

Redescription and new synonyms of the cosmopolitan species *Lamprochernes savignyi* (Simon) (Chernetidae: Pseudoscorpionida)

Mark S. Harvey

Division of Entomology, CSIRO,
G.P.O. Box 1700,
Canberra,
A.C.T., 2601, Australia*

Summary

The adult and all nymphal stages of *Lamprochernes savignyi* (Simon) are described and the following species are found to be junior synonyms: *Chelifer pygmaeus* L. Koch (Australia), *Chelifer brevifemorus* Balzan (Paraguay and Argentina), *Chelifer celerrimus* With (Grenada), *Chelifer godfreyi* Kew (Britain), *Pycnochernes linsdalei* Chamberlin (U.S.A.) and *Muscichernes katoi* Morikawa (Japan). *Muscichernes* Morikawa is newly synonymised with *Lamprochernes* Tömösváry. *Lamprochernes savignyi* is found to have a world-wide distribution.

Introduction

Populations of a small species of *Lamprochernes* have recently been found in disturbed habitats in south-eastern Australia, and examination of the literature indicated that the specimens were very similar to published descriptions of *L. savignyi* (Simon) (e.g. Beier, 1932) and *L. godfreyi* (Kew) (e.g. Beier, 1963a), among others. This prompted a complete review of *L. savignyi* and the results of this study are presented below. Along with six new synonyms of *L. savignyi* and a new generic synonym of *Lamprochernes*, *L. savignyi* is revealed as a world-wide, synanthropic species, with a distribution rivalling those of other well-known pseudoscorpion species such as *Chelifer cancroides* (Linnaeus) and *Withius piger* (Simon).

Materials and Methods

Specimens were borrowed from or lodged in the following institutions: Australian Museum, Sydney (AM), American Museum of Natural History, New York (AMNH), Australian National Insect Collection, Canberra (ANIC), British Museum of Natural History, London (BMNH), Division of Scientific and Industrial Research, Auckland (DSIR), Ehime University, Matsuyama (EU), J. C. Chamberlin collection, Pacific University, Portland (JCC), M. Judson collection, Leeds (MJ), Museum of Victoria, Abbotsford (NMV), National Museum of Ireland, Dublin (NMI) and Queensland Museum, Fortitude Valley (QM).

Specimens were mounted on microscope slides in Canada Balsam or Euparal. Measurements were taken from ten adults of each sex, and five nymphs of each stage, as well as from all available type material, except for the type series of *C. pygmaeus* from which only five

specimens were measured. One male and one female were critical point dried, mounted on points and gold coated for examination in a JEOL JSM-35C Scanning Electron Microscope. Morphological terminology follows Chamberlin (1931). TS refers to the distance of the tactile seta from the proximal end of the tarsus of leg IV divided by the length of the tarsus.

Family CHERNETIDAE Menge

Subfamily Lamprochernetinae Beier

Genus *Lamprochernes* Tömösváry

Chernes (*Lamprochernes*) Tömösváry, 1882: 185. Type species *Chelifer nodosus* Schrank, 1803, by subsequent designation of Beier, 1932 (erroneously claimed to be by original designation).

Lamprochernes Tömösváry: Beier, 1930: 200; Beier, 1932: 82; Hoff, 1949: 450; Beier, 1963a: 249-250; Murthy & Ananthkrishnan, 1977: 135.

Pycnochernes Beier, 1932: 136; Beier, 1933: 522; Chamberlin, 1952: 274-275. Type species *Chelifer cerrimus* With, 1908, by original designation. Synonymised by Muchmore, 1975: 19.

Muscichernes Morikawa, 1960: 140. Type species *Muscichernes katoi* Morikawa, 1960, by original designation. NEW SYNONYMY.

Diagnosis

Leg IV with three tactile setae: one distally on telofemur; one distally on tibia; and one sub-medially or sub-proximally on tarsus. Trichobothrium *it* closer to *ist* than to tip of fixed chelal finger. Females with spermatheca consisting of a long T-shaped tube. Males without medio-dorsal protuberance on palpal tibia. Tarsal claws simple.

Remarks

Morikawa (1960) claimed that *Muscichernes* differed from *Lamprochernes* by lacking tactile setae from the pedipalpal femur, tibia and chelal hand. However, *Lamprochernes* also lacks such tactile setae. Morikawa also cited the sub-medial position of the tactile seta of tarsus IV as a distinguishing characteristic of *Muscichernes*, but, as shown below, it is barely of specific importance, and is thus disregarded as a generic character. *Muscichernes* is therefore here considered a synonym of *Lamprochernes*.

Lamprochernes savignyi (Simon) (Figs. 1-17)

Chelifer savignyi Simon, 1881: 12-13.

Chelifer nodosus Schrank: Hansen, 1884: 548-549 (misidentification, in part); Ellingsen, 1907: 156 (misidentification); Kew, 1909: 259 (misidentification).

Chelifer pygmaeus L. Koch, 1885: 49-50, pl. 6, figs. 8, 8a-b; With, 1905: 110. NEW SYNONYMY.

Chelifer brevifemorus Balzan, 1890: 420-421, figs. 7, 7a-c; With, 1908: 284. NEW SYNONYMY.

Chelifer (Trachychernes) brevifemorus Balzan: Balzan, 1892: 548; Ellingsen, 1905: 324.

Chelifer (Chernes) brevifemorus Balzan: Ellingsen, 1902: 156-158.

Chelifer celerrimus With, 1908: 285-286, figs. 23a-e. NEW SYNONYMY.

Chelifer (Chernes) godfreyi Kew, 1911: 42, fig. 2; Kew, 1916: 78. Synonymised with *C. celerrimus* by Muchmore, 1975: 19.

Lamprochernes savignyi (Simon): Beier, 1932: 86, fig. 105; Beier, 1947: 569; Beier, 1953: 73; Vachon, 1954: 590; Beier, 1958: 175;

*Present address: Biological Survey Department,
Museum of Victoria,
71 Victoria Crescent,
Abbotsford,
Victoria, 3067, Australia

Beier, 1963b: 195; Beier, 1964: 75; Beier, 1965: 374; Beier, 1969: 413; Beier, 1974: 1010; Mahnert, 1975: 545; Beier, 1976: 213; Mahnert, 1978: 884.

Lamprochernes godfreyi (Kew): Beier, 1932: 86-87; Lohmander, 1939: 293-294, fig. 6; Evans & Browning, 1954: 18, fig. 19; Hoff & Bolsterli, 1956: 166-167; Hoff, 1958: 20; Beier, 1963a: 250; Howes, 1972a: 109; Howes, 1972b: 122; Legg, 1972: 579, fig. 1 (6c); Jones, 1978: 90; Jones, 1980: map 14.

Haplochernes pygmaeus (L. Koch): Beier, 1932: 110-111; Harvey, 1981: 246; Harvey, 1985: 134.

Pycnochernes celerrimus (With): Beier, 1932: 137; Beier, 1933: 522.

Pycnochernes brevifemoratus (Balzan): Beier, 1932: 137; Beier, 1933: 522; Feio, 1945: 7.

Pycnochernes linsdalei Chamberlin, 1952: 275-277, fig. 4a-i; Hoff, 1958: 21; Muchmore, 1975: fig. 7. NEW SYNONYMY.

Muscichernes katoi Morikawa, 1960: 140-141, pl. 3 fig. 7, pl. 7 fig. 16, pl. 9 fig. 19. NEW SYNONYMY.

Lamprochernes cf. *savignyi* (Simon): Mahnert, 1982: 692-693, fig. 1.

Types

Chelifer savignyi: Holotype, sex unknown, Ramlé [= Ramleh, a suburb of Alexandria], Egypt, in house, M. A. Letourneaux (not in Muséum National d'Histoire Naturelle, Paris), lost.

Chelifer pygmaeus: Lectotype ♀ (present designation) (with brood-sac), 39 paralectotype ♀ (some with brood-sacs), Gayndah, Queensland, Australia (BMNH, 1913.9.1.357-396) (spirit and slides). 7 paralectotype ♀ (some with brood-sacs), same data as lectotype (BMNH, 1891.8.1.1078-1084) (spirit). 3 paralectotype ♀, same data as lectotype (NMV, K336-338) (spirit and slide).

Chelifer brevifemoratus: Syntypes (not examined; not in Muséum National d'Histoire Naturelle, Paris): unknown number of specimens, Ascuncion, Paraguay. 1 specimen, Resistencia, Argentina.

Chelifer celerrimus: Holotype ♀, Balthazar, Grenada, half shady place in a mixture of earth and old manure, 9 March, H. H. Smith (BMNH, 1985.11.1.1) (slide), examined.

Chelifer godfreyi: Syntypes (not examined; not in BMNH or NMI): Petersham, [England], in manure-heap; Newport, Isle of Wight, [England], in manure-heap, E. A. Butler; Hatfield [England], ex fly, F. G. Pitts; South Norwood, [England], ex fly, in house, Aug. 1906, H. Hill; Oban, [Scotland], ex moss, C. D. Soar; Rathmines, County Dublin, [Ireland], ex fly, N. E. Stephens.

Pycnochernes linsdalei: Holotype ♀, Frances Simes Hastings Natural History Reservation, Monterey County, California, U.S.A., 30 May 1940, J. M. Linsdale (AMNH, JC-1225.08001) (slide), examined. Paratype ♀, Stanford University, California, U.S.A., under tub in moist soil, 9 October 1923, B. C. Cain (JCC, JC-264.01001), not examined.

Muscichernes katoi: Holotype ♀, Shakujii, Tokyo, Japan, ex *Musca vicina* Macquart [= *Musca domestica* Linnaeus (Muscidae: Diptera)], 3 July 1958, M. Kato (EU), not examined.

Other material examined

AUSTRALIA: Australian Capital Territory: 1 ♂, 1 ♀, Ainslie, ex mouldy grass pile, 5 Jan. 1984,

J. Lawrence (ANIC); 2 ♂, 6 ♀, Cook, ex compost heap, 6 July 1984, M. S. Harvey (ANIC). New South Wales: 1 ♀, Sydney (AM, KS14013). Victoria: 1 ♀, Balwyn, ex ♀ of *Fannia canicularis* (Linnaeus) (Fanniidae: Diptera), 21 March 1981, M. S. Harvey (NMV, MH280.01); 1 ♀, Boronia, ex ♀ of *Drosophila melanogaster* Meigen (Drosophilidae: Diptera), 30 April 1980, B. Lobert (NMV, MH195.01); 2 ♀, same data as above except ex ♂ of *D. hydei* Sturtevant, 1 May 1980 (NMV, MH196.01-02); 3 ♀, Doncaster, ex ♀ of *M. domestica*, 10 March 1964, R. Jenz (NMV); 7 ♂, 5 ♀, Mt. Waverley, ex compost heap, 23 Sept. 1982, R. C. Brown (NMV, MH452.01-12); 169 ♂, 129 ♀ (some with brood-sacs), 231 tritonymphs, 260 deutonymphs, 59 protonymphs, same data as above except 14 Oct. 1982 (NMV, ANIC, AM, QM, MH458.01-848); 7 ♀, Wesburn, ex 4 ♂ of *M. domestica*, 18 Feb 1984, J. Bennett (NMV, MH546.01-07). ENGLAND: 1 ♂, 3 ♀, Cassisbury Park, Watford, ex oak leaf litter, 7 May 1977, M. Judson (BMNH); 4 ♂, 4 ♀, same data as above (MJ). IRELAND: 1 ♀, Glasnevin, ex fly (NMI). NEW ZEALAND: North Island: 1 ♀, Lynfield, 15 July 1975, G. Kuschel (DSIR). SUDAN: 1 ♀, Wad Medani, in fly trap, 12 Nov. 1945, D. J. Lewis (BMNH, 1946.11.7.2).

Diagnosis

Lamprochernes savignyi is one of the smallest species in the genus [chela (with pedicel) 0.685-0.75 (♂), 0.75-0.85 mm (♀) in length] and the tarsal tactile seta of leg IV is slightly more distal than in most species [TS = 0.36-0.43 (♂), 0.33-0.47 (♀)].

