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Comparative Morphology of the Alimentary Canal and Reproductive Organs of the Terrestrial Caraboidea (Coleoptera: Adephaga) Part 3

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Abstract. This is the third in a series of papers describing and comparing, by means of dissection and light microscopy, the alimentary canal and reproductive organs of the carabid beetles. This paper covers the subfamilies Elaphrinae, Scaritinae, Broscinae, Trechinae, Bembidiinae, Patrobinae, Pterostichinae, Zabrinae, Harpalinae, Licininae, Callistinae, Odacanthinae, Pentagonicinae, Lebiinae, Zuphinae, and Brachininae.

Key words: terrestrial Caraboidea; comparative morphology; alimentary canal; reproductive organ.

Introduction

The superfamily Caraboidea is one of the largest group of the order Coleoptera comprising more than 30,000 species from the world and about 1,300 species from Japan at present.

Though their classification into higher taxa above and below the tribe level is fairly stable and accepted by many authors, the phylogenetic system above the subfamily level and the ranking of higher taxa are in the state of discordance and various systems have been proposed based on the morphology and anatomy of the various organs, larvae, and molecular data by Jeannel (1941-42), Reichenbach-Klinke (1953), Crowson (1955), Bell (1967), Lindroth (1961-69), Kryzhanovsky (1976), Burmeister (1976), Bils (1976), Baehr (1979), Erwin and Sims (1984), Deuve (1988), Beutel (1992), Maddison *et al.* (1999), Shull *et al.* (2001), Beutel *et al.* (2008).

The present study aims to contribute to the phylogenetic system of the terrestrial Caraboidea on the basis of the comparative morphology of the alimentary canal and reproductive organs of many species. The first part (Yahiro, 1996) covered the families Rhysodidae, Paussidae, Omophronidae and Cicindelidae, and the second part (Yahiro, 1998) covered subfamilies Carabinae and Nebrinae in the family Carabidae. This third part treats the subfamilies Elaphrinae, Scaritinae, Broscinae, Trechinae, Bembidiinae, Patrobinae, Pterostichinae,

Zabrinae, Harpalinae, Licininae, Callistinae, Odacanthinae, Pentagonicinae, Lebiinae, Zuphinae, and Brachininae in the family Carabidae.

Materials and methods

1. Material examined

The following taxa were used.

Elaphrinae: *Elaphrus comatus* Goulet, 1983.

Scaritinae: *Scarites acutidens* Chaudoir, 1855, *S. aterrimus* Morawitz, 1863, *S. sulcatus* Oliver, 1795.

Broscinae: *Broscosoma doenitzi* (Harold, 1881), *Craspedonotus tibialis* Schaum, 1863.

Trechinae: Perileptini, *Perileptus japonicus* Bates, 1873; Trechini, *Epaphiosis janoi* (Jeannel, 1937), *Trechus ephippiatus* Bates, 1873.

Bembidiinae: Tachyini, *Tachyura fumicata* (Motchulsky, 1851), *T. laetifica* (Bates, 1873), Bembidiini, *Bembidion tetraporum* Bates, 1883.

Patrobinae: *Archipatrobus flavipes* (Motchulsky, 1864), *Apatrobus kurosawai* Morita, 1986, *Diplous caligatus* Bates, 1873.

Pterostichinae: Morionini, *Morion boniense* Kasahara et Sato, 1990; Pterostichini, *Trigonotoma lewisii* Bates, 1873, *Pterostichus planicollis* (Motchulsky, 1860); Platynini, *Platynus magnus* (Bates, 1873), *Colpodes buehneri* Hope, 1831, *Colpodes lampros* Bates, 1873, *Colpodes rubriolus* Bates, 1883, *Dolichus halensis*

(Schaller, 1783), *Synuchus dulcigradus* (Bates, 1873).

Zabrinae: *Amara congrua* Morawitz, 1862.

Harpalinae: Anisodactylini, *Anisodactylus punctatipennis* Morawitz, 1862; Harpalini, *Harpalus capito* Morawitz, 1862, *H. vicarius* Harold, 1878.

Licininae: *Diplocheila zeelandica* (Redtenbacher, 1868)

Panagaeinae: *Dischissus japonicus* Andrewes, 1933.

Callistinae: *Haplochaenius costiger* (Chaudoir, 1856), *Chlaenius variicornis* Morawitz, 1863, *C. naeviger* Morawitz, 1862, *Lithochlaenius noguchii* (Bates, 1873).

Odacanthinae: *Archicolliuris bimaculata nipponica* Habu, 1963, *Ophionea ishii* Habu, 1962.

Pentagonicinae: *Pentagonica daimiela* Bates, 1892, *P. angulata* Bates, 1883.

Lebiinae: *Lebidia octoguttata* Morawitz, 1862, *L. bifenestrata* Morawitz, 1862, *Apristus cuprascens* Bates, 1873.

Zuphinae: *Galerita orientalis* Schmidt-Gobel, 1846, *Planetes puncticeps* Andrewes, 1919.

Brachininae: *Pheropsophus jessoensis* Morawitz, 1862, *P. javanus* (Dejean, 1825), *Brachinus scotomedes* Redtenbacher, 1868, *B. stenoderus* Bates, 1873.

2. Methods for dissection and observation

Living or preserved specimens in 70% alcohol were used. After measuring the body length, the elytra and hind wings were removed, and dissected in about 80 % alcohol solution under a binocular stereo microscope. The thoracic nota and the abdominal terga were also removed, then the alimentary canals and reproductive organs were taken out from the body and examined on slide glass after treating by 10% KOH solution over a water bath (60C°) for 10 to 15 minutes. These two organs were stained with hematoxylin or Bouin's fluid *in situ*. They were drawn and were finally measured.

3. Terminology

Terminology used for the various parts of the alimentary canal and reproductive organs was followed those outlined by Smrz (1982), Deuve (1991) and Yahiro (1996).

Results

1. Family Carabidae

1.1. Subfamily Elaphrinae

Elaphrus comatus Goulet, 1983.

(Fig. 1)

Alimentary canal

Alimentary canal 11.2 mm in length, almost 1.5 times as long as body; relative lengths of fore gut, mid gut, and hind gut 40 : 35 : 25.

Fore gut with oesophagus straight; crop large and bulbous; in proventriculus, main longitudinal folds with hairs along lateral margins, weakly convex, not sclerotized, while intermediate longitudinal folds not hairy, slightly convex, not sclerotized.

Mid gut curved to right and forming one dextral coil posteriorly, joining hind gut at 3rd abdominal segment; crypts rod-shaped, dense.

Hind gut with ileum meandering to left side; rectum medium in size; rectal glands elliptical, lying in ring around anterior of rectum.

Reproductive organs

Male. Testis small; vas deferens not coiled, vesicula seminalis absent; accessory glands long, curved to right side, contiguous to each other.

Female. Bursa copulatrix large and prolonged to right side; vagina narrow; spermatheca cylindrical, entering into basal part of bursa copulatrix; spermathecal duct short or poorly delineated.

1.2. Subfamily Scaritinae

Scarites acutidens Chaudoir, 1855

(Fig. 2)

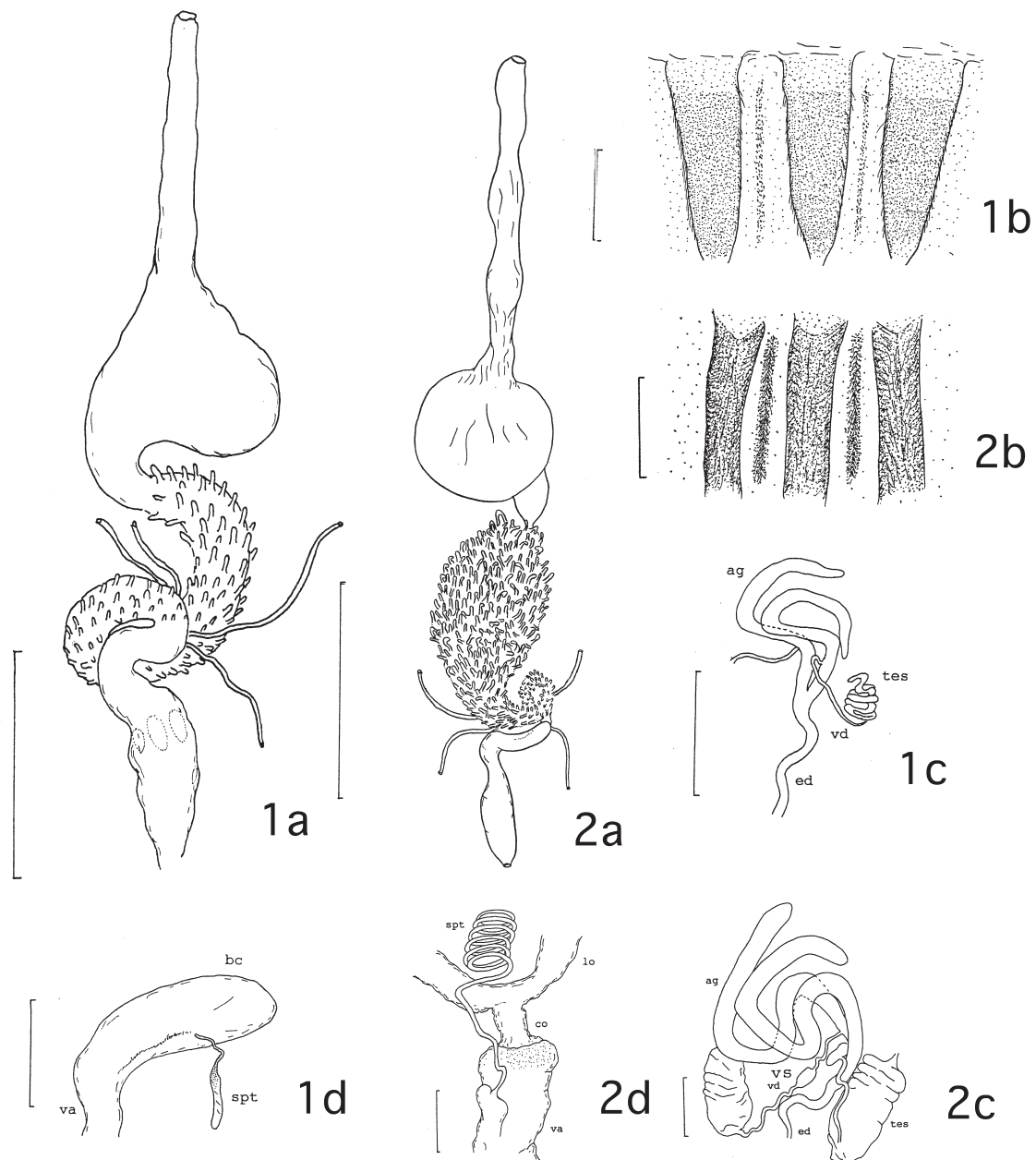
Alimentary canal

Alimentary canal 27.1 mm in length, almost 1.5 times as long as body; relative lengths of fore gut, mid gut and hind gut 37 : 33 : 30.

Fore gut with oesophagus straight; crop very large and bulbous; proventriculus moderately complicated, its main longitudinal folds strongly hirsute along entire length, strongly convex and with longitudinal ridge in center, not sclerotized, while intermediate longitudinal folds bearing hairs along center line, well convex, not sclerotized.

Mid gut with anterior part small, then swollen and broadest one fifth of way from cardia, gradually narrowing posteriorly, then curving to left and form one dextral coil, finally joining hind gut at 3rd abdominal segment; crypts long, rod-shaped, dense.

Hind gut with ileum curved upward to right side, then



Figs. 1-2. Alimentary canal and reproductive organ of *Elaphrus comatus* (Fig. 1), and *Scarites acutidens* (Fig. 2). a, alimentary canal; b, proventriculus; c, male reproductive organ; d, female reproductive organ. Scales: 2.5mm for 1a; 0.3mm for 1b; 0.5mm for 1c-d, 2b, and 2d; 5mm for 2a; 1.0mm for 2c.

meandering to left to form U-shape, joining rectum at center of 5th abdominal segment at angle of 90; rectum medium in size.

Reproductive organs

Male. Testis ovoid; vas deferens not coiled, with vesicula seminalis distinct; accessory glands long, curved to right side and forming S-shape, contiguous to each other.

Female. Spermatheca very long, tubular, entering into

dorsal side of vagina; vagina swollen at deriving point of spermatheca; common oviduct directly connecting to vagina.

Scarites aterrimus Morawitz, 1863

(Fig. 3)

Alimentary canal

Alimentary canal 15.5 mm in length, almost 1.5 times as long as body; relative lengths of fore gut, mid gut and

hind gut 43 : 33 : 24.

Fore gut with oesophagus straight and small; crop medium in size; proventriculus moderately complicated, its main longitudinal folds strongly hirsute along hairs in entire length, strongly convex with longitudinal ridge at center, not sclerotized, while intermediate longitudinal folds hairy along center line, well convex, not sclerotized.

Mid gut with anterior part straight and posterior part slightly curved, joining hind gut in right side of 3rd abdominal segment; crypts long, rod-shaped, dense.

Hind gut with ileum slightly meandering, joining rectum in center of 5th abdominal segment; rectum medium in size.

Reproductive organs

Male. Testis ovoid; vas deferens not coiled, with distinct vesicula seminalis; accessory glands long, curved to right side and forming S-shape, contiguous to each other.

Female. Spermatheca very long, tubular, entering into dorsal side of vagina; vagina swollen at deriving point of spermatheca; common oviduct directly connecting to vagina.

Scarites sulcatus Oliver, 1795

(Fig. 4)

Alimentary canal

Alimentary canal 27.1 mm in length, almost 1.4 times as long as body; relative lengths of fore gut, mid gut and hind gut 37 : 33 : 30.

Fore gut with oesophagus straight and small; crop small; proventriculus moderately complicated, its main longitudinal folds strongly hirsute along entire length, strongly convex with longitudinal ridge in center, not sclerotized, while intermediate longitudinal folds hairy in center line, well convex, not sclerotized.

Mid gut with anterior part straight, gradually narrowing posteriorly, then curved to left and forming one dextral coil, joining hind gut in right side of 3rd abdominal segment; crypts long, rod-shaped, dense.

Hind gut with ileum curved to left side and forming C-shape, joining rectum in center of 5th abdominal segment; rectum medium in size.

Reproductive organs

Male. Testis ovoid; vas deferens not coiled, with distinct vesicula seminalis; accessory glands long, curved to right side and forming S-shape, contiguous to each other.

Female. Spermatheca very long, tubular, entering into vagina through dorsal side; vagina swollen at deriving point of spermatheca; accessory gland present on right side; common oviduct directly connecting to vagina.

1.3. Subfamily Broscinae

Broscosoma doenitzi (Harold, 1881)

(Fig. 5)

Alimentary canal

Alimentary canal 15.2 mm in length, almost 1.7 times as long as body; relative lengths of fore gut, mid gut and hind gut 46 : 30 : 24.

Fore gut with oesophagus straight and thin; crop small; in proventriculus, main longitudinal folds simple with hairs on lateral margins, not sclerotized, while intermediate longitudinal folds weakly convex, hairy along center line, slightly convex, not sclerotized.

Mid gut with anterior part about twice as broad as posterior part, extending from 1st to 4th abdominal segment, then curving to right to form one dextral coil, joining hind gut in left side of 3rd abdominal segment; crypts short, rod-shaped, dense.

Hind gut with ileum meandering to form S-shape in 4th abdominal segment; rectum medium in size; rectal glands elliptical, lying in single ring around anterior part of rectum.

Reproductive organs

Male. Testis ovoid; vas deferens slightly meandering, vesicula seminalis absent; accessory glands long and curved.

Female. Spermatheca long, tubular, with acuminate sclerite in basal part; vagina with accessory gland on right side; common oviduct directly connecting to vagina.

Craspedonotus tibialis Schaum, 1863

(Fig. 6)

Alimentary canal

Alimentary canal 32.5 mm in length, almost 1.5 times as long as body; relative lengths of fore gut, mid gut, and hind gut 41 : 33 : 26.

