Brignoli 1978b).

Discussion

Twenty-three Tegenaria species have now been reported from Turkey, including the newly described species. Only four of them (T. agrestis, T. atrica, T. domestica and T. *parietina*) have broad distribution ranges, whereas 16 species are endemic to Turkey. Among the species restricted to Turkey or to the eastern Mediterranean, 14 are known exclusively from females and only four species are known from both sexes. All species known from only one sex were described by Brignoli (1972; 1978 a,b). Reasoning from the illustrations of Brignoli (1972; 1978 a,b) and knowing that the epigyne of Tegenaria is rather simple, it can be assumed that some of Brignoli's species names will be synonymized in the future. Nevertheless, the diversity of *Tegenaria* in Turkey is very high compared to other regions. The Turkish fauna includes more species than some well studied and species-rich countries as Italy and Spain (15 species of Tegenaria in each) (Helsdingen 2009). Neighbouring Bulgaria has only 12 species reported (Deltshev 1995). Of course, it is possible that some of the species known from females may belong to the closely related genus Malthonica (sensu Guseinov et al. 2005). If one compares the species diversity of the genera Tegenaria and Malthonica, the species richness of both in Turkey (31 species) is higher than in other countries: 27 in continental Italy, 23 in Bulgaria and France, and 22 in Spain.

Although the currently known diversity of *Tegenaria* and *Malthonica* in Turkey is already extraordinarily high, the actual diversity may be even higher. Many caves, a favourite habitat for *Tegenaria*, have never been studied or sampled for spiders in Turkey. Therefore, we expect that more new species will be found in the future.

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RESEARCH ARTICLE



Taxonomic study of subgenus *Plastus* s. str. (Coleoptera, Staphylinidae, Osoriinae) in China, with descriptions of five new species

Jie Wu^{1,†}, Hong-Zhang Zhou^{2,‡}

l Key Laboratory of Zoological Systematics and Evolution, Institute of Zoology, Chinese Academy of Sciences, 1 Beichenxi Rd., Chaoyang District, Beijing 100101, P. R. China **2** Shanghai Entomological Museum, Chinese Academy of Sciences, 300 Fenglin Rd., Xuhui District, Shanghai 200032, P. R. China

† urn:lsid:zoobank.org:author:4F975D7D-59D0-4D18-88DA-A1B6FE92FD33 ‡ urn:lsid:zoobank.org:author:0CCACC79-9829-44FE-8069-6FBCD1EA269F

Corresponding author: Hong-Zhang Zhou (zhouhz@ioz.ac.cn)

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Abstract

This paper treats Chinese species of the rove beetle genus *Plastus* Bernhauer, 1903, subgenus *Plastus* s. str. (Coleoptera, Staphylinidae, Osoriinae). None of the 87 previously described species of this subgenus are known from China. The following five new species are described and illustrated: *Plastus* (s. str.) *amplus* Wu & Zhou, **sp. n.** from Xizang, *P.* (s. str.) *biconcavus* Wu & Zhou, **sp. n.** from Guangxi, *P.* (s. str.) *rhombicus* Wu & Zhou, **sp. n.** from Yunnan, *P.* (s. str.) *shanghaiensis* Wu & Zhou, **sp. n.** from Shanghai, and *P.* (s. str.) *tuberculatus* Wu & Zhou, **sp. n.** from Hainan. A key to adults of the five known Chinese species is provided.

Keywords

Staphylinidae, Plastus s. str., new species, China

Introduction

The subgenus *Plastus* s. str. Bernhauer, 1903, is a species rich rove beetle group with 87 previously recorded species (Herman 2001, Wu and Zhou 2007). Most of them are known to be closely associated with dead wood habitats in the tropical and subtropi-

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cal forests of south and east Asia and the islands of South Pacific, with a few species in Madagascar (Cameron 1930, Greenslade 1971, Herman 2001, Wu and Zhou 2007). This subgenus was originally erected by Bernhauer (1903) as a subgenus of the genus *Priochirus* (sensu lato) Sharp, 1887, and this taxonomic treatment was accepted for long time (Bernhauer 1903, Cameron 1930, Greenslade 1971, Naomi 1996). Wu and Zhou (2007) studied the phylogeny of the groups related to the genus *Priochirus* (sensu lato), and found that the genus was not a monophyletic taxon. Thus, improved taxonomy was proposed: *Plastus* was raised to a valid genus and the genus *Priochirus* was retained. Consequently their taxonomic definitions were changed (Wu and Zhou 2007). The genus *Plastus* Bernhauer, 1903 (sensu Wu and Zhou 2007) includes the following 8 subgenera: *Leiochirus* Greenslade, 1971, *Exochirus* Greenslade, 1971, *Syncampsochirus* Bernhauer, 1903, *Eutriacanthus* Jakobson, 1908, *Plastus* s. str., *Barychirus* Greenslade, 1971, *Stigmatochirus* Bernhauer, 1903 and *Sinumandibulus* Wu & Zhou, 2007. These 7 taxa were originally in the genus *Priochirus* sens. lat. (Greenslade 1971). This emended classification is adopted in this study.

Previously one species, *Plastus brachycerus* (Kraatz, 1859), was erroneously recorded from China (Wu and Zhou 2007), which is a misidentification of *P. shanghaiensis* sp. n. Five new species are discovered and here described from China: *Plastus* (s. str.) *amplus* Wu & Zhou, sp. n. from Xizang, *P.* (s. str.) *biconcavus* Wu & Zhou, sp. n. from Guangxi, *P.* (s. str.) *rhombicus* Wu & Zhou, sp. n. from Yunnan, *P.* (s. str.) *shanghaiensis* Wu & Zhou, sp. n. from Shanghai, *P.* (s. str.) *tuberculatus* Wu & Zhou, sp. n. from Hainan. An earlier confusion (Wu and Zhou 2007) between *P. brachycerus* (Kraatz, 1859) and *P. shanghaiensis* sp. n. is resolved. Our study suggests that the subgenus *Plastus* s. str. is widely distributed from southwest to east China. This information may shed light on the origin and dispersal of *Plastus* s. str. in tropical and subtropical Asia.

Material and methods

All specimens examined were measured using a compound microscope (Leica MZ12). Before dissection the specimens were relaxed in warm water (60°C) for 3–5 hours, then male genitalia were separated from terminal abdominal segment by dissecting needle, macerated in 10% KOH solution, rinsed in distilled water, and preserved in 75% alcohol for consequent observation. Measurements and photographs were taken by using CCD Scientific Cameras (Motic 252A) and digital microscopy software (Motic Images Advanced 3.2 and Multi-Focus 1.0).

The morphological terminology follows mainly that used by Wu and Zhou (2007) and Greenslade (1971, 1972).

The following abbreviations are used in the text: HL, head length (measured from anterior margin of frontal angle to the posterior margin of head capsule); PL, pronotum length (measured along medial line of the disc); EL, elytron length (measured from the humeral margin to the most distal margin); HW, head width (maximal, excluding eyes); PW, pronotum width (maximal); EW, elytra width (maximal).

Depositories

Specimens from this study are deposited in the following collections:

- IZ-CAS Institute of Zoology, the Chinese Academy of Sciences, Beijing
- SEM-CAS Shanghai Entomological Museum, the Chinese Academy of Sciences, Shanghai

Results

Genus Plastus Bernhauer, 1903

Bernhauer 1903: 142, 160 (as subgenus of *Priochirus*); Wu and Zhou 2007: 81, 85 (valid genus, emended).

Type species: *Leptochirus convexus* Laporte, 1835, fixed by subsequent designation (Lucas 1920).

Subgenus Plastus s. str. Bernhauer, 1903

Diagnosis. This subgenus may be distinguished from the other subgenera by having the head with a pair of distinct lateral teeth; outer lateral teeth on head often present, but never lateral to, nor in the same horizontal plane as main lateral teeth; frontal tooth on anterior margin of frontal impression of head, if present, never single and centrally placed (Bernhauer 1903, Greenslade 1971).

Key to the species of subgenus Plastus s. str. from China

1.	Frontal impression on head rhomboid in shape, anterior margin strongly con-
	vex in middle (Fig. 8); epipleural line on elytron absent <i>P. rhombicus</i> sp. n.
_	Frontal impression of head never rhomboid in shape, anterior margin not
	convex in middle (Figs 6, 7, 9, 10); epipleural line on elytron present2
2.	Frontal impression about 5 times as wide as long (Fig. 7); central disc of pro-
	notum with two distinct fovae on sides of longitudinal median sulcus
	P. biconcavus sp. n.
_	Frontal impression at most 4 times as wide as long (Figs 6, 9, 10); central disc
	of pronotum without fovae
3.	Anterior margin of frontal impression of head without frontal tooth at each
	side (Fig. 9); mentum ventrally with coarse and mutually contiguous ridges,
	disc rugose without polished region (Fig. 14) P. shanghaiensis sp. n.
_	Anterior margin of frontal impression of head with frontal tooth at each side
	(Figs 6, 10); mentum ventrally with three transverse ridges, disc between last
	posterior ridge and basal margin polished (Figs 11, 15)4

Plastus (s. str.) amplus Wu & Zhou, sp. n.

urn:lsid:zoobank.org:act:15E05BCE-416D-45FA-8B60-8A2573E1721D Figs 1, 6, 11, 16, 17

Type material. Holotype male, Xizang: Motuo, 1370 m, 18.ix.1979, Gentao Jin and Jianyi Wu coll. (SEM-CAS). Paratypes (13 spp.): 2 males and 9 females, same data as for holotype; male, Xizang: Motuo: Kabu, 1100 m, 8.v.1980, Gentao Jin and Jianyi Wu coll. (SEM-CAS); female, Xizang: Motuo, 1000–1200 m, 11.ii.1983, Yinheng Han coll. (IZ-CAS).

Description. Measurement. Body length: 10.04–11.13 mm; HL: 0.74–0.82 mm; HW: 1.58–1.70 mm; PL: 1.70–1.97 mm; PW: 2.23–2.47 mm; EL: 2.49–2.58 mm; EW: 2.35–2.54 mm.

Coloration. Head black with labrum red-brown, mandibles black with inner side red-brown (Fig. 6). Pronotum and elytra black (Fig. 1). Abdomen black except for 8th segment slightly brown. Antennae brown. Femora black, tibiae black at base and gradually becoming brown apically. Tarsi slightly yellow-brown.

Structural attributes. Head transverse (Fig. 6), about twice as long as wide, sides slightly concave in middle and slightly convex outward basally; frontal impression strongly transverse, about 3.5 times as wide as long, anterior margin slightly arc-shaped and weakly emarginate in middle with two small granulated frontal teeth on sides, distance between apices of two frontal teeth almost as wide as 2/3 of frontal impression, posterior margin slightly emarginate in middle and slightly obliquely convergent posteriorly; lateral teeth blunt and distinctly convergent anteriorly with apices slightly introflexed, on apical 1/3 of ventral side with distinct subsidiary denticle apically pointed and curved forward, on inner side with row of 5-6 long setae extending onto anterior margin of frontal impression; lateral impression triangularly and widely depressed along almost whole external side of lateral tooth and anterior margin of frontal angle of head, bearing 4–6 short setae; anterior margin of frontal angle of head slightly convex forming small and blunt outer lateral tooth; median sulcus on vertex about twice as long as frontal impression, gradually broadened posteriorly, but abruptly divergent at posterior 1/3, the posterior end of which is almost twice as wide as middle; clypeus short and steeply inclined, anterior margin slightly rounded, baso-laterally with 3-5 long setae; eye glabrous and convex, almost occupying half side of head; vertex moderately convex, in depressed regions near frontal impression with shallow longitudinal depression



Figures 1–5. General habitus, dorsal view: 1 *Plastus* (s. str.) *amplus* sp. n. 2 *P*. (s. str.) *biconcavus* sp. n. 3 *P*. (s. str.) *rhombicus* sp. n. 4 *P*. (s. str.) *shanghaiensis* sp. n. 5 *P*. (s. str.) *tuberculatus* sp. n. (scale bar = 1 mm).

on each side of median sulcus, surface evenly covered with fine micropunctures, along lateral and postero-lateral margin with some scattered punctures and long setae, at each side of posterior end of median sulcus with 4–7 setiferous punctures concentrated in shallow foveae.

Antennae subgeniculate, antennomere I baculiform and apically slightly depressed to form shallow sulcus on dorsal side, antennomere II smallest, slightly transverse; antennomere III elongate about 1.7 times as long as II; antennomeres IV and V almost quadrate; antennomeres VI–X gradually more transverse apically; antennomere XI elongate, apically rounded, about twice as long as X.



Figures 6–10. Head, dorsal view: 6 *Plastus* (s. str.) *amplus* sp. n. 7 *P*. (s. str.) *biconcavus* sp. n. 8 *P*. (s. str.) *rhombicus* sp. n. 9 *P*. (s. str.) *shanghaiensis* sp. n. 10 *P*. (s. str.) *tuberculatus* sp. n. (scale bar = 0.5 mm).

Mentum trapeziform (Fig. 11), frontal angle slightly rounded, anterior margin weakly depressed in middle, with small pointed median denticle, ventral surface setose, with three transverse ridges, first distinct and almost straight, second and third slightly wrinkled and indistinct, disc between third ridge and posterior margin polished and with 4 or 5 larger setiferous punctures scattered along base of third ridge.

Pronotum transverse, distinctly wider than head, anterior margin weakly bisinuate, sides almost parallel, median longitudinal sulcus deep and narrow, slightly broadened posteriorly, not reaching either anterior nor posterior margins; lateral marginal area with 30–35 setiferous punctures, punctures on upper half distinctly larger than on lower half, disc polished, with indistinct micropunctures evenly distributed.

Protibiae externally furnished with 11–15 denticles, which gradually become shorter basally.

Elytra almost quadrate, epipleural line complete, setiferous punctures on lateral marginal side sparser and less distinct than those on sides of pronotum.

Abdomen cylindrical, along anterior and posterior margin of III–VI segments respectively with row of setae, but VI segment distinctly with additional median row of setae extending to central disc, segments VII and VIII densely setose, disc of III–VI segment densely punctured except for transverse glabrous region near to posterior margin, basal distinctly denser than apical, on disc of VII and VIII, centrally with longitudinal glabrous region, narrow and extending to basal region. Aedeagus submembranous (Figs 16, 17), basal part of median lobe slightly bulbous and strongly curved behind basal orifice, almost L-shaped in lateral view; posterior part baculiform, slightly narrower than basal bulbous part, sides almost parallel, distinctly sclerotised on both ventral and lateral sides, with apex membranous and protruding; parameres elongate and weakly curved with apices not extending beyond apical level of basal protruding part, anterior margin strongly convex and pointed near base; basal part protruding ventrally, but not connecting to each other below basal orifice.

Remarks. This new species is similar to *P*. (s. str.) *brachycerus* (Kraatz, 1859), but can be distinguished from the latter by more transverse frontal impression, anteriorly convergent lateral teeth and small outer lateral teeth on anterior margin of frontal angle of head (Fig. 6).

Distribution. Only known from type locality in Xizang, elevations of 1000–1370 m.

Etymology. The species name is derived from Latin word '*amplus*' (broad) to indicate distinctly transverse frontal impression of head.

Plastus (s. str.) biconcavus Wu & Zhou, sp. n.

urn:lsid:zoobank.org:act:F7BDE46E-673A-462B-BE3D-9484B4B89FC1 Figs 2, 7, 12

Type material. Holotype male, Guangxi: Longsheng: Neicujiang, 840 m, 7.vi.1963, Shuyong Wang coll. (IZ-CAS).

Description. Measurement. Body length: 9.84 mm. HL: 0.71 mm; HW: 1.48 mm; PL: 1.56 mm; PW: 2.07 mm; EL: 2.18 mm; EW: 2.09 mm.

Coloration. Head black with labrum red-brown, mandibles black with inner side reddish brown (Fig. 7). Pronotum and elytra slightly dark brown (Fig. 2). Abdomen black except for 8th segment slightly rufous. Antennae dark red brown. Femora and tibiae slightly dark red brown. Tarsi brown.

Structural attributes. Head transverse (Fig. 7), twice as long as wide, sides slightly concave in middle; frontal impression strongly transverse, about 5 times as wide as median length, anterior margin almost straight in middle, posterior margin slightly rounded posteriorly; lateral teeth blunt and straightly projecting, middle of ventral side with bluntly convex subsidiary denticle, on inner side with row of 4–6 long setae extending onto anterior margin of frontal impression; lateral impression narrow, along posterior half of external side of lateral tooth, almost not reaching anterior margin of frontal angle of head, bearing 3 or 4 short setae; anterior margin of frontal angle of head rounded, without tooth; median sulcus on vertex about 3 times as long as median length of frontal impression, gradually broadened posteriorly, but abruptly divergent at posterior 1/4, posterior end of which almost twice as wide as middle; clypeus steeply inclined and rounded anteriorly, with shallow depression behind anterior margin, baso-laterally with 2 or 3 long setae; eye glabrous and convex, almost occupying half side of head; vertex broadly convex, between frontal angle and base of lateral tooth with luniform depression, in depressed region near posterior margin of frontal impression



Figures 11–15. Mentum, ventral view: 11 *Plastus* (s. str.) *amplus* sp. n. 12 *P*. (s. str.) *biconcavus* sp. n. 13 *P*. (s. str.) *rhombicus* sp. n. 14 *P*. (s. str.) *shanghaiensis* sp. n. 15 *P*. (s. str.) *tuberculatus* sp. n. (scale bar = 0.25 mm).

with two distinct punctures in line on each side of median sulcus, surface polished and evenly covered with fine micropunctures, along lateral and postero-lateral margin with some scattered punctures and long setae, at each side of posterior end of median sulcus without distinct fovea.

Antennae subgeniculate, antennomere I baculiform and apically slightly depressed, antennomere II smallest, slightly transverse; antennomere III elongate about 2 times as long as II; antennomeres IV quadrate; antennomeres V–X gradually more transverse apically; antennomere XI elongate, apically rounded, about 2 times as long as X.

Mentum trapeziform (Fig. 12), frontal angle slightly rounded, anterior margin weakly depressed in middle, with small indistinct median denticle, ventral surface with three transverse and waved ridges, but third indistinct and vague, space between ridges setose and rugose, but disc between last posterior ridge and basal margin glabrous and polished, with two large setiferous punctures on sides.

Pronotum transverse, distinctly wider than head, anterior margin weakly bisinuate, sides almost parallel, median longitudinal sulcus deep, broadest in middle and gradually narrowed anteriorly and posteriorly, not reaching either anterior or posterior margins; lateral marginal area with 21–23 setiferous punctures, punctures on upper half not distinctly larger than on lower, disc polished, surface evenly with fine micropuncture scattered, centrally with two distinct fovea on sides of longitudinal sulcus.

Protibiae externally furnished with 13 or 14 denticles, which gradually become shorter basally.

Elytra slightly longer than wide, epipleural line complete, setiferous punctures on lateral marginal side sparser and less distinct than those on side of pronotum.

Abdomen cylindrical, along anterior and posterior margin of III–VI segments respectively with row of setae, segments VII and VIII densely setose, disc of III–VI



Figures 16, 17. Aedeagus of *Plastus* (s. str.) *amplus* sp. n.: **16** ventral view **17** lateral view (scale bar = 0.5 mm).

segment densely punctured, except for broad and transverse glabrous region near posterior margin, basal denser than apical, central disc of VII evenly punctured, VIII centrally with narrow longitudinal glabrous region.

Remarks. This new species can easily be distinguished from other members of the subgenus *Plastus* s. str. by its strongly transverse frontal impression (about 5 times as wide as long) and two distinct foveae on sides of pronotal disc. *Plastus* (s. str.) *taprobanus* (Cameron, 1930) also has strongly transverse frontal impression and distinct fovea on either side of pronotum, but its lateral teeth are distinctly shorter than those in this new species.

Distribution. Known from the type locality in Guangxi, elevation of 840 m.

Etymology. The species name is derived from Latin words '*bi*-' (double) and '*con-cavus*' (concave) to indicate two distinct fovae on pronotum of this species.

Plastus (s. str.) *rhombicus* Wu & Zhou, sp. n. urn:lsid:zoobank.org:act:91C17665-3964-4AD5-AA9C-B83CE75140F4 Figs 3, 8, 13, 18, 19

Type material. Holotype male, Yunnan: Tengchong: Jietou (25.697°N, 98.68059°E), 1865 m, 14.v.2006, H.B. Liang coll. (IZ-CAS). Paratypes (2 spp.): 2 females, same data as for holotype (IZ-CAS).

Description. Measurement. Body length: 10.43–11.78 mm. HL: 0.56–0.70 mm; HW: 1.43–1.52 mm; PL: 1.46–1.67 mm; PW: 1.99–2.22 mm; EL: 2.01–2.21 mm; EW: 2.09–2.25 mm.



Figures 18, 19. Aedeagus of *Plastus* (s. str.) *rhombicus* sp. n.: **18** ventral view **19** lateral view (scale bar = 0.5 mm).

Coloration. Head black with labrum red-brown (Fig. 8), mandibles black with inner side red-brown. Pronotum, elytra and abdomen black (Fig. 3). Antennae dark brown. Femora black, tibiae black at base and gradually become red-brown apically. Tarsi brown.

Structural attributes. Head (Fig. 8) transverse, about twice as long as wide, sides slightly divergent anteriorly; frontal impression deep and rhomboid, with anterior margin medially convex and slightly turned up, posterior margin slightly convergent posteriorly, about 3 times as wide as long; lateral teeth blunt with apices slightly divergent forward, on apical 1/3 of ventral side with triangularly convex subsidiary denticle (in front of which, additional small denticle present in one examined female specimen), on inner side with row of 5-7 long setae, not extending onto anterior margin of frontal impression; along external side of lateral tooth, lateral impression very short and narrow, not extending to front angle of head, bearing 2-4 short setae, anterior margin of frontal angle of head rounded; median sulcus on vertex almost twice as long as median length of frontal impression, gradually broadened posteriorly, the posterior end of which is almost 2 times as wide as middle; clypeus elongate and rounded anteriorly, with shallow depression behind anterior margin, along lateral side with 4 or 5 long setae scattered; eye glabrous and convex, occupying about 3/5 of side of head; vertex strongly convex near frontal angle, central disc polished and covered with fine micropunctures, along lateral and postero-lateral margin with some scattered punctures and long setae, at each side of posterior end of median sulcus with indistinct fovea bearing 2 or 3 long setae.



Figures 20, 21. Aedeagus of *Plastus* (s. str.) *tuberculatus* sp. n.: **20** ventral view **21** lateral view (scale bar = 0.5 mm).

Antennae subgeniculate, antennomere I baculiform and apically slightly depressed to form shallow sulcus on dorsal side, antennomere II smallest, slightly transverse; antennomere III elongate about 1.5 times as long as II; antennomeres IV–VI slightly quadrate; VII–X gradually more transverse apically; antennomere XI elongate, apically rounded, about 1.5 times as long as X. Mentum trapeziform (Fig. 13), frontal angle slightly rounded, anterior margin weakly depressed in middle, with indistinct median denticle, ventral surface setose, with three wrinkled ridges, last posterior one less distinct than anterior two, disc surface with 4 large setiferous punctures along posterior margin, space between those punctures slightly rugose.

Pronotum transverse (Fig. 3), distinctly wider than head, anterior margin weakly bisinuate, sides rounded and slightly convergent anteriorly, median longitudinal sulcus deep and narrow, slightly broadened posteriorly, not reaching either anterior or posterior margins; lateral marginal area with 24–37 setiferous punctures, punctures on upper half slightly larger than those on lower half, disc polished, with fine micropuncture evenly distributed.

Protibiae externally furnished with 11–14 denticles, which gradually become shorter basally.

Elytra almost quadrate, epipleural line absent, setiferous punctures on lateral marginal side sparser and less distinct than those on side of pronotum.

Abdomen cylindrical, along anterior and posterior margin of III–VI segments respectively with row of setae, disc of each segments densely punctured, except for broad glabrous region near posterior margin, basal distinctly denser than apical, segments VII and VIII densely setose and punctured, with longitudinal glabrous region in central.

Male: aedeagus almost membranous (Figs 18, 19), basal part of median lobe strongly bulbous and curved behind basal orifice; posterior part baculiform, distinctly narrower than basal part, sides almost parallel, only ventral side sclerotised; parameres elongate and strongly curved with apices far below level of basal protruding apices, anterior margin near base rounded; basal parts protruding ventrally, apically weakly separated below basal orifice.

Remarks. This species can be distinguished from other members of subgenus *Plastus* s. str. by the rhomboid shape of frontal impression of head (Fig. 8). The anterior margin of frontal impression in this species is convex upward in middle. This structure is slightly similar in position to the central tooth in the subgenus *Eutriacanthus*, but never pointed and protruding anteriorly as the single central tooth in the latter. Thus, this new species has a clinal morphological characteristics between subgenera *Eutriacanthus* and *Plastus* s. str..

Distribution. Known from the type locality in Yunnan, elevation of 1865 m.

Etymology. The species name derived from a Latin word '*rhombicus*' (rhombic) to indicate the shape of its frontal impression.

Plastus (s. str.) *shanghaiensis* Wu & Zhou, sp. n. urn:lsid:zoobank.org:act:DBDA5500-9257-452F-9C87-8C92A0B2DD05 Figs 4, 9, 14

Type material. Holotype female, Zi Ka Wei (Shanghai: Xujiahui), 4.v.1939, collector unknown (IZ-CAS).

Description. Measurement. Body length: 9.75 mm. HL: 0.72 mm; HW: 1.42 mm; PL: 1.63 mm; PW: 2.02 mm; EL: 2.05 mm; EW: 2.14 mm.

Coloration. Head black with labrum red-brown (Fig. 9), mandibles black with inner side red-brown. Pronotum and elytra black (Fig. 4). Abdomen black with posterior margin of VII and whole VIII segment rufous. Antennae brown. Femora black, tibiae black at base and gradually become red-brown apically. Tarsi red-brown.

Structural attributes. Head (Fig. 9) transverse, twice as long as wide, sides almost parallel, slightly concave in middle; frontal impression transverse, about 2 times as wide as median length, anterior margin almost semicircular, posterior margin rounded; lateral teeth straight and blunt, ventral side medially with weakly convex subsidiary denticle, on inner side with row of 2 or 3 long setae extending onto lateral anterior margin of frontal impression; lateral impression narrowly depressed at outer base of lateral tooth, bearing 2 or 3 short setae, anterior margin of frontal angle of head weakly convex and forming small granulated tooth; median sulcus on vertex about 1.5 times as long as median length of frontal impression, gradually broadened posteriorly, but abruptly divergent at posterior 1/4, the posterior end of which is almost 2.5 times as

wide as middle; clypeus short and steeply inclined, anterior margin moderately rounded, with 3–5 long setae scattered along lateral side; eye glabrous and convex, occupying about 3/5 of side of head; vertex moderately convex, gradually inclining in regions near posterior margin of frontal impression, without distinct depression on each side of median sulcus, surface almost polished and covered with fine micropunctures, along lateral and postero-lateral margin with some scattered punctures and long setae, at each side of posterior end of median sulcus with indistinct fovea bearing 2 or 3 setiferous punctures.

Antennae subgeniculate, antennomere I baculiform and apically slightly depressed to form shallow sulcus on dorsal side, antennomere II smallest, slightly transverse; antennomere III elongate about 2 times as long as II; antennomeres IV–V slightly quadrate; VI–X gradually transverse; antennomere XI elongate, apically rounded, about 1.8 times as long as X.

Mentum trapeziform (Fig. 14), frontal angle slightly rounded, anterior margin weakly depressed in middle, with indistinct median denticle, ventral surface with coarse and mutually contiguous ridges, behind which disc strongly rugose and setose.

Pronotum transverse (Fig. 4), distinctly wider than head, anterior margin slightly bisinuate, sides almost parallel, but slightly convex at anterior angle, median longitudinal sulcus deep and narrow, not distinctly broadened posteriorly, not reaching either anterior or posterior margins; lateral marginal area with 17–20 setiferous punctures, punctures on upper half not larger than on those lower half, disc polished, with fine micropuncture evenly distributed, in central with two indistinct punctures at sides of sulcus.

Protibiae externally furnished with 10 denticles, which gradually become shorter basally.

Elytra almost quadrate, epipleural line complete, setiferous punctures on lateral marginal side sparser and less distinct than those on side of pronotum.

Abdomen cylindrical, along anterior and posterior margin of III–VI segments respectively with row of setae, but VI segment with additional median row of setae, segments VII and VIII densely setose, disc of III–VI segments densely punctured, without distinct glabrous region near posterior margin, basal distinctly denser than apical, VII punctured, centrally without longitudinal glabrous region, glabrous region on VIII short and not extending to basal half.

Remarks. Wu and Zhou (2007) misidentified this species as *P*. (s. str.) *brachycerus* (Kraatz, 1859) (tables 1, 2; figures 1–4; and locality error in Wu and Zhou 2007). *Plastus* (s. str.) *shanghaiensis* sp. n. is closely allied to *P*. (s. str.) *brachycerus* in the shape of lateral teeth and frontal impression, but can be distinguished from the latter by more depressed lateral impression at the outer base of lateral tooth, and anterior margin of frontal angle of head is furnished with a small granulate tooth.

Distribution. Known from type locality in Shanghai.

Etymology. The specific name '*shanghaiensis*' is derived from the name of the type locality, Shanghai.

Plastus (s. str.) tuberculatus Wu & Zhou, sp. n.

urn:lsid:zoobank.org:act:A4D0B921-8BB3-4802-B6E7-06AF37BEC6E9 Figs 5, 10, 15, 20, 21

Type material. Holotype male, Hainan: Diaoluoshan, 14.i.1985, Gentao Jin and Zurao Liu coll. (SEM-CAS). Paratypes (18 spp.): 11 males, 6 females, same data as for holotype (SEM-CAS); male, Hainan: Limushan: Sanquling, 30.xi.2007, 830 m, Zhuo Yang coll. (IZ-CAS).

Description. Measurement. Body length: 9.80–10.35 mm. HL: 0.61–0.66 mm; HW: 1.47–1.65 mm; PL: 1.63–1.81 mm; PW: 2.15–2.29 mm; EL: 2.14–2.32 mm; EW: 2.17–2.22 mm.

Coloration. Head black with labrum red-brown (Fig. 10), mandibles black with inner side red-brown. Pronotum and elytra black (Fig. 5). Abdomen black, except for 8th segment slightly rufous. Antennae brown. Femora black, tibiae slightly red-brown. Tarsi slightly yellow-brown.

Structural attributes. Head (Fig. 10) transverse, twice as long as wide, lateral sides slightly concave in middle; frontal impression strongly transverse, about 4 times as wide as long, anterior margin deeply emarginate in middle, with two triangularly convex and pointed frontal teeth at sides, distance between apices of two frontal teeth almost as wide as 3/5 of frontal impression, posterior margin slightly obliquely convergent backwards; lateral teeth straight and blunt, on apical 1/3 of ventral side with distinct pointed subsidiary denticle, on inner side with row of 5-8 long setae extending onto outer base of frontal tooth; lateral impression triangularly and widely depressed at outer base of lateral tooth, bearing 5 or 7 short setae; anterior margin of frontal angle of head slightly convex and depressed inside, forming blunt outer lateral tooth; median sulcus about 1.5 times as long as median length of frontal impression, distinctly divergent posteriorly, almost triangular, the posterior end of which is almost two times as wide as middle; clypeus short and steeply inclined, anterior margin moderately rounded, with 3-5 long setae scattered along lateral side; eye glabrous and strongly convex, occupying about 3/5 of side of head; vertex strongly and tuberculately convex at dorsal base of lateral tooth, gradually inclining in regions near posterior margin of frontal impression, without distinct depression on each side of median sulcus, surface almost polished and covered with fine micropunctures, along lateral and postero-lateral margin with some scattered punctures and long setae, at each side of posterior end of median sulcus with distinct fovea bearing 5-7 setiferous punctures.

Antennae subgeniculate, antennomere I baculiform and apically slightly depressed to form shallow sulcus on dorsal side, antennomere II smallest, slightly transverse; antennomere III elongate about 2 times as long as II; antennomeres IV–X gradually transverse, X about 2.5 times as wide as long; antennomere XI elongate, apically rounded, about 2.5 times as long as X.

Mentum trapeziform (Fig. 15), frontal angle slightly rounded, anterior margin weakly depressed in middle, with indistinct median denticle, ventral surface with three

transverse and slightly waved ridges, disc between last posterior ridge and basal margin moderately polished, with 5 or 6 large setiferous punctures.

Pronotum transverse (Fig. 5), distinctly wider than head, anterior margin very weakly bisinuate, sides slightly convergent anteriorly at anterior 1/4; median longitudinal sulcus deep and narrow, slightly broadened at posterior end, not reaching either anterior or posterior margins; lateral marginal area with 30–40 setiferous punctures, punctures on upper half distinctly larger than on those lower half, disc polished, with fine micropuncture evenly distributed.

Protibiae externally furnished with 11–13 denticles, which gradually become shorter basally.

Elytra almost quadrate, epipleural line complete, setiferous punctures on lateral marginal side sparser and less distinct than those on side of pronotum.

Abdomen cylindrical, along anterior and posterior margin of III–VI segments respectively with row of setae, but VI segment with additional median row of setae, segments VII and VIII densely setose, disc of III–VI segment densely punctured, basal distinctly denser than apical, but near posterior margin with small glabrous region in middle, on disc of VII and VIII, glabrous region narrow and extending to basal region.

Male aedeagus almost membranous (Figs 20, 21), basal part of median lobe bulbous and curved behind basal orifice; posterior part baculiform, almost as broad as basal part, sides slightly constricted in middle, distinctly sclerotised on both ventral and lateral sides, with membranous and protruding apex; parameres elongate and weakly curved with apices not extending beyond level of basal protruding apices, slightly broadened near base with anterior margin rounded; basal parts protruding ventrally, apically widely separated below basal orifice.

Remarks. This species is allied to *P*. (s. str.) *kimurai* (Naomi, 1996) in the shape of lateral and outer lateral teeth on head, but can be distinguished from the latter by following features: anterior margin of frontal impression with two distinct frontal teeth, dorsal base of lateral teeth tuberculately convex and median sulcus on head distinctly broadened posteriorly (Fig. 10).

Distribution. Known from type locality in Hainan, elevation about 800 m.

Etymology. The species name is derived from Latin word '*tuberculatus*' (tuberculate) to indicate vertex tuberculately convex at base of lateral teeth.

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RESEARCH ARTICLE



Revision of the Afrotropical species of Zaprionus (Diptera, Drosophilidae), with descriptions of two new species and notes on internal reproductive structures and immature stages

Amir Yassin^{1,2,†}, Jean R. David^{1,3,‡}

Laboratoire Evolution, Génomes et Spéciation (LEGS), Centre National de la Recherche Scientifique (CNRS), av. de la Terrasse, 91198 Gif-sur-Yvette Cedex; Université Paris-Sud XI, 91400 Orsay; France **2** Sackler Institute for Comparative Genomics, Department of Invertebrate Systematics, American Museum of Natural History (AMNH), New York, USA **3** Département Systématique et Evolution, Muséum National d'Histoire Naturelle (MNHN), Paris, France

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Corresponding author: Amir Yassin (yassin@legs.cnrs-gif.fr)

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Abstract

A new classification of the subgenus Zaprionus is proposed in light of recent phylogenetic findings. The boundaries of the armatus and inermis species groups are redefined. The vittiger subgroup is upgraded to the level of a species group. The tuberculatus subgroup is transferred from the armatus to the inermis group. A new monotypic group, neglectus, is erected. Full morphological descriptions of four species belonging to the vittiger group are given: Z. lachaisei sp. n. from Tanzania and Z. santomensis sp. n. from São Tomé and Principé, and two cryptic species of the indianus complex, Z. africanus Yassin & David and Z. gabonicus Yassin & David. Three nominal species are synonymised: Z. beninensis Chassagnard & Tsacas, syn. n. with Z. koroleu Burla, Z. simplex Chassagnard & McEvey, syn. n. with Z. neglectus Collart, and Z. megalorchis Chassagnard & Tsacas, syn. n. with Z. ornatus Séguy. Half of the 46 species of the subgenus are available as laboratory strains and this has allowed full descriptions of the internal structure of their reproductive systems and their immature stages.

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Keywords

classification, reproductive system, immature stages, taxonomy, cryptic species, Tropical Africa

Introduction

The drosophilid genus Zaprionus Coquillett, 1902 is characterized by the presence of longitudinal white stripes on the frons and the mesonotum (Fig. 1). It is a Paleotropical genus whose species are classified under two subgenera: Zaprionus sensu stricto in the Afrotropical region (48 species), and Anaprionus in the Oriental and Australasian regions (11 species) (Okada and Carson 1983; Markow and O'Grady 2006; Brake and Bächli 2008). The two subgenera are distinguished on the basis of the number of their mesonotal stripes, being even in Zaprionus s.s. and odd in Anaprionus. Flies of the subgenus Zaprionus form an important component of the Afrotropical drosophilid fauna, in terms of number of species, relative abundance and large body size (Tsacas et al. 1981; Yassin and David in press.). Chassagnard and Tsacas (1993) classified those species under two groups: the armatus group with ornamented forefemora, and the *inermis* group with unornamented forefemora. Recent phylogenetic revisions using molecular and morphological characters have shown Zaprionus s.s. species to be monophyletic, but both species groups to be polyphyletic (Yassin et al. 2008a, 2010, in press).

In this paper, we propose a new classification based on recent phylogenetic findings, describe two new species, and provide a taxonomic key to all African *Zaprionus* species. In the early 1990s, several taxonomic keys were published for African *Zaprionus* (Tsacas and Chassagnard 1990; Chassagnard and McEvey 1992; Chassagnard and Tsacas 1993), but these usually treated some species subgroups or geographical localities and covered only 76% of the then known species. Since 1993, eight species were described including the two new ones described here. Twenty three species were available as laboratory strains, and this allowed us to also provide descriptions of internal reproductive system and premature morphology.

Materials and methods

Specimens examined

Examined specimens were museum-preserved material or laboratory strains. Laboratory strains in the Laboratoire Evolution, Génomes et Spéciation (LEGS) belonged to 23 species (Table 1), and they were used in describing internal structures of the male and female reproductive systems and immature stages. As shown in Table 1, a congeneric Oriental species, *Z. (Anaprionus) bogoriensis* Mainx, was added to the analysis.



Figure 1. Frons and mesonotum of Zaprionus (Anaprionus) bogoriensis Mainx, 1954 a, Z. (Zaprionus) ghesquierei Collart, 1937a b, Z. (Z.) litos Chassagnard & McEvey, 1992 c, Z. (Z.) sexstriatus Chassagnard, 1996 d, Z. (Z.) cercus Chassagnard & McEvey, 1992 e, Z. (Z.) kolodkinae Chassagnard & Tsacas, 1987 f, Z. (Z.) verruca Chassagnard & McEvey, 1992 g, Z. (Z.) multivittiger Chassagnard, 1996 h, and Z. (Z.) davidi Chassagnard & Tsacas, 1993 i.

Morphological description

Formal morphological description of the new species followed standard *Drosophila* terminology and index formulae as in McEvey (1990). Specimens were deposited in Laboratoire Evolution, Génomes et Spéciation, Gif-sur-Yvette, France (LEGS)

Species	Founder females collection data
Subgenus Anaprionus	
Z. bogoriensis Mainx	India: Bangalore; 2004, J. R. David
Subgenus Zaprionus s.s.	
Z. africanus Yassin & David	Uganda: Kibale (1100 m); vii.2003, D. Lachaise
Z. burlai Yassin	Tanzania: East Usambara Mt, Amani (900 m); 25-
	ix-2002, D. Lachaise
Z. camerounensis Chassagnard & Tsacas	Tanzania: East Usambara Mt, Amani (900 m); 25-
	ix-2002, D. Lachaise
Z. capensis Chassagnard & Tsacas	South Africa: Cape Town; ii.1984, J. R. David
Z. cercus Chassagnard & McEvey	Madagascar: Maroantsetra; 18-26.x.1987, S. F.
	McEvey, J. R. David & S. Aulard
Z. davidi Chassagnard & Tsacas	Congo: Brazzaville; iii.2006, J. Vouidibio
Z. gabonicus Yassin & David	Gabon: Ogoué-Ivindo, Makoukou (500 m);
	i.2004, F. Mavoungou
Z. ghesquierei Collart	Congo: Brazzaville; iii.2006, J. Vouidibio
Z. indianus Gupta	Brazil: Rio de Janeiro, Tijuca; 2001, J. R. David
Z. inermis Collart	Uganda: Kibale (1100 m); vii.2003, D. Lachaise
Z. kolodkinae Chassagnard & Isacas	Madagascar: Antananarivo, Isimbazaza (1200 m);
7 1 1	11.2008, A. Yassin & J. R. David T_{max} (000) 25
Z. lachaisei sp. n.	in 2002 D. Lashaira Mit, Amani (900 m); 25-
7 manufininin Traccas & David	IX-2002, D. Lachaise
Z. mastariensis Isacas & David	Madagaagar Andagiba ii 2008 A Vasin & L D
Z. neglectus Collart	David
7 arratus Segur	Congo: Brazzaville: iii 2006 I Vouidibiou
Z. provinus Collart	Kenva: S Dunas
7 santomensis sp. p	Sao Tomé & Príncipe: Pico de São Tomé Park
<i>D. sumonensis</i> sp. 11.	(1500 m): iii.2001. D. Lachaise
Z. sepsoides Duda	Congo: Brazzaville: iii.2006. I. Vouidibiou
Z. taronus Chassagnard & Tsacas	Kenva: S. Dupas
Z. tsacasi Yassin	Sao Tomé & Príncipe: Pico de São Tomé Park
	(1500 m); iii.2001, D. Lachaise
Z. tuberculatus Malloch	Congo: Brazzaville; iii.2006, J. Vouidibiou
Z. verruca Chassagnard & McEvey	Madagascar: Antananarivo, Tsimbazaza (1200 m);
	ii.2008, A. Yassin & J. R. David
Z. vittiger Coquillett	South Africa: Cape Province, Stellarbush; xii.2006,
	M. Debiais-Thibaud

 Table 1. List of laboratory strains used in studying internal reproductive structures and immature stages.

as living cultures, frozen and alcohol-preserved material and microscopic preparations, and in Muséum National d'Histoire Naturelle, Paris, France (MNHN) as pinned material.
Morphological structures are abbreviated as: fw = front width; fl = front length; hw = head width; o = maximum diameter of the eye; j = width of gena in line with o; ch = maximum width of gena; or1 = proclinate orbital seta; or2 = anterior reclinate orbital seta; or3 = posterior reclinate orbital seta; oc = ocellar seta; poc = post-ocellar seta; iv = inner vertical seta; ov = outer vertical seta; acs = acrostichal setulae; adc = anterior dorsocentral; pdc = posterior dorsocentral; psc = prescutullar seta; bsc = basal scutellar seta; asc = apical scutellar seta; F1 = forefemur; WL = wing length; Wl = wing width; TL = thorax length; WV = width of white vittae at adc; BV = width of black vittae surrounding WV at adc; A = number of abdominal bristles summed over successive sternites. Measurements on immature stages were taken from uncrowded cultures grown under the same conditions (at 21°C). Measurements are abbreviated as: EL = egg length; El = egg width; PF = length of egg posterior filament; PL = puparium length; Pl = puparium width; H (horn index) = the ratio of the length of the anterior spiracles to the total length of the puparium × 100.

Anatomy of the internal reproductive system

Mature, about 10 days old adults were dissected in a Drosophila Ringer solution. For the male reproductive system (see drawings in Lachaise 1972; Araripe et al. 2004), testes were uncoiled before a linear measurement could be done. This operation was facilitated by allowing the Ringer solution to evaporate a little so that the testis loses its rigidity. Linear measurements were done with a stereomicroscope equipped with a micrometer. Six lengths were measured: TST = testis; SV = seminal vesicle; VD = vas deferens; PAR = paragonia (accessory gland); EC = ejaculatory canal; EB = ejaculatory bulb; and CAE = caecum. PAR and EB are glandular structures and their measurements are variable according to the reproductive status of the dissected male. They do not provide thus reliable taxonomic information. For the female (cf. Lachaise 1972), the lengths of two organs were measured after dissection: SR = seminal receptacle and SP = spermatheca length. The SR also makes irregular coils at the junction between the oviduct and uterus, and was uncoiled with tiny needles before measurement. As with immature stages, two or three individuals from almost each species were measured and the results were very similar. Multiple measurements were not taken for all species, but slight differences were only found within those for which multiple measurements were taken.

A key to African Zaprionus

1	F1 without a row of spines (Fig. 2a,b)	2
_	F1 with a row of spines (Fig. 2c–f)	19
2(1)	F1 with a protruding tubercule bearing a bristle (Fig. 2b)	3
_	F1 without a protruding tubercule (Fig. 2a)	7

3(2)	Frons without a median white stripe; $\partial A = 46-57$; aedeagus subterminally
	concave (Fig. 3a); spermatheca smooth (Fig. 3c)
	[Madagascar; Mauritius; Mayotte (France) (loc. n.); La Réunion (France)]
-	From swith a median white stripe; $\bigcirc A = 22-3/$; aedeagus subterminally con-
((2))	vex (Fig. 3e,i); spermatheca rough (Fig. 3g, k)4
4(3)	TST = 1-2 mm; spermatheca very papillate (Fig. 3g); posterior egg filament
	spatulate (Fig. 3h)
-	TST = 3-5 mm; spermatheca somewhat papillate (Fig. 3k); posterior egg fila-
	ment not spatulate (Fig. 3l)
5(4)	$O'WV = 1.5 - 1.8 \ \mu m; TST = 2.0 \ mm$
	[Benin; Cameroon; Côte d'Ivoire; Gabon; Congo; Madagascar; Malawi;
	South Africa; Uganda]
-	$\partial WV = 1.9-2.5 \ \mu m; TST = 1.2 \ mmZ. tsacasi$
	[São Tomé and Principé]
6(3)	TST = 3.2 mmZ. tuberculatus
	[Cameroon; Canary Islands (Spain); Cabo Verde; Central African Republic;
	Chad; Congo; Côte d'Ivoire; Cyprus; Democratic Republic of Congo; Egypt;
	Gabon; Greece; Kenya; Israel; Madagascar; Malawi; Malta; Mauritius; May-
	otte (France) (loc. n.); Mozambique; Niger; Nigeria; La Réunion (France);
	Zambia; Seychelles; South Africa; St. Helena; Tanzania; Uganda; Zimbabwe]
_	TST = 4.4 mm
	[Tanzania]
7(2)	Frons without a median stripe
_	Frons with a median stripe14
8(7)	Scutum velvety black, especially posteriorly; scutellum with a white spot at
	tip (Fig. 1b)
	[Benin; Cameroon; Congo; Côte d'Ivoire; Democratic Republic of Congo;
	Gabon; Kenya; Madagascar; Malawi; Niger; Nigeria; São Tomé and Prin-
	cipé; Swaziland; Tanzania; Turkey; Uganda; Hawaii Islands (United States of
	America); Zimbabwe]
_	Scutum and scutellum not as above9
9(8)	Scutellum entirely and scutum posteromedially black (Fig. 1c)
	[Madagascar]
_	Scutellum and scutum not as above10
10(9)	Wing darkened anteriorly
_	Wing uniformally hyaline
11(10)	Thorax and abdomen entirely dark brown (Fig. 4a)
	[Côte d'Ivoire; Democratic Republic of Congo]
_	Thorax and abdomen yellow (Fig. 4b)
	[Côte d'Ivoire]
12(10)	♂ basitarsus without a hairy brush (Fig. 5a)
	[Côte d'Ivoire; Democratic Republic of Congo; Madagascar]
_	👌 basitarsus with a hairy brush (Fig. 5b-d)

13(12)	Thorax yellow; the last 3 abdominal segments shining dark brown (Fig. 4c) .
	Z. niabu
	[Côte d'Ivoire]
-	Thorax reddish yellow; abdomen shining yellow (Fig. 4d)
	[Côte d'Ivoire; Democratic Republic of Congo]
14(7)	Scutum with 6 longitudinal white stripes (Fig. 1d)15
_	Scutum with 4 longitudinal white stripes (Fig. 1e)16
15(14)	Aedeagal flap smooth and pointed basally (Fig. 6a) Z. sexvittatus
	[Democratic Republic of Congo; Kenya]
-	Aedeagal flap finely serrated and truncated basally (Fig. 6b) Z. sexstriatus
	[South Africa]
16(14)	Cercus with elongate, ventromedial expansion (Fig. 7a,b)17
_	Cercus without ventromedial expansion (Figs 7c,d)18
17(16)	Thorax with a faint median white stripe (Fig. 1e); \bigcirc WL:TL = 2.02–2.15;
	abdomen with dark spots at the base of tergal bristles; cercal prominence long
	and basomedially setulate (Fig. 7b)Z. cercus
	[Madagascar]
_	Thorax without a faint median white stripe; \bigcirc WL:TL = 2.25–2.35; abdomen
	without dark spots at the base of tergal bristles; cercal prominence short and
	almost entirely setulate along median edge (Fig. 7a)
	[Cameroon; Central African Republic; Congo; Côte d'Ivoire; Democratic
	Republic of Congo; Gabon; Kenya; Uganda]
18(16)	BV = 9–11 μ m (Fig. 1f); testis short; epandrial phragma with a broad hump
	at the middle of the anterior margin (Fig. 7c); spermatheca smooth
	[Madagascar]
-	$BV = 6-8 \ \mu m$ (Fig. 1g); testis long; epandrial phragma with a narrow hump
	at the dorsal quarter of the anterior margin (Fig. 7d); spermatheca papillate;
	F1 sometimes with a minute tubercule
	[Madagascar]
19(1)	F1 with spines not fused with long bristles at their bases (Figs 2c,d, 8)20
_	F1 with spines fused with long bristles at their bases (Figs 2e,f)
20(19)	F1 with 2 spines pointed in opposite orientation (Fig. 2c)21
-	F1 with more than 2 spines usually pointed to the same direction (Fig. 2d)22
21(20)	F1 small (Figs 2c, 8a); abdomen with dark spots at base of bristles
	Z. campestris
	[Cameroon; Côte d'Ivoire; Madagascar, Sao Tomé and Principé]
-	F1 large (Fig. 8b); abdomen without dark spots at base of bristles
	Z. montanus
	[Burundi; Côte d Ivoire; Democratic Republic of Congo; Kenya; Rwanda;
22(20)	South Africa
22(20)	\sim basitarsus without a hairy brush
_	\odot basitarsus with a hairy brush

23(22)	F1 with 3-4 spines; basalmost spine strong (Fig. 8c)
	[Cameroon; Côte d'Ivoire; Democratic Republic of Congo]
-	F1 with 5 spines internally and sometimes 2 spines externally (Fig. 8d)
	Z. spineus
	[Democratic Republic of Congo]
24(22)	F1 spines differentiated; basalmost spine strong (Figs 2d, 8e)Z. serratus
	[Cameroon; Democratic Republic of Congo; Uganda]
_	F1 spines undifferentiated (Fig. 8f-n)25
25(24)	Wing anterior margin black or darkened (Fig. 9a-c)26
_	Wing hyaline (Fig. 9d)
26(25)	Wing anterior margin black (Fig. 9a,b); F1 spines fine (Fig. 8f, g)27
-	Wing anterior margin darkened (Fig. 9c); F1 spines robust (Fig. 8h, i)28
27(26)	F1 with 2–3 spines (Fig. 8g) Z. fumipennis
	[Congo; Côte d'Ivoire; Democratic Republic of Congo; Kenya]
_	F1 with 5–6 spines (Fig. 8f)
	[Congo; Côte d'Ivoire; Democratic Republic of Congo; Gabon; Tanzania;
	Uganda]
28(26)	F1 middle bristle borne on a tubercule (Fig. 8h) Z. tuberarmatus
	[Cameroon; Democratic Republic of Congo]
_	F1 middle bristle not borne on a tubercule (Fig. 8i) Z. hoplophorus
	[Cameroon; Congo]
29(25)	Aedeagal flap absent (Fig. 6c, d)30
-	Aedeagal flap present
30(29)	F1 with a hairy tuft proximally (Fig. 8j); aedeagus short and robust
	Z. armatus
	[Democratic Republic of Congo]
_	F1 without a hairy tuft proximally (Fig. 8k); aedeagus very long and slender
	Z. enoplomerus
	[Cameroon; Côte d'Ivoire]
31(29)	F1 middle bristle borne on a minute tubercule (Fig. 8l); spermatheca volumi-
	nous, sclerified at apex and with deep apical introvert (Fig. 6e) Z. spinipes
	[Cameroon]
-	F1 middle bristle not borne on a tubercule (Fig. 8m,n); spermatheca not as
	above
32(31)	F1 not broadened, with a series of short bristles (Fig. 8m); spermatheca scleri-
	fied (Fig. 6f)Z. seguyi
	[Cameroon; Congo; Democratic Republic of Congo]
-	F1 broadened, with a few long bristles (Fig. 8n); spermatheca smooth
	(Fig. 6g)Z. spinormatus
	[Cameroon; Côte d'Ivoire; Nigeria]
33(19)	WV < 15 µm; thorax and abdomen blackish brown
	[Cameroon; Malawi; Tanzania (loc. n.); Uganda]

-	WV > 15 μ m; thorax and abdomen not black
34(33)	Abdominal tergal bristles with dark spots basally
- 35(34)	Thorax with two incomplete submedian white stripes between two complete
55(51)	dorsocentral stripes (Fig. 1h)
	[Kenva; Rwanda]
_	Thorax without submedian stripes
36(35)	F1 setiferous spines differentiated; basalmost borne on a protruding tubercule
	(Fig. 2e)
	[Kenya; Uganda]
-	F1 setiferous spines undifferentiated
37(36)	BV enlarged posteriorly; abdomen dark brown (Fig. 10b, d, e)
- 20(27)	Ab domain darker than the rear (Fig. 10b) 7 house
38(37)	Benin: Côte d'Ivoire
_	Abdomen and thorax concolorous (Fig. 10d) 39
39(38)	First and second tarsomeres of the foreleg with strong black spines (Fig. 5c);
0 / (0 -)	♂TL = 1.62–1.68 mm (Fig. 10e); H = 5.2 (Fig. 11d) Z. lachaisei sp. n.
	[Tanzania]
_	First and second tarsomeres of the foreleg without strong black spines; $\ensuremath{}\xspace{-1pt}{} TL$
	= 1.44–1.56 mm (Fig. 10d); H = 9.6 (Fig. 11e)
	[Cameroon; Ethiopia; Madagascar; Malawi; South Africa]
40(37)	Head orange tan lighter than thorax (Fig. 10f); hairy brush $1/3$ \bigcirc basitarsus
	(Fig. 5e); spermatheca without introvert (Fig. 13d) Z. santomensis sp. n.
	[Sao Iome and Principe] Head and there is a concelerous reddish brown heiry brush $2/3$ $\frac{1}{2}$ besiterous
_	spermethece with an introvert (Fig. 12) 41
41(40)	δ aedeagal flap highly serrated apically (Fig. 12a) : oviscape constricted basal-
()	ly with 8 (rarely 7) peg-like ovisensilla (Fig. 12b); spermatheca length:width
	= 0.62–0.84 (Fig. 12c) Z. africanus
	[Gabon ; Uganda]
-	$\stackrel{\scriptstyle <}{\scriptstyle \bigcirc}$ aedeagal flap highly smooth apically (Fig. 12d,g); oviscape with 6 peg-like
	ovisensilla (Fig. 12e,h); spermatheca length:width = 0.95–1.16 (Fig. 12f,i)42
42(41)	aedeagal flap smooth basally (Fig. 12d) Z. gabonicus
	$\begin{bmatrix} Gabon \end{bmatrix}$
-	• acceagal hap servated basally (Fig. 12g)
	Congo: Côte d'Ivoire: Foynt: India: Iran: Israel: Italy: Kenya: Madagascar:
	Madeira (Portugal): Malawi; Mauritius; Morocco (loc. n.): Mozambique;
	Niger; Nigeria; Panama; La Réunion (France); São Tomé and Principé;
	Saudi Arabia; Seychelles; South Africa; Tanzania; United States of America;
	Uruguay]

43(34)	Abdomen yellow with brown posterior fine stripes on tergites II to IV; TST >
	12.0 mm; spermatheca elongated (Fig. 14a)
	[Cameroon; Côte d'Ivoire; Congo; Gabon; Madagascar; South Africa]
_	Abdomen uniformally yellow; TST < 6.0 mm; spermatheca globulous
	(Figs 14b,c,e)
44(43)	TST = 2.6 mm; spermatheca chitinized at base and apex (Fig. 14b); egg with
	2 filaments
	[Congo; São Tomé and Principé (loc. n.)]
_	TST = 4.0–5.2 mm; egg with 4 filaments
45(44)	$\partial TL = 1.56-1.70 \text{ mm}; \partial$ epandrium not expanded dorsally (Fig. 14d); sper-
	matheca (Fig. 14c)
	[Congo (loc. n.); Gabon; Kenya; Malawi; São Tomé and Principé (loc. n.)]
_	∂TL = 1.44–1.50 mm; ∂ epandrium expanded dorsally (Fig. 14e); sper-
	matheca (Fig. 14f)
	[South Africa]

Revised classification of Zaprionus s.s.

Chassagnard and Tsacas (1993) divided Zaprionus s.s. into two groups: *inermis* and *armatus*, the latter comprising three subgroups: *armatus*, *tuberculatus* and *vittiger*. The phylogenetic revision of Yassin et al. (2008a) revealed both groups and subgroups to be polyphyletic. However, almost half of the species used in their study lacked DNA sequences, and the discovery and the subsequent molecular analysis of some of these species revealed some new insights (Yassin et al., in press). In light of these findings, a new classification scheme is proposed (Table 2).

Table 2 also shows the breeding niche and the possibility to rear in the laboratory for some species. These two attributes are interrelated, as generalist fruit-breeding species are usually those that can be reared with ease on standard *Drosophila* medium. Lachaise and Tsacas (1983) reviewed the breeding niche for 12 Zaprionus s.s. species. With the exception of the curious entomophagous ecology of some Afrotropical drosophilids, Zaprionus species share almost all of the known breeding niches of the Afrotorpical fauna, *i.e.* fruit, flower and decaying tree trunk breeding. Most species are fruit breeders. Some species (e.g., Z. badyi, Z. momorticus, and Z. neglectus) are generalist flower-breeders, whereas two species of the armatus group (Z. fumipennis and Z. vrydaghi) breed exclusively in flowers of Costus afer (Tsacas and Chassagnard 1990). Records of Z. montanus suggest this species to mine bamboo leaves or stems (Graber 1957; Chassagnard 1989). The breeding niche of its sibling species, Z. campestris, is unknown as it was collected by non-selective light or Malaise traps. Zaprionus koroleu was bred from cut palm trunks along with other palm breeding drosophilids of the genera Chymomyza and Scaptodrosophila. However, it appears that no strict association with palm trees has yet evolved in this species as it was able to be reared in the laboratory (although the strain has been lost due to the difficulty of rearing). Other Zaprionus



Figure 2. Forefemur of *Zaprionus cercus* Chassagnard & McEvey, 1992 a, *Z. mascariensis* Tsacas & David, 1975 b, *Z. campestris* Chassagnard, 1989 c, *Z. serratus* Chassagnard, 1989 d *Z. proximus* Collart, 1937 e, and *Z. indianus* Gupta, 1970 f.

species that were also bred from cut tree trunks included *Z. armatus*, *Z. inermis* and *Z. ghesquierei*.

It is still difficult to estimate with certainty the niches for some of the problematic species in Lachaise and Tsacas's (1983) review. For example, Z. indianus had almost 80 host plants being the most ecologically diverse drosophilid in the Afrotropical fauna. However, most of the ecological records prior to Tsacas' (1980) re view confused this species with other species of the vittiger group, and even after its identity has been established (Tsacas 1985) the recent discovery of two cryptic species, one of which is also widespread in tropical Africa (Yassin et al. 2008b), sheds doubt on its hosts there. Indeed, Lachaise and Tsacas (1983) described three native host plants from Makokou (Gabon), a locality where the two cryptic species coexist (Yassin et al. 2008b). Although the breeding niches of Z. indianus have been properly determined in its introduced regions in Brazil (Silva et al. 2005; Tidon 2006; Garcia et al. 2008) and the Palearctic region (Yassin et al. 2009), attention has to be paid in the future to determine its breeding niche in its zone of origin. We excluded also the records on the tuberculatus subgroup predating Tsacas et al.'s (1977) discrimination of two sibling species Z. sepsoides and Z. tuberculatus. Records on the Gabonese strain of Z. ornatus in Lachaise and Tsacas (1983) were assigned to Z. taronus since Chassagnard and Tsacas (1993) showed this strain to be misidentified with Z. ornatus by Tsacas (1980).

The armatus group

The *armatus* group was initially erected to include three subgroups: *armatus*, *tuber-culatus* and *vittiger* (Chassagnard and Tsacas 1993). We transferred the *tuberculatus*

TR = decaying tree trunk. Ability	
<i>aprionus</i> . Breeding niches are abbreviated as: FL = flowers; FR = fruits; and	r species that are reared and (•) for species that are not.
Je 2. Classification and ecology of the subgenus \hat{z}	be reared in the laboratory (L) is indicated as ($+$) for

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to be reared in	ssuitcation and e n the laboratory	(L) is indicated a	genus <i>zaprionus.</i> as (+) for species	that are reared and (-) for species	as: r = = s that are	Howers; $\mathbf{F}\mathbf{A} = \text{truits}$; and $\mathbf{I}\mathbf{A} = \text{decaying tree t}$ not.	trunk. Abuity
Group	Subgroup	Complex	Species	Authorship	L Bre	eding niche	Reference
armatus	armatus	armatus	armatus	Collart, 1937a	- TR	: Ficus sp. (Moraceae)	C37a
					FR	: Myrianthus sp. (Cercopiaceae)	TC90
			enoplomerus	Chassagnard, 1989	+ FR (M	: Ficus macrosperma (Moraceae); Ficus sur oraceae); Ficus capensis (Moraceae)	C89
			seguyi	Tsacas & Chassagnard, 1990	- FR		TC90
			spinipes	Tsacas & Chassagnard, 1990	۸. ۱		TC90
			spinoarmatus	Tsacas & Chassagnard, 1990	- FR:	: Dacryodes sp. (Burseraceae)	TC90
					TR	: Raphia sp. (Arecaceae)	B54
		hoplophorus	hoplophorus	Tsacas & Chassagnard, 1990	<u>م</u> .		
			tuberarmatus	Tsacas & Chassagnard, 1990	<u>م</u> .		
		vrydaghi	fumipennis	Séguy, 1938	- FL:	Costus afer (Costaceae)	TC90
			vrydaghi	Collart, 1937a	- FL:	Costus afer (Costaceae)	B76,C86
	montanus		campestris	Chassagnard, 1989	۸. ۱		C89
			montanus	Collart, 1937b	- TR	: Andropoganeae (Poaceae)	G57
					TR	: Bambuseae (Poaceae)	C89
	spinosus		servatus	Chassagnard, 1989	- FL:	Bignoniaceae	C89
			spineus	Tsacas & Chassagnard	۸. ۱		TC90
			spinosus	Collart, 1937a	۸. ۱		
inermis			arduus	Collart, 1937b	- FR:	: Musa sp. (Musaceae)	C37b
			badyi	Burla, 1954	- FR		B54
			ghesquierei	Collart, 1937a	- FR Rol (R. T_{dir}	: Citrus sinensis (Rutaccae); Coffea sp. ibiaceae); Cola acuminata (Malvaceae); linia sieberi (Annonaceae); Sarocephalus (Rubiaceae); Psidium sp. (Myrtaceae); minalia sp. (Combredaceae); Murraya exotica ttaceae); Pseudospondia sp. (Anacridaceae); rianthus sp. (Cercopiaceae); Dorstenia sp. oraceae); Uanaca sp. (Phyllanthaceae)	C37a

Group	Subgroup	Complex	Species	Authorship	L Bre	eeding niche	Reference
					FR (O) (O) (A) (AF	: Musa sp. (Musaceae), Averrhoa carambola xalidaceae); Turraeanthus africana eliaceae); Conopharyngia dusissima oocynaceae),	B54
					$\begin{array}{c} \operatorname{FR}_{a}\\ \operatorname{Car}_{a}\\ $: Mangifera indica (Anacardiaceae); rica papaya (Caricaceae); Persea americana uraceae); Ficus ovata (Moraceae); Musa sp. usaceae); Averrhoa carambola (Oxalidaceae); bhonandra betacea (Solanaceae); Solanum gilo lanaceae)	B76
					FR. Den	: <i>Polyalthia sauveolens</i> (Annonaceae); <i>tarium senegalense</i> (Caesalpiniaceae)	LT83
					FR (Lii <i>per</i> j	: Dacryodes sp. (Burseraceae); Hugonia sp. naceae); Parinari sp. (Rosaceae); Gambeya pulchra (Sapotaceae)	L79
					FR	: Cocos romanzoffiana (Palmaceae)	L47
					FR	: <i>Pancovia bijuga</i> (Sapindaceae)	L74
					TR	.: Elaeis guinensis (Palmaceae)	L47
					FR	: Ficus thonningii (Moraceae)	C97
			momorticus	Graber, 1957 -	- FL:	: Momordica pterocarpa (syn. M. runsorrica) curbitaceae)	G57
					FL: Cri	: <i>Crinum sanderianum</i> (Amaryllidaceae); <i>inum jagus</i> (Amaryllidaceae)	L79
					FL:	: <i>Rothmania whitfieldi</i> (Rubiacea)	L74
			niabu	Burla, 1954	- FR	: Carica papaya (Caricaceae)	B54
	inermis		Cercus	Chassagnard & McEvey	+ FR	: ex-banana trap	CM92
			inermis	Collart, 1937a	+ FR	: Eugenia malaccensis (Myrtaceae)	C37a
					FR	: Citrus sp. (Rutaceae); Carica papaya	B54
					TR (C	aricaceae); :: <i>Raphia</i> sp. (Arecaceae)	B54

Group	Subgroup	Complex	Species	Authorship	L	Breeding niche	Reference
c	0	0	0	(FR: Musa sapientum (Musaceae)	LT83
						TR: Elaeis guineensis (Arecaceae)	LT83
	tuberculatus		kolodkinae	Chassagnard & Tsacas, 1987	+	FR: ex-banana trap	CT87
			mascariensis	Tsacas & David, 1975	+	FR: ex-banana trap	TD75
		sepsoides	sepsoides	Duda, 1939	+	FR: Dacryodes sp. (Burseraceae); Hugonia	L79
						sp. (Linaceae); Guarea cedrata (Meliaceae);	
						<i>Iurraeanthus africanus</i> (Mellaceae); <i>Parmari</i> sp. (Chrysobalanaceae)	
						FR: Ficus sur (Moraceae); Ficus lynata	L82
						(Moraceae); Ficus macrosperma (Moraceae);	
						Ficus elasticoides (Moraceae); Ficus ovata	
						(Moraceae); Ficus sp. (Moraceae)	
						FR: Pandanus candelabrum (Pandanaceae)	R83
						FR: Spondias mombin (Anacardiaceae);	C86
						Detarium senegalense (Cesalpinaceae);	
						Pentadesma butyraceae (Guttifereae); Treculia	
						africana (Moraceae); Hirtella sp. (Rosaceae);	
						Parinari excelsa (Rosaceae); Nauclea poheguinii	
						(Rubiaceae); Gambeya taiensis (Sapotaceae);	
						Tieghemella heckelii (Sapotaceae)	
			tsacasi	Yassin, 2008	+	FR: ex-banana trap	Y08
		tuberculatus	burlai	Yassin, 2008	+	FR: ex-banana trap	Y08
			tuberculatus	Malloch, 1932	+	FR: Santiria trimera (Burseraceae); Dacryodes	L79
						sp. (Burseraceae); Guarea cedrata (Meliaceae);	
						Parinari sp. (Rosaceae); Parinari excelsa	
						(Rosaceae); Tieghemella heckelii (Sapotaceae)	
						FR: Ficus sur (Moraceae); Ficus saussureana	L82, LT83
						(Moraceae); Ficus mucuso (Moraceae); Ficus	
						lutea (Moraceae); Ficus natalensis (Moraceae);	