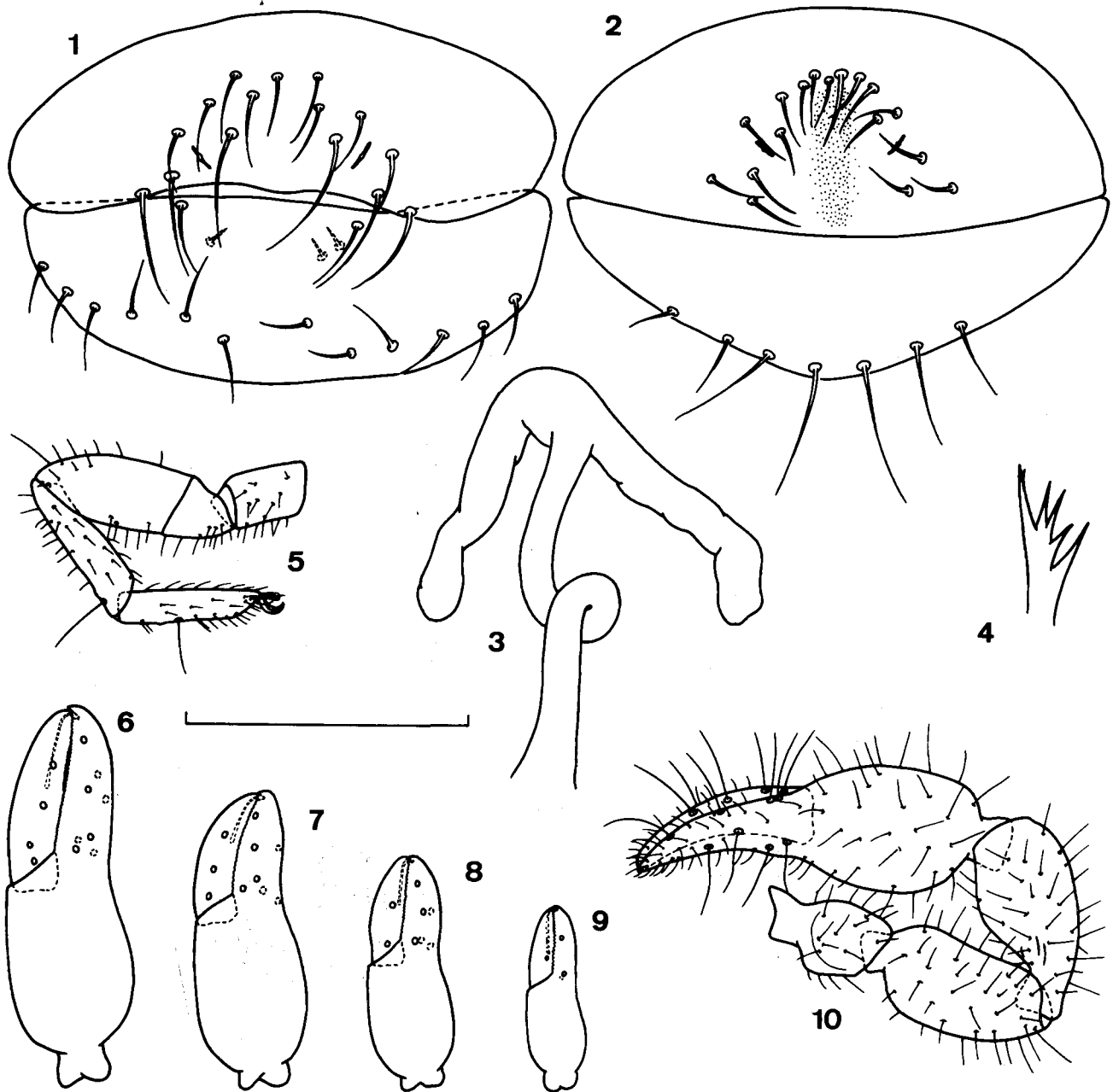
Description

Adults: Derm generally smooth, lateral margins of carapace and internal margins of pedipalpal trochanter, femur, tibia and chela moderately granulate. Pleural membrane longitudinally striate. Pedipalps (Fig. 10): Trochanter with dorsal protuberance, 1.63-1.93 (♂), 1.70-2.00 (♀), femur abruptly pedicellate, widest subproximally, 2.08-2.34 (♂), 2.24-2.43 (♀), tibia 2.03-2.22 (♂), 2.05-2.24 (♀), chela (with pedicel) 2.90-3.13 (♂), 2.70-3.06 (♀), chela (with pedicel) 2.65-2.90 (♂), 2.48-2.84 (♀) times longer than broad. Fixed chelal finger with eight trichobothria, moveable chelal finger with four trichobothria (Fig. 6); *it* closer to *ist* than to tip of fixed finger; *est* slightly distal to *ist*. Venom apparatus present in moveable finger terminating in nodus ramosus midway between *st* and *t*. Fixed finger with 30-34 (♂), 29-31 (♀) marginal teeth, plus 3-4 (♂), 2-3 (♀) external and one internal accessory teeth; moveable finger with 32-36 (♂), 31-34 (♀) marginal teeth, plus three (♂), 2-3 (♀) external and one internal accessory teeth. Several sense spots present basally on external face of moveable finger and on both faces of fixed finger. Chelicera with five setae on hand, *sbs* and *bs* with 2-3 small spinules; serrula exterior with 16-18 (♂), 17-20 (♀) lamellae; flagellum of three blades, anterior blade longest and widest, each blade with spinules on anterior face; galea of ♂ simple, of ♀ with several rami (Fig. 4). Carapace with 9-11 (♂), 8-11 (♀) setae on posterior margin, 1.18-1.39 (♂), 1.05-1.33 (♀)