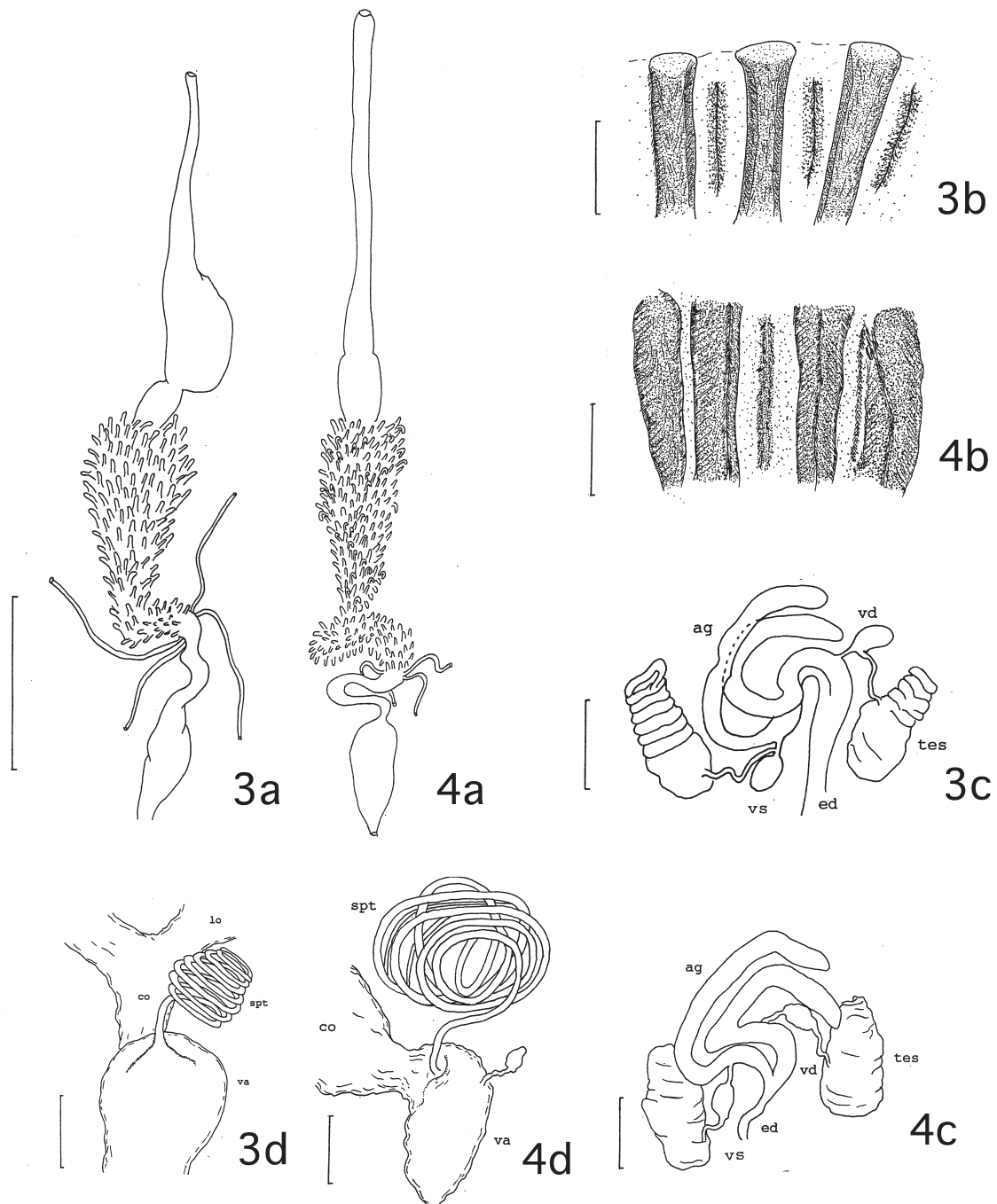
Fore gut with oesophagus straight and short; crop large, bulbous; in proventriculus, main longitudinal folds simple with hairs on lateral margins, weakly convex, while intermediate longitudinal folds hairy in center, slightly convex, not sclerotized.

Mid gut with anterior part straight and then curved to left, joining hind gut in left side of 3rd abdominal segment; crypts short, rod-shaped, dense.

Hind gut with ileum slightly meandering in 4th abdominal segment; rectum medium in size; rectal glands elliptical, lying in single ring around anterior part of rectum.

Reproductive organs

Male. Testis ovoid; vas deferens slightly meandering, vesicula seminalis absent; accessory glands long and



Figs. 3-4. Alimentary canal and reproductive organ of *Scarites aterrimus* (Fig. 3), and *Scarites sulcatus* (Fig. 4). a, alimentary canal; b, proventriculus; c, male reproductive organ; d, female reproductive organ. Scales; 5.0mm for 3a and 4a; 0.5mm for 3b; 1.0mm for 3c-d and 4b-d.

S-shaped.

Female. Spermatheca clavate; spermathecal duct short, entering into acuminate vaginal sclerite; vagina with accessory gland on right side; common oviduct directly connecting to vagina.

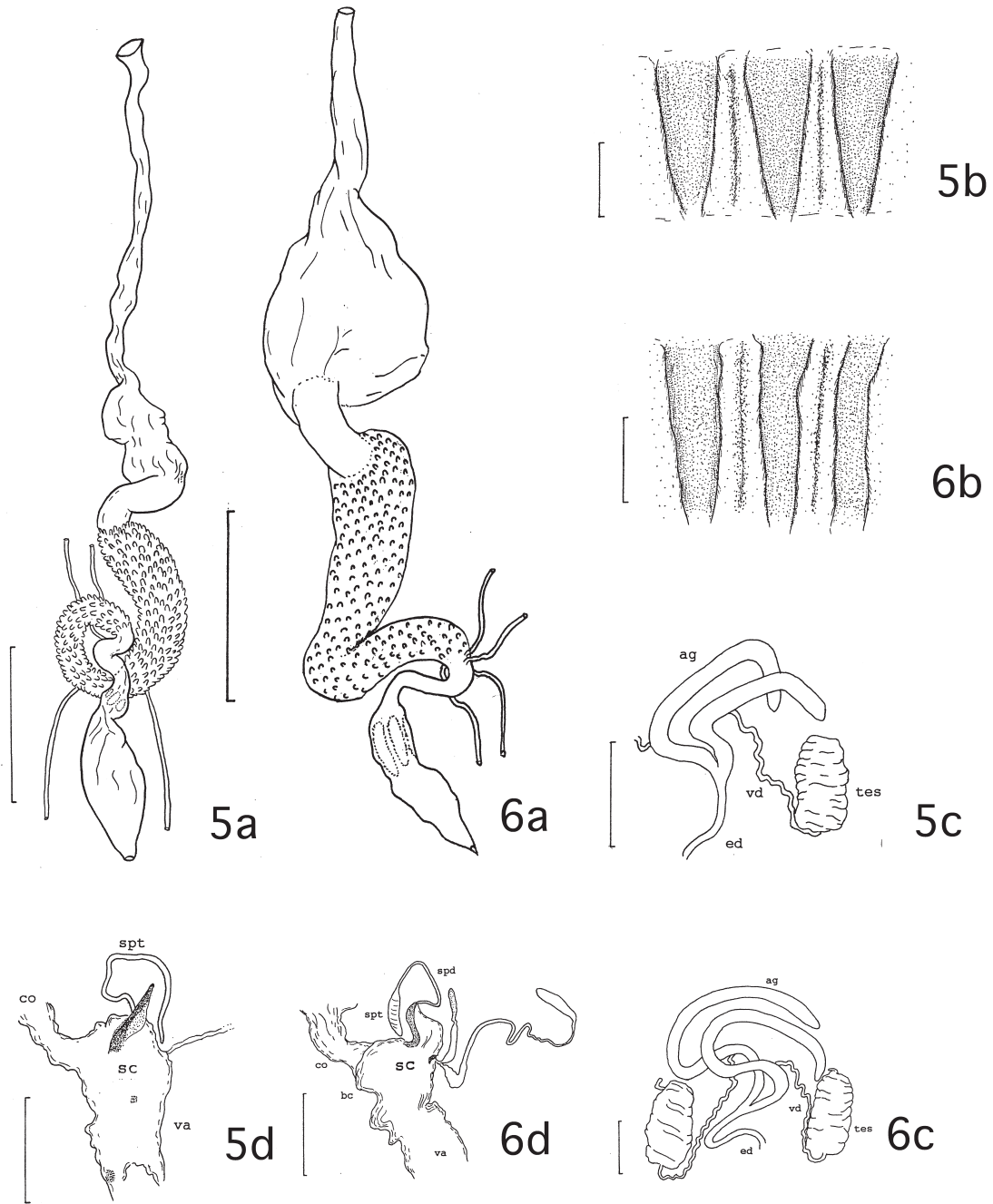
1.4. Subfamily Trechinae

Perileptus japonicus Bates, 1873

(Fig. 7)

Alimentary canal

Alimentary canal 2.9 mm in length, almost 1.4 times as long as body; relative lengths of fore gut, mid gut, and



Figs. 5-6. Alimentary canal and reproductive organ of *Broscosoma doenitzi* (Fig. 5), and *Craspednotus tibialis* (Fig. 6). a, alimentary canal; b, proventriculus; c, male reproductive organ; d, female reproductive organ. Scales; 3.0mm for 5a; 0.3mm for 5b; 0.5mm for 5c-d; 5.0mm for 6a; 1.0mm for 6b-d.

hind gut 41 : 25 : 34.

Fore gut with oesophagus straight; crop small; proventriculus moderately complicated, its main longitudinal folds with hairs along lateral margins, knobby posteriorly, not sclerotized, while intermediate longitudinal folds with short hairs along median ridge and with horizontal furrows, well convex, not sclerotized.

Mid gut straight; crypts long, rod-shaped, sparse.

Hind gut with ileum curved to right and forming one dextral coil; rectum medium in size.

Reproductive organs

Male. Testis ovoid; vas deferens short, vesicula seminalis absent; accessory glands elliptical, with narrow ducts leading into subconical swollen parts, latter fused at midline.

Female. Bursa copulatrix bulbous; spermatheca

clavate, sclerotized, abruptly bent at midlength; spermathecal duct long, gently curved, entering into right side of bursa copulatrix.

Epaphiosis janoi (Jeannel, 1937)

(Fig. 8)

Alimentary canal

Alimentary canal 4.5 mm in length, almost 1.5 times as long as body; relative lengths of fore gut, mid gut, and hind gut 54 : 20 : 26.

Fore gut with oesophagus straight; crop small; proventriculus moderately complicated, its main longitudinal folds hairy along a lateral margins, and minutetriangular spinules anterior end, and minute knobs at posterior end, not sclerotized, while intermediate longitudinal folds with short hairs along median ridge and with horizontal furrows, well convex, not sclerotized.

Mid gut straight; crypts long, rod-shaped, dense.

Hind gut with ileum curved to right and forming one dextral coil; rectum medium in size; rectal glands elliptical, lying in ring around anterior part of rectum.

Reproductive organs

Male. Testis ovoid; vas deferens short, vesicula seminalis absent; accessory glands with ovoid posterior part connected via long, curved duct to clavate proximal part.

Female. Bursa copulatrix bulbous; spermatheca clavate, sclerotized, entering anteriorly into right side of bursa copulatrix.

Trechus ephippiatus Bates, 1873

(Fig. 9)

Alimentary canal

Alimentary canal 3.9 mm in length, almost 1.1 times as long as body; relative lengths of fore gut, mid gut, and hind gut 49 : 21 : 30.

Fore gut with oesophagus straight; crop small; proventriculus moderately complicated, its main longitudinal folds with hairs along lateral margins, knobby posteriorly, not sclerotized, while intermediate longitudinal folds with short hairs on median ridge and with horizontal furrows, well convex, not sclerotized.

Mid gut straight; crypts long, rod-shaped, sparse.

Hind gut with ileum curved to right and forming one dextral coil; rectum medium in size; rectal glands elliptical, lying in ring around anterior part of rectum.

Reproductive organs

Male. Vas deferens short, vesicula seminalis absent; accessory glands U-shaped, thick, fused at their slightly hooked distal ends both thick, at hooked base, confused.

Female. Bursa copulatrix bulbous; with lobe-like process on left side; spermatheca oval, sclerotized, enter-

ing into process of bursa copulatrix.

1.5. Subfamily Bembidiinae

Tachyura fumicata (Motschulsky, 1851)

(Fig. 10)

Alimentary canal

Alimentary canal 2.8 mm in length, almost 1.4 times as long as body; relative lengths of fore gut, mid gut, and hind gut 45 : 25 : 30s.

Fore gut with oesophagus straight; crop bulbous; proventriculus complicated, its main longitudinal folds tongue-like, knobby and sclerotized posteriorly, with hairs on lateral margins and dense hairs anteriorly, while intermediate longitudinal folds with short hairs on median ridge and with horizontal furrows, well convex, not sclerotized.

Mid gut gently curved to right side; crypts long stick-shaped.

Hind gut with ileum curved to right and forming one dextral coil; rectum medium in size; rectal glands elliptical, lying in ring around anterior part of rectum.

Reproductive organs

Male. Testis subglobular; vas deferens short, vesicula seminalis absent; accessory glands thick, short.

Female. Bursa copulatrix bulbous; spermatheca clavate; spermathecal duct long, sinuate, entering into bursa copulatrix from ventral side; spermathecal gland tubular, derived from about middle of spermatheca; common oviduct connecting with bursa copulatrix on upper side.

Tachyura laetifica (Bates, 1873)

(Fig. 11)

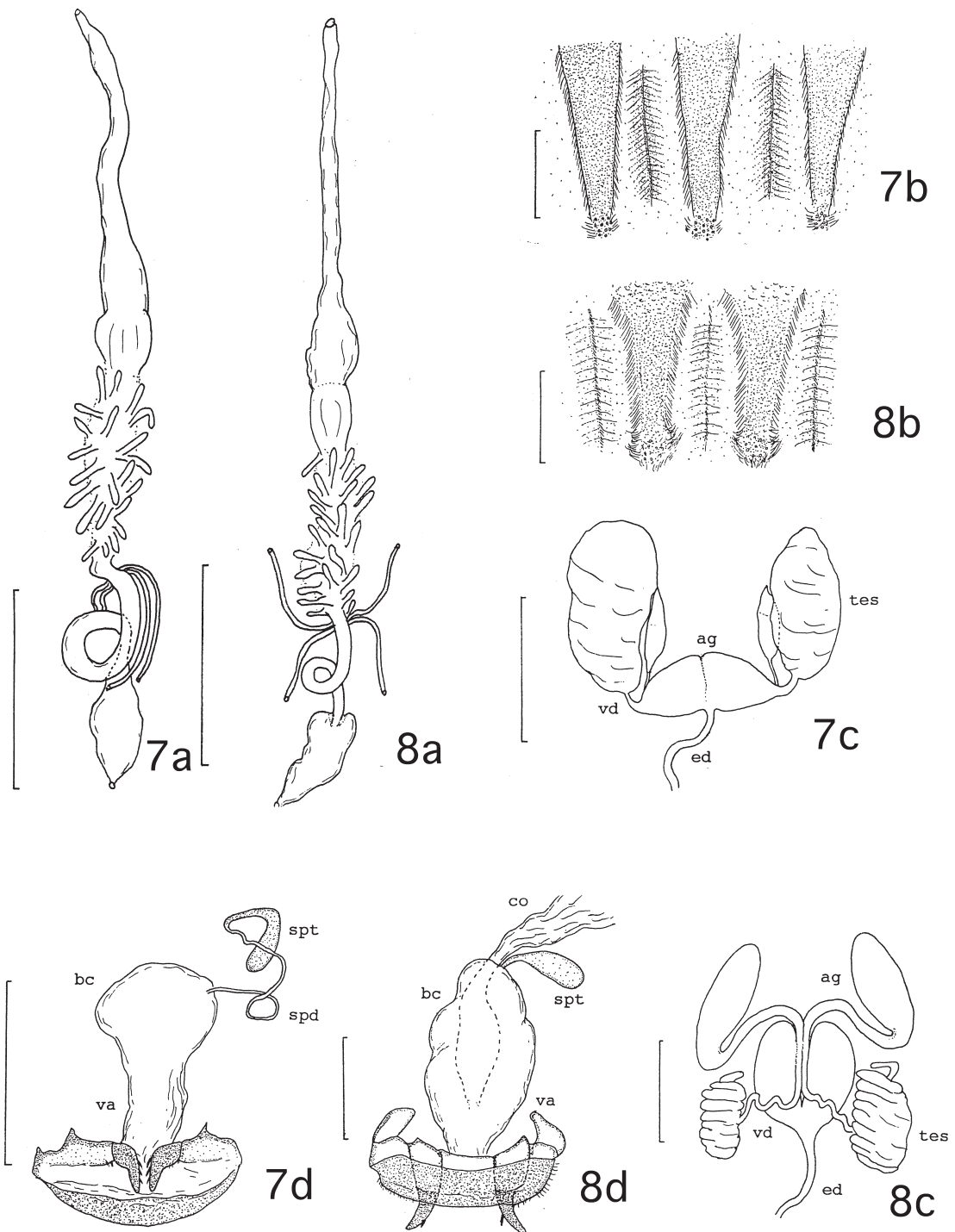
Alimentary canal

Alimentary canal 3.3 mm in length, almost 1.3 times as long as body; relative lengths of fore gut, mid gut, and hind gut 42 : 26 : 32.