Group	Subgroup	Complex	Species	Authorship L	Breeding niche	Reference
					FR: Spondias mombin (Anacardiaceae); Detarium senegalense (Cesalpinaceae); Artocarpus sp. (Moraceae); Hirtella sp. (Rosaceae); Uncaria sp. (Rubiaceae); Gambeya taiensis (Sapotaceae)	C86
			рентиса	Chassagnard & McEvey, + 1992	FR: ex-banana trap	CM92
neglectus			neglectus	Collart, 1937 +	FR	B54
					FL: <i>Ipomoea digitata</i> (Convolvulaceae)	B54
					FL: Crinum jagus (Amaryllidaceae); Pentadesma butyracea (Guttiferae); Rothmania whifieldi (Rubiaceae)	C86
					FR: Ficus ovata (Moraceae)	L79
					FR: Treculia africana (Moraceae)	C86
vittiger		davidi	davidi	Chassagnard & Tsacas, 1993 +	FR: ex-banana trap	CT93
			taronus	Chassagnard & Tsacas, 1993 +	FR: Polyalthia sauveolens (Annonaceae); Staudtia	LT83
					gabonensis (Myristicaceae); Cissus dinklagei (Vitaceae)	
		indianus	africanus	Yassin & David, 2008 +	FR: ex-banana trap	Y08b
			gabonicus	Yassin & David, 2008 +	FR: ex-banana trap	Y08b
			indianus	Gupta, 1970 +	FR: ex-banana trap	Y08b
					FR: date palm, guava and citrus	Y09
		ornatus	litos	Chassagnard & McEvey, - 1992	~-	CM92
			ornatus	Séguy, 1933 +	FR: Averrhoa carambola (Oxalidaceae)	B54
					FR: Spondias mombin (Anacardiaceae); Gambeya taiensis (Sapotaceae)	C86
					FR: Ficus sur (Moraceae)	L76

Group	Subgroup	Complex	Species	Authorship	Г	Breeding niche	Reference
						FR: Ficus macrosperma (Moraceae); Ficus sausureana (Moraceae); Ficus elasticoides (Moraceae); Ficus vogeliana (Moraceae); Ficus mucuso (Moraceae); Ficus ovata (Moraceae); Ficus lutea (Moraceae); Ficus thoningii (Moraceae)	L82, LT83
						FL: Rothmania whitfieldii (Rubiaceae)	L74
		proximus	capensis	Chassagnard & Tsacas, 1993	+	FR: ex-banana trap	CT93
			proximus	Collart, 1937b	+	FR: Cussonia sp. (Araliaceae)	C37b
		sexvittatus	multivittiger	Chassagnard, 1996	+	FR: Rhamnus prinoides (Rhamnaceae)	C96
			sexstriatus	Chassagnard, 1996	+	FR?	
			sexvittatus	Collart, 1937c	ı	FR: Acokanthera sp. (Apocynaceae)	C37c
						FR: Juniperus procera (Cupressaceae)	C96
		vittiger	camerounensis	Chassagnard & Tsacas, 1993	+	FR: ex-banana trap	CT93
			koroleu	Burla, 1954	+	FR: ex-banana trap	
						TR: Raphia sp. (Arecaceae)	B54
			lachaisei	sp. n.	+	FR: ex-banana trap	
			santomensis	sp. n.	+	FR: ex-banana trap	
			vittiger	Coquillett, 1902	+	FR: ex-banana trap	YP

References: B54: Burla 1954; B76 = Buruga 1976; C37a = Collart 1937a; C37b = Collart 1937b; C86 = Couturier et al. 1986; C89 = Chassagnard 1989; C96 = cas 1993; G57 = Graber 1957; L47 = Lepesme 1947; L74 = Lachaise 1974; L76 = Lachaise 1976; L79 = Lachaise 1979; L82 = Lachaise et al. 1982 LT83 = Lachaise Chassagnard 1996; C97 = Chassagnard et al. 1997; CM92 = Chassagnard and McEvey 1992; CT87 = Chassagnard and Tsac and Tsacas 1983; R83 = Rio et al. 1983; TC90 = Tsacas and Chassagnard 1990; TD75 = Tsacas and David, 1975; Y08 = Yassin 2008; Y08b = Yassin et al. 2008b; Y09 = Yassin et al. 2009; YP = Yassin et al., in press.



Figure 3. Distiphallus, testis and accessory gland, spermatheca and egg of *Zaprionus mascariensis* Tsacas & David **a–d**, *Z. sepsoides* Duda, 1939 **e–h**, and *Z. tuberculatus* Malloch, 1932 **i–l** [From Tsacas et al. 1977; courtesy of M. T. Chassagnard].

subgroup to the *inermis* group and upgraded the *vittiger* subgroup to a species group hence restricting the *armatus* group to the 14 species of the previous *armatus* subgroup bearing a simple row of spines on F1 (Tsacas and Chassagnard 1990; Fig. 2c, d; Fig. 8). Tsacas and Chassagnard (1990) further subdivided the 14 species of the *armatus* subgroup to three 'Ensembles' I, II and III on the basis of the differentiation of the F1 spines. Yassin et al. (2008a) suggested, using morphological characters of the male genitalia, this subgroup to be polyphyletic. Nonetheless, molecular sequences became later available from a single species, *Z. campestris*, and its phylogenetic position did not confirm Yassin et al.'s (2008a) placement (Yassin et al., in press). Therefore, Tsacas and Chassagnard's (1990) subclassification will be retained with slight modifications until new molecular sequences become available. The *armatus* group is now subdivided into



Figure 4. Dorsal views of *Zaprionus momorticus* Graber, 1957 a, *Z. badyi* Burla, 1954 b, abdomen of *Z. niabu* Burla, 1954 c, and lateral view of *Z. arduus* Collart, 1937 d.

three subgroups: the *montanus* subgroup with two species bearing two oppositely oriented F1 spines (Ensemble I); the *spinosus* subgroup with three species bearing a row of differentiated F1 spines (Ensemble II); and the *armatus* subgroup with nine species bearing a row of undifferentiated F1 spines (Ensemble III). The *armatus* subgroup is further subdivided into three complexes: the *hoplophorus* complex with two species bearing differentially oriented strong F1 spines; the *armatus* complex with five species bearing undifferentially oriented strong F1 spines; and the *vrydaghi* complex with two species bearing undifferentially oriented fine F1 spines and wings blackened anteriorly.

The inermis group

The *inermis* group comprises species with spineless F1 (Figs 2a, b). The F1 spinelessness is also found in the Oriental subgenus *Anaprionus*, suggesting a plesiomorphy, and the monophyly of this group was questionable (Chassagnard and Tsacas 1993). Yassin et al. (2008a) suggested on the basis of morphological characters that this group was polyphyletic with two species *Z. litos* and *Z. neglectus* being closely related to the *arma*-



Figure 5. Tarsomeres of male foreleg of *Zaprionus neglectus* Collart, 1937 a, *Z. kololdkinae* Chassagnard & Tsacas, 1987 b, *Z. lachaisei* Yassin & David, sp. n. c, *Z. taronus* Chassagnard & Tsacas, 1993 d, and *Z. santomensis* Yassin & David, sp. n. e.

tus and the vittiger groups. These suggestions were confirmed by later molecular analyses (Yassin et al., in press) which also suggested that two other species (Z. sexstriatus and Z. sexvittatus) formed the sister clade with the vittiger group. Four species of the inermis group (Z. arduus, Z. badyi, Z. momorticus and Z. niabu) have not been included in any of these previous studies and their phylogenetic placement remains thus uncertain. Zaprionus ghesquierei forms the earliest branch for the remaining species that are classified here under two subgroups: the inermis subgroup with two species having the short straight aedeagus; and the tuberculatus subgroup with seven species having the curved robust aedeagus. The F1 of several species of tuberculatus subgroup carries a tubercule (Fig. 2b). These two subgroups are closely related to each other as they share the bare and bristleness epandrium (Fig. 7) and the fine serration on the dorsal margin of the aedeagus. These synapomorphies are absent in Z. ghesquierei, Z. arduus, Z. badyi and Z. momorticus. No male specimen has ever been collected for Z. niabu. The tuberculatus



Figure 6. Ventral views of distiphallus of *Zaprionus sexvittatus* Collart, 1937 a, *Z. sexstriatus* Chassagnard, 1996 b, *Z. armatus* Collart, 1937 c, and *Z. enoplomerus* Chassagnard, 1989 d; spermatheca of *Z. spinipes* Tsacas & Chassagnard, 1990 e, *Z. seguyi* Tsacas & Chassagnard, 1990 f, and *Z. serratus* Chassagnard, 1989 g [From Chassagnard 1989, 1996; Tsacas and Chassagnard 1990; courtesy of M. T. Chassagnard].

subgroup contains two species complexes as suggested by Yassin (2008): the *sepsoides* complex with two species having short testicules; and the *tuberculatus* complex with three species having long testicules.

The neglectus group

Zaprionus (Zaprionus) neglectus Collart

Z. simplex Chassagnard and McEvey 1992, syn. n.

Discussion. Zaprionus neglectus is a continental species lacking F1 ornamentation and the hairy brush on F1 basitarsus in males (Collart 1937b; Fig. 5a). It is the only species previously belonging to the *inermis* group to lack such a secondary sexual character. Two species of the *spinosus* subgroup of the *armatus* group also lack the male hairy brush. Burla (1954) and Lachaise and Tsacas (1983) described that Z. neglectus bred on decaying fruits and in flowers of *Ipomoea* and *Crinum*. Chassagnard and McEvey (1992) described a species, Z. simplex, lacking F1 ornamentation and the male hairy brush from Madagascar. They also noted that some specimens were "collected from *Crinum* sp. flowers but no evidence was found that it bred therein" (p. 322).

We have recently collected a strain of *Z. simplex* from *Crinum* sp. in Madagascar and reared it in the laboratory. Burla (1954) noted the presence of two long caecae around



Figure 7. Lateral views of male epandrium and cercus and ventral views of aedeagus and hypandrium of *Zaprionus inermis* Collart, 1937 **a**, *Z. cercus* Chassagnard & McEvey, 1992 **b**, *Z. kolodkinae* Chassagnard & Tsacas, 1987 **c**, **e**, and *Z. verruca* Chassagnard & McEvey, 1992 **d**, **f** [From Chassagnard and Tsacas 1987; Chassagnard and McEvey 1992; courtesy of M. T. Chassagnard].

the ejaculatory bulb in males of *Z. neglectus*. Dissection of cultured males of *Z. simplex* also revealed the presence of long caecae in the Malagasy strain. Wing shape indices were also strongly similar in the original descriptions of the two species. Hence, *Z. simplex* Chassagnard & McEvey is considered a junior synonym to *Z. neglectus* Collart. Yassin et al. (2008a) suggested in light of morphological characters *Z. simplex*, syn. n. to belong to the *armatus* group, but in the lack of molecular data of any species of this group such relation remains questionable. Indeed, the species has more than 2 epandrial bristles and lacks any F1 ornamentation. Molecular analysis of the Malagasy strain showed the species to be the earliest branch of the subgenus not belonging to any of the three other species groups (Yassin et al., in press). Thus, a group is erected for this single species.



Figure 8. Ventral views of forefemur of Zaprionus campestris Chassagnard, 1989 a, Z. montanus Collart, 1937 b, Z. spinosus Collart, 1937 c Z. spineus Tsacas & Chassagnard, 1990 d, Z. serratus Chassagnard, 1989 e, Z. fumipennis Séguy, 1938 f, Z. vrydaghi Collart, 1937 g, Z. tuberarmatus Tsacas & Chassagnard, 1990 h, Z. hoplophorus Tsacas & Chassagnard, 1990 i, Z. armatus Collart, 1937 j, Z. enoplomerus Chassagnard, 1989 k, Z. spinipes Tsacas & Chassagnard, 1990 l, Z. seguyi Tsacas & Chassagnard, 1990 m, and Z. spinoarmatus Tsacas & Chassagnard, 1990 n [From Chassagnard 1989; Tsacas and Chassagnard 1990; courtesy of M. T. Chassagnard].

The vittiger group

The *vittiger* group comprises 17 species with usually hairy epandrium carrying more than 2 posterior bristles (Fig. 14d, f). It is mainly characterized by the relatively deep serration of the aedeagal flap. The F1 of most of its species carry composite spines that have bristles fused at their bases and usually are borne on protruding tubercules (Fig. 2e, f). Three species (*Z. sexstriatus*, *Z. sexvittatus* and *Z. litos*) have the unarmed F1 and have been classified in the *inermis* group (Chassagnard and Tsacas 1993; Chassagnard 1996). Species with F1 bearing composite spines are classified into six complexes: the *sexvittatus* complex with three species having two additional submedian silvery longitudinal stripes on the thorax (Fig. 1); the *ornatus* complex



Figure 9. Wing of *Zaprionus fumipennis* Séguy, 1938 **a**, and dorsal views of *Z. vrydaghi* Collart, 1937 **b**, *Z. hoplophorus* Tsacas & Chassagnard, 1990 **c**, and *Z. tuberarmatus* Tsacas & Chassagnard, 1990 **d**.

with two species having the aedeagal flap weakly serrate apically and smooth basally and greatly extended basally and tapering to a point; the *indianus* complex with three species having the entirely hairy epandrium and hypandrium and the smooth spermatheca (Fig. 12); the *davidi* complex with two species having the partially hairy epandrium and rough spermatheca (Fig. 14); the *proximus* complex with two species having the epandrium enlarged dorsally and tapered ventrally (Fig. 14), the broadened hypandrium and the voluminous cercus lobate at the dorsal margin; and the *vittiger* complex with five species having the partially hairy epandrium and the smooth spermatheca.



Figure 10. Lateral and dorsal views of *Zaprionus koroleu* Burla, 1954 **a**, **b**, *Z. vittiger* Coquillett, 1902 **c**, **d**, *Z. lachaisei* Yassin & David, sp. n. **e**, *Z. santomensis* Yassin & David, sp. n. **f**, and *Z. camerounensis* Chassagnard & Tsacas, 1993 **g**, **h**.

Zaprionus (Zaprionus) ornatus Séguy

Z. megalorchis Chassagnard and Tsacas 1993, syn. n.

Discussion. Séguy (1933) described a species of the *vittiger* group from Côte d'Ivoire, which has differentiated F1 composite spines; *i.e.* the spines are borne on protruding tubercules that decrease in size distally. He called the species *Z. ornatus*. Collart (1937a) considered this character an intraspecific variation and synonymised *Z. ornatus* with *Z. vittiger*. Chassagnard and Tsacas (1993) redescribed Séguy's female holotype and illustrated the distinctive elongated spermatheca that had also been previously illustrated by Burla (1954) for *Z.* aff. *vittiger*. In the same paper, they also described a new species from Congo with the distinctive elongated spermatheca and F1 ornamentation. They called the new species *Z. megalorchis* and noted that the only difference between it and *Z. ornatus* was the presence of silver pilosity on the inner side of flagellomere I in *Z. ornatus*. Yassin et al. (2008a) erected the *megalorchis* species complex for the two species. However,



Figure 11. Puparium of *Zaprionus neglectus* Collart, 1937 **a**, *Z. inermis* Collart, 1937 **b**, *Z. cercus* Chassagnard & McEvey, 1992 **c**, *Z. santomensis* Yassin & David, sp. n. **d**, *Z. lachaisei* Yassin & David, sp. n. **e** and *Z. vittiger* Coquillett, 1902 **f**.

we have examined a number of strains collected from the type locality of *Z. megalorchis* and found the flagellomere I pilosity to be polymorphic. We consider thus *Z. megalorchis* Chassagnard & Tsacas, syn. n. and *Z.* aff. *vittiger* Burla, syn. n. to be junior synonyms to *Z. ornatus* Séguy. Yassin et al. (2008b) have also considered *Z. megalorchis* (and thus *Z. ornatus*) a member of the *indianus* species complex, but it is considered here as belonging to an independent, monophyletic complex along with *Z. litos* (Yassin et al., in press).

Zaprionus (Zaprionus) africanus Yassin & David in Yassin et al. 2008b

Diagnosis. This species resembles *Z. indianus* and *Z. gabonicus*, but can be distinguished from them by the deep serration of the apical margin of the aedeagal flap, the shape of the spermatheca being wider than long and the presence of 8 (rarely 7) peglike ovisensilla on the oviscape, which is constricted ventrally (Fig. 12).



Figure 12. Distiphallus, oviscape and spermatheca of *Zaprionus africanus* Yassin & David in Yassin et al., 2008b **a-c**, *Z. gabonicus* Yassin & David in Yassin et al., 2008b **d-f**, and *Z. indianus* Gupta, 1970 **g-i**.

Description. \mathcal{J} . TL = 1.38 mm.

Head. Arista with 3 dorsal and 2 ventral rays plus terminal fork; pedicel white, flagellomere I dark brown. Frons orange, without a median stripe but with orbital stripes inwardly bordered with black; ocellar triangle concolorous with frons; hw:fw = 2.42, fw:fl = 0.96. Orbital setae in straight line; or1:or2:or3 = 3:2:3, orbito-index = 1.1, oc:or1 = 1.45, poc:oc = 0.63, iv:ov = 0.88. Face whitish yellow; carina broad and bulbous. Gena broad, o:j = 9.3, o:ch = 6.2. Eye red.

Thorax. Scutum brown, darker than frons, with 2 silvery white stripes. acs in 6 rows in front of adc; adc:pdc = 0.8. Scutellum darker than scutum, with black borders of the stripes expanded posteriorly; bsc:asc = 0.7. Pleura yellow; sterno-index = 0.38. Forefemur with 4–5 spines borne on warts on the anteroventral margin. Male basitarsus with a hairy brush.

Wing. Yellowish. C-index = 2.5, 4v-index = 1.3, 4c-index = 0.9, 5x-index = 1.0, M-index = 0.4, ac-index = 2.5, b/c = 0.7, C3 fringe = 47%, and WL = 2.90 mm.

Abdomen. Entirely yellow with deep dark spots at the bases of tergal setae.



Figure 13. Male genitalia and spermatheca of *Z. lachaisei* Yassin & David, sp. n. **a**, **b**, and *Z. santomensis* Yassin & David, sp. n. **c**, **d**.

Terminalia. Epandrium densely pubescent throughout its entire length; posterior margin pubescent at dorsal portion with 4 long setae; epandrial ventral lobe with 3 long setae. Surstylus quadrate with two rows of prensisetae. Cercus triangular laterally. Hypandrium densely pubescent at the lateral portion of the paraphyses. Aedeagus expanded apically with a hook-like appendix; aedeagal flap expanded and deeply serrated. Apodeme subequal in length to aedeagus.

 \bigcirc . TL = 1.39 mm, resembling male.

Terminalia. Oviscape constricted ventrally, with 8 peg-like and 6 short, marginal setae plus 4 supernumeraries. Spermatheca wide, campaniform and smooth.

Egg. Elliptical with 4, equally long and fine filaments.

Larva. Escaping the culture medium when crowded.

Puparium. Horn-index 9.8.

Zaprionus (Zaprionus) gabonicus Yassin & David in Yassin et al. 2008b

Diagnosis. This species resembles *Z. indianus*, but it can be distinguished from it by the small body size and the total lack of serration on the aedeagal flap (Fig. 12)

Description. \mathcal{O} . TL = 1.40 mm.

Head. Arista with 3 dorsal and 2 ventral rays plus terminal fork; pedicel white, flagellomere I dark brown. Frons orange, sometimes with highly vestigial median



Figure 14. Spermatheca and male epandrium of *Zaprionus ornatus* Séguy, 1933 **a**, *Z. davidi* Chassagnard & Tsacas, 1993 **b**, *Z. taronus* Chassagnard & Tsacas, 1993 **c**, **d**, and *Z. capensis* Chassagnard & Tsacas, 1993 **e**, **f** [Illustrations from Chassagnard and Tsacas 1993; courtesy of M. T. Chassagnard].

stripe plus orbital stripes inwardly bordered with black; ocellar triangle concolorous with frons; hw:fw = 2.45, fw:fl = 0.85. Orbital setae in straight line; or1:or2:or3 = 1.1:1.0:1.2, orbito-index = 1.1, oc:or1 = 1.4, poc:oc = 0.7, iv:ov = 0.7. Face whitish yellow; carina broad and bulbous. Gena narrow; o:j = 10, o:ch = 4.9. Eye red.

Thorax. Scutum brown, darker than frons, with 2 silvery white stripes. acs in 6 rows in front of adc; adc:pdc = 0.75. Scutellum darker than scutum, with black borders of the stripes expanded posteriorly; bsc:asc = 0.9. Pleura yellow; sterno-index = 0.44. Forefemur with 4–5 spines borne on warts on the anteroventral margin. Male basitarsus with a hairy brush.

Wing. Yellowish. C-index = 2.3, 4v-index = 1.4, 4c-index = 0.8, 5x-index = 1.0, M-index = 0.4, ac-index = 2.2, b/c = 0.6, C3 fringe = 52%, and WL = 2.7 mm.

Abdomen. Entirely yellow with deep dark spots at the bases of tergal setae.



Figure 15. Larval cephalopharyngeal skeleton of Zaprionus sepsoides Duda, 1939.

Terminalia. Epandrium densely pubescent throughout its entire length; posterior margin pubescent at dorsal portion with 4 long setae; epandrial ventral lobe with 3 long setae. Surstylus quadrate with two rows of prensisetae. Cercus triangular laterally. Hypandrium densely pubescent at the lateral portion of the paraphyses. Aedeagus slender expanded apically without a hook-like appendix; aedeagal flap expanded and not serrated. Apodeme subequal in length to aedeagus.

 \bigcirc . TL = 1.34 mm, resembling male.

Terminalia. Oviscape not constricted ventrally, with 6 (rarely 7) peg-like and 6 short, marginal setae plus 4 supernumeraries. Spermatheca globulous and smooth, not wider than longer.

Egg. Elliptical with 4 equally long and fine filaments. *Larva.* Escaping the culture medium when crowded. *Puparium.* Horn-index 10.4.

Zaprionus (Zaprionus) koroleu Burla

Z. (Z.) beninensis Chassagnard and Tsacas 1993, syn. n.

Discussion. The identity of the dark species *Z. koroleu* has long been problematic since its description by Burla (1954) from lowland rainforests in Côte d'Ivoire. It had often been confused with another montane dark species in Uganda (Buruga 1976) and Cameroon (Tsacas 1980; Bennet-Clark et al. 1980), which was later described as *Z. camerounensis* by Chassagnard and Tsacas (1993). Chassagnard and Tsacas (1993) re-examined Burla's type and considered the enlargement and fusion of BV on the scutellum a characteristic trait of *Z. koroleu* in the lack of distinctive features of the male genitalia. However, the examination of different strains of *Z. vittiger* has shown this character to be polymorphic and not exclusive to *Z. koroleu*. Chassagnard and Tsacas (1993) also noted that *Z. koroleu* is distinguishable from *Z. beninensis* in having the thorax and abdomen darker than the frons, whereas in *Z. beninensis* the abdo-

men is darker than the frons and the thorax as confirmed by re-examining the type series of *Z. beninensis*. All species of the *vittiger* complex are found in high latitudes or altitudes with the exception of *Z. koroleu* and *Z. beninensis*. Burla (1954) noted that *Z. koroleu* was bred in Côte d'Ivoire from decaying *Raphia* trunk along with other palm breeding drosophilids of the genera *Chymomyza* and *Scaptodrosophila*, and this was similar to the breeding niche of *Z. beninensis* in Benin (fallen trunks of coconut palm; J. R. David, unpublished observations). Both species are, however, generalists as Burla (1954) bred *Z. koroleu* also from fermenting fruits and as *Z. beninensis* was maintained in laboratory for almost ten years (Chassagnard and Tsacas 1993). On the basis of these geographical and ecological considerations, only slight differences in pigmentation observed in *Z. beninensis* and the great morphological similarity of male genitalia, *Z. beninensis* Chassagnard & Tsacas syn. n. is considered a junior synonym to *Z. koroleu* Burla.

Zaprionus (Zaprionus) lachaisei Yassin & David, sp. n. urn:lsid:zoobank.org:act:842BCF21-9ACF-48C1-9B53-9DAC95C49554

Diagnosis. This species resembles *Z. vittiger*, but has the bigger body size (TL > 1.60 mm), spiniform spines enlarged and blackened on the first two tarsomeres of the foreleg (Fig. 5), and shorter puparial anterior spiracles (H = 5) (Fig. 11). It is also distinguishable by a peculiar behavior of the larvae which do not leave the culture bottle when disturbed or crowded.

Description. \mathcal{C} . TL = 1.68 mm.

Head. Arista with 3 dorsal and 2 ventral rays plus a terminal fork, pedicel tan. Frons orange-tan with lateral white stripes; median white stripe absent; ocellar triangle raised and darker; hw:fw = 2.04, fw:fl = 1.05. Face pale; carina large; palpus yellow. Gena broad, o:j = 10.2, o:ch = 5.2. Orbital bristles in straight line; or2 very minute, or1:or2:or3 = 7:2:5, orbito-index = 1.4. Ocellar setae long, divergent; oc:or1 = 1.3, poc:oc = 0.5, iv:ov = 0.6. Eye red and densely pilose.

Thorax. Scutum tan, darker than frons, with four white longitudinal stripes continuing on scutellum; white stripes narrow, bordered with large black stripes, especially on the inner side; acs in 6 regular rows anterior to adc and 4 irregular rows between them; psc enlarged, adc:psc = 1.5; adc:pdc = 0.6. Scutellum slightly pointed at the apex, where white spot absent; bsc:asc = 1.3. Sterno-index = 0.6. F1 with 4 setiferous spines not borne on tubercules on the anteroventral margin. Basitarsus of the foreleg with a hairy brush on the ventral margin. Spiniform spines of the first and second tarsomeres of the foreleg enlaged and blackened.

Wing. Dusky; WL:WW = 2.3, C-index = 3.0, 4v-index = 1.5, 4c-index = 0.8, 5x-index = 0.7, M-index = 0.3, ac-index = 2.5, b/c = 0.6, C3 fringe 0.45, WL = 3.8 mm.

Abdomen. Uniformly tan, with dark spots at the bases of tergal bristles.

Terminalia (Fig. 13a). Epandrium densely pubescent at ventral portion; posterior margin pubescent at dorsal portion with 5 long bristles; anterior phragma narrow;

epandrial ventral lobe with 3 long bristles. Surstylus quadrate with two rows of prensisetae. Cercus triangular laterally. Hypandrium with a small pubescent patch at the lateral portion of the paraphyses. Aedeagus expanded apically; aedeagal flap expanded and deeply serrate. Apodeme subequal in length to aedeagus.

 \bigcirc . TL = 1.76 mm, resembling male.

Terminalia. Oviscape with 8 peg-like and 7 short, marginal setae plus 4 supernumary. Spermatheca large, globulous and smooth (Fig. 13b).

Egg. Elliptical with 4 equally long and fine filaments.

Larva. Not escaping the culture medium when disturbed or crowded.

Puparium. H = 5.0 (Fig. 11d).

Distribution. Tanzania.

Type material. Holotype (male) and allotype (female), **Tanzania:** East-Usambara Mountains, Amani (870 m), ex type strain ZMI.12, 11-VIII-2008, founder female coll. 25-IX-2002, D. Lachaise. Paratypes: 10 males and 10 females with the same label. Types deposited in MNHN.

Discussion. Attempts to hybridize this strain with others belonging to the *vittiger* complex have all failed. The species is very prolific and easy to breed in the laboratory.

Etymology. Patronym, in honor of the French *Drosophila* systematist Dr. Daniel Lachaise (1948–2006), collector of the types of two new species described here.

Zaprionus (Zaprionus) santomensis Yassin & David, sp. n. urn:lsid:zoobank.org:act:4DE262CC-1AD9-4D00-827B-FC62FC28BACD

Zaprionus sp. B in Araripe et al. 2004

Diagnosis. This species resembles those of the *indianus* complex in having abdominal tergal spots and F1 spines not borne on protruding tubercule. It can be distinguished from them by the bigger body size, the darker body color mainly in contrast with the frons which is bright orange (Fig. 10f), the wings being dusky rather than hyaline, the smaller hairy brush of the male basitarsus (1/3 of basitarsus) (Fig. 5e), and the lack of an apical introvert in the spermatheca (Fig. 13d).

Description. \mathcal{O} . TL = 1.40 mm.

Head. Arista with 2 dorsal and 3 ventral rays plus terminal fork; pedicel dark brown. Frons orange tan, with vestigial median stripe plus orbital stripes inwardly bordered with black; ocellar triangle blackened; hw:fw = 2.16, fw:fl = 0.8. Orbital setae in straight line; or1:or2:or3 = 3:2:3, orbito-index = 1.8, oc:or1 = 1.5, poc:oc=0.6, iv:ov = 0.4. Face tan. Gena narrow, o:j = 7.6, o:ch = 5.1. Eye red.

Thorax. Scutum brown, darker than frons, with 2 silvery white stripes. acs in 6 rows in front of adc; adc:pdc = 0.9. Scutellum darker than scutum, with black borders of the stripes expanded posteriorly; bsc:asc = 1.2. Pleura with white pilosity; sterno-index = 0.4. Forefemur with 4 spines not borne on warts on the anteroventral margin. Male basitarsus with a hairy brush.

Wing. Dusky; WL:WW = 2.3, C-index = 2.8, 4v-index = 1.4, 4c-index = 0.8, 5x-index = 0.9, M-index = 0.3, ac-index = 2.7, b/c = 0.6, C3 fringe 0.40, and WL = 3.2 mm.

Abdomen. Entirely yellowish, lighter than thorax, with faint dark spots at the bases of tergal setae.

Terminalia (Fig. 13c). Epandrium densely pubescent at ventral portion; posterior margin pubescent at dorsal portion with 3 long setae; anterior phragma slightly humped dorsally; epandrial ventral lobe with 4 long setae. Surstylus quadrate with two rows of prensisetae. Cercus triangular laterally. Hypandrium densely pubescent at the lateral portion of the paraphyses. Aedeagus expanded apically; aedeagal flap expanded and deeply serrate. Apodeme subequal in length to aedeagus.

 \bigcirc . TL = 1.50 mm, resembles male.

Terminalia. Oviscape with 8 peg-like and 6 short, marginal setae plus 4 supernumeraries. Spermatheca globulous and smooth (Fig. 13d).

Egg. Elliptical with 4 equally long and fine filaments.

Larva. Escaping the culture medium when crowded.

Puparium. Horn-index 10.6.

Distribution. Sao Tomé and Príncipe.

Type material. Holotype (male) and allotype (female), **Sao Tomé and Príncipe:** Pico de São Tomé Park (1,500 m), ex type strain ZNG, 11-VIII-2008, founder female coll. III-2001, D. Lachaise. Paratypes: 10 males and 10 females with the same label. Types deposited in MNHN.

Discussion. This species resembles *Z. proximus*, from which it can be distinguished on the basis of F1 ornamentation. An important physiological difference also exists between these species, as *Z. santomensis* is a very heat-sensitive species since a growth temperature of 25°C is lethal for both sexes and males are sterile at 23 and 24°C (cf. Araripe *et al.* 2004).

Etymology. The species epithet is in reference to the type locality.

Comparative anatomy of reproductive system

Many authors described the internal anatomy of some *Zaprionus* species that can be grown in laboratory (Burla 1954; Throckmorton 1962; Lachaise 1972; Araripe et al. 2004); but with the exception of Tsacas et al.'s (1977) study on the *tuberculatus* subgroup, little attention has been paid to quantify the differences between the species. Table 3 shows the measurements of some structures in the laboratory strains used in this study. As shown, many measurements give insightful taxonomic differences.

Male reproductive system

Testis length (TST) ranges from 1.0 mm in *Z. kolodkinae* to 12.4 mm in *Z. ornatus*. The Oriental species, *Z. (A.) bogoriensis*, has TST of 4.4 mm which approaches that of

	Male						Female		
	TST	SV	VD	PAR	EC	EB	CAE	SR	SP
Subgenus Anaprionus									
Z. (A.) bogoriensis	4.4	2.0	0.80	2.6	2.2	0.30	0.6	3.8	0.07
Subgenus Zaprionus									
<i>neglectus</i> group									
Z. (Z.) neglectus	2.8	1.0	0.60	0.7	2.4	0.20	2.0	3.2	0.06
<i>inermis</i> group									
Z. (Z.) ghesquierei	1.2	0.6	0.04	2.0	1.1	0.22	1.0	1.5	0.04
Z. (Z .) inermis	1.5	1.1	0.20	2.6	2.1	0.32	0.4	1.0	0.09
Z. (Z.) cercus	1.4	0.9	0.16	2.2	2.0	0.22	1.6	0.9	0.08
Z. (Z.) mascariensis	4.4	0.9	0.40	3.2	1.1	0.22	0.5	7.2	0.12
Z. (Z.) kolodkinae	1.0	0.7	0.20	1.6	2.1	0.20	0.8	0.8	0.06
Z. (Z.) sepsoides	2.0	0.6	0.20	3.2	1.6	0.20	0.1	1.0	0.04
Z. (Z.) tsacasi	1.3	0.8	0.40	3.6	1.2	0.20	0.4	1.2	0.06
Z. (Z.) tuberculatus	3.2	1.2	0.70	2.2	0.9	0.20	0.3	3.6	0.06
Z. (Z.) burlai	4.4	1.0	1.10	2.0	1.3	0.12	0.3	6.3	0.06
Z. (Z.) verruca	3.8	1.6	0.80	2.0	2.0	0.20	1.2	4.0	0.06
<i>vittiger</i> group									
Z. (Z.) ornatus	12.4	7.2	2.20	3.6	0.9	0.30	0.7	12.0	0.18
Z. (Z.) indianus	5.3	2.2	1.30	2.2	1.5	0.30	0.7	4.8	0.16
Z. (Z.) africanus	5.4	1.0	0.70	1.6	1.3	0.30	0.8	3.8	0.07
Z. (Z.) gabonicus	2.5	0.7	0.40	0.7	0.7	0.16	0.4	3.5	0.06
Z. (Z.) davidi	2.6	1.4	0.80	2.0	1.6	0.30	0.6	3.0	0.06
Z. (Z.) taronus	5.2	1.4	1.40	3.2	2.2	0.30	0.8	4.6	0.06
Z. (Z.) capensis	4.0	2.0	0.80	2.6	1.2	0.30	0.6	4.6	0.07
Z. (Z.) proximus	3.6	2.4	2.00	1.4	2.0	0.28	0.3	4.2	0.06
Z. (Z.) santomensis sp. n.	3.6	1.6	1.20	2.0	1.6	0.34	0.7	3.2	0.10
Z. (Z.) lachaisei sp. n.	4.4	2.4	1.30	2.0	2.1	0.30	0.7	4.6	0.10
Z. (Z.) vittiger	4.4	2.4	1.30	2.0	2.4	0.30	0.8	4.2	0.12
Z. (Z.) camerounensis	4.2	2.0	0.70	3.2	1.2	0.20	0.6	4.5	0.09

Table 3. Comparative morphometry of internal structures of male and female reproductive systems in *Zaprionus*.

TST = testis; **SV** = seminal vesicle; **VD** = vas deferens; **PAR** = paragonia (accessory gland); **EC** = ejaculatory bulb; **CAE** = caecum; **SR** = seminal receptacle; **SP** = spermatheca.

the mean of the African species $(3.7 \pm 0.5 \text{ mm})$. Species of the *inermis* group can be classidfied under two categories: those with small testis ranging from 1.0 to 2.0 mm (*Z. inermis, Z. cercus, Z. kolodkinae, Z. sepsoides* and *Z. tsacasi*), and those with large testis ranging from 3.2 to 4.4 mm (*Z. mascariensis, Z. tuberculatus, Z. burlai* and *Z. verruca*). Species of the last category are all members of the *tuberculatus* subgroup which also include some species of the first category, and TST presents a very informative taxonomic

	Egg		Puparium	
	EL:El	PF:EL	PL:Pl	Н
Subgenus Anaprionus				
Z. (A.) bogoriensis	3.45	1.13	2.54	9.3
Subgenus Zaprionus				
neglectus group				
Z. (Z.) neglectus	2.90	0.83	2.31	15.3
<i>inermis</i> group				
Z. (Z.) ghesquierei	3.00	0.54	2.54	9.4
Z. (Z.) inermis	3.26	1.13	2.62	13.1
Z. (Z.) cercus	2.90	0.97	2.40	10.3
Z. (Z.) mascariensis	2.91	0.73	2.47	6.8
Z. (Z.) kolodkinae	2.75	0.97	2.43	9.0
Z. (Z.) sepsoides	3.10	0.90	2.57	8.6
Z. (Z.) tsacasi	2.73	0.90	2.53	8.4
Z. (Z.) tuberculatus	2.86	0.90	2.59	7.0
Z. (Z.) burlai	3.00	0.91	2.29	7.2
Z. (Z.) verruca	3.40	0.88	2.31	10.6
<i>vittiger</i> group				
Z. (Z.) ornatus	3.18	1.14	2.52	10.0
Z. (Z.) indianus	3.44	0.81	2.49	8.3
Z. (Z.) africanus	3.26	0.90	2.46	9.8
Z. (Z.) gabonicus	3.33	0.83	2.43	10.4
Z. (Z.) davidi	3.05	1.16	2.54	10.5
Z. (Z.) taronus	2.87	0.91	2.29	12.0
Z. (Z.) capensis	2.43	1.00	2.45	9.8
Z. (Z.) proximus	3.67	1.06	2.44	10.6
Z. (Z.) santomensis sp. n.	2.86	0.60	2.24	10.6
Z. (Z.) lachaisei sp. n.	3.28	0.78	2.64	5.0
Z. (Z.) vittiger	3.20	1.06	2.65	9.3
Z. (Z.) camerounensis	3.00	0.93	2.56	11.0

Table 4. Measurements of immature stages in *Zaprionus* species grown under the same laboratory conditions.

EL = egg length; **El** = egg width; **PL** = puparium length; **Pl** = puparium width; **H** = horn-index.

clue (Fig. 3; Tsacas et al. 1977; Yassin 2008). In the *vittiger* group, *Z. ornatus* with its very long testis (TST = 12.4 mm) is particular. The remaining species can be classified under four discontinuous categories: *Z. gabonicus* and *Z. davidi* with TST from 2.5 to 2.6 mm; *Z. proximus* and *Z. santomensis* sp. n. with TST of 3.6 mm; *Z. capensis, Z. camerounensis, Z. vittiger* and *Z. lachaisei* sp. n. with TST from 4.0 to 4.4 mm; and *Z. indianus, Z. africanus* and *Z. taronus* with TST from 5.2 to 5.4 mm. Unlike in the *inermis* group, the categories of the *vittiger* group do not reflect any phylogenetic trend.

The seminal vesicle (SV) is the part of the vas deferens that has undergone a differentiation for sperm storage. It ranges from 0.6 mm in *Z. ghesquierei* and *Z. sepsoides* to 7.2 mm in *Z. ornatus*, with the mean of 1.6 ± 0.3 mm in African Zap-

rionus. Species of the *inermis* group tend to have small SV, ranging from 0.6 to 1.6 mm, whereas species of the *vittiger* group have larger SV, ranging from 0.7 to 2.4 mm (excluding *Z. ornatus*).

The vas deferens (VD) ranges from 0.04 mm in Z. ghesquierei to 2.20 mm in Z. ornatus. The quasi-absence of VD in Z. ghesquierei is exceptional as the next value to it is 0.20 mm in a number of species of the *inermis* group (Z. inermis, Z. kolodkinae and Z. sepsoides). Indeed, Throckmorton (1962) described VD morphology in a laboratory strain of Z. ghesquierei. The 12 males he dissected "were variable, showing two major types with only slight integradation between them" (pp. 232). The VDs of three males were quasi-absent like the one described here, whereas those of the remaining nine males were "somewhat longer and associates closely with the ventral surface of the paragonia." We did not find this polymorphism in the few individuals dissected. The longest VD in the *inermis* group is found in Z. burlai (VD = 1.1 mm), and it is greater than VDs of its two relatives (0.7 mm in Z. tuberculatus and 0.8 mm in Z. verruca).

The ejaculatory bulb of *Zaprionus* species is moderately large, rounded and bearing long posterior caecae (Throckmorton 1962). In the *vittiger* species group, the posterior caecae are branched several times, whereas in the remaining African and Oriental species the caecae are unbranched. The length of the caecae (CAE) ranges from 0.1 mm in *Z. sepsoides* to 2.0 mm in *Z. neglectus*. The long CAE of *Z. neglectus* is exceptional (Burla 1954) and it was used as one of the arguments to synonymize *Z. neglectus* Burla with *Z. simplex* Chassagnard & McEvey. CAE can also be used to distinguish *Z. cercus* (CAE = 1.6 mm) from its sibling species *Z. inermis* (CAE = 0.4 mm), which has particularly small CAE. Lachaise (1972) also noted that CAE of *Z. inermis* was about 0.6 mm. *Zaprionus verruca* has exceptional long CAE of 1.2 mm in the *tuberculatus* subgroup, that can easily distinguish it from its two sibling species *Z. tuberculatus* and *Z. burlai* (CAE = 0.3 mm).

Female reproductive system

The seminal receptacle (SR) ranges from 0.8 mm in *Z. kolodkinae* to 12.0 mm in *Z. ornatus*. As with TST, species of the *vittiger* group tend to have larger SR than those of the *inermis* group. The correlation between TST and SR is a well-established fact in the Drosophilidae, although the correlation is thought to be functional rather than genetic (Joly and Bressac 1994). This correlation is obvious in *Zaprionus* (r = 0.93; P < 0.001). SR can distinguish *Z. burlai* females (SR = 6.3 mm) from *Z. tuberculatus* (SR = 3.6 mm), and *Z. indianus* (SR = 4.8 mm) from *Z. africanus* (SR = 3.8 mm) and *Z. gabonicus* (SR = 3.5 mm).

Burla (1954) provided the first account of the morphology of the spermatheca (SPR) in *Zaprionus* species from Côte d'Ivoire, and illustrations of spermathecae became a taxonomic routine in all descriptions following his study (Figs 3, 6, 12, 13). The elongate form of the spermatheca of *Z. ornatus* is characteristic and it was one of the arguments for considering *Z. megalorchis* Chassagnard and Tsacas syn. n. and *Z.*

aff. *vittiger* Burla as junior synonyms for this species (Fig. 13). We dissected 10 females per species in the *indianus* complex and found that in *Z. africanus* the width of the spermatheca was always relatively greater than its length, whereas in its two cryptic species *Z. indianus* and *Z. gabonicus*, the spermatheca length and width were subequal (Fig. 12). In the *tuberculatus* species subgroup, it is the shape rather than the length of the spermatheca which provides the best taxonomic clues (Fig. 3).

Immature stages

Egg

The eggs of species of the Oriental subgenus *Anaprionus* have two filaments (Bock 1966; Bock and Baimai 1967), whereas in African *Zaprionus* s.s. they have four filaments. A single exception in *Zaprionus* s.s. is *Z. davidi* whose eggs have also two filaments (Chassagnard and Tsacas 1993). However, they still can be distinguished from those of the Oriental species by the presence in the latter of a thin, chitinized crest at the apex of the operculum.

The length of the filaments varies between species (Table 3). In *Z. momorticus*, the four filaments are very short (Graber 1957). In most species, however, the posterior (dorsal) filaments are usually longer than the anterior (ventral) ones. In some species (*Z. mascariensis*, *Z. kolodkinae*, *Z. sepsoides* and *Z. tsacasi*) of the *Z. tuberculatus* species subgroup (Fig. 3), the posterior filaments are usually elongated and spatulate near the apex.

Larva

Larvae of the genus *Zaprionus* are all of the amphipneustic type as in other drosophilid flies (Okada 1968). In all instars of both subgenera, the larval cephalopharyngeal skeleton is smooth lacking any dentition (Fig. 15). In all species, when cultures are crowded, the mature larvae climb up the bottle and often escape through the plug, and die from desiccation (Bock 1966; David et al. 2006). *Zaprionus lachaisei* sp. n. is the only species of which larvae do not show this peculiar behavior, and this makes its laboratory culture an easier.

Puparium

Puparia of the two subgenera are reddish brown in color (Fig. 11). The puparial length (PL) ranges from 2.82 mm in *Z. gabonicus* to 4.58 mm in *Z. inermis*, in complete concordance with the differences of body size in the adults (Yassin and David, in prep.). The only other species with PL exceeding 4.00 mm are *Z. lachaisei* sp. n. (PL = 4.30 mm) and *Z. bogoriensis* (PL = 4.20 mm). The puparial shape (PL:Pl) ranges from 2.24

in Z. santomensis sp. n. to 2.65 in Z. vittiger. Interestingly this ratio can serve in discriminating puparia of some close species such as between: Z. inermis (2.62) and Z. cercus (2.40), and Z. tuberculatus (2.59) and Z. burlai (2.29).

The horn-index (H) is a classical taxonomic measurement in drosophilid systematics. H ranges from 5.0 in *Z. lachaisei* sp. n. (Fig. 11D) to 15.3 in *Z. neglectus* (Fig. 11A) with the mean of 9.7 ± 0.4 in African *Zaprionus* (9.3 in the Oriental species *Z. bogoriensis*). With the exception of the two extremes, H ranges from 6.8 to 13.1. In the *tuberculatus* species complex, H discriminates *Z. verruca* (H = 10.6) from its two sibling species, *Z. tuberculatus* (H = 7.0) and *Z. burlai* (H = 7.2).

Another important taxonomic character of the puparium is the branches of the anterior spiracle. In all *Zaprionus* species, these branches are of the clubbed type (Okada 1968). The arrangement of the branches on the stalk is of the type Y in which pseudocentral branches (*sensu* Okada 1968) are absent. The number of branches tends to vary from 11 to 14 in the *inermis* species group, and from 15 to 17 in the *vittiger* group. A particular exception is found in *Z. inermis* where the number of branches ranges from 18 to 21 (Fig. 11b). This facilitates the discrimination of its puparia from those of its sibling species, *Z. cercus*, which has 11 to 13 branches (Fig. 11c).

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RESEARCH ARTICLE



Insects attracted to Maple Sap: Observations from Prince Edward Island, Canada

Christopher G. Majka

Research Associate, Nova Scotia Museum, 1747 Summer Street, Halifax, Nova Scotia, Canada, B3H 3A6

Corresponding author: Christopher G. Majka (c.majka@ns.sympatico.ca)

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Abstract

The collection of maple sap for the production of maple syrup is a large commercial enterprise in Canada and the United States. In Canada, which produces 85% of the world's supply, it has an annual value of over \$168 million CAD. Over 38 million trees are tapped annually, 6.5% of which use traditional buckets for sap collection. These buckets attract significant numbers of insects. Despite this, there has been very little investigation of the scale of this phenomenon and the composition of insects that are attracted to this nutrient source. The present paper reports the results of a preliminary study conducted on Prince Edward Island, Canada. Twenty-eight species of Coleoptera, Lepidoptera, and Trichoptera were found in maple sap buckets, 19 of which are known to be attracted to saps and nectars. The physiological role of sap feeding is discussed with reference to moths of the tribe Xylenini, which are active throughout the winter, and are well documented as species that feed on sap flows. Additionally, 18 of the 28 species found in this study are newly recorded in Prince Edward Island.

Keywords

Coleoptera, Nitidulidae, Lepidoptera, Xylenini, Trichoptera, Prince Edward Island, Canada, maple sap, maple syrup, biodiversity

Introduction

The collection of maple sap for the production of maple sugar has a long history in North America. Before the arrival of European settlers, native people in northeastern North America collected maple sap, pouring it into hollowed-out logs in which heated stones were placed to evaporate the water and concentrate the syrup. In the 1880's a significant innovation was the introduction of the forerunner to the contemporary flue pan evaporator (Chapeske and Henderson 2007). Two species of trees, sugar maple (*Acer saccharum* Marsh.) and black maple (*Acer nigrum* Michx.) are employed in maple sugar production, although the former accounts for the majority of trees tapped (Chapeske and Henderson 2007).

Canada produces 85% of the world's maple syrup; the United States the other 15%. Annual Canadian production in 2007 was 5.235 million gallons of syrup valued at over \$168 million CAD. Québec accounts for 91.1% of domestic production followed by New Brunswick (4.5%), Ontario (3.9%), and Nova Scotia (0.5%). Small volumes are also produced in Prince Edward Island. In the United States, production in 2006 was 1.449 million gallons from producers in Vermont (32%), Maine (21%), New York (17%), Wisconsin (7%), Michigan (5%), Ohio (5%), Pennsylvania (5%), New Hampshire (4%), Massachusetts (3%), and Connecticut (0.7%) (Agriculture and Agri-Food Canada 2007).

In 2006 in Canada, 9,731 maple sugar producers had an average per-farm tap number of 3,913 indicating that approximately 38,077,400 trees were being tapped. Two collection methods are used: the traditional bucket system placed on trees, and plastic tube collection. In Ontario 78% of collection is with plastic tubing and 22% is by traditional buckets (Chapeske and Henderson 2007). In Québec 97.7% collection is with plastic tubing, and only 2.3% with traditional buckets (Johannie Coiteux, Federation of Quebec Maple Syrup Producers, pers. comm.). Employing these percentages indicates that in Canada some 1.5 million trees are tapped using traditional buckets.

Despite the long history of maple syrup production, which has evolved to become a significant industry in Canada and the northeastern United States, and the very sizeable number of trees that are tapped over a considerable portion of the continent, there has been remarkably little attention paid to the insects that are attracted to maple sap during extraction and collection. Sap is largely contained with the plastic tubing collection method and except for local spots surrounding the borehole, there is little opportunity for insects to avail themselves of this resource. In traditional bucket collection the opportunity for attracting insects to sap is considerably greater. Maple sap typically consists of 97.5% water, 2.4% sugars (primarily sucrose with small amounts of glucose), and 0.1% minerals (primarily potassium and calcium, with smaller quantities of zinc and manganese, and trace amounts of other minerals). There are also trace amounts of phenolic compounds, primary amines, peptides, amino acids, and other organic compounds. (Ball 2007).

Many species of moths attracted to sugar solutions on trees, indeed "sugaring" for moths is an important collection technique for many species of nocturnal Lepidoptera. In a poetic essay entitled "Sugaring for Moths" in The Moth Book, Holland (1903: 146–150), an important figure in the history of North American lepidopterology, outlined the technique in a lyrical style, now long vanished from entomological literature. Smith (1900) noted the propensity of many moths to be attracted to the sap of trees, particularly that of sugar maples. He highlighted *Xylena* spp., *Eupsilia* spp., *Metalepsis* *salicarum* (Walker), *Orthosia hibisci* (Guenee), and *Xystopeplus rufago* (Hübner) (all Noctuidae) as species particularly attracted to maple sap. Miller (1997) noted that adult moths of four families – Noctuidae, Sphingidae, Geometridae, and Tortricidae – are attracted to natural sap flows.

Amongst Coleoptera, members of Nitidulidae (sap beetles) are well known to be attracted to natural sap flows on a variety of trees. Vogt (1950) documented 33 species of nitidulids at sap flows, primarily on white oak (*Quercus alba* L.), but also on post oak (*Quercus stellata* Wang.), chinkapin oak (*Quercus muhlenbergia* Engelm.), red maple (*Acer rubrum* L.), and river birch (*Betula nigra* L.). In addition to these nitidulids, Vogt (1950) also found representatives of Mycetophagidae (2 species), Histeridae (2 species), Carabidae (1 species), Silvanidae (1 species), Laemophloeidae (1 species), Tenebrionidae (1 species), and Nosodendridae (1 species) at such sap flows.

There has been considerable interest in sap flows caused by Yellow-bellied Sapsuckers (*Sphyrapicus varius* Linnaeus) (Aves: Picidae) and the insects attracted to these. Studies such as Foster and Tate (1966) and Rissler et al. (1995) recorded a large diversity of insects in Lepidoptera, Hymenoptera, Diptera, Coleoptera, Hemiptera, Homoptera, Collembola, and Psocoptera frequenting sapsucker induced flows. Unfortunately, in many instances identifications were done only to the level of Family.

There are few references in entomological literature of insects specifically associated with the collection of maple sap. Arnett (2000) noted that *Hypogastrura nivicola* (Fitch) (Collembola: Poduridae), the common and familiar "snow flea", is attracted to maple sap and can attain pest status in buckets during periods of harvest. Rings (1969, 1973) drew attention to *Lithophane antennata* (Walker), *Lithophane laticinerea* Grote, and *Lithophane unimoda* (Lintner) (Lepidoptera: Noctuidae) as moths attracted to maple sap, which can become a nuisance by accumulating on the surface in collection buckets. Dearborne (1999) reported that adult *Ellychnia corrusca* (Linnaeus) (Coleoptera: Lampyridae) often become a pest by falling into maple sap buckets.

Methods

On 4 April 2010 while at a maple sugar collection site in Woodville Mills, Prince Edward Island, (46°14'22"N; 62°31'04"W), insects in maple sap collection buckets (n=70) were surveyed. The forest stand (4.2 hectares) consists of primarily deciduous trees [sugar maple, red oak (*Quercus rubra* L.), yellow birch (*Betula alleghaniensis* Britt), linden (*Tilia europea* L), pin cherry (*Prunus pensylvanica* L.f.), and others) with occasional intermixed conifers [red spruce (*Picea rubens* Sarg,), white spruce (*Picea glauca* (Moench) Voss), balsam fir (*Abies balsamaea* (L.) Mill)]. It is bounded along its lower margin by a small stream flowing from a marsh and beaver pond, along its upper margin by an apple orchard, and along both sides by agricultural fields. The spacing of sap collection buckets varied within this area. In some instance as many as three buckets were place on a single tree; in other instances buckets were as much as 10 meters apart, depending on the size and spacing of the sugar maple trees.

All buckets had covers on them to prevent extraneous debris from falling into the maple sap. Therefore insects present inside would almost certainly have had to actively enter the buckets, either from beneath the lids (where there was a gap at the front of the bucket) or in the small open area near the spigot. Thus, the suite of insects present would largely represent species actively attracted to maple sap, or seeking shelter in the buckets, as opposed to specimens that had accidentally fallen into the containers.

It was not possible to strictly quantify the results, since different buckets had been hanging with uncollected sap for varying periods (1–4 days) due to the impending conclusion of the sap collection season. Nevertheless general categories of abundance [scarce, fewer than 10 specimens; abundant, 10–30 specimens; very abundant, more than 30 specimens] were assigned for each of the species found.

Results and discussion

The results of this investigation are shown in Table 1. Diptera were also present but were not collected. Twenty-eight species were recorded including 18 Coleoptera, eight Lepidoptera, and two Trichoptera. After reviewing the biology of each species, it was possible to categorize them as species associated with sap and nectar, or accidental visitors.

Due in large measure to the comparative dearth of entomological research on Prince Edward Island, it is possible to report that 18 of the 28 species found in this study are newly recorded in the province. In the case of some species of Coleoptera (i.e., *Ellychnia corrusca, Cyphon variabilis, C. confusus,* and *Nudobius cephalus* (Say)) these new records represent broadly distributed species that belong to groups that have not yet been surveyed on Prince Edward Island. However the Prince Edward Island Curculionidae were surveyed by Majka et al. (2007), the Nitidulidae were surveyed by Majka and Cline (2006a), and the Maritime Provinces Aleocharinae by Majka and Klimaszewski (2010) so the new records of *Trypodendron retusum* (LeConte), *Xyloborinus alni* (Niisima), *Cryptarcha ampla* Erichson and *Silusa californica* Bernhauer are additions to a fauna which has already received recent attention.

Similarly, although some research has been conducted on the Noctuidae of Prince Edward Island, the fauna remains poorly known and none of the species recorded herein have previously been recorded from the province (Troubridge and Lafontaine 2004).

Coleoptera: species associated with sap and nectar

Two species were hyper-abundant (more than 100 individuals each) in the sap buckets: *E. corrusca* and *C. variabilis*. Rooney and Lewis (2000) reported that adult *E. corrusca* feed actively on floral nectarines of Norway maple (*Acer platanoides* L.) and are attracted to natural sap flows on *A. saccharum*. As previously noted, Dearborne (1999) remarked on how this species was attracted to maple sap, often becoming a pest in sap buckets.

Table 1. Insects collected in maple sap, Woodville Mills, PEI, April 2010

Species	Abundance	PEI Status ¹
COLEOPTERA		· ·
Carabidae		
Dromius piceus Dejean	scarce	
Coccinellidae		
Anatis mali (Say)	scarce	
Corylophidae		
Orthoperus suturalis LeConte	scarce	
Curculionidae		
Trypodendron retusum (LeConte)	abundant	new in PEI
Xyloterinus politus (Say)	scarce	
Xyloborinus alni (Niisima) †	scarce	new in PEI
Dermestidae		
Anthrenus castanae Melsheimer	scarce	
Histeridae		
Euspilotus assimilis (Paykull)	scarce	
Lampyridae		
Ellychnia corrusca (Linnaeus)	very abundant	new in PEI
Nitidulidae		
Cryptarcha ampla Erichson	scarce	new in PEI
Glischrochilus fasciatus (Olivier)	abundant	
Glischrochilus quadrisignatus (Say)	abundant	
Glischrochilus sanguinolentus (Olivier)	scarce	
Glischrochilus siepmanni Brown	scarce	
Scirtidae		
Cyphon confusus Brown	scarce	new in PEI
<i>Cyphon variabilis</i> (Thunberg) *	very abundant	new in PEI
Staphylinidae		
Silusa californica Bernhauer	scarce	new in PEI
Nudobius cephalus (Say)	scarce	new in PEI
LEPIDOPTERA		
Noctuidae		
Crocigrapha normani (Grote)	scarce	new in PEI
Eupsilia vinulenta (Grote)	abundant	new in PEI
Eupsilia tristigmata (Grote)	abundant	new in PEI
Lithophane innominata (J.B. Smith)	abundant	new in PEI
Lithophane petulca Grote	scarce	new in PEI
Lithophane pexata Grote	scarce	new in PEI
<i>Xylena cineritia</i> (Grote)	scarce	new in PEI
Tortricidae		
Acleris chalybeana (C.H. Fernald)	abundant	new in PEI
TRICHOPTERA		
Limnephilidae		
Glyphopsyche irrorata (Fabricius)	scarce	new in PEI
Limnephilus ornatus Banks	scarce	new in PEI

Notes: †, adventive Palaearctic species; *, Holarctic species.

¹ No entry indicates the species has previously been recorded in the province.

Klausnitzer (2009) described *C. variabilis* as a eurotypic species found in moderately acid *Sphagnum* moorlands, near eutrophic waters, beside muddy ditches, and along the banks of ponds. The species has not been generally associated with sap flows or the collection of maple sap in the literature, although Wolcott and Montgomery (1933) did note a specimen on a tamarack trunk, "feeding at small spot of exuding sap." The collection site is approximately 0.25 km from a small beaver pond and associated marsh that provide a suitable site for *C. variabilis*, however, the large number of specimens attracted to maple sap (and smaller numbers of the related *Cyphon confusus* Brown) is unexpected, apparently reflecting an aspect of the biology of these marsh beetles not hitherto noted in the literature.

Trypodendron retusum, Xyloterinus politus (Say), and Xyloborinus alni are all ambrosia beetles (Curculionidae: Scolytinae) wherein adults excavate galleries beneath bark of unhealthy or dying trees. These galleries are inoculated with symbiotic fungi carried in mycangial pits on the heads of the beetle. Adults and larvae feed on the resulting growth of fungal hyphae. Bark beetles are known to be attracted to tree volatiles such as terpenes and oleoresins, so it may be that these species are attracted to the maples via these chemicals signals, and in seeking their source, the beetles secondarily fall into the maple sap. Trypodendron retusum is associated with poplars (Populus grandidentata Michx. and Populus tremuloides Michx.) and is newly recorded on Prince Edward Island (Wood 1982; Majka et al. 2007). Xyloterinus politus is associated with a wide variety of primarily deciduous hosts (occasionally coniferous ones) including species of Acer, Alnus, Betula, Carya, Castanea, Fagus, Fraxinus, Quercus, Picea, Pinus, Tsuga, and Ulmus (Wood 1982). Xyloborinus alni is an adventive Oriental species recently found in North America (Haack 2006). The species was originally detected in 1995 in British Columbia, and 1996 in Washington State, and later reported in several eastern states in the USA (Haack 2006). This is the first report of this species from Prince Edward Island. In North America the only reported hosts are *Alnus* spp. (Haack 2006).

Cryptarcha ampla, Glischrochilus fasciatus (Olivier), *Glischrochilus quadrisignatus* (Say), *Glischrochilus sanguinolentus* (Olivier), and *Glischrochilus siepmanni* Brown are all sap beetles (Nitidulidae: Cryptarchinae) well known to be attracted to a variety of saps and liquids. Vogt (1950) recorded *C. ampla, G. fasciatus,* and *G. quadrisignatus* from sap flows on maples. Parsons (1943) also noted that *C. ampla* occurs on sap flows on maple. Williams et al. (1992) collected large numbers of all five of these species from a variety of baits including fermenting bread dough, a fermenting brown sugar solution, and decaying cantaloupes and bananas. Majka and Cline (2006a) noted that in the Maritime Provinces *G. sanguinolentus* was primarily found associated with coniferous trees (*Pinus* and *Picea* spp.) but was also occasionally found on sap flows on trembling aspen (*Populus tremuloides*) and red oak (*Quercus rubra* L.).

Although *Anthrenus* larvae such as *Anthrenus castanae* Melsheimer, like other dermestids, feed on dried animal and plants products, adults mate in the field and feed on nectar and pollen (Bousquet 1990). Consequently, like other nectarivourous species, the single specimen collected may have been attracted to sugars found in maple sap.

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Coleoptera: accidental species

Dromius piceus Dejean is a nocturnal, arboreal predaceous ground beetle found in deciduous, coniferous and mixed forests (Larochelle and Larivière 2003). One specimen was found, and is likely an accidental collection. Similarly Nudobius cephalus (Say) is a nocturnal, predaceous rove beetle found under the bark of trees feeding on various insects found in such habitats (Smetana 1982). The species is primarily associated with coniferous trees, but is occasionally found on deciduous trees (Acer, Betula, Populus spp.) (Smetana 1982). The single individual found may also have been an accidental collection in the course of nocturnal foraging activities. Anatis mali (Say) is a large lady beetle, frequently associated with conifer trees and an important predator of the balsam twig aphid (Mindarus abietinus Koch) (Bethiaume et al. 2004), and its presence in maple sap is probably accidental. Like other corylophids, adults of Orthoperus suturalis LeConte feed on fungal spores and are found in decompositional environments. Majka and Cline (2006b) reported it from Sphagnum bogs and red spruce (Picea rubens Sarg.) forests. Therefore its presence in maple sap is probably accidental. The histerid *Euspilotus assimilis* (Paykull) is commonly found on carrion (Bousquet and Laplante 2006). Its presence in maple sap is also probably accidental. Silusa californica is a widely distributed boreal rove beetle found in forest litter, wet moss, on dung and fungi in coniferous, deciduous, and mixed forests (Klimaszewski et al. 2003). Its presence in maple sap is also probably accidental.

Lepidoptera: species associated with sap and nectar

Xylena cineritia (Grote), Lithophane innominata (J.B. Smith), Lithophane petulca Grote, Lithophane pexata Grote, Eupsilia vinulenta (Grote), and Eupsilia tristigmata (Grote) (Noctuiodae: Cuculliinae: Xylenini) were well represented in the maple sap buckets. They are all members of genera well known to be attracted to maple sap (Rings 1969, 1973; Smith 1900). The physiology and behaviour of moths in these genera (specifically L. innominata, E. tristigmata, and E. vinulenta), all of which are active during the winter months whenever ambient temperatures rise above 0°C, was thoroughly investigated by Heinrich (1987). He found that they are active at low temperatures because they maintain thoracic temperatures 10°C higher than other moths. This is accomplished through a combination of behavioural adaptations (shivering to warm the thorax, which can commence at temperatures of -2°C, much lower than in other Lepidoptera) and anatomical features (a thick pile on the head and thorax, a series of abdominal air sacks that act as insulators, and an aortic configuration that acts as a thoracic heat exchanger). The moths obtain the energy for these physiological processes and activities by utilizing sugar saps. Heinrich (1987) observed that, given the opportunity, these moths will bloat themselves by consuming saps, increasing their body weight by up to 94.5%.

Heinrich (1987) used sugar solutions containing approximately 10 times as much sugar as found in maple sap, and calculated that a meal of this kind contained energy

reserves that would last a single moth 31 days. Presumably, a meal of maple sap, containing 10% of the concentration employed by Heinrich (1987), would yield a moth approximately 3 days of energy reserves. Thus, the presence of a diversity of species and substantial numbers of moths in the genera *Eupsilia, Lithophane,* and *Xylena* in maple sap buckets is not unexpected.

In addition to the noctuids discussed above, one tortricid, *Acleris chalybeana* (C.H. Fernald), was abundant in maple sap buckets. This is a widespread species whose hosts include apple, beech, birch, maple, and oak (Covell 1984). Tortricids are one of the four families of moths noted by Miller (1997) and Foster and Tate (1966) that are attracted to natural sap flows. *Acleris chalybeana* is known to defoliate sugar maple under certain circumstances (Horsley et al. 2002; Hallett et al. 2006). A specific attraction of this species to maple sap, and what role it may play in the physiology of the moth, have not been documented.

Lepidoptera: accidental species

The one noctuid collected which is not a member of this suite of moths, was a single specimen of *Crocigrapha normani* (Grote), a species whose hosts include apple, cherry, oak, and other deciduous trees (Covell 1984). It would appear that its presence in the maple sap buckets was accidental.

Trichoptera

Almost all adult Trichoptera are liquid feeders, consuming sap and floral nectar (Malicky 2004). Single individuals of two species of caddisflies, *Glyphopsyche irrorata* (Fabricius) and *Limnephilus ornatus* Banks, were found in the maple sap buckets. *Glyphopsyche irrorata* is a caddisfly which over-winters as an adult and, like moths of the genera *Eupsilia, Lithophane,* and *Xylena,* is regularly active in the winter months at temperatures near 0°C (Berté and Prichard 1983; South 1983).

Conclusion

In summary, 28 species of Coleoptera, Lepidoptera, and Trichoptera were recovered from maple sap buckets at one site in Prince Edward Island. Nineteen of these are known to be attracted to sap and nectar. Two species, *Cyphon variabilis* and *C. confusus*, have not been documented as exhibiting an association with such substances, but the hyper abundance of the former species in collection vessels appears to indicate that an association does exist and reflects a hitherto undocumented feature of the biology of these species of marsh beetles. The remaining seven species (all represented by single

individuals) are mostly found in deciduous forest stands, and their presence in maple sap containers would appear to be accidental.

Given that some 1.5 million are tapped in Canada employing traditional buckets, the number of insects collected annually through such activities must be considerable. This phenomenon may have both ecological repercussions, in terms of the impact of removing a sizeable number of adults from the population early in the reproductive season, as well as an economic impact in terms of the removal of drowned insects in the maple sap before processing. This preliminary study suggests further research on this phenomenon is needed to document not only a more complete taxon list, but also to aid the maple syrup industry in controlling unwanted insect contaminants through methods utilizing the biology of the species.

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