times longer than broad; eye spots absent; single, median transverse furrow present. Tergites II-X and sternites IV-X divided. Tergal chaetotaxy: ♂, 15-19 : 18-23 : 18-22 : 19-25 : 21-27 : 20-24 : 20-24 : 19-24 : 18-28 : 16-19 : T2-3T2-3T2-3T : 2; ♀, 16-20 : 19-23 : 19-22 : 21-25 : 20-26 : 20-27 : 22-26 : 20-28 : 19-26 : 18-24 : T2-3T1-2T2-3T : 2. Sternal chaetotaxy: ♂, 0 : 15-22 : (3)10-14[3-5](2-4) : (3-4)7-16(4) : 21-26 : 21-28 : 22-27 : 21-27 : 20-25 : 18-20 : T2-3T2-3T2-3T : 2; ♀, 0 : 16-21 : (3-4)5-8(3-4) : (3-4)7-11(3-4) : 16-25 : 22-28 : 23-27 : 20-27 : 21-26 : 18-23 : T2-3T2-3T1-3T : 1-2. Coxal chaetotaxy: ♂, 13-17 : 14-19 : 13-19 : 27-38; ♀, 13-17 : 15-18 : 16-22 : 36-46 (the latter includes several setae on dorsal edge above pedal foramen). Male genital opercula (Fig. 1) with three to four pairs of long setae,

three to five pairs of short setae and one pair of slit sensilla on anterior operculum. Female genital opercula (Fig. 2) with two to three pairs of long setae, four to five pairs of slightly shorter setae and one pair of slit sensilla on anterior operculum; anterior operculum with medial stripe. Male genitalia large and conspicuous, with no obvious distinctive characters. Female genitalia with long, T-shaped spermathecae (Fig. 3). Leg IV (Fig. 5) with three tactile setae: one distally on telofemur; one distally on tibia; and one submedially on tarsus, TS = 0.36-0.43 (♂), 0.33-0.47 (♀). All tarsi with proximal elevated slit sensillum (Figs. 16-17). Claws simple.

Dimensions (mm) ♂ (♀): Body length 1.2-1.7 (1.4-2.4); pedipalps: trochanter 0.24-0.275/0.135-0.155



Figs. 1-10: *Lamprochernes savignyi* (Simon). **1** Genital opercula, ventral view, male, MH458.01; **2** Same, female, MH458.11; **3** Spermathecae, female, MH458.11; **4** Galea, female, MH458.11; **5** Left leg IV, lateral view, male, MH458.01; **6** Left chela, lateral view, male, MH458.01; **7** Same, tritonymph, MH458.299; **8** Same, deutonymph, MH458.530; **9** Same, protonymph, MH458.790; **10** Right pedipalp, dorsal view, male, MH458.01. Scale line = 0.12 mm (1-3), 0.09 mm (4), 0.50 mm (5-10).

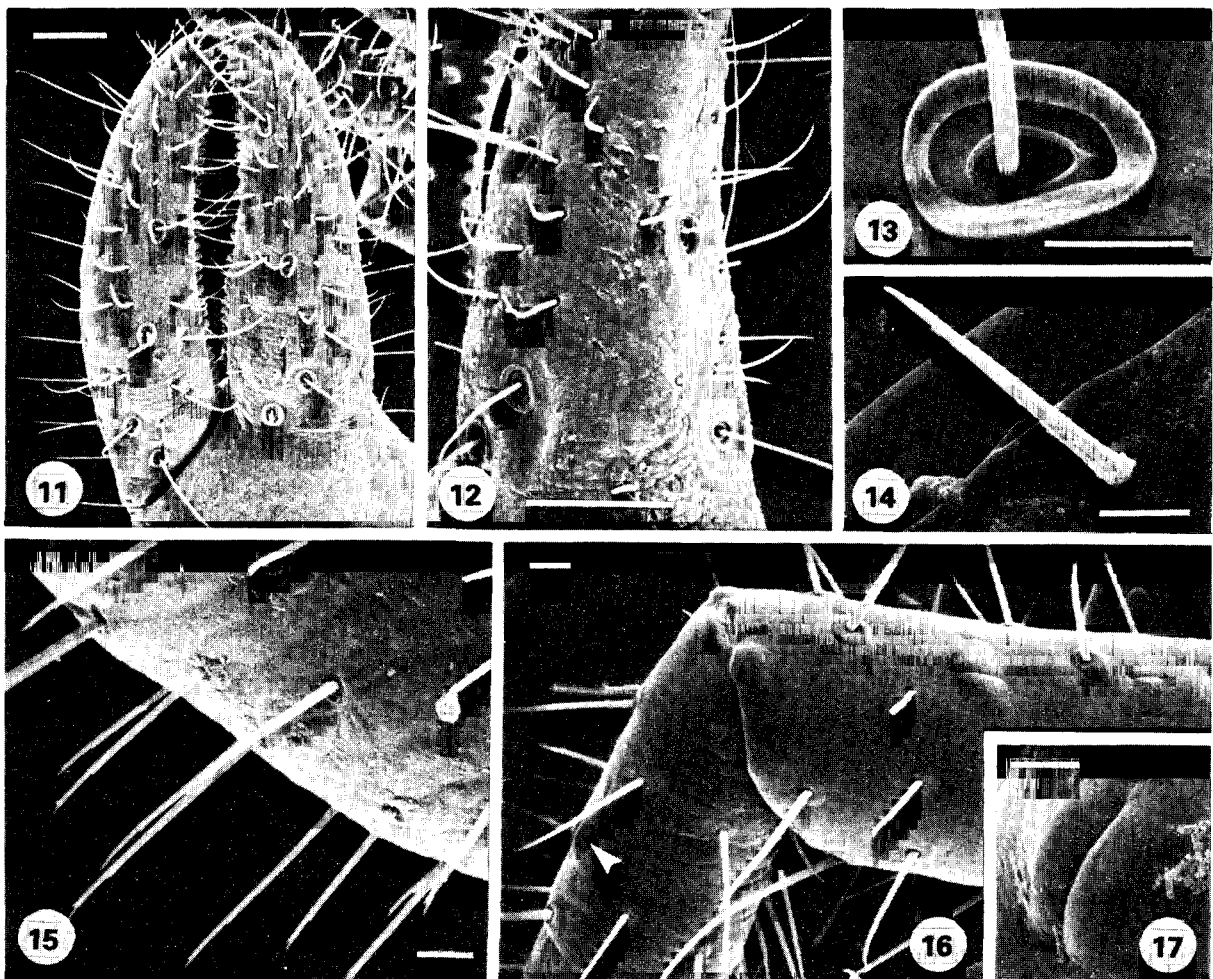
(0.27-0.315/0.14-0.17), femur 0.365-0.42/0.165-0.185 (0.405-0.46/0.17-0.20), tibia 0.365-0.41/0.18-0.19 (0.405-0.455/0.185-0.215), chela (with pedicel) 0.685-0.75/0.22-0.245 (0.75-0.85/0.255-0.30), chela (without pedicel) 0.625-0.695 (0.695-0.77), moveable finger length 0.32-0.375 (0.365-0.405); chelicera 0.19-0.20/0.08-0.10 (0.205-0.23/0.09-0.11), moveable finger length 0.155-0.17 (0.155-0.18); carapace 0.455-0.525/0.36-0.405 (0.52-0.67/0.405-0.535); leg I: trochanter 0.10-0.105/0.075-0.085 (0.115-0.13/0.085-0.10), basifemur 0.12-0.155/0.075-0.11 (0.145-0.17/0.085-0.115), telofemur 0.195-0.23/0.085-0.095 (0.215-0.24/0.085-0.10), tibia 0.19-0.215/0.065-0.07 (0.21-0.24/0.065-0.075), tarsus 0.205-0.235/0.045-0.05 (0.225-0.26/0.05-0.055); leg IV: trochanter 0.15-0.18/0.095-0.11 (0.18-0.23/0.11-0.13), basifemur 0.135-0.15/0.095-0.11 (0.16-0.19/0.11-0.125), telofemur 0.265-0.29/0.115-0.13 (0.29-0.33/0.12-0.14), tibia 0.275-0.335/0.075-0.085 (0.295-0.34/0.085-0.10), tarsus 0.25-0.275/0.055-0.06 (0.27-0.315/0.06-0.07), distance of tarsal tactile seta from proximal margin 0.095-0.115 (0.09-0.145).

Tritonymphs: Pedipalp: trochanter 1.58-1.83, femur 2.07-2.25, tibia 1.84-2.06, chela (with pedicel) 2.67-2.86, chela (without pedicel) 2.56-2.64 times longer than broad. Fixed chelal finger with seven trichobothria

(*ist* absent), moveable chelal finger with three trichobothria (*sb* absent) (Fig. 7); one sense spot present distal to *eb*. Serrula exterior of chelicera with 16-17 lamellae; galea generally trifurcate, sometimes with further bifurcations. Carapace with 8-9 setae on posterior margin. Tergal chaetotaxy: 12 : 12-15 : 12-16 : 14-17 : 15-19 : 16-18 : 15-18 : 16-17 : 15-17 : 16-17 : T2T1-2T1-2T : 2. Sternal chaetotaxy: 0 : 3-4 : (2)4-6(2-3) : (3)6-8(3) : 16-17 : 17-18 : 16-18 : 14-18 : 15-18 : 14-16 : T1-2T2-3T1-2T : 2. Coxal chaetotaxy: 5-10 : 8-10 : 9-10 : 17-20.

Dimensions (mm): Body length 1.5-1.8; pedipalps: trochanter 0.19-0.22/0.12, femur 0.30-0.315/0.14-0.15, tibia 0.285-0.32/0.155, chela (with pedicel) 0.565-0.61/0.205-0.215, chela (without pedicel) 0.53-0.565, moveable finger length 0.275-0.295.

Deutonymphs: Pedipalp: trochanter 1.45-1.76, femur 1.90-2.11, tibia 1.81-1.91, chela (with pedicel) 2.87-2.96, chela (with pedicel) 2.70-2.81 times longer than broad. Fixed chelal finger with six trichobothria (*esb* and *ist* absent), moveable chelal finger with two trichobothria (*sb* and *st* absent) (Fig. 8); no sense spots present. Serrula exterior of chelicera with 13-15 lamellae; galea with two small distal and two medial rami. Carapace with 6-7 setae on posterior margin.



Figs. 11-17: *Lamprochernes savignyi* (Simon), scanning electron micrographs. 11-15, 17 male, MH458.61; 16 female, MH458.62. **11** Left chela, lateral view; **12** Same, dorsal view; **13** Trichobothrium *t*; **14** Seta of tergite I; **15** Distal end of pedipalpal femur, dorsal view; **16** Tibia and tarsus of right leg IV, arrow shows elevated slit sensillum of tarsus; **17** Elevated slit sensillum of left tarsus IV. Scale lines = 0.05 mm (11-12), 0.01 mm (13-16), 0.005 mm (17).

Tergal chaetotaxy: 9-10 : 9-10 : 9-10 : 10 : 10-11 : 9-10 : 10-11 : 9-11 : 10-11 : 10 : T1T2T1T : 2. Sternal chaetotaxy: 0 : 0 : (1)4-6(1) : (2)5-8(2) : 8-10 : 9-12 : 8-11 : 10-12 : 10 : 10-11 : T1T2T1T : 2. Coxal chaetotaxy: 4-5 : 6 : 6 : 6-9.

Dimensions (mm): Body length 1.1-1.3; pedipalps: trochanter 0.14-0.155/0.085-0.10, femur 0.19-0.225/0.095-0.11, tibia 0.19-0.215/0.105-0.115, chela (with pedicel) 0.39-0.43/0.135-0.15, chela (without pedicel) 0.365-0.405, moveable finger length 0.19-0.205.

Protonymphs: Pedipalp: trochanter 1.40-1.71, femur 1.75-1.88, tibia 1.75-1.88, chela (with pedicel) 3.00-3.10, chela (without pedicel) 2.86-2.95 times longer than broad. Fixed chelal finger with three trichobothria (*eb*, *et* and *isb* present), moveable chelal finger with one trichobothrium (*t* present) (Fig. 9); no sense spots present. Serrula exterior of chelicera with 12-13 lamellae; hand with four setae, *sbs* and *gs* absent; galea with one sub-basal and two distal rami. Carapace with 6 setae on posterior margin. Tergal chaetotaxy: 6 : 6 : 6 : 6 : 6 : 6 : 6 : 6 : TTTT : 2. Sternal chaetotaxy: 0 : 0 : (0)2(0) : (1-2)4(1-2) : 6 : 6 : 6 : 6 : 6 : 6 : TTTT : 2. Coxal chaetotaxy: 4 : 4-5 : 5 : 5.

Dimensions (mm): Body length 0.8-0.9; pedipalps: trochanter 0.105-0.12/0.07-0.075, femur 0.14-0.16/0.08-0.085, tibia 0.14-0.16/0.08-0.085, chela (with pedicel) 0.315-0.325/0.105, chela (without pedicel) 0.30-0.31, moveable finger length 0.15-0.165.

Remarks

The holotype of *C. savignyi* is lost (Mahnert, 1982; J. Heurtault, pers. comm.), but the redescription given by Beier (1932) for *L. savignyi* (possibly of the holotype) is well within the range noted above. The types of *C. brevifemoratus* are not present in the Muséum National d'Histoire Naturelle, Paris (J. Heurtault, pers. comm.), but the description presented by Balzan (1890, 1892), especially the measurements of the chelal segments, indicates that it is synonymous with *L. savignyi*. The type material of *C. godfreyi* is not present in BMNH or NMI and could not be located for study. Nevertheless, several specimens from the British Isles (including a female identified by H. W. Kew as *C. godfreyi* from Ireland; J. P. O'Connor, pers. comm.) have been examined and they undoubtedly represent *L. savignyi*. No important differences could be detected between the type material of *C. pygmaeus*, *C. celerrimus* and *P. linsdalei* and the remaining specimens which would warrant the retention of separate species. Morikawa's description of *M. katoi* is sufficient to indicate that it too is synonymous with *L. savignyi*.

Lamprochernes savignyi is widely distributed, undoubtedly due to human introductions. It has been recorded from Egypt, Israel, Sudan, Chad, South Africa, Mauritius, Reunion Is., Seychelles Is., Britain, Denmark, India, Japan, Argentina, Paraguay, Uruguay, Brazil, Ecuador, Grenada, U.S.A., New Zealand, Australia and possibly Kenya. It appears to be most commonly found near human habitations, and like other members of the genus (Beier, 1948; Jones,

1978) is not uncommonly phoretic on flies. The native distribution of this species is difficult to ascertain, but many of the African specimens appear to have been collected away from sites of human habitation, and it is likely that this represents its source.

The sub-medial position of the tarsal tactile seta of leg IV has often been cited as a specific character for this species, but even though the TS ratios are higher than those of other species, there is considerable overlap. For example, Gabbutt (1972) recorded for *L. nodosus* TS ratios of 0.32-0.39 (♂) and 0.31-0.39 (♀), whereas the ratios of *L. savignyi* are slightly higher: 0.36-0.43 (♂), 0.33-0.47 (♀).

Klausen & Totland (1977) examined the setae of six species of Chernetidae and found that those of *L. nodosus* invariably possess five spines. *Lamprochernes savignyi* differs in possessing only three (occasionally four) such spines (Figs. 14-16).

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