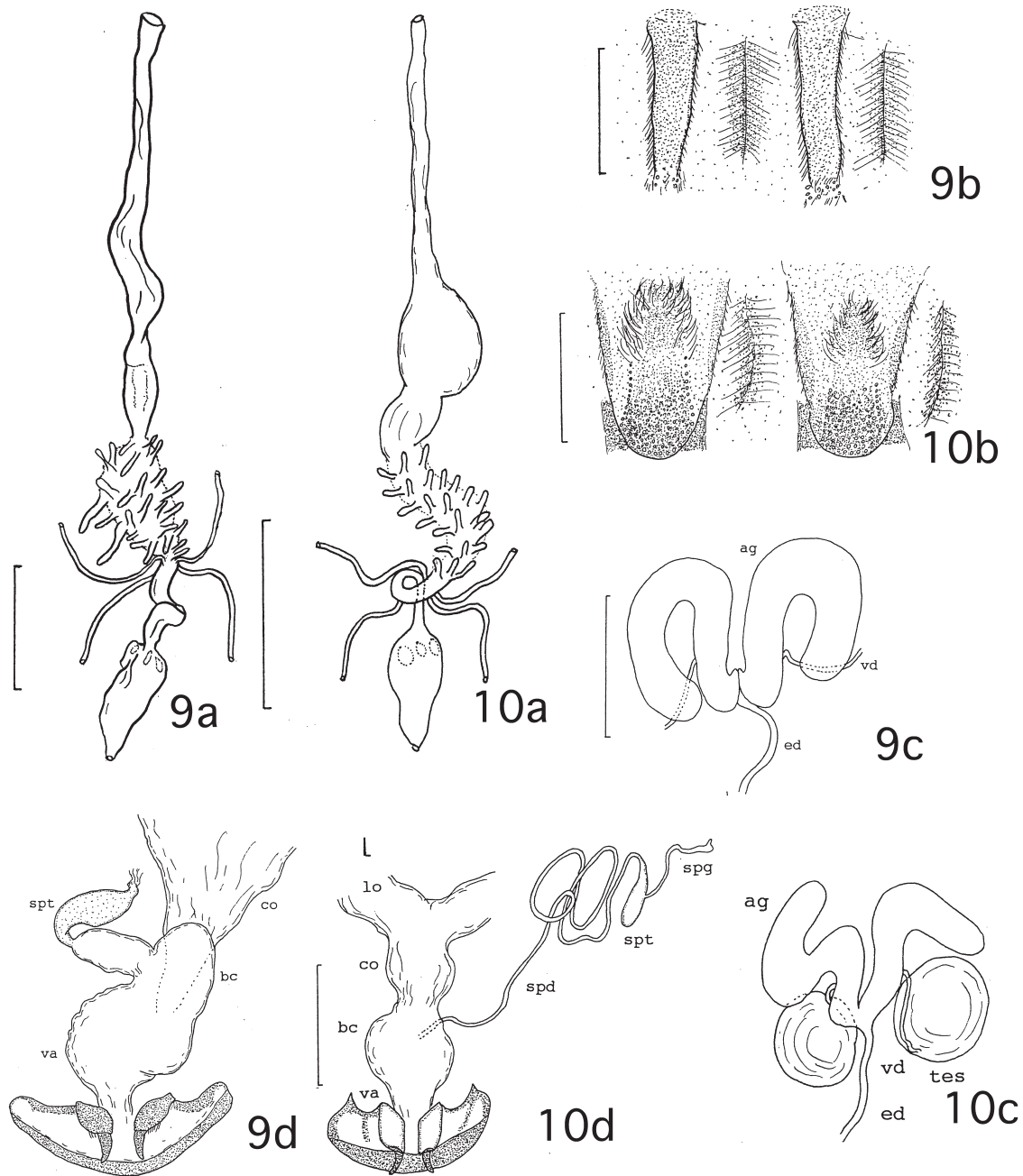
Fore gut with oesophagus straight; crop bulbous; proventriculus complicated, its main longitudinal folds tongue-like, knobby and sclerotized posteriorly, with hairs on lateral margins and dense hairs in center and strong setae anteriorly, while intermediate longitudinal folds with short hairs on median ridge and with horizontal furrows, well convex, not sclerotized.

Mid gut gently curved to right side; crypts long, rod-shaped.

Hind gut with ileum curved to right and forming one dextral coil; rectum medium in size; rectal glands elliptical, lying in ring around anterior part of rectum.



Figs. 7-8. Alimentary canal and reproductive organ of *Perileptus japonicus* (Fig. 7), and *Epaphiosis janoi* (Fig. 8). a, alimentary canal; b, proventriculus; c, male reproductive organ; d, female reproductive organ. Scales; 0.6mm for 7a; 0.1mm for 7b; 0.5mm for 7c-d and 8c-d; 1.0mm for 8a; 0.3mm for 8b.



Figs. 9-10. Alimentary canal and reproductive organ of *Trechus ephippiatus* (Fig. 9), and *Tachyura fumicata* (Fig. 10). a, alimentary canal; b, proventriculus; c, male reproductive organ; d, female reproductive organ. Scales; 1.0mm for 9a; 0.5mm for 9b-d, 10a, and 10c-d; 0.2mm for 10b.

Reproductive organs

Male. Testis subglobular; vas deferens short, vesicula seminalis absent; accessory glands thick, short.

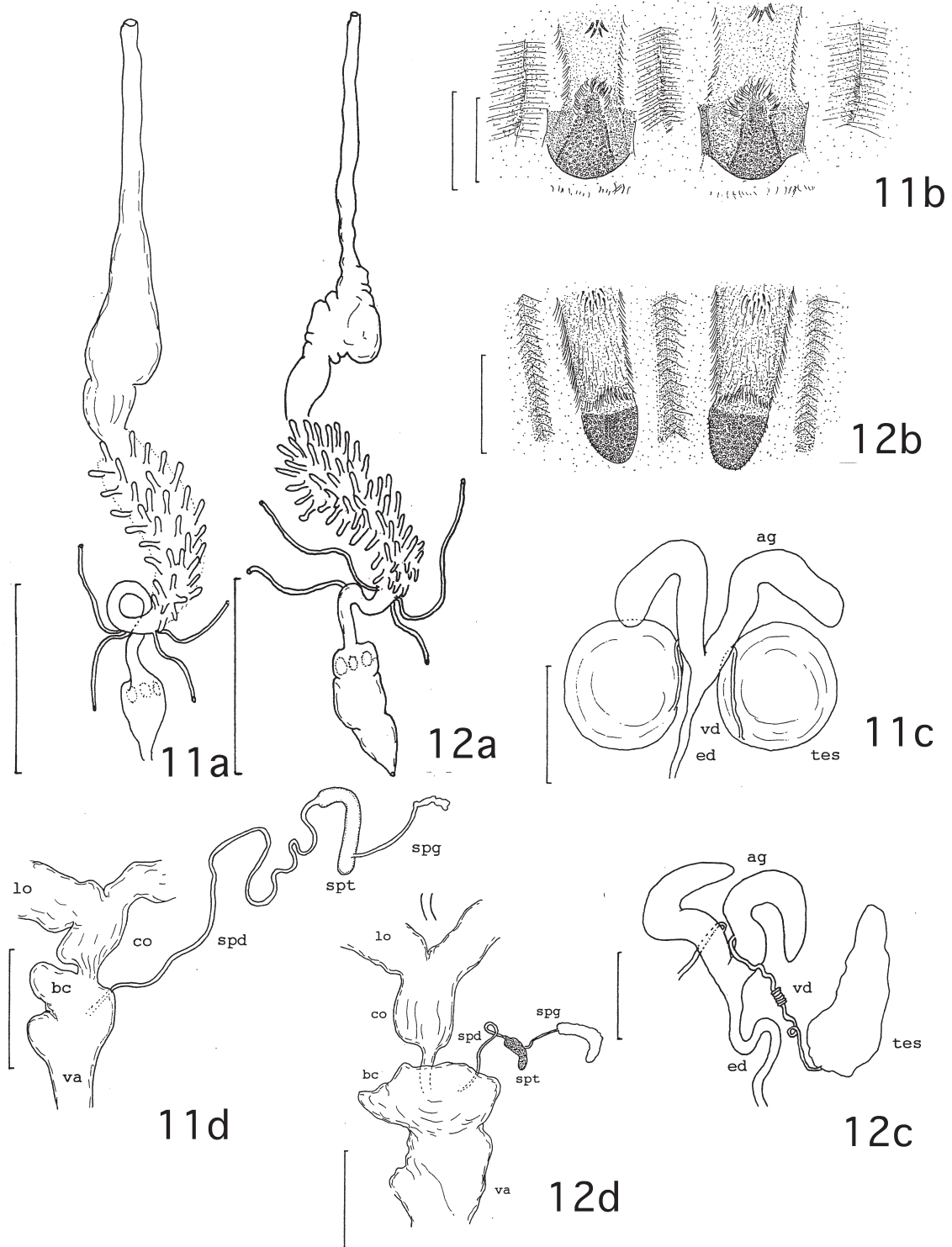
Female. Bursa copulatrix bulbous; spermatheca sous-age-shaped and bent; spermathecal duct long, sinuate, entering into bursa copulatrix from ventral side; spermathecal gland tubular, derived from near apex of spermatheca; common oviduct connecting with bursa copulatrix

on upper side.

***Bembidion tetraporum* Bates, 1883**
(Fig. 12)

Alimentary canal

Alimentary canal 4.8 mm in length, almost 1.1 times as long as body; relative lengths of fore gut, mid gut, and hind gut 46 : 21 : 33.



Figs. 11-12. Alimentary canal and reproductive organ of *Tachyura laetifica* (Fig. 11), and *Bembidion tetraporum* (Fig. 12). a, alimentary canal; b, proventriculus; c, male reproductive organ; d, female reproductive organ. Scales; 0.7mm for 11a; 0.1mm for 11b; 0.5mm for 11c; 0.2mm for 11d and 12b-c; 1.0mm for 12a; 0.3mm for 12d.

Fore gut with oesophagus straight; crop small; proventriculus complicated, its main longitudinal folds finger-like, knobby and sclerotized posteriorly, with hairs in entire length, especially with strong setae anteriorly, not sclerotized, while intermediate longitudinal folds with short hairs on median ridge and with horizontal furrows, well convex, not sclerotized.

Mid gut gently curved to right side; crypts rod-shaped, dense.

Hind gut with ileum meandering to left side; rectum medium in size; rectal glands elliptical, lying in ring around anterior part of rectum.

Reproductive organs

Male. Testis ovoid; vas deferens coiled at middle part, vesicula seminalis absent; accessory glands short, thick, curved to right side, narrowed toward apex.

Female. Bursa copulatrix transverse; spermatheca strongly sclerotized; spermathecal duct medium in length, entering into bursa copulatrix from ventral side; spermathecal gland from basal part to middle part small tubular and the remaining part larger and soft, derived from middle of spermatheca; common oviduct connecting with bursa copulatrix on ventral side.

1.6. Subfamily Patrobinae

Archipatrous flavipes (Motschulsky, 1864)

(Fig. 13)

Alimentary canal

Alimentary canal 19.0 mm in length, almost 1.3 times as long as body; relative lengths of fore gut, mid gut, and hind gut 36 : 21 : 33.

Fore gut with oesophagus straight and narrow; crop medium in size; proventriculus complicated, its main longitudinal folds finger-like, scattered setal lines at anterior part, knobby and sclerotized posteriorly, with hairs in entire length, while intermediate longitudinal folds not haired, weakly convex, not sclerotized.

Mid gut gently curved to right and forms one dextral coil; crypts hemispherical, dense.

Hind gut with ileum curved to right and forms one dextral coil; rectum large; rectal glands elliptical, lying in ring around anterior part of rectum.

Reproductive organs

Male. Testis ovoid; vas deferens coiled in entire length, vesicula seminalis absent; accessory glands straight, constricted and bent at apex.

Female. Bursa copulatrix ovoid, with crack longitudinally, with ring-like sclerite at left side of dorsal surface, ventral half weakly sclerotized; vagina with round sclerite at dorsal side; spermatheca narrow, stick shapedly;

spermathecal duct medium in length, entering into bursa copulatrix from dorsal side; spermathecal gland from basal part to middle part small tubular and the remaining part larger and soft, derived from near basal part of spermathecal duct; common oviduct connecting with bursa copulatrix on ventral side.

Apatrobus kurosawai Morita, 1986

(Fig. 14)

Alimentary canal

Alimentary canal 14.0 mm in length, almost 1.4 times as long as body; relative lengths of fore gut, mid gut, and hind gut 43 : 32 : 25.

Fore gut with oesophagus straight and narrow; crop large, bulbous; proventriculus complicated, its main longitudinal folds finger-like, scattered setal lines anteriorly, knobby and sclerotized posteriorly, and with hairs in entire length, while intermediate longitudinal folds not haired, weakly convex, not sclerotized.

Mid gut curved to right and forms one dextral coil; crypts hemispherical, dense.

Hind gut with ileum straight, then meandering to left side; rectum medium in size; rectal glands elliptical, lying in ring around anterior part of rectum.

Reproductive organs

Male. Testis ovoid; vas deferens coiled in entire length, vesicula seminalis absent; accessory glands straight, constricted and bent at apex.

Female. Bursa copulatrix ovoid, with crack longitudinally, with ring-like sclerite at dorsal left surface; vagina with longitudinal sclerite at dorsal side; spermatheca narrow, cord-like; spermathecal duct medium in length, entering into bursa copulatrix from dorsal side; spermathecal gland from basal part to middle part small tubular and the remaining part larger and soft, derived from basal part of spermathecal duct rounded; common oviduct connecting with bursa copulatrix on dorsal side; common oviduct swollen.

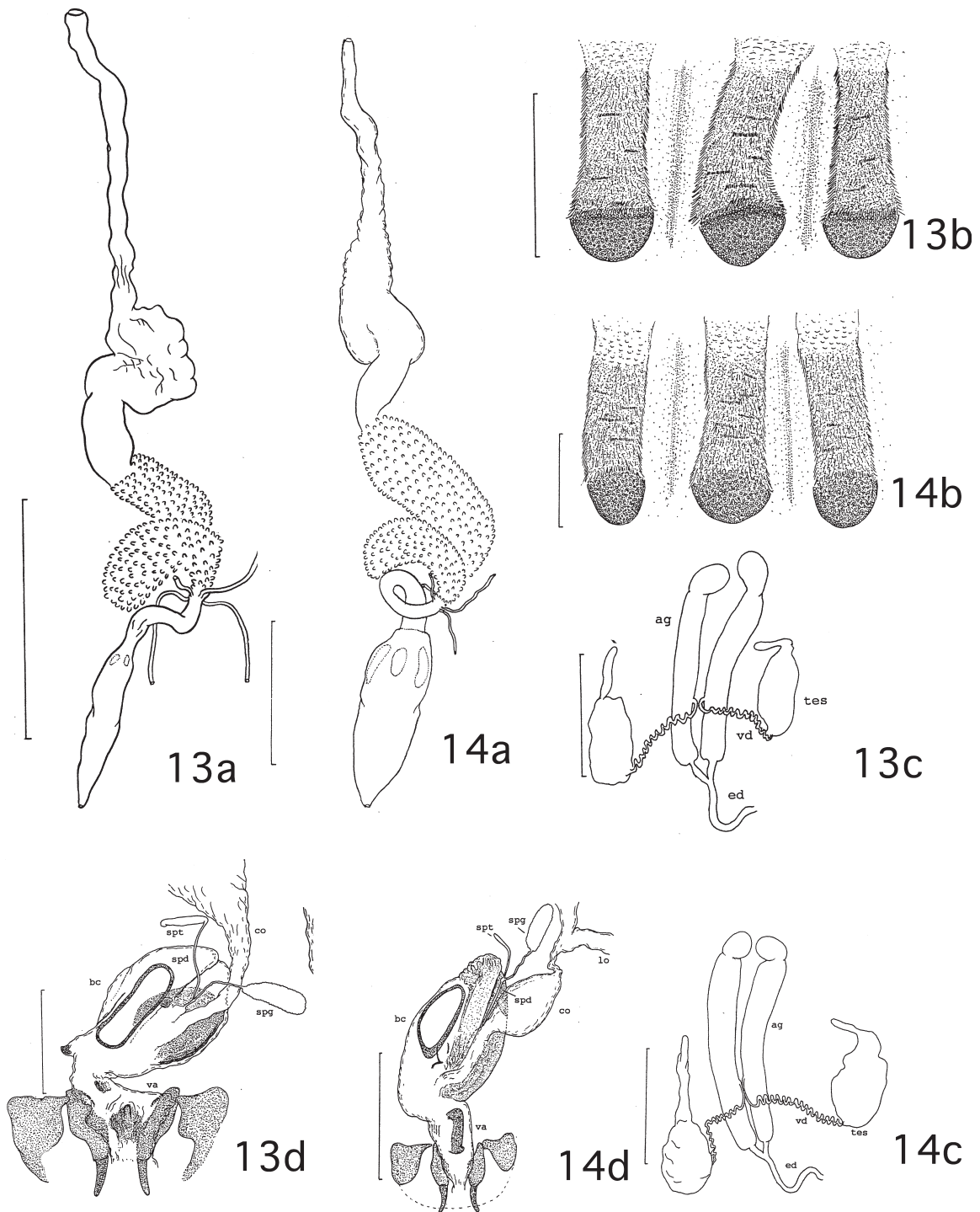
Diplous caligatus Bates, 1873

(Fig. 15)

Alimentary canal

Alimentary canal 18.5 mm in length, almost 1.5 times as long as body; relative lengths of fore gut, mid gut, and hind gut 38 : 32 : 30.

Fore gut with oesophagus straight and narrow; crop medium in size; proventriculus complicated, its main longitudinal folds finger-like, scattered setal lines anteriorly, knobby and sclerotized posteriorly, with hairs in entire length, while intermediate longitudinal folds not haired, weakly convex, not sclerotized.



Figs. 13-14. Alimentary canal and reproductive organ of *Archipatrobus flavipes* (Fig. 13), and *Apatrobus kurosawai* (Fig. 14). a, alimentary canal; b, proventriculus; c, male reproductive organ; d, female reproductive organ. Scales; 2.5mm for 13a; 0.4mm for 13b and 14b; 3.0mm for 13c and 14a; 1.5mm for 13d; 2.0mm for 14c; 1.3mm for 14d.

Mid gut curved to right and forms one dextral coil; crypts hemispherical, dense.

Hind gut with ileum straight, then meandering to left side; rectum medium in size; rectal glands elliptical, lying in ring around anterior part of rectum.

Reproductive organ

Male. Testis ovoid; vas deferens coiled in entire length, vesicula seminalis absent; accessory glands straight, constricted and bent at apex.

Female. Bursa copulatrix ovoid, with ring-like sclerite at ventral side; vagina with many small sclerite at dorsal side and two round sclerites at posterior part; spermatheca clavate; spermathecal duct short, entering into bursa copulatrix from right side; spermathecal gland from basal part to middle part small tubular and the remaining part larger and soft, derived from basal part of spermatheca; common oviduct directly connecting with upper side on bursa copulatrix.

1.7. Subfamily Pterostichinae

Morion boniense Kasahara et Sato, 1990

(Fig. 16)

Alimentary canal

Alimentary canal 18.0 mm in length, almost 1.2 times as long as body; relative lengths of fore gut, mid gut, and hind gut 44 : 22 : 35.

Fore gut with oesophagus straight; crop small; proventriculus moderately complicated, its main longitudinal folds with hairs in entire length, with scale-like ctenidia anteriorly, weakly knobby posteriorly, while intermediate longitudinal folds, not haired, weakly convex, not sclerotized.

Mid gut gently curved to left side; crypts rod-shaped, dense.

Hind gut with ileum meandering to left side; rectum medium in size; rectal glands elliptical, lying in ring around anterior part of rectum.

Reproductive organs

Male. Testis ovoid; vas deferens spiraled, long, between the middle of it and testis, vesicula seminalis absent; accessory glands S-shaped.

Female. Bursa copulatrix transverse, with very small sclerotized part at dorsal surface; spermatheca bipartite, one clavate, the other tubular, gently curved and tapered apically, sclerotized at basal part; spermathecal gland small tubular at base, with larger and ovoid apex, derived from middle part of spermatheca; common oviduct entering to bursa copulatrix on ventral side.

Trigonotoma lewisii Bates, 1873

(Fig. 17)

Alimentary canal

Alimentary canal 22.4 mm in length, almost 1.4 times as long as body; relative lengths of fore gut, mid gut, and hind gut 44 : 27 : 29.

Fore gut with oesophagus straight; crop medium in size; proventriculus complicated, its main longitudinal folds with hairs in entire length, with scale-like ctenidia anteriorly, weakly knobby posteriorly, intermediate longitudinal folds, not haired, weakly convex, not sclerotized.

Mid gut gently curved to left side; crypts rod-shaped, dense.

Hind gut with ileum meandering to left side; rectum medium in size; rectal glands elliptical, lying in ring around anterior part of rectum.

Reproductive organ

Male. Testis ovoid; vas deferens spiraled, long, between the middle of it and testis, vesicula seminalis absent; accessory glands S-shaped.

Female. Bursa copulatrix transverse, with very small sclerotized part at dorsal surface; spermatheca bipartite, one clavate, the other tubular, gently curved and tapered apically, sclerotized at basal part; spermathecal gland small tubular at base, with larger and ovoid apex, derived from middle part of spermatheca; common oviduct entering to bursa copulatrix on ventral side.

Pterostichus planicollis (Motschulsky, 1860)

(Fig. 18)

Alimentary canal

Alimentary canal 15.5 mm in length, almost 1.3 times as long as body; relative lengths of fore gut, mid gut, and hind gut 45 : 29 : 26.

Fore gut with oesophagus straight; crop small; proventriculus moderately complicated, its main longitudinal folds with hairs in entire length, knobby and sclerotized anteriorly, with scale-like ctenidia posteriorly, while intermediate longitudinal folds not haired, weakly convex, not sclerotized.

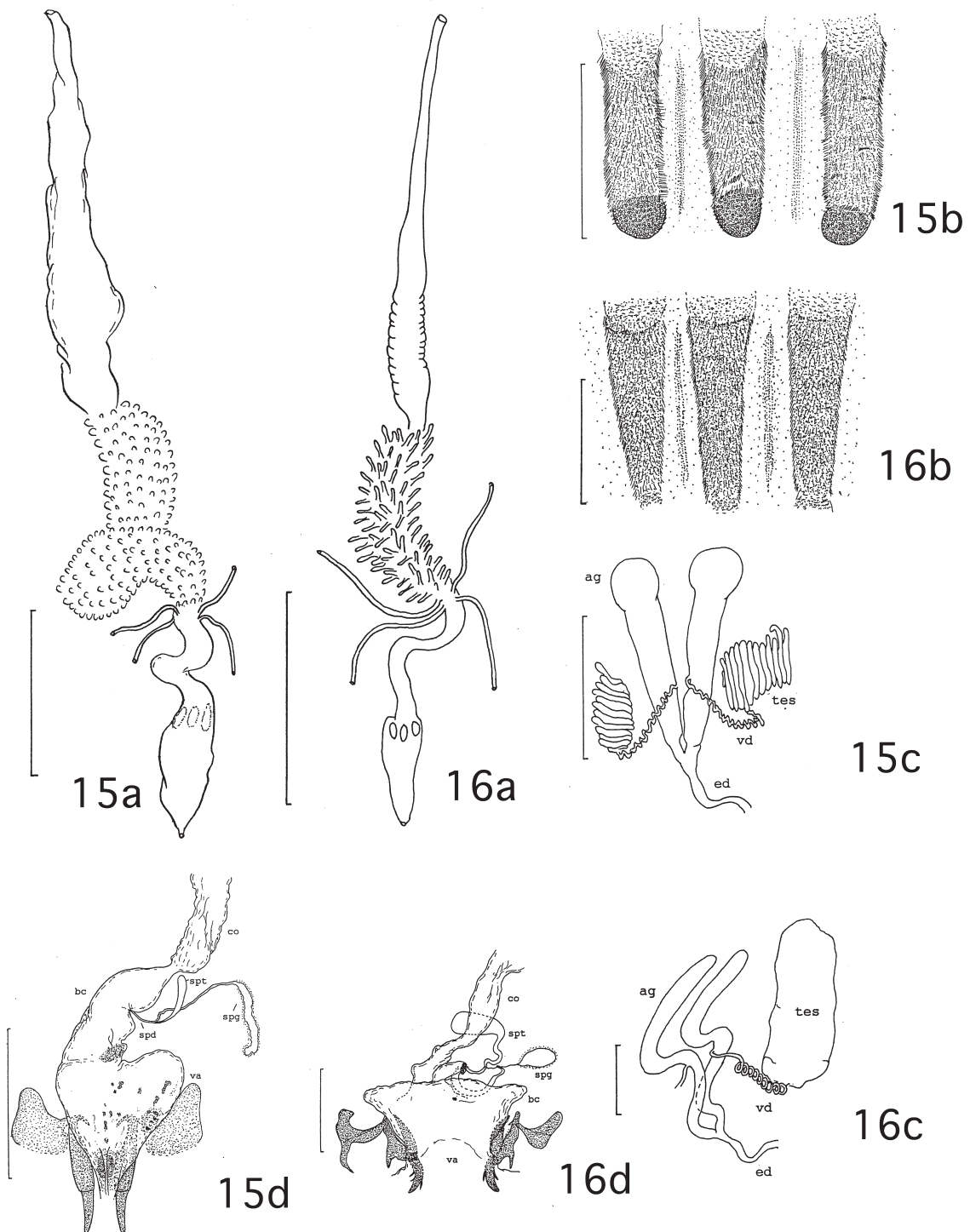
Mid gut straight, then curved to right side and forms one dextral coil; crypts long rod-shaped, dense.

Hind gut with ileum curved to right and forms one dextral coil; rectum medium in size; rectal glands large, elliptical, lying in ring around anterior part of rectum.

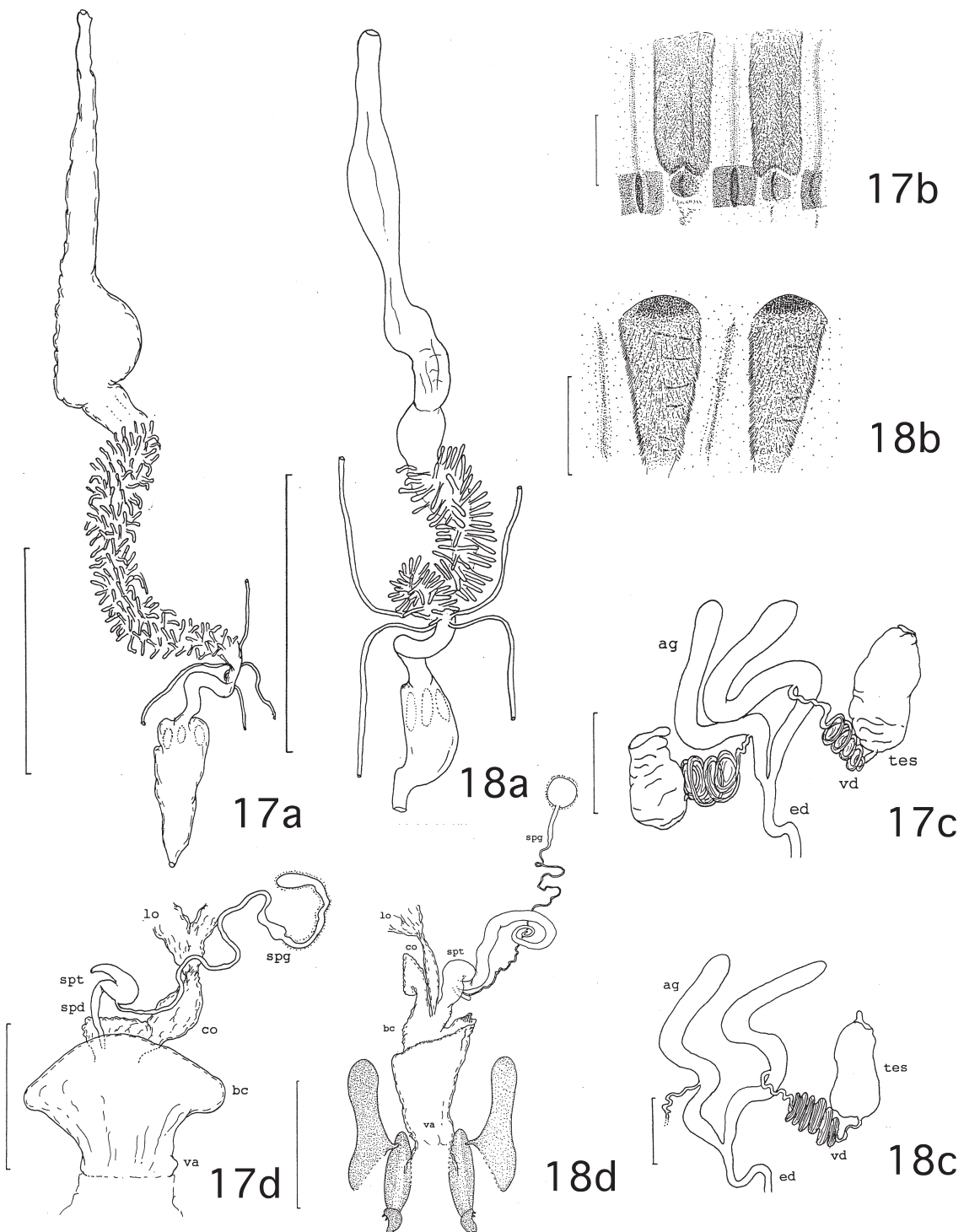
Reproductive organ

Male. Testis ovoid; vas deferens spiraled between the middle of it and testis, vesicula seminalis absent; accessory glands long, S-shaped.

Female. Bursa copulatrix produced anteriorly as a



Figs. 15-16. Alimentary canal and reproductive organ of *Diplous caligatus* (Fig. 15), and *Morion boniense* (Fig. 16). a, alimentary canal; b, proventriculus; c, male reproductive organ; d, female reproductive organ. Scales; 2.5mm for 15a; 0.6mm for 15b; 2.0mm for 15c; 1.5mm for 15d; 3.5mm for 16a; 0.5mm for 16b-c; 1.0mm for 16d.



Figs. 17-18. Alimentary canal and reproductive organ of *Trigonotoma lewisii* (Fig. 17), and *Pterostichus planicollis* (Fig. 18). a, alimentary canal; b, proventriculus; c, male reproductive organ; d, female reproductive organ. Scales; 5.0mm for 17a and 18a; 0.5mm for 17b and 18a-b; 1.0mm for 17c and 18c; 1.5mm for 17d and 18d.

bent sac at left side, weakly sclerotized at right side; spermatheca comma-shaped at basal part and tubular and coiled at apical part; spermathecal duct short, entering into bursa copulatrix at ventral side; spermathecal gland long tubular, with globular apex, derived from basal part of spermatheca; common oviduct derived from right base of sac-like part of bursa copulatrix.

***Platynus magunus* (Bates, 1873)**

(Fig. 19)

Alimentary canal

Alimentary canal 21.5 mm in length, almost 1.4 times as long as body; relative lengths of fore gut, mid gut, and hind gut 37 : 42 : 21.

Fore gut with oesophagus straight; crop small; proventriculus moderately complicated, its main longitudinal folds with hairs in entire length, with scale-like ctenidia at anterior part, weakly knobby at posterior part, while intermediate longitudinal folds with short hairs, well convex, not sclerotized, with small scale-like ctenidia posteriorly.

Mid gut curved to right and forms one dextral coil; crypts long, rod-shaped, dense.

Hind gut with ileum curved to right and forms one dextral coil; rectum medium in size; rectal glands elliptical, lying in ring around anterior part of rectum.

Reproductive organ

Male. Testis ovoid; vas deferens long, spiraled between the middle of it and testis, long, vesicula seminalis absent; accessory glands long, contiguous to each other.

Female. Bursa copulatrix produced longitudinally; spermatheca stick-shaped, gently curved; spermathecal gland long tubular at base, larger and ovoid at apex, derived from part of spermatheca; common oviduct swollen at basal part, derived from upper side of bursa copulatrix.

***Colpodes buchanani* Hope, 1831**

(Fig. 20)

Alimentary canal

Alimentary canal 14.0 mm in length, almost 1.2 times as long as body; relative lengths of fore gut, mid gut, and hind gut 44 : 28 : 28.

Fore gut with oesophagus straight; crop small; proventriculus moderately complicated, its main longitudinal folds with hairs in entire length, with scale-like ctenidia at anterior part, weakly knobby posteriorly, while intermediate longitudinal folds with short hairs, well convex, not sclerotized.

Mid gut curved to left; crypts long, rod-shaped, dense.

Hind gut with ileum meandering to left; rectum

medium in size; rectal glands elliptical, lying in ring around anterior part of rectum.

Reproductive organ

Male. Testis ovoid; vas deferens spiraled, long, vesicula seminalis absent; accessory glands long, contiguous to each other.

Female. Bursa copulatrix produced cylindrical; vagina with evaginate part and sclerite; spermatheca clavate; spermathecal duct short, entering into upper side of bursa copulatrix; spermathecal gland tubular, with larger and ovoid apex, derived from basal part of spermatheca; common oviduct swollen at basal part, derived from upper side on bursa copulatrix.

***Colpodes lampros* Bates, 1873**

(Fig. 21)

Alimentary canal

Alimentary canal 10.7 mm in length, almost 1.2 times as long as body; relative lengths of fore gut, mid gut, and hind gut 39 : 23 : 38.

Fore gut with oesophagus straight; crop small; proventriculus moderately complicated, its main longitudinal folds with hairs in entire length, with scale-like ctenidia at anterior part, weakly knobby at posterior part, while intermediate longitudinal folds with short hairs, well convex, not sclerotized.

Mid gut straight, lying from 1st to 4th abdominal segments; crypts long, rod-shaped, dense.

Hind gut with ileum curved to right and forms one dextral coil; rectum medium in size; rectal glands elliptical, lying in ring around anterior part of rectum.

Reproductive organ

Male. Testis ovoid; vas deferens spiraled, long, between the middle of it and testis, vesicula seminalis absent; accessory glands long, contiguous to each other.

Female. Bursa copulatrix cylindrical; spermatheca stick-shaped, narrowed apically; spermathecal duct short, entering into upper side of bursa copulatrix; spermathecal gland tubular, with larger and ovoid apex, derived from basal part of spermatheca; common oviduct derived from upper side on bursa copulatrix.

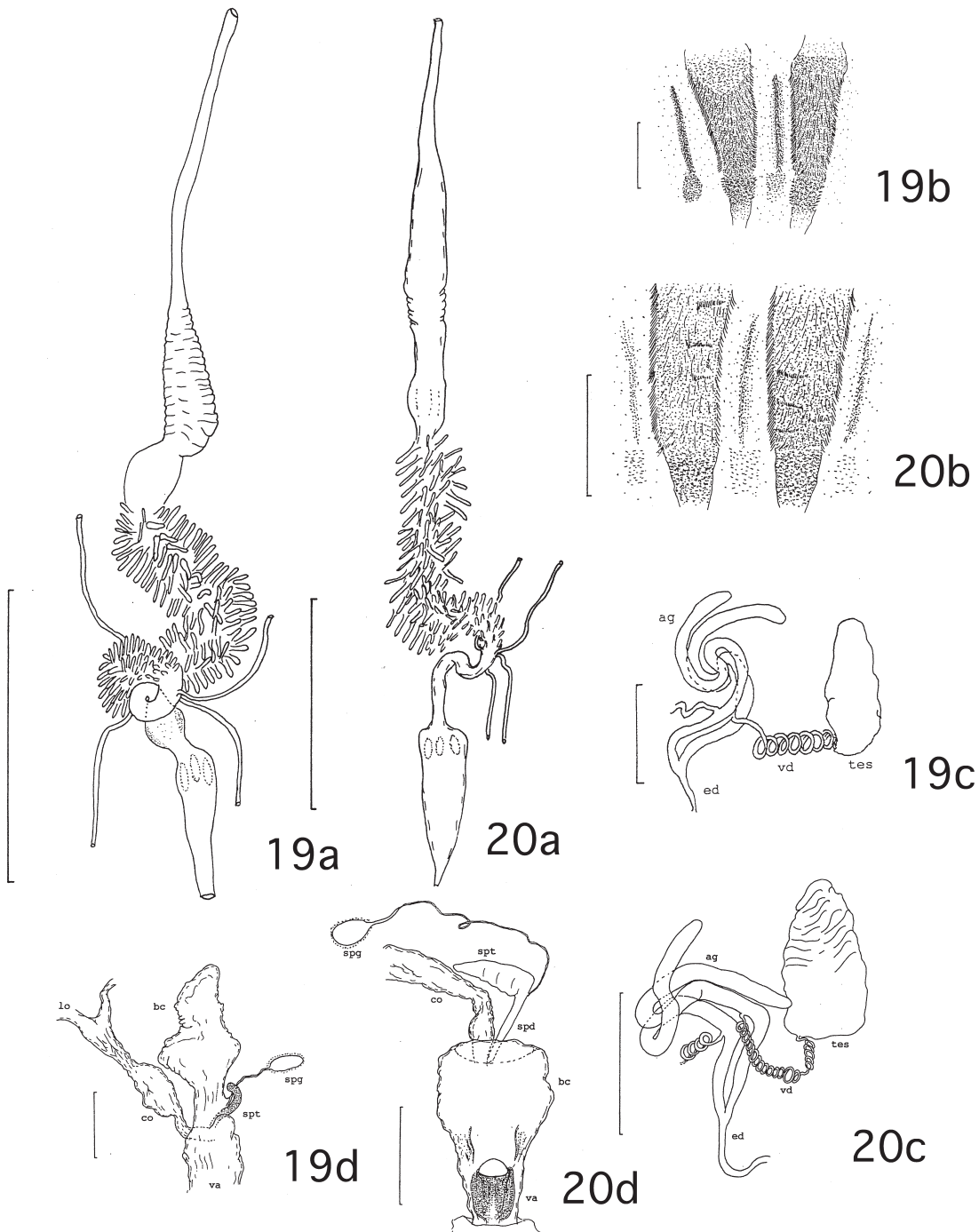
***Colpodes rubriolus* Bates, 1883**

(Fig. 22)

Alimentary canal

Alimentary canal 9.8 mm in length, almost 1.2 times as long as body; relative lengths of fore gut, mid gut, and hind gut 38 : 26 : 36.

Fore gut with oesophagus straight; crop small; proventriculus moderately complicated, its main longitudinal folds with hairs in entire length, with scale-like ctenidia at



Figs. 19-20. Alimentary canal and reproductive organ of *Platynus magnus* (Fig. 19), and *Colpodes buehneri* (Fig. 20). a, alimentary canal; b, proventriculus; c, male reproductive organ; d, female reproductive organ. Scales; 5.0mm for 19a; 0.3mm for 19b and 20b; 1.5mm for 19c; 0.5mm for 19d; 3.0mm for 20a; 2.5mm for 20c; 0.8mm for 20d.

anterior part, weakly knobby at posterior part, while intermediate longitudinal folds not haired, well convex, not sclerotized.

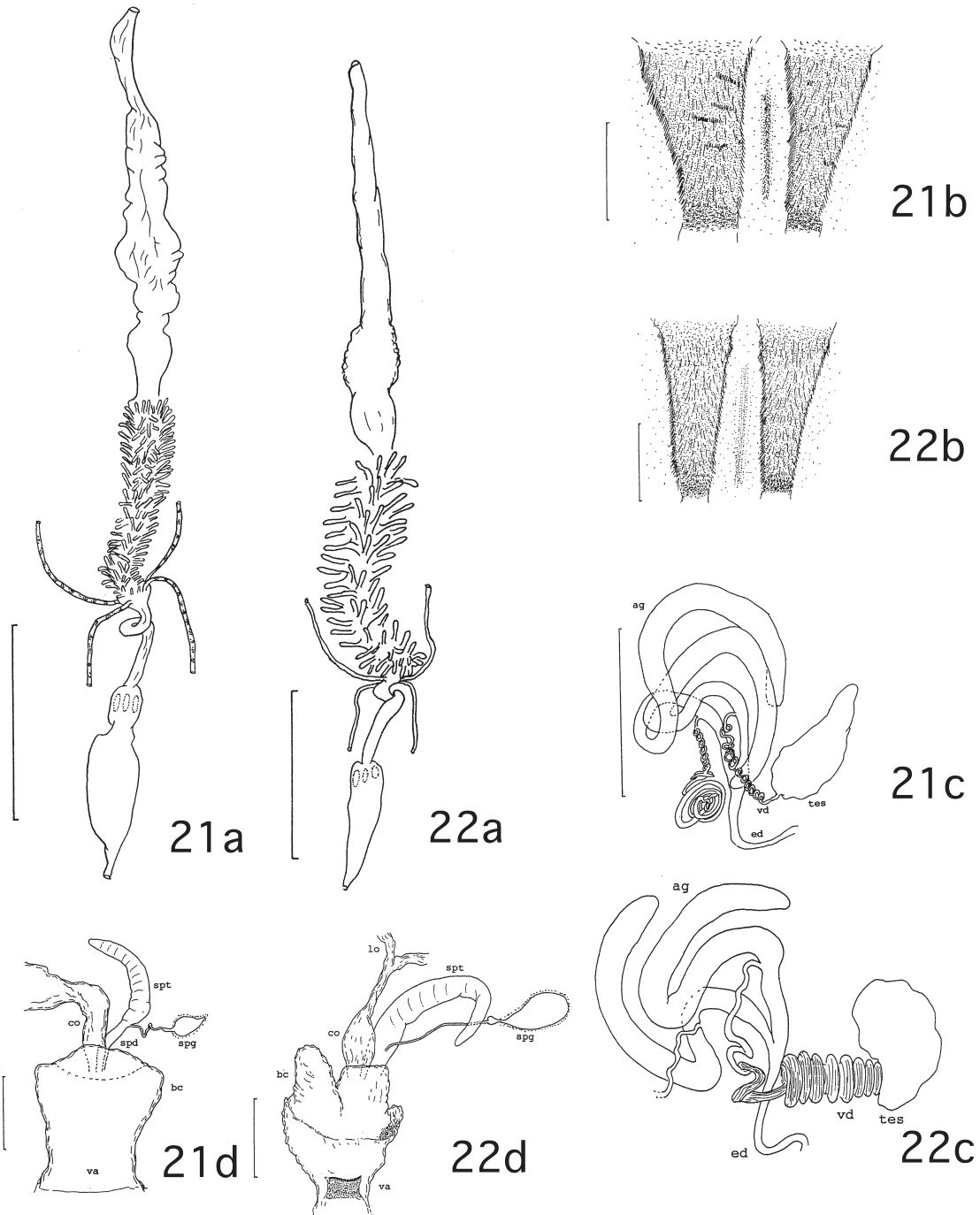
Mid gut curved to left and forms one dextral coil; crypts long, stick-shaped, dense.

Hind gut with ileum curved to right and forms one

dextral coil; rectum medium in size; rectal glands elliptical, lying in ring around anterior part of rectum.

Reproductive organ

Male. Testis ovoid; vas deferens spiraled between the middle of it and testis, vesicula seminalis absent; accessory glands long, S-shaped, contiguous to each other.



Figs. 21-22. Alimentary canal and reproductive organ of *Colpodes lampros* (Fig. 21), and *Colpodes rubriolus* (Fig. 22). a, alimentary canal; b, proventriculus; c, male reproductive organ; d, female reproductive organ. Scales; 2.0mm for 21a; 0.3mm for 21b and 22b; 2.5mm for 21c; 0.5mm for 21d and 22d; 1.5mm for 22a; 1.0mm for 22c.

Female. Bursa copulatrix longitudinally at left side, weakly sclerotized at right side; vagina with transverse sclerite at posterior part; spermatheca tubular, bent and narrowed apically; sousage-shaped, narrowed apically; spermathecal gland long tubular, with larger and ovoid apex, derived from basal part of spermatheca; common

oviduct derived from upper side on bursa copulatrix.

Dolichus halensis (Schaller, 1783)
(Fig. 23)

Alimentary canal

Alimentary canal 19.0 mm in length, almost 1.1 times

as long as body; relative lengths of fore gut, mid gut, and hind gut 32 : 32 : 36.

Fore gut with oesophagus straight; crop small; proventriculus moderately complicated, its main longitudinal folds with hairs in entire length, with scale-like ctenidia anteriorly, weakly knobby posteriorly, while intermediate longitudinal folds with short hairs, well convex, not sclerotized.

Mid gut straight, then curved to right and forms one dextral coil; crypts long, rod-shaped, dense.

Hind gut with ileum curved to right and forms one dextral coil; rectum medium in size; rectal glands elliptical, lying in a ring around anterior part of rectum.

Reproductive organ

Male. Testis ovoid; vas deferens spiraled, long, between the middle of it and testis, long, between the middle of it and testis, long, vesicula seminalis absent; accessory glands long, contiguous to each other.

Female. Bursa copulatrix longitudinal; vagina weakly sclerotized at dorsal and ventral side; spermatheca stick-shaped, gently curved; spermathecal gland long, tubular, derived from basal part of spermatheca with anchor-like apex and its basal part swollen; common oviduct derived from upper side on bursa copulatrix.

Synuchus dulcigradus (Bates, 1873)

(Fig. 24)

Alimentary canal

Alimentary canal 13.5 mm in length, almost 1.5 times as long as body; relative lengths of fore gut, mid gut, and hind gut 46 : 17 : 37.

Fore gut with oesophagus straight; crop medium in size; proventriculus moderately complicated, its main longitudinal folds with hairs in entire length, with scale-like ctenidia at anterior part, weakly knobby posteriorly, while intermediate longitudinal folds not haired, well convex, not sclerotized.

Mid gut straight, lying from 1st to 4th abdominal segments; crypts long, rod-shaped, dense.

Hind gut with ileum curved to right and forms one dextral coil; rectum medium in size; rectal glands elliptical, lying in ring around anterior part of rectum.

Reproductive organ

Male. Testis ovoid; vas deferens spiraled, long, between the middle of it and testis, long, between the middle of it and testis, long, vesicula seminalis absent; accessory glands thick, bent at apex.

Female. Bursa copulatrix transverse; spermatheca sausage-shaped; spermathecal duct short, entering into right side of common oviduct; spermathecal gland tubular, derived from basal part of spermatheca, with larger and

globular apex, junction of spermatheca and common oviduct derived from lateroventral side on bursa copulatrix.

1.8. Subfamily Zabrinae

Amara congrua Morawitz, 1862.

(Fig. 25)

Alimentary canal

Alimentary canal 14.3 mm in length, almost 1.8 times as long as body; relative lengths of fore gut, mid gut, and hind gut 37 : 29 : 34.

Fore gut with oesophagus straight; crop medium in size; proventriculus simple, its main longitudinal folds with hairs at lateral margins, with scale-like ctenidia posteriorly, not sclerotized, while intermediate longitudinal folds undeveloped, not haired, not sclerotized.

Mid gut curved to right and forms one dextral coil at posterior part; crypts rod-shaped, dense.

Hind gut with ileum curved to right and forms one dextral coil; rectum medium in size; rectal glands elliptical, lying in ring around anterior part of rectum.

Reproductive organ

Male. Testis ovoid, small; vas deferens long, spiraled between the middle of it and testis, between the middle of it and testis, long, between the middle of it and testis, long, vesicula seminalis absent; accessory glands long, contiguous to each other.

Female. Bursa copulatrix bulbous; spermatheca stick-shaped; spermathecal duct short, entering into right side of bursa copulatrix; spermathecal gland tubular, with enlarged apex, derived from basal part of spermatheca, junction of spermatheca and spermathecal gland swollen at ventral side; common oviduct derived from ventral side of bursa copulatrix.

1.9. Subfamily Harpalinae

Anisodactylus punctatipennis Morawitz, 1862

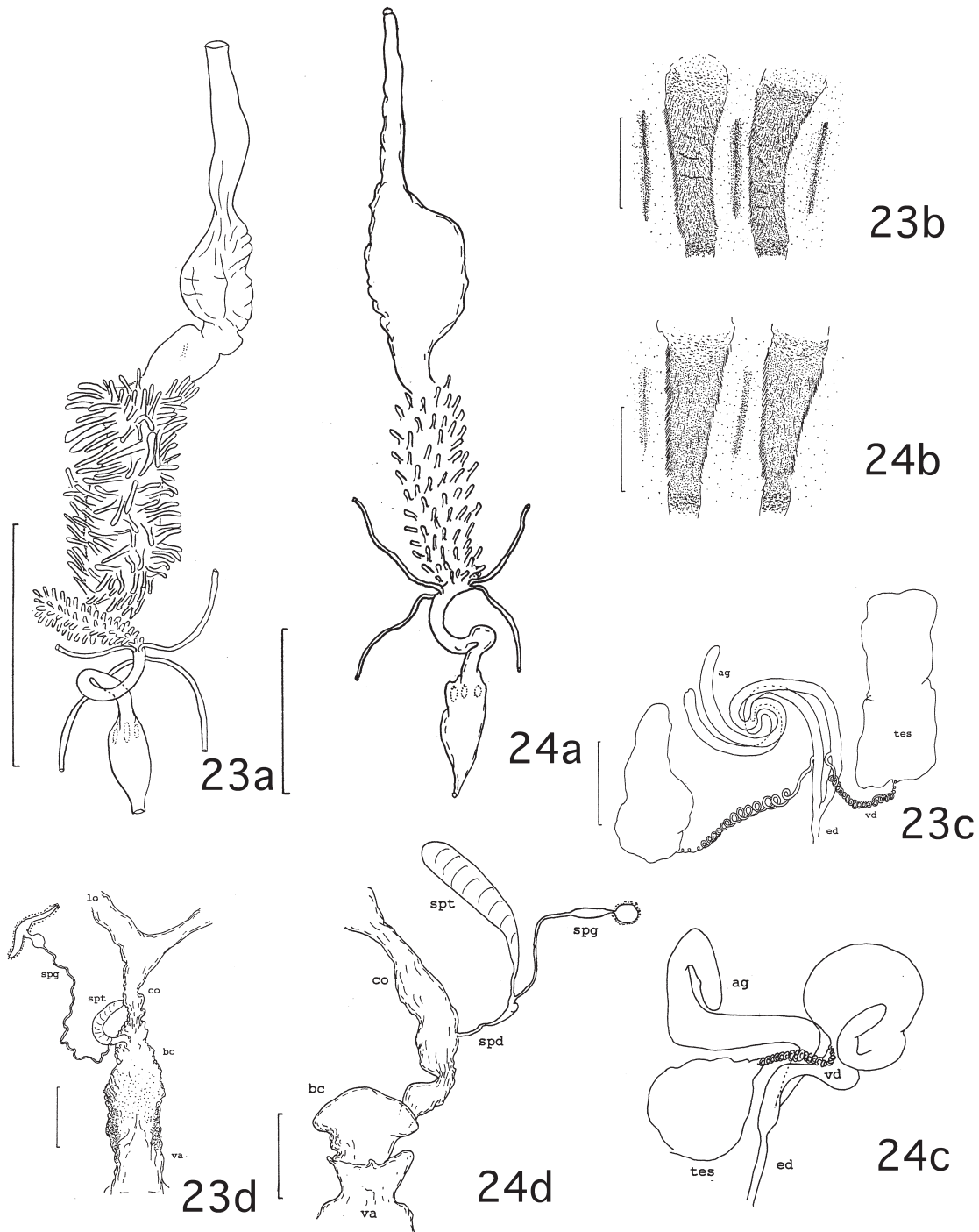
(Fig. 26)

Alimentary canal

Alimentary canal 14.5 mm in length, almost 1.3 times as long as body; relative lengths of fore gut, mid gut, and hind gut 41 : 24 : 35.

Fore gut with oesophagus straight; crop bulbous; proventriculus moderately complicated, its main longitudinal folds with hairs in entire length, with long setae anteriorly, weakly knobby posteriorly, not sclerotized, while intermediate longitudinal folds not haired, weakly convex, not sclerotized.

Mid gut straight, lying from 1st to 4th abdominal seg-



Figs. 23-24. Alimentary canal and reproductive organ of *Dolichus halensis* (Fig. 23), and *Synuchus dulcigradus* (Fig. 24). a, alimentary canal; b, proventriculus; c, male reproductive organ; d, female reproductive organ. Scales; 5.0mm for 23a; 0.5mm for 23b and 24d; 1.0mm for 23d and 24c; 1.5mm for 23c; 3.0mm for 24a; 0.3mm for 24b.

ments; crypts rod-shaped, dense.

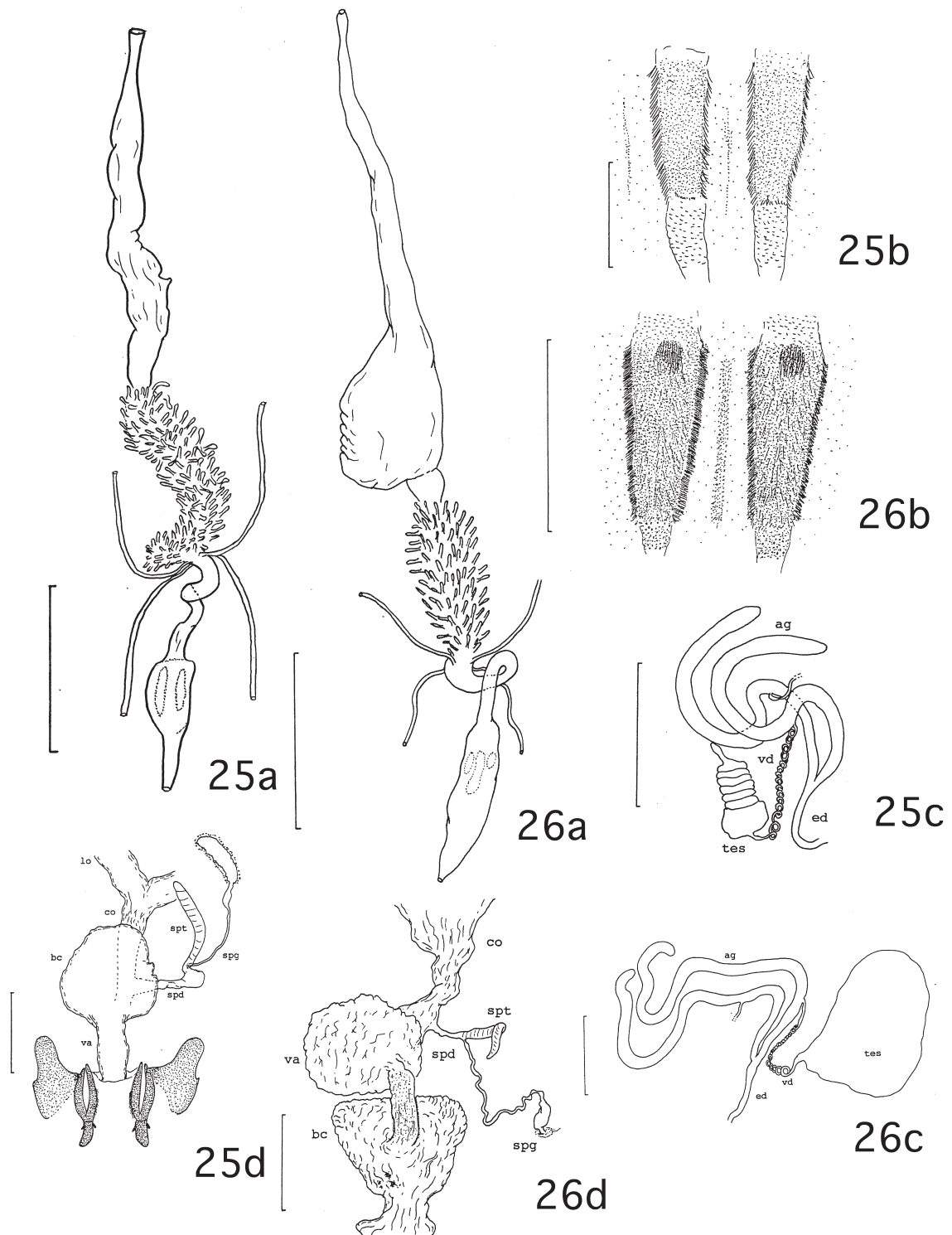
Hind gut with ileum curved to right and forms one dextral coil; rectum medium in size; rectal glands elliptical, lying in two rings around anterior part of rectum.

Reproductive organ

Male. Testis ovoid, small; vas deferens spirald, long,

vesicula seminalis absent; accessory glands long, contiguous to each other.

Female. Bursa copulatrix bulbous, with small sclerotized part at dorsal surface; spermatheca stick-shaped, gently curved apically; spermathecal duct very short, entering into basal part of common oviduct; spermathecal



Figs. 25-26. Alimentary canal and reproductive organ of *Amara congrua* (Fig. 25), and *Anisodactylus punctatipennis* (Fig. 26). a, alimentary canal; b, proventriculus; c, male reproductive organ; d, female reproductive organ. Scales; 2.5mm for 25a; 0.3mm for 25b; 1.0mm for 25c; 0.5mm for 25d and 26b; 2.5mm for 26a; 1.0mm for 26c-d.

gland tubular, long, with larger apex, derived from basal part of spermatheca; vagina visible beyond bursa copulatrix.

Harpalus capito Morawitz, 1862

(Fig. 27)

Alimentary canal

Alimentary canal 25.7 mm in length, almost 1.5 times as long as body; relative lengths of fore gut, mid gut, and hind gut 51 : 23 : 26.

Fore gut with oesophagus straight; crop large, bulbous; proventriculus moderately complicated, its main longitudinal folds with hairs in entire length, with long setae anteriorly, not sclerotized, while intermediate longitudinal folds not haired, weakly convex, not sclerotized.

Mid gut straight curved to right and forms one dextral coil, lying from 1st to 4th abdominal segments; crypts bottle-shaped, dense.

Hind gut with ileum meandering to left; rectum medium in size; rectal glands elliptical, lying in two rings around anterior part of rectum.

Reproductive organ

Male. Testis ovoid, small; vas deferens sinuate, long, vesicula seminalis absent; accessory glands long, contiguous to each other.

Female. Bursa copulatrix bulbous; spermatheca stick-shaped, sclerotized at basal part; spermathecal duct short, entering into near base of common oviduct; spermathecal gland tubular, long, derived from basal part of spermatheca.

Harpalus vicarious Harold, 1878.

(Fig. 28)

Alimentary canal

Alimentary canal 19.0 mm in length, almost 1.2 times as long as body; relative lengths of fore gut, mid gut, and hind gut 42 : 37 : 21.

Fore gut with oesophagus straight; crop medium in size; proventriculus moderately complicated, its main longitudinal folds with hairs in entire length, with long setae at anterior part, not sclerotized, while intermediate longitudinal folds not haired, weakly convex, not sclerotized.

Mid gut straight curved to right and forms one dextral coil, lying from 1st to 4th abdominal segments; crypts rod-shaped, dense.

Hind gut with ileum curved to right and forms one dextral coil; rectum medium in size; rectal glands elliptical, lying in two rings around anterior part of rectum.

Reproductive organ

Male. Testis ovoid; vas deferens spiraled, long, vesicula seminalis absent; accessory glands long, contiguous to

each other.

Female. Bursa copulatrix bulbous; spermatheca stick-shaped; spermathecal duct very short, entering into basal part of common oviduct; spermathecal gland tubular, long, with larger apex, derived from basal part of spermatheca; common oviduct entering into dorsal side of bursa copulatrix.

1.10. Subfamily Licininae

Diplocheila zeelandica (Redtenbacher, 1868)

(Fig. 29)

Alimentary canal

Alimentary canal 19.0 mm in length, almost 1.4 times as long as body; relative lengths of fore gut, mid gut, and hind gut 40 : 30 : 30.

Fore gut with oesophagus straight; crop small; proventriculus moderately complicated, its main longitudinal folds with strong hairs in entire length, with long setae at anterior part, not sclerotized, while intermediate longitudinal folds with hairs at center line, well convex, not sclerotized.

Mid gut curved to right and forms one dextral coil, lying from 1st to 4th abdominal segments; crypts rod-shaped, dense.

Hind gut with ileum meandering to left side; rectum medium in size; rectal glands elliptical, lying in one ring around anterior part of rectum.

Reproductive organ

Male. Vas deferens sinuate, long, vesicula seminalis absent; accessory glands long, gently curved, contiguous to each other.

Female. Bursa copulatrix cylindrical, weakly sclerotized; spermatheca stick-shaped, gradually narrowed posteriorly, from middle to end reddish, curved at apex; spermathecal duct very short, entering into basal part of common oviduct; spermathecal gland tubular, long, with larger apex, derived from basal part of spermatheca.

1.11. Subfamily Panagaeinae

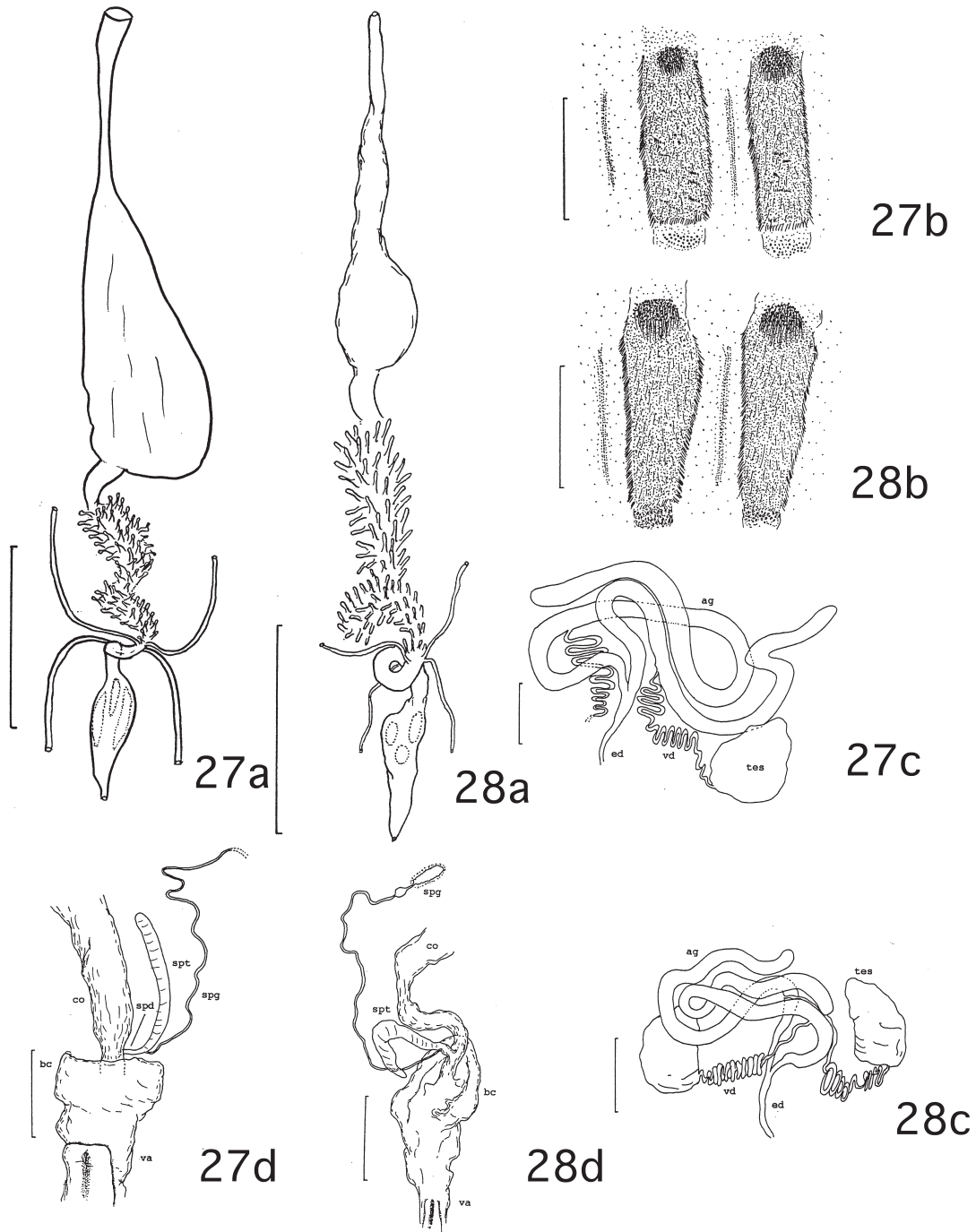
Dischissus japonicus Andrewes, 1933.

(Fig. 30)

Alimentary canal

Alimentary canal 12.5 mm in length, almost 1.5 times as long as body; relative lengths of fore gut, mid gut, and hind gut 36 : 32 : 32.

Fore gut with oesophagus straight; crop small; proventriculus moderately complicated, its main longitudinal folds with hairs in entire length, knobby and sclerotized anteriorly, while intermediate longitudinal folds with



Figs. 27-28. Alimentary canal and reproductive organ of *Harpalus capito* (Fig. 27), and *Harpalus vicarius* (Fig. 28). a, alimentary canal; b, proventriculus; c, male reproductive organ; d, female reproductive organ. Scales; 5.0mm for 27a; 0.5mm for 27b and 28b; 1.0mm for 27c-d and 28d; 4.0mm for 28a; 2.0mm for 28c.

hairs at center line, weakly convex, not sclerotized.

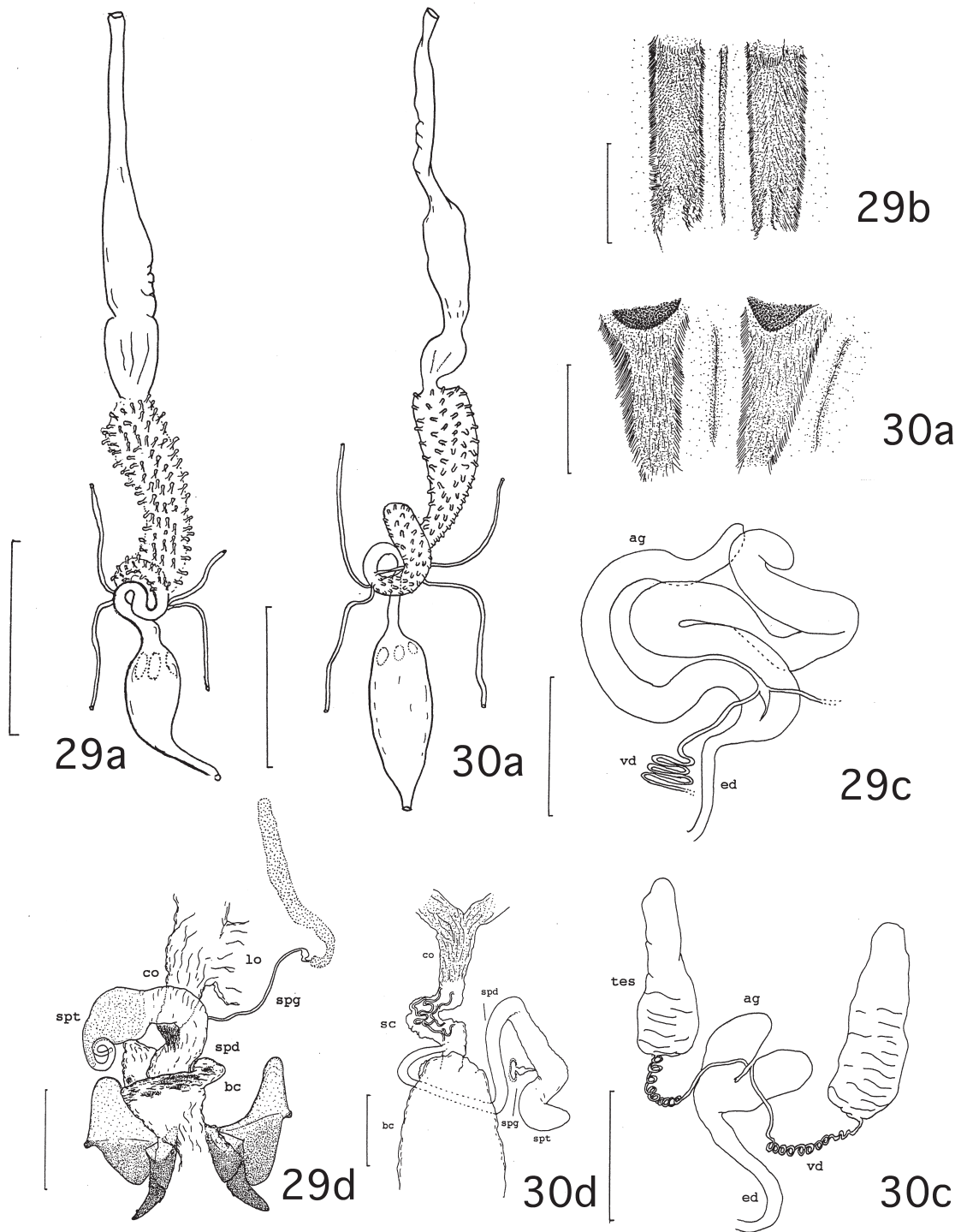
Mid gut curved to right side and forms one dextral coil in 4th abdominal segment; crypts cone-shaped, dense.

Hind gut with ileum curved to right and forms one dextral coil; rectum medium in size; rectal glands elliptical, lying in one ring around anterior part of rectum.

Reproductive organs

Male. Testis narrow; vas deferens spiraled, long, vesicula seminalis absent; accessory glands short, heart-shaped.

Female. Bursa copulatrix longitudinal; spermatheca comma-shaped; spermathecal duct long, entering into



Figs. 29-30. Alimentary canal and reproductive organ of *Diplocheila zeelandica* (Fig. 29), and *Dischissus japonicus* (Fig. 30). a, alimentary canal; b, proventriculus; c, male reproductive organ; d, female reproductive organ. Scales; 6.0mm for 29a; 1.0mm for 29b; 4.5mm for 29c; 2.0mm for 29d and 30a; 0.3mm for 30b; 0.5mm for 30c-d.

basal part of common oviduct; spermathecal gland tubular, small, with larger apex, derived from basal part of spermatheca; common oviduct with coiled, weak sclerite at basal part.

1.12. Subfamily Callistinae

Haplochlaenius costiger (Chaudoir, 1856)

(Fig. 31)

Alimentary canal

Alimentary canal 35.5 mm in length, almost 1.6 times as long as body; relative lengths of fore gut, mid gut, and hind gut 38 : 31: 31.

Fore gut with oesophagus straight; crop small; proventriculus complicated, its main longitudinal folds with hairs in entire length, well convex, not sclerotized, while intermediate longitudinal folds knobby and sclerotized posteriorly.

Mid gut straight and gently curved posteriorly; crypts rod-shaped, dense.

Hind gut with ileum meandering to right side; rectum small; rectal glands elliptical, lying in one ring around anterior part of rectum.

Reproductive organ

Male. Testis ovoid; vas deferens medium in size, vesicula seminalis present; accessory glands curved and narrowed apically, contiguous to each other.

Female. Bursa copulatrix cylindrical; spermatheca small; spermathecal duct long, entering into basal part of common oviduct; spermathecal gland tubular, small, with larger apex, derived from basal part of spermatheca.

Chlaenius variicornis Morawitz, 1863

(Fig. 32)

Alimentary canal

Alimentary canal 17.5 mm in length, almost 1.5 times as long as body; relative lengths of fore gut, mid gut, and hind gut 45 : 20: 35.

Fore gut with oesophagus straight; crop medium in size; proventriculus complicated, its main longitudinal folds with hairs in entire length, well convex, not sclerotized, while intermediate longitudinal folds knobby and sclerotized posteriorly.

Mid gut straight; crypts rod-shaped, dense.

Hind gut with ileum meandering to left side; rectum medium in size; rectal glands elliptical, lying in one ring around anterior part of rectum.

Reproductive organ

Male. Testis ovoid; vas deferens medium in size, vesicula seminalis absent; accessory glands short.

Female. Bursa copulatrix cylindrical; spermatheca

comma-shaped, with a small lobe at base; spermathecal duct long, entering into basal part of common oviduct; spermathecal gland tubular, small, with larger apex, derived from basal part of spermatheca; common oviduct with a cord-like sclerite at basal part.

Chlaenius naeviger Morawitz, 1862

(Fig. 33)

Alimentary canal

Alimentary canal 23.2 mm in length, almost 1.6 times as long as body; relative lengths of fore gut, mid gut, and hind gut 43 : 30: 27.

Fore gut with oesophagus straight; crop large, bulbous; proventriculus complicated, its main longitudinal folds with hairs in entire length, not sclerotized, while intermediate longitudinal folds knobby and sclerotized posteriorly.

Mid gut gently curved to right side and then forms to one dextral coil posteriorly; crypts bottle-shaped, dense.

Hind gut with ileum straight and then curved upward to left side; rectum medium in size; rectal glands elliptical, lying in one ring around anterior part of rectum.

Reproductive organ

Male. Testis narrow; vas deferens sinuate, vesicula seminalis absent; accessory glands short, gently curved apex, contiguous to each other.

Female. Bursa copulatrix cylindrical; spermatheca short, stick-shaped; spermathecal duct long; spermathecal gland tubular, small, with larger apex; common oviduct with a cord-like sclerite at basal part.

Lithochlaenius noguchii (Bates, 1873)

(Fig. 34)

Alimentary canal

Alimentary canal 20.5 mm in length, almost 1.5 times as long as body; relative lengths of fore gut, mid gut, and hind gut 49 : 24: 27.

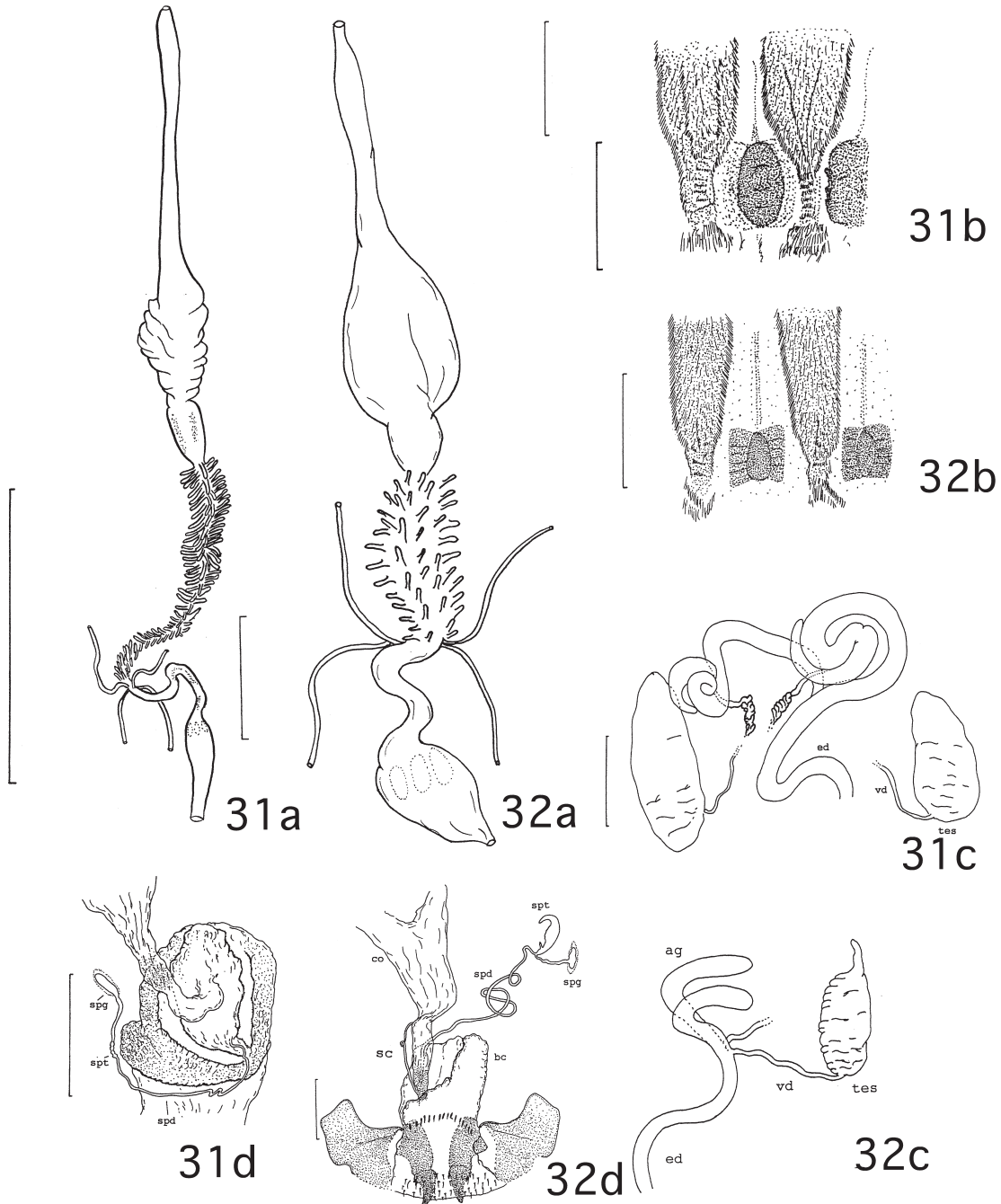
Fore gut with oesophagus straight; crop large, bulbous; proventriculus complicated, its main longitudinal folds with hairs in entire length, not sclerotized, while intermediate longitudinal folds knobby and sclerotized posteriorly.

Mid gut gently curved to right side; crypts bottle-shaped, dense.

Hind gut with ileum straight and then forms one dextral coil; rectum medium in size; rectal glands elliptical, lying in one ring around anterior part of rectum.

Reproductive organ

Male. Testis ovoid; vas deferens spiraled, vesicula seminalis absent; accessory glands S-shaped, short, contiguous to each other.



Figs. 31-32. Alimentary canal and reproductive organ of *Haplochlaenius costiger* (Fig. 31), and *Chlaenius variicornis* (Fig. 32). a, alimentary canal; b, proventriculus; c, male reproductive organ; d, female reproductive organ. Scales; 5.0mm for 31a; 1.0mm for 31b, 31d, and 32c; 2.0mm for 31c and 32a; 0.5mm for 32b and 32d.

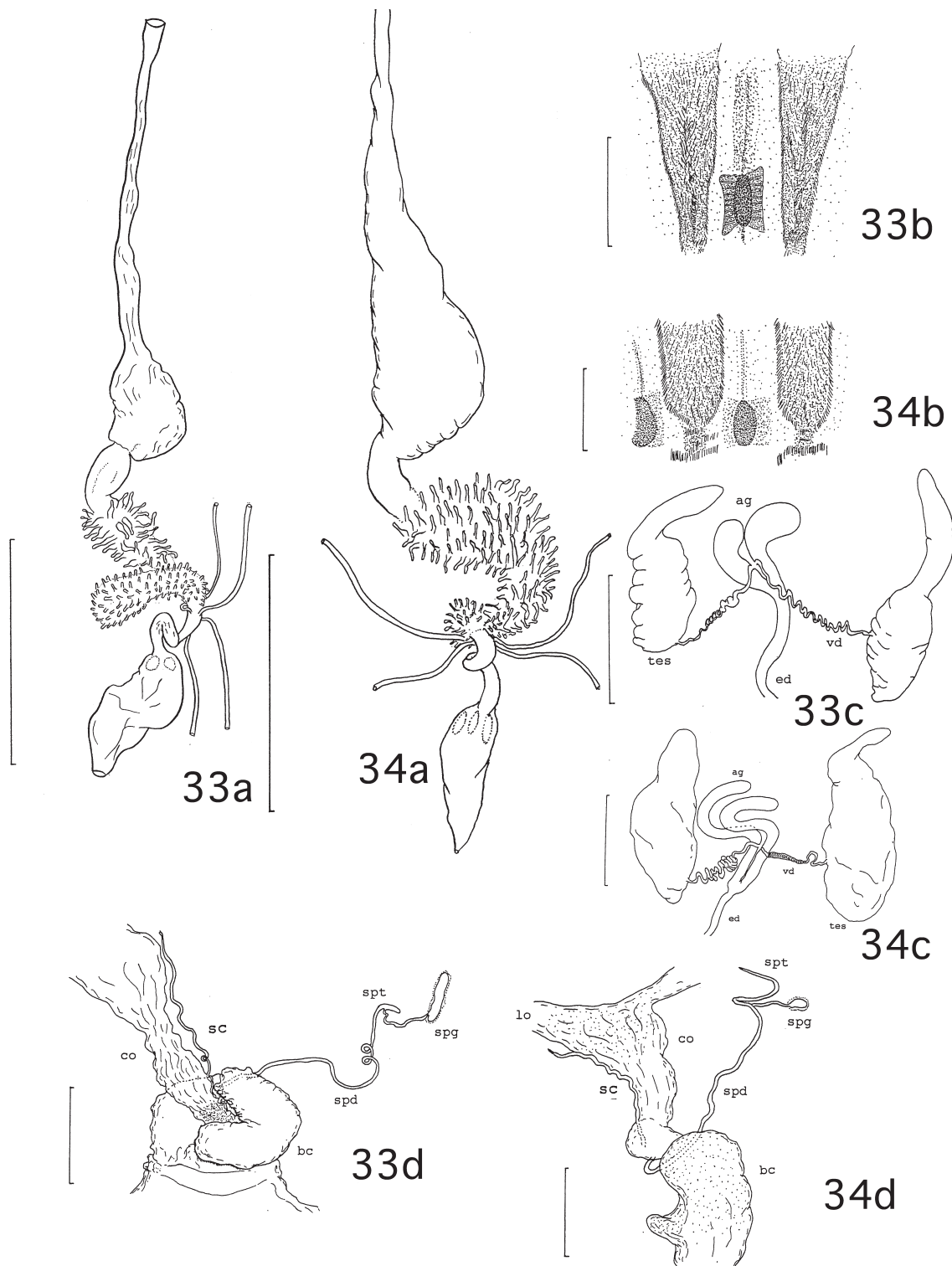
Female. Bursa copulatrix bulbous, weakly sclerotized at dorsal surface; spermatheca cord-like, narrow; spermathecal duct long; spermathecal gland tubular, small, with larger apex; common oviduct with a cord-like sclerite at basal part.

1.13. Subfamily Odacanthinae

Archicolliuris bimaculata nipponica Habu, 1963
(Fig. 35)

Alimentary canal

Alimentary canal 16.5 mm in length, almost 1.4 times as long as body; relative lengths of fore gut, mid gut, and



Figs. 33-34. Alimentary canal and reproductive organ of *Chlaenius naeviger* (Fig. 33), and *Lithochlaenius noguchii* (Fig. 34). a, alimentary canal; b, proventriculus; c, male reproductive organ; d, female reproductive organ. Scales: 5.0mm for 33a and 34a; 0.5mm for 33b, 33d, 34b, and 34d; 1.0mm for 33c; 2.0mm for 34c.

hind gut 43 : 27: 30.

Fore gut with oesophagus straight; crop medium in size; proventriculus complicated, finger-like, its main longitudinal folds with hairs in entire length, with scale-like ctenidia posteriorly, intermediate longitudinal folds with hairs at center line, knobby posteriorly, well convex.

Mid gut gently curved to left side; crypts rod-shaped, dense.

Hind gut with ileum meandering to form S-shape; rectum medium in size; rectal glands elliptical, lying in one ring around anterior part of rectum.

Reproductive organ

Male. Testis ovoid; vas deferens medium in length, vesicula seminalis absent; accessory glands thick, short, contiguous to each other.

Female. Bursa copulatrix cylindrical, weakly sclerotized; spermatheca bipartite, with a basal part and an apical bulbs; spermathecal duct short, bulbous, joined common oviduct by U-shaped sclerite; spermathecal gland tubular, small, with larger apex, derived from spermathecal apical bulb.

***Ophionea ishii* Habu, 1962.**

(Fig. 36)

Alimentary canal

Alimentary canal 7.2 mm in length, almost 1.1 times as long as body; relative lengths of fore gut, mid gut, and hind gut 70 : 17: 13.

Fore gut with oesophagus straight; crop medium in size; proventriculus complicated, finger-like, its main longitudinal folds with hairs in entire length, with scale-like ctenidia at posterior part, knobby and sclerotized at posterior part, while intermediate longitudinal folds with hairs at center line, knobby at posterior part, well convex.

Mid gut gently curved to left side; crypts rod-shaped, dense.

Hind gut with ileum meandering to forms S-shape; rectum medium in size; rectal glands elliptical, lying in one ring around anterior part of rectum.

Reproductive organ

Male. Testis ovoid; vas deferens medium in length, vesicula seminalis absent; accessory glands thick, short, contiguous to each other.

Female. Bursa copulatrix cylindrical, with small sclerotized part; spermatheca bipartite, with a basal part and an apical bulbs; spermathecal duct short, bulbous, joined common oviduct by U-shaped sclerite; spermathecal gland tubular, small, with larger apex, derived from spermathecal apical bulb.

1.14. Subfamily Pentagonicinae

***Pentagonica daimiela* Bates, 1892**

(Fig. 37)

Alimentary canal

Alimentary canal 5.9 mm in length, almost 1.2 times as long as body; relative lengths of fore gut, mid gut, and hind gut 54 : 20: 26.

Fore gut with oesophagus straight; crop large, bulbous; proventriculus complicated, main longitudinal folds with hairs at lateral margins, knobby and sclerotized posteriorly, while intermediate longitudinal folds knobby and sclerotized posteriorly.

Mid gut gently curved to right side; crypts bottle-shaped, dense.

Hind gut with ileum gently curved to right side; rectum medium in size; rectal glands elliptical, lying in one ring around anterior part of rectum.

Reproductive organ

Male. Testis ovoid; vas deferens spiraled, vesicula seminalis absent; accessory glands S-shaped, contiguous to each other.

Female. Bursa copulatrix bulbous; spermatheca bipartite, with a basal part and an apical bulbs; spermathecal duct short, bulbous, joined common oviduct by U-shaped sclerite; spermathecal gland tubular, small, with larger apex, derived from spermathecal apical bulb.

***Pentagonica angulata* Bates, 1883**

(Fig. 38)

Alimentary canal

Alimentary canal 5.4 mm in length, almost 1.2 times as long as body; relative lengths of fore gut, mid gut, and hind gut 50 : 20: 30.

Fore gut with oesophagus straight; crop large, bulbous; proventriculus complicated, main longitudinal folds with hairs at lateral margins, knobby and sclerotized at posterior part, intermediate longitudinal folds knobby and sclerotized at posterior part.

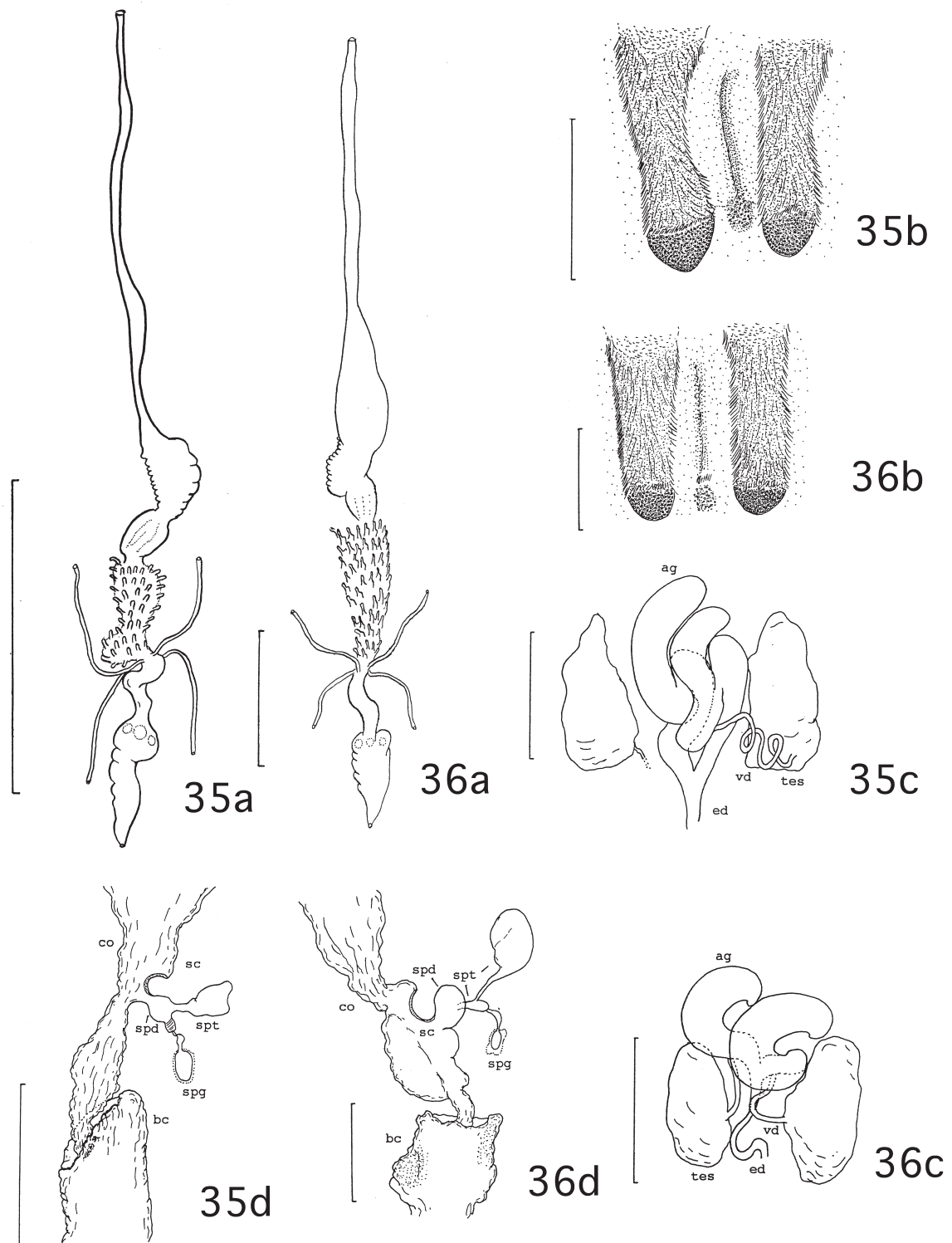
Mid gut straight; crypts bottle-shaped, dense.

Hind gut with ileum gently curved to right side; rectum medium in size; rectal glands elliptical, lying in one ring around anterior part of rectum.

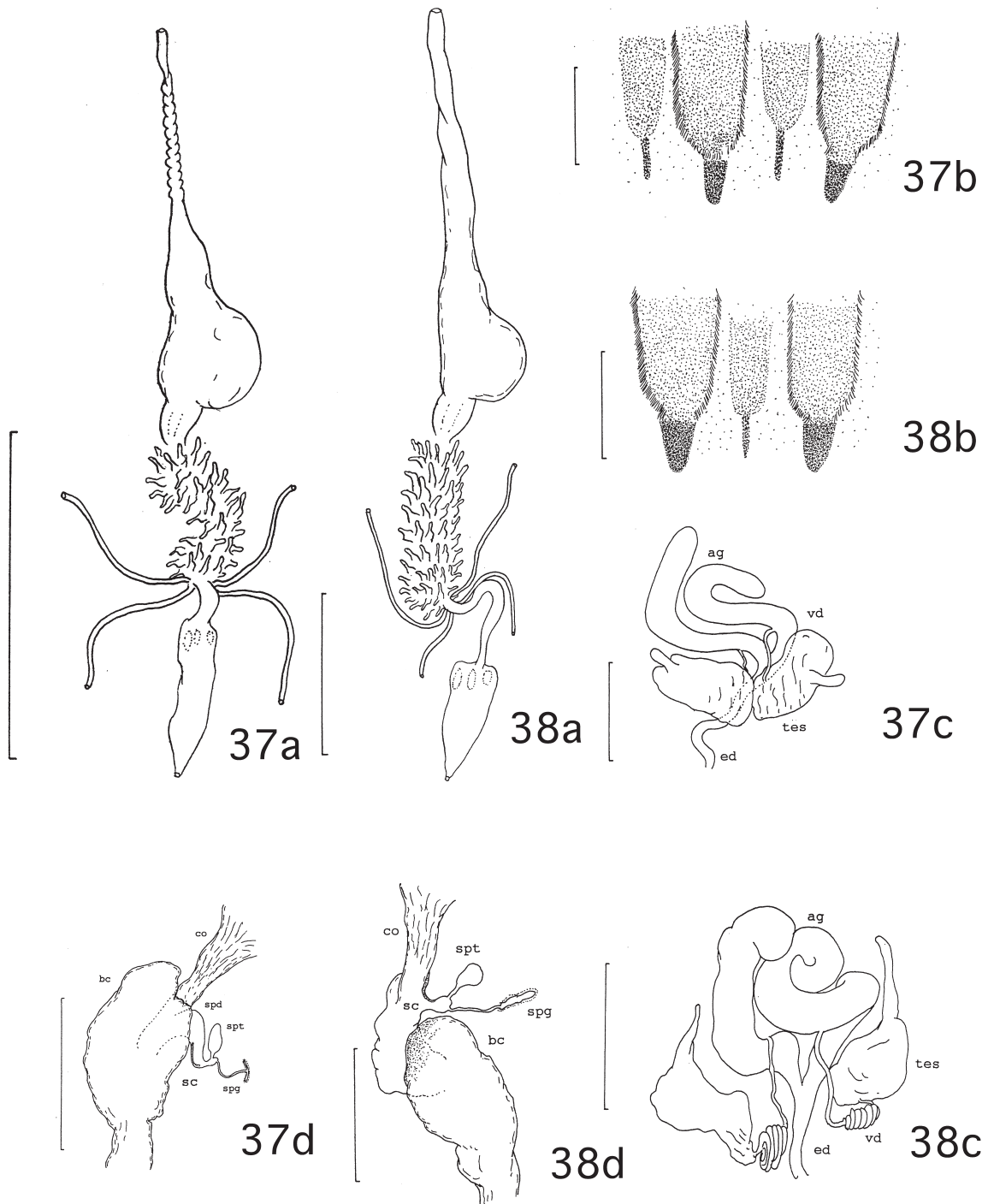
Reproductive organ

Male. Testis ovoid; vas deferens spiraled, vesicula seminalis absent; accessory glands S-shaped, contiguous to each other.

Female. Bursa copulatrix bulbous; spermatheca bipartite, with a basal part and an apical bulbs; spermathecal duct short, bulb-like, joined common oviduct by U-shaped sclerite; spermathecal gland tubular, small, with larger



Figs. 35-36. Alimentary canal and reproductive organ of *Archicolliuris bimaculata nipponica* (Fig. 35), and *Ophionea ishii* (Fig. 36). a, alimentary canal; b, proventriculus; c, male reproductive organ; d, female reproductive organ. Scales; 3.0mm for 35a; 0.3mm for 35b and 36b; 1.0mm for 35c, 36a and 36c; 0.5mm for 35d; 0.2mm for 36b.



Figs. 37-38. Alimentary canal and reproductive organ of *Pentagonica daimiela* (Fig. 37), and *Pentagonica angulata* (Fig. 38). a, alimentary canal; b, proventriculus; c, male reproductive organ; d, female reproductive organ. Scales; 2.0mm for 37a; 0.2mm for 37b; 0.5mm for 37c-d and 38c-d; 1.0mm for 38a; 0.2mm for 38b.

apex, derived from spermathecal apical bulb.

1.15. Subfamily Lebiinae

Lebidia octoguttata Morawitz, 1862

(Fig. 39)

Alimentary canal

Alimentary canal 16.5 mm in length, almost 1.4 times as long as body; relative lengths of fore gut, mid gut, and hind gut 43 : 27: 30.

Fore gut with oesophagus straight; crop large, bulbous; proventriculus moderately complicated, finger-like, its main longitudinal folds with hairs in entire length, knobby and sclerotized posteriorly, while intermediate longitudinal folds not haired, not sclerotized, weakly convex.

Mid gut gently curved to left side; crypts rod-shaped, dense.

Hind gut with ileum gently curved to forms S-shape; rectum medium in size; rectal glands elliptical, lying in one ring around anterior part of rectum.

Reproductive organ

Male. Testis ovoid; vas deferens spiraled, vesicula seminalis absent; accessory glands S-shaped, contiguous to each other.

Female. Bursa copulatrix bulbous; spermatheca bipartite, with a basal part and an apical bulbs; spermathecal duct short, bulb-like, joined common oviduct by U-shaped sclerite; spermathecal gland tubular, medium in size, with larger apex, derived from spermathecal apical bulb; vagina visible beyond bursa copulatrix.

Lebidia bifenestrata Morawitz, 1862

(Fig. 40)

Alimentary canal

Alimentary canal 6.8 mm in length, almost 1.5 times as long as body; relative lengths of fore gut, mid gut, and hind gut 40 : 30: 30.

Fore gut with oesophagus straight; crop large, bulbous; proventriculus moderately complicated, finger-like, its main longitudinal folds with hairs at lateral margins, knobby and sclerotized posteriorly, while intermediate longitudinal folds not haired, not sclerotized, weakly convex.

Mid gut gently curved to left side; crypts rod-shaped, dense.

Hind gut with ileum meandering to left side; rectum medium in size; rectal glands elliptical, lying in one ring around anterior part of rectum.

Reproductive organ

Male. Vas deferens sinuate, vesicula seminalis absent; accessory glands short, gently curved, contiguous to each

other.

Female. Bursa copulatrix bulbous, sclerotized at dorsal surface margin; spermatheca bipartite, with a basal and an apical bulbs; spermathecal duct short, sclerotized; spermathecal gland tubular, long, with larger apex, derived from spermathecal apical bulb.

Apristus cuprascens Bates, 1873

(Fig. 41)

Alimentary canal

Alimentary canal 4.2 mm in length, almost 1.4 times as long as body; relative lengths of fore gut, mid gut, and hind gut 52 : 17: 31.

Fore gut with oesophagus straight; crop large, bulbous; proventriculus moderately complicated, its main longitudinal folds with hairs in entire length, knobby and sclerotized at posterior part, while intermediate longitudinal folds undeveloped, not haired, not sclerotized.

Mid gut gently curved to right side; crypts rod-shaped, dense.

Hind gut with ileum straight; rectum medium in size; rectal glands elliptical, lying in one ring around anterior part of rectum.

Reproductive organ

Male. Testis ovoid; vas deferens spiraled, vesicