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

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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.

**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.

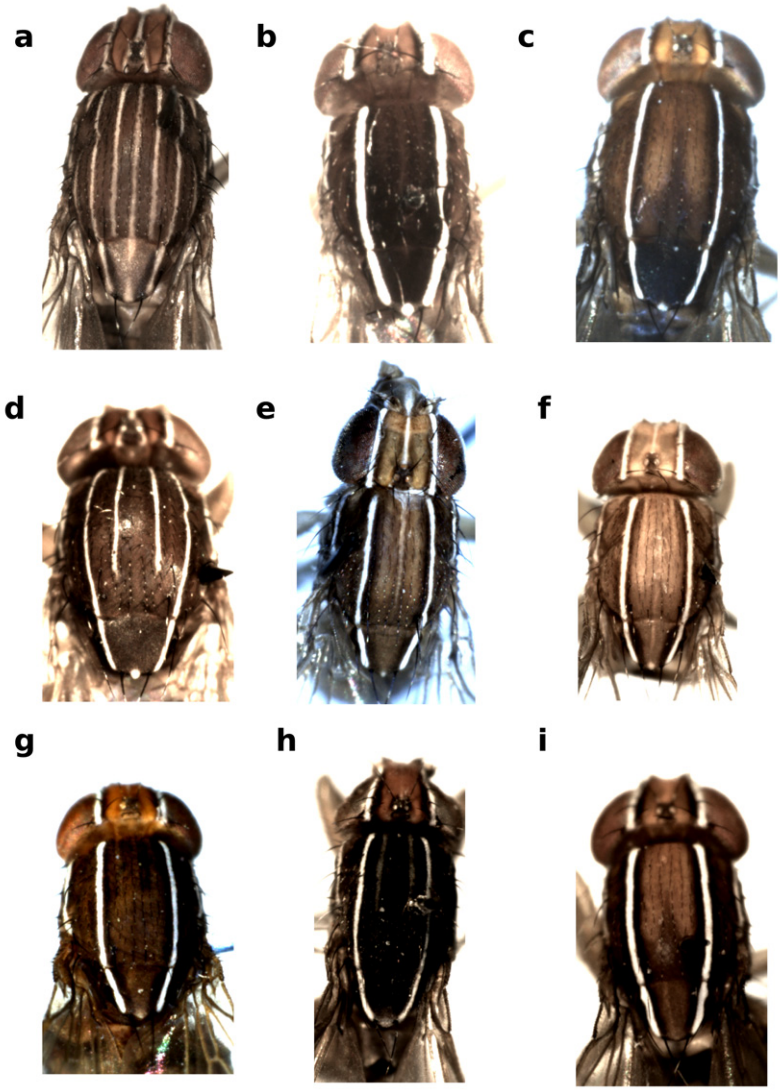


**Figure 1.** Frons and mesonotum of *Zaprionus* (*Anaprionus*) *bogoriensis* Mainx, 1954 **a**, *Z.* (*Zaprionus*) *ghesquierei* Collart, 1937a **b**, *Z.* (*Z.*) *litos* Chassagnard & McEvey, 1992 **c**, *Z.* (*Z.*) *sexstriatus* Chassagnard, 1996 **d**, *Z.* (*Z.*) *cercus* Chassagnard & McEvey, 1992 **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)

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

| 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 & Tsacas | Madagascar: Antananarivo, Tsimbazaza (1200 m); ii.2008, A. Yassin & J. R. David |
| *Z. lachaisei* sp. n. | Tanzania: East Usambara Mt, Amani (900 m); 25-ix-2002, D. Lachaise |
| *Z. mascariensis* Tsacas & David | La Reunion (France): 2004, P. Capy |
| *Z. neglectus* Collart | Madagascar: Andasibe; ii.2008, A. Yassin & J. R. David |
| *Z. ornatus* Séguy | Congo: Brazzaville; iii.2006, J. Vouidibiou |
| *Z. proximus* Collart | Kenya: S. Dupas |
| *Z. santomensis* sp. n. | Sao Tomé & Príncipe: Pico de São Tomé Park (1500 m); iii.2001, D. Lachaise |
| *Z. sepsoides* Duda | Congo: Brazzaville; iii.2006, J. Vouidibiou |
| *Z. taronus* Chassagnard & Tsacas | Kenya: 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 |

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; ♂A = 46–57; aedeagus subterminally concave (Fig. 3a); spermatheca smooth (Fig. 3c) ..... ***Z. mascariensis*** [Madagascar; Mauritius; Mayotte (France) (**loc. n.**); La Réunion (France)]

– Frons with a median white stripe; ♂A = 22–37; aedeagus subterminally convex (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) ..... **5**

– TST = 3–5 mm; spermatheca somewhat papillate (Fig. 3k); posterior egg filament not spatulate (Fig. 3l) ..... **6**

5(4) ♂WV = 1.5–1.8 μm; TST = 2.0 mm ..... ***Z. sepsoides*** [Benin; Cameroon; Côte d'Ivoire; Gabon; Congo; Madagascar; Malawi; South Africa; Uganda]

– ♂WV = 1.9–2.5 μm; TST = 1.2 mm ..... ***Z. tsacasi*** [São Tomé and Principé]

6(3) TST = 3.2 mm ..... ***Z. 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; Mayotte (France) (**loc. n.**); Mozambique; Niger; Nigeria; La Réunion (France); Zambia; Seychelles; South Africa; St. Helena; Tanzania; Uganda; Zimbabwe]

– TST = 4.4 mm ..... ***Z. burlai*** [Tanzania]

7(2) Frons without a median stripe ..... **8**

– Frons with a median stripe ..... **14**

8(7) Scutum velvety black, especially posteriorly; scutellum with a white spot at tip (Fig. 1b) ..... ***Z. ghesquierei*** [Benin; Cameroon; Congo; Côte d'Ivoire; Democratic Republic of Congo; Gabon; Kenya; Madagascar; Malawi; Niger; Nigeria; São Tomé and Principé; Swaziland; Tanzania; Turkey; Uganda; Hawaii Islands (United States of America); Zimbabwe]

– Scutum and scutellum not as above ..... **9**

9(8) Scutellum entirely and scutum posteromedially black (Fig. 1c) ..... ***Z. litos*** [Madagascar]

– Scutellum and scutum not as above ..... **10**

10(9) Wing darkened anteriorly ..... **11**

– Wing uniformally hyaline ..... **12**

11(10) Thorax and abdomen entirely dark brown (Fig. 4a) ..... ***Z. momorticus*** [Côte d'Ivoire; Democratic Republic of Congo]

– Thorax and abdomen yellow (Fig. 4b) ..... ***Z. badyi*** [Côte d'Ivoire]

12(10) ♂ basitarsus without a hairy brush (Fig. 5a) ..... ***Z. neglectus*** [Côte d'Ivoire; Democratic Republic of Congo; Madagascar]

– ♂ basitarsus with a hairy brush (Fig. 5b-d) ..... **13**

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) ..... ***Z. arduus***
[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); ♂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; ♂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) ..... ***Z. inermis***
[Cameroon; Central African Republic; Congo; Côte d'Ivoire; Democratic Republic of Congo; Gabon; Kenya; Uganda]

18(16) BV = 9–11 μm (Fig. 1f); testis short; epandrial phragma with a broad hump at the middle of the anterior margin (Fig. 7c); spermatheca smooth..... ..... ***Z. kolodkinae***
[Madagascar]

– BV = 6–8 μm (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 ..... ***Z. verruca***
[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) ..... **33**

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, São 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; South Africa]

22(20) ♂ basitarsus without a hairy brush ..... **23**

– ♂ basitarsus with a hairy brush ..... **24**

23(22) F1 with 3–4 spines; basalmost spine strong (Fig. 8c) ..... ***Z. spinosus***
[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) ..... **29**

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)..... ***Z. vrydaghi***
[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 ..... **31**

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 voluminous, 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**

32(31) F1 not broadened, with a series of short bristles (Fig. 8m); spermatheca sclerified (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.....***Z. camerounensis***
[Cameroon; Malawi; Tanzania (**loc. n.**); Uganda]

– WV > 15 µm; thorax and abdomen not black.....**34**
34(33) Abdominal tergal bristles with dark spots basally .....**35**
– Abdominal tergal bristles without dark spots basally .....**43**
35(34) Thorax with two incomplete submedian white stripes between two complete dorsocentral stripes (Fig. 1h).....***Z. multivittiger***
[Kenya; Rwanda]
– Thorax without submedian stripes .....**36**
36(35) F1 setiferous spines differentiated; basalmost borne on a protruding tubercule (Fig. 2e) ..... ***Z. proximus***
[Kenya; Uganda]
– F1 setiferous spines undifferentiated .....**37**
37(36) BV enlarged posteriorly; abdomen dark brown (Fig. 10b, d, e) .....**38**
– BV not enlarged posteriorly; abdomen light yellow.....**40**
38(37) Abdomen darker than thorax (Fig. 10b)..... ***Z. koroleu***
[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); ♂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; ♂TL = 1.44–1.56 mm (Fig. 10d); H = 9.6 (Fig. 11e) .....***Z. vittiger***
[Cameroon; Ethiopia; Madagascar; Malawi; South Africa]
40(37) Head orange tan lighter than thorax (Fig. 10f); hairy brush 1/3 ♂ basitarsus (Fig. 5e); spermatheca without introvert (Fig. 13d)..... ***Z. santomensis* sp. n.**
[São Tomé and Principé]
– Head and thorax concolorous reddish brown; hairy brush 2/3 ♂ basitarsus; spermatheca with an introvert (Fig. 12) .....**41**
41(40) ♂ aedeagal flap highly serrated apically (Fig. 12a) ; oviscape constricted basally with 8 (rarely 7) peg-like ovisensilla (Fig. 12b); spermatheca length:width = 0.62–0.84 (Fig. 12c) ..... ***Z. africanus***
[Gabon ; Uganda]
– ♂ 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***
[Gabon]
– ♂ aedeagal flap serrated basally (Fig. 12g).....***Z. indianus***
[Argentina; Austria; Benin; Brazil; Cabo Verde; Canary Islands (Spain); Congo; Côte d'Ivoire; Egypt; 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) ..... ***Z. ornatus***
[Cameroon; Côte d'Ivoire; Congo; Gabon; Madagascar; South Africa]

– Abdomen uniformally yellow; TST < 6.0 mm; spermatheca globulous (Figs 14b,c,e) ..... **44**

44(43) TST = 2.6 mm; spermatheca chitinized at base and apex (Fig. 14b); egg with 2 filaments ..... ***Z. davidi***
[Congo; São Tomé and Principé (**loc. n.**)]

– TST = 4.0–5.2 mm; egg with 4 filaments ..... **45**

45(44) ♂TL = 1.56–1.70 mm; ♂ epandrium not expanded dorsally (Fig. 14d); spermatheca (Fig. 14c) ..... ***Z. taronus***
[Congo (**loc. n.**); Gabon; Kenya; Malawi; São Tomé and Principé (**loc. n.**)]

– ♂TL = 1.44–1.50 mm; ♂ epandrium expanded dorsally (Fig. 14e); spermatheca (Fig. 14f) ..... ***Z. capensis***
[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*

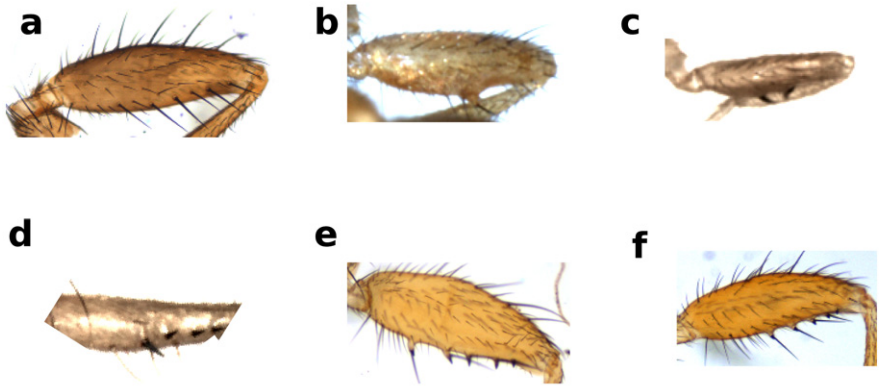


**Figure 2.** Forefemur of *Zaprionus cercus* Chassagnard & McEvey, 1992 **a**, *Z. mascariensis* Tsacas & David, 1975 **b**, *Z. campestris* Chassagnard, 1989 **c**, *Z. serratus* Chassagnard, 1989 **d** *Z. proximus* Collart, 1937 **e**, and *Z. indianus* Gupta, 1970 **f**.

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*, *tuberculatus* and *vittiger* (Chassagnard and Tsacas 1993). We transferred the *tuberculatus*

**Table 2.** Classification and ecology of the subgenus *Zaprionus*. Breeding niches are abbreviated as: **FL** = flowers; **FR** = fruits; and **TR** = decaying tree trunk. Ability to be reared in the laboratory (**L**) is indicated as (**+**) for species that are reared and (**-**) for species that are not.

| Group | Subgroup | Complex | Species | Authorship | L | Breeding niche | Reference |
|---|---|---|---|---|---|---|---|
| *armatus* | *armatus* | *armatus* | *armatus* | Collart, 1937a | - | TR: *Ficus* sp. (Moraceae) | C37a |
| | | | | | | FR: *Myrianthus* sp. (Cercopiaceae) | TC90 |
| | | | *enoplomerus* | Chassagnard, 1989 | + | FR: *Ficus macrosperma* (Moraceae); *Ficus sur* (Moraceae); *Ficus capensis* (Moraceae) | C89 |
| | | | *seguyi* | Tsacas & Chassagnard, 1990 | - | FR | TC90 |
| | | | *spinipes* | Tsacas & Chassagnard, 1990 | - | ? | TC90 |
| | | | *spinoarmatus* | Tsacas & Chassagnard, 1990 | - | FR: *Dacryodes* sp. (Burseraceae) | TC90 |
| | | | | | | TR: *Raphia* sp. (Arecaceae) | B54 |
| | | *hoplophorus* | *hoplophorus* | Tsacas & Chassagnard, 1990 | - | ? | |
| | | | *tuberarmatus* | Tsacas & Chassagnard, 1990 | - | ? | |
| | | *vrydaghi* | *fumipennis* | Séguy, 1938 | - | FL: *Costus afer* (Costaceae) | TC90 |
| | | | *vrydaghi* | Collart, 1937a | - | FL: *Costus afer* (Costaceae) | B76,C86 |
| | *montanus* | | *campestris* | Chassagnard, 1989 | - | ? | C89 |
| | | | *montanus* | Collart, 1937b | - | TR: Andropoganeae (Poaceae) | G57 |
| | | | | | | TR: Bambuseae (Poaceae) | C89 |
| | *spinosus* | | *serratus* | Chassagnard, 1989 | - | FL: Bignoniaceae | C89 |
| | | | *spineus* | Tsacas & Chassagnard | - | ? | TC90 |
| | | | *spinosus* | Collart, 1937a | - | ? | |
| *inermis* | | | *arduus* | Collart, 1937b | - | FR: *Musa* sp. (Musaceae) | C37b |
| | | | *badyi* | Burla, 1954 | - | FR | B54 |
| | | | *ghesquierei* | Collart, 1937a | - | FR: *Citrus sinensis* (Rutaceae); *Coffea* sp. (Rubiaceae); *Cola acuminata* (Malvaceae); *Rollinia sieberi* (Annonaceae); *Sarcocephalus* sp. (Rubiaceae); *Psidium* sp. (Myrtaceae); *Terminalia* sp. (Combredaceae); *Murraya exotica* (Rutaceae); *Pseudospondia* sp. (Anacridaceae); *Myrianthus* sp. (Cercopiaceae); *Dorstenia* sp. (Moraceae); *Uapaca* sp. (Phyllanthaceae) | C37a |

| Group | Subgroup | Complex | Species | Authorship | L | Breeding niche | Reference |
|---|---|---|---|---|---|---|---|
| | | | | | | FR: *Musa* sp. (Musaceae), *Averrhoa carambola* (Oxalidaceae); *Turraeanthus africana* (Meliaceae); *Conopharyngia dusissima* (Apocynaceae), | B54 |
| | | | | | | FR: *Mangifera indica* (Anacardiaceae); *Carica papaya* (Caricaceae); *Persea americana* (Lauraceae); *Ficus ovata* (Moraceae); *Musa* sp. (Musaceae); *Averrhoa carambola* (Oxalidaceae); *Cyphonandra betacea* (Solanaceae); *Solanum gilo* (Solanaceae) | B76 |
| | | | | | | FR: *Polyalthia sauveolens* (Annonaceae); *Detarium senegalense* (Caesalpiniaceae) | LT83 |
| | | | | | | FR: *Dacryodes* sp. (Burseraceae); *Hugonia* sp. (Linaceae); *Parinari* sp. (Rosaceae); *Gambeya perpulchra* (Sapotaceae) | L79 |
| | | | | | | FR: *Cocos romanzoffiana* (Palmaceae) | L47 |
| | | | | | | FR: *Pancovia bijuga* (Sapindaceae) | L74 |
| | | | | | | TR: *Elaeis guinensis* (Palmaceae) | L47 |
| | | | | | | FR: *Ficus thonningii* (Moraceae) | C97 |
| | | | *momorticus* | Graber, 1957 | - | FL: *Momordica pterocarpa* (syn. *M. runsorrica*) (Cucurbitaceae) | G57 |
| | | | | | | FL: *Crinum sanderianum* (Amaryllidaceae); *Crinum jagus* (Amaryllidaceae) | L79 |
| | | | | | | FL: *Rothmania whitfieldi* (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* (Caricaceae); | B54 |
| | | | | | | TR: *Raphia* sp. (Arecaceae) | B54 |

| Group | Subgroup | Complex | Species | Authorship | L | Breeding niche | Reference |
|---|---|---|---|---|---|---|---|
| | | | | | | 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* sp. (Linaceae); *Guarea cedrata* (Meliaceae); *Turraeanthus africanus* (Meliaceae); *Parinari* sp. (Chrysobalanaceae) | L79 |
| | | | | | | FR: *Ficus sur* (Moraceae); *Ficus lyrata* (Moraceae); *Ficus macrosperma* (Moraceae); *Ficus elasticoides* (Moraceae); *Ficus ovata* (Moraceae); *Ficus* sp. (Moraceae) | L82 |
| | | | | | | FR: *Pandanus candelabrum* (Pandanaceae) | R83 |
| | | | | | | FR: *Spondias mombin* (Anacardiaceae); *Detarium senegalense* (Cesalpinaceae); *Pentadesma butyraceae* (Guttifereae); *Treculia africana* (Moraceae); *Hirtella* sp. (Rosaceae); *Parinari excelsa* (Rosaceae); *Nauclea poheguinii* (Rubiaceae); *Gambeya taiensis* (Sapotaceae); *Tieghemella heckelii* (Sapotaceae) | C86 |
| | | | *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* sp. (Burseraceae); *Guarea cedrata* (Meliaceae); *Parinari* sp. (Rosaceae); *Parinari excelsa* (Rosaceae); *Tieghemella heckelii* (Sapotaceae) | L79 |
| | | | | | | FR: *Ficus sur* (Moraceae); *Ficus saussureana* (Moraceae); *Ficus mucuso* (Moraceae); *Ficus lutea* (Moraceae); *Ficus natalensis* (Moraceae); | L82, LT83 |

| 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 |
| | | | *verruca* | Chassagnard & McEvey, 1992 | + | FR: ex-banana trap | CM92 |
| *neglectus* | | | *neglectus* | Collart, 1937 | + | FR | B54 |
| | | | | | | FL: *Ipomoea digitata* (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 gabonensis* (Myristicaceae); *Cissus dinklagei* (Vitaceae) | LT83 |
| | | *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 | L | Breeding niche | Reference |
|---|---|---|---|---|---|---|---|
| | | | | | | FR: *Ficus macrosperma* (Moraceae); *Ficus saussureana* (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 | - | 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 = Chassagnard 1996; C97 = Chassagnard et al. 1997; CM92 = Chassagnard and McEvey 1992; CT87 = Chassagnard and Tsacas 1987; CT93 = Chassagnard and Tsacas 1993; G57 = Graber 1957; L47 = Lepesme 1947; L74 = Lachaise 1974; L76 = Lachaise 1976; L79 = Lachaise 1979; L82 = Lachaise et al. 1982 LT83 = Lachaise 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.

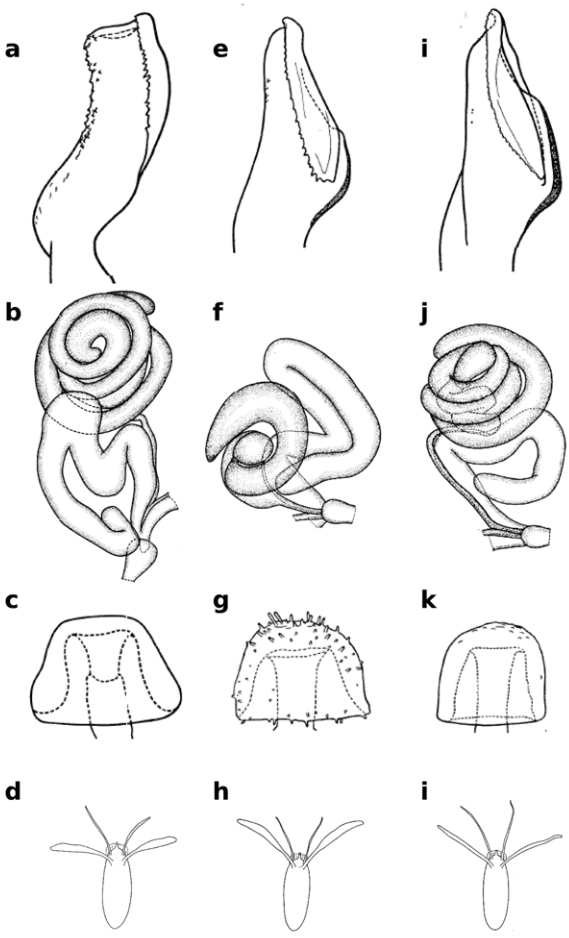


**Figure 3.** Distiphallus, testis and accessory gland, spermatheca and egg of *Zaprionus mascariensis* Tsacas & David **a–d**, *Z. sepsoides* Duda, 1939 **e–h**, and *Z. tuberculatus* Malloch, 1932 **i–l** [From Tsacas et al. 1977; courtesy of M. T. Chassagnard].

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

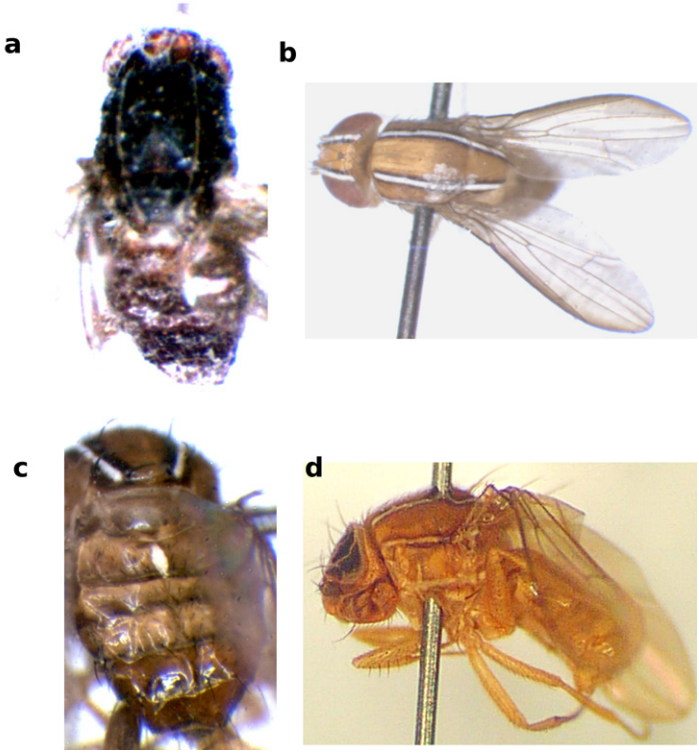


**Figure 4.** Dorsal views of *Zaprionus momorticus* Graber, 1957 **a**, *Z. badyi* Burla, 1954 **b**, abdomen of *Z. niabu* Burla, 1954 **c**, and lateral view of *Z. arduus* Collart, 1937 **d**.

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*

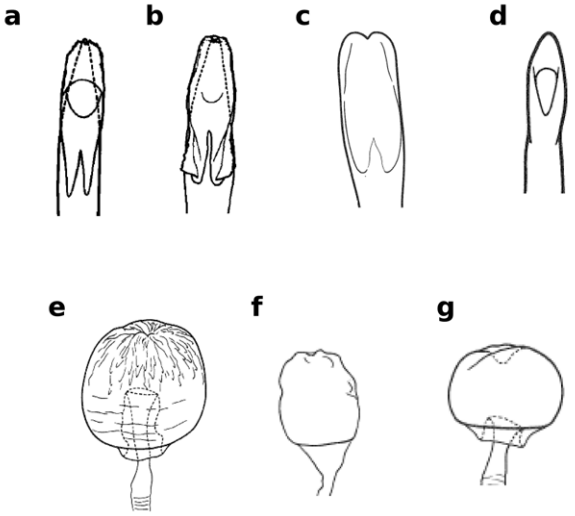


**Figure 6.** Ventral views of distiphallus of *Zaprionus sexvittatus* Collart, 1937 **a**, *Z. sexstriatus* Chassagnard, 1996 **b**, *Z. armatus* Collart, 1937 **c**, and *Z. enoplomerus* Chassagnard, 1989 **d**; spermatheca of *Z. spinipes* Tsacas & Chassagnard, 1990 **e**, *Z. seguyi* Tsacas & Chassagnard, 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

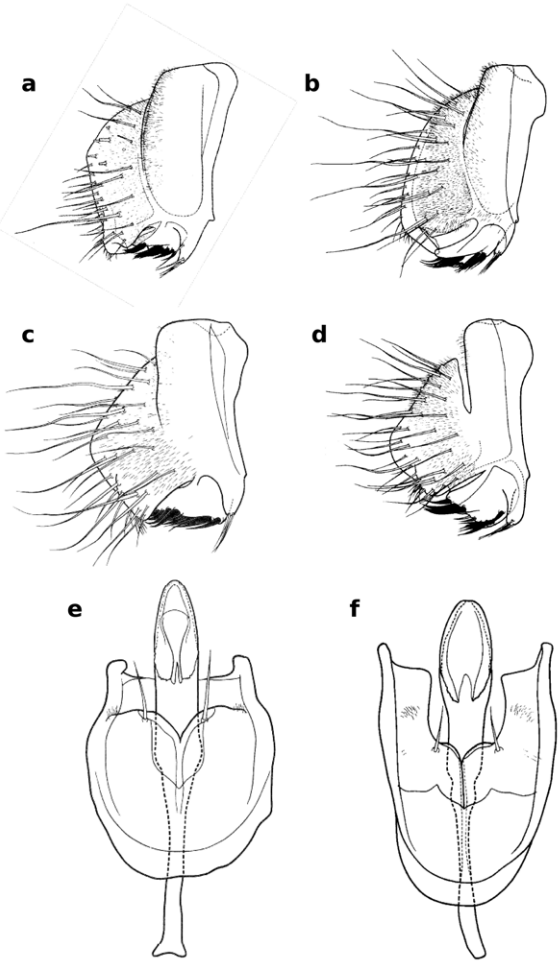


**Figure 7.** Lateral views of male epandrium and cercus and ventral views of aedeagus and hypandrium of *Zaprionus inermis* Collart, 1937 **a**, *Z. cercus* Chassagnard & McEvey, 1992 **b**, *Z. kolodkinae* Chassagnard & Tsacas, 1987 **c, e**, and *Z. verruca* Chassagnard & McEvey, 1992 **d, f** [From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

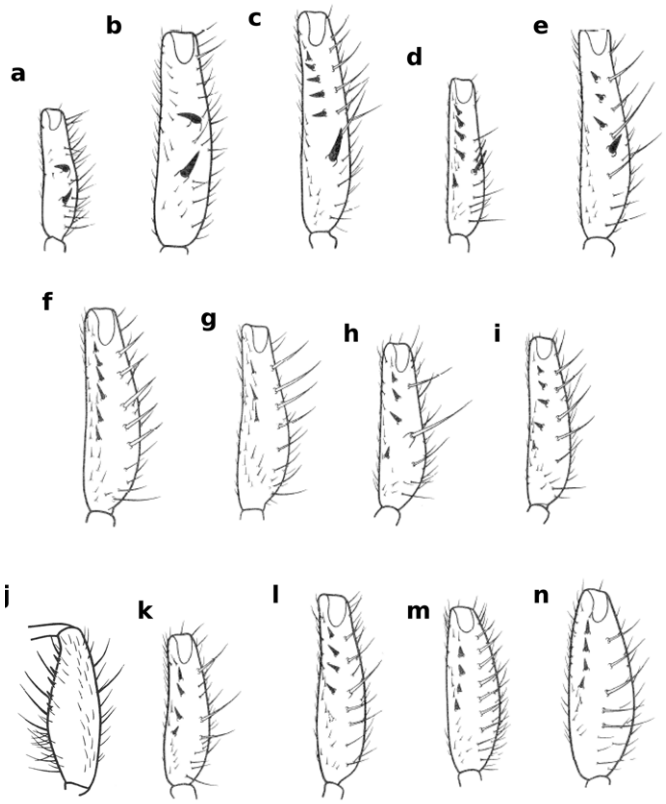


**Figure 8.** Ventral views of forefemur of *Zaprionus campestris* Chassagnard, 1989 **a**, *Z. montanus* Collart, 1937 **b**, *Z. spinosus* Collart, 1937 **c** *Z. spineus* Tsacas & Chassagnard, 1990 **d**, *Z. serratus* Chassagnard, 1989 **e**, *Z. fumipennis* Séguy, 1938 **f**, *Z. vrydaghi* Collart, 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

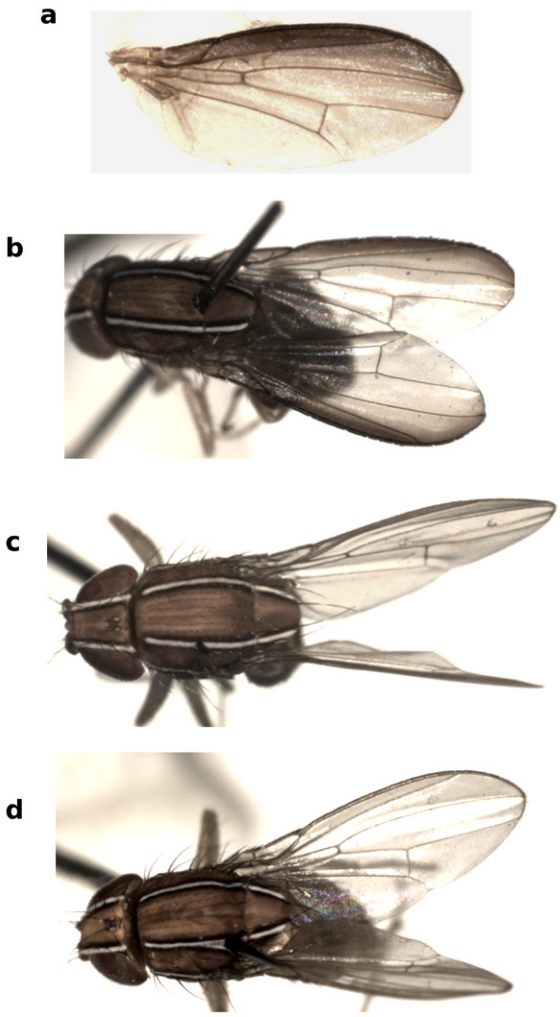


**Figure 9.** Wing of *Zaprionus fumipennis* Séguy, 1938 **a**, and dorsal views of *Z. vrydaghi* Collart, 1937 **b**, *Z. hoplophorus* Tsacas & Chassagnard, 1990 **c**, and *Z. tuberarmatus* Tsacas & Chassagnard, 1990 **d**.

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.

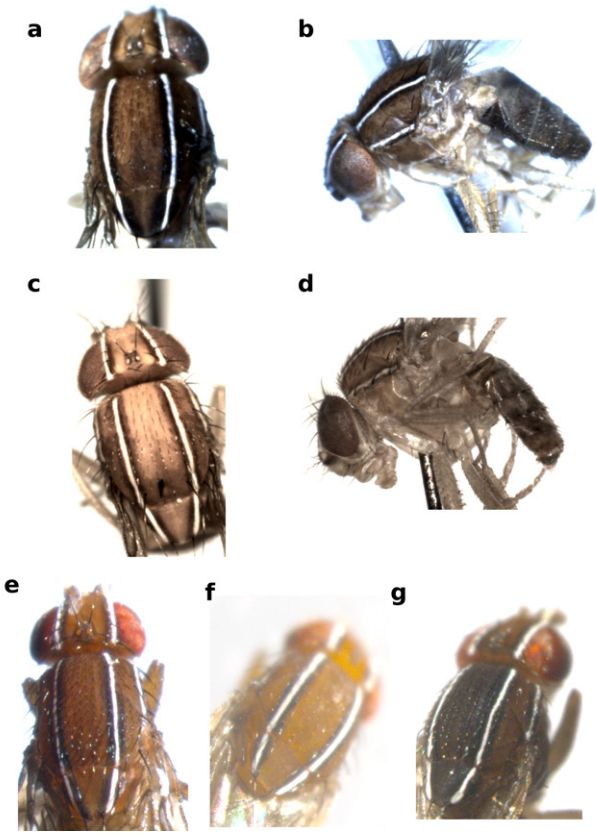


**Figure 10.** Lateral and dorsal views of *Zaprionus koroleu* Burla, 1954 **a, b**, *Z. vittiger* Coquillett, 1902 **c, d**, *Z. lachaisei* Yassin & David, sp. n. **e**, *Z. santomensis* Yassin & David, sp. n. **f**, and *Z. camerounensis* Chassagnard & Tsacas, 1993 **g, h**.

### *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,

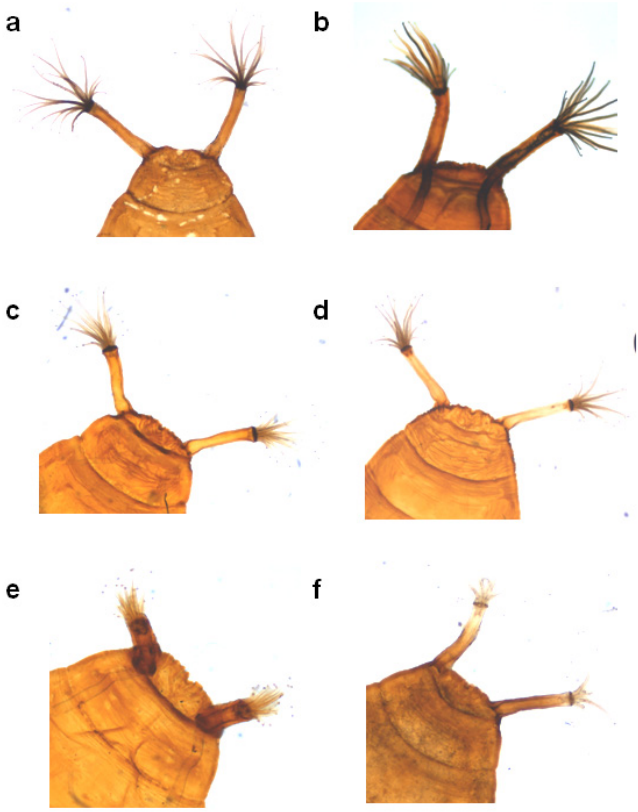


**Figure 11.** Puparium of *Zaprionus neglectus* Collart, 1937 **a**, *Z. inermis* Collart, 1937 **b**, *Z. cercus* Chassagnard & McEvey, 1992 **c**, *Z. santomensis* Yassin & David, sp. n. **d**, *Z. lachaisei* Yassin & David, sp. n. **e** and *Z. vittiger* Coquillett, 1902 **f**.

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) peg-like ovisensilla on the oviscape, which is constricted ventrally (Fig. 12).

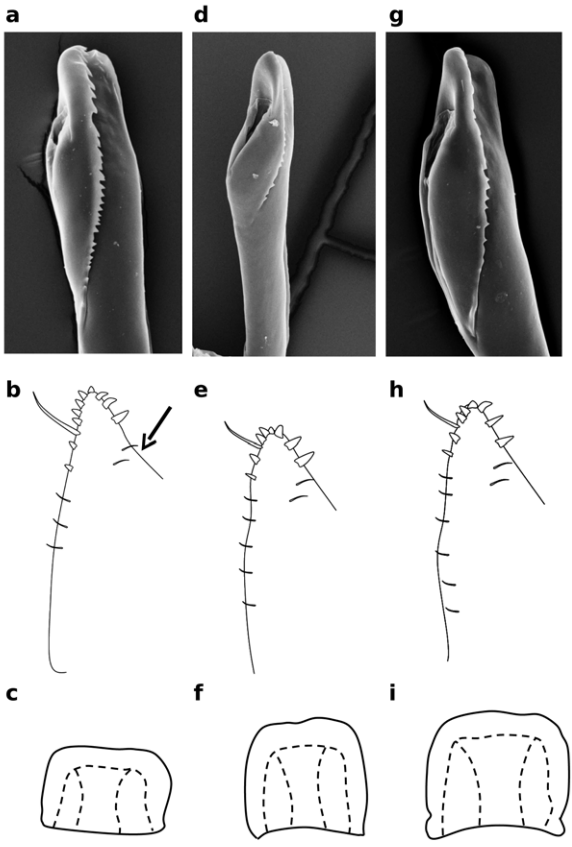


**Figure 12.** Distiphallus, oviscape and spermatheca of *Zaprionus africanus* Yassin & David in Yassin et al., 2008b **a-c**, *Z. gabonicus* Yassin & David in Yassin et al., 2008b **d–f**, and *Z. indianus* Gupta, 1970 **g–i**.

**Description.** ♂. 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.

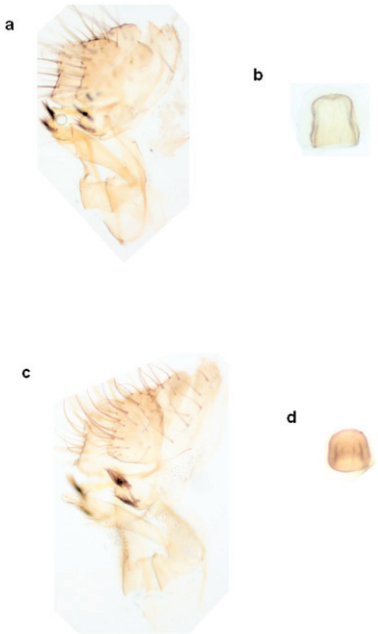


**Figure 13.** Male genitalia and spermatheca of *Z. lachaisei* Yassin & David, sp. n. **a, b**, and *Z. santomensis* Yassin & David, sp. n. **c, d**.

*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.

♀. 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.** ♂. 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

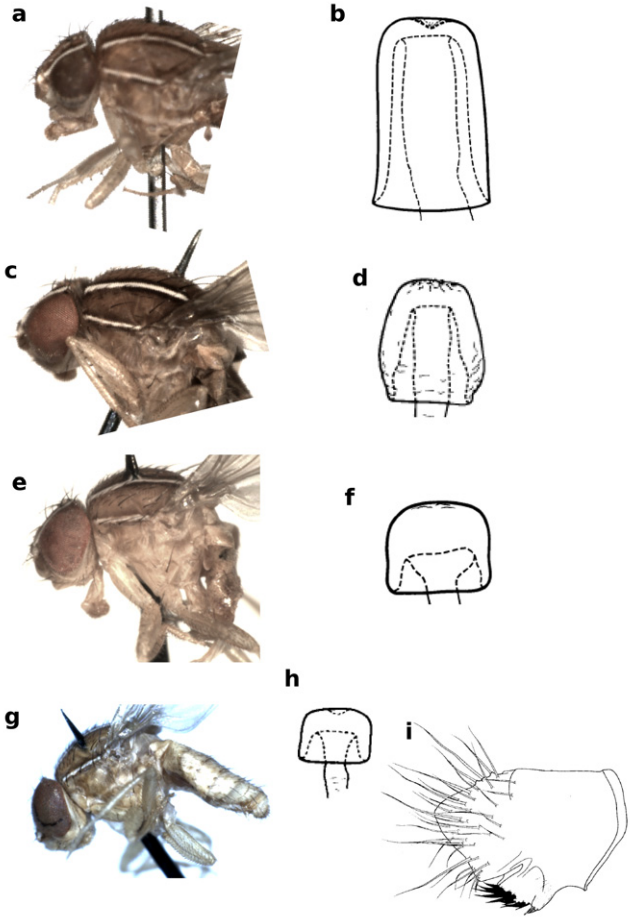


**Figure 14.** Spermatheca and male epandrium of *Zaprionus ornatus* Séguy, 1933 **a**, *Z. davidi* Chassagnard & Tsacas, 1993 **b**, *Z. taronus* Chassagnard & Tsacas, 1993 **c, d**, and *Z. capensis* Chassagnard & Tsacas, 1993 **e, f** [Illustrations from Chassagnard and Tsacas 1993; courtesy of M.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

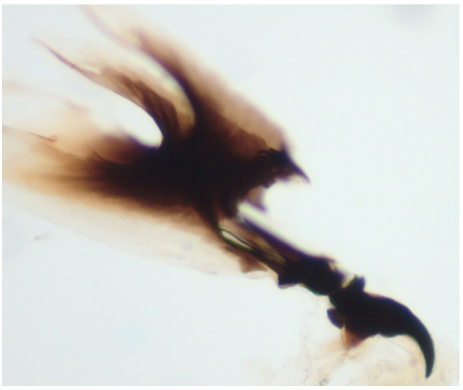

**Figure 15.** Larval cephalopharyngeal skeleton of *Zaprionus sepsoides* Duda, 1939.

*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.

♀. 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.** ♂. 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.

♀. 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.** ♂. 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.

♀. 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

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

| | 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*** | | | | | | | | | |
| ***neglectus* group** | | | | | | | | | |
| *Z.* (*Z.*) *neglectus* | 2.8 | 1.0 | 0.60 | 0.7 | 2.4 | 0.20 | 2.0 | 3.2 | 0.06 |
| ***inermis* 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 |
| ***vittiger* 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 |

**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 ± 0.5 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

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

| | Egg | | Puparium | |
|---|---|---|---|---|
| | EL:El | PF:EL | PL:Pl | H |
| **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 |
| ***inermis* 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 |
| ***vittiger* 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 |

**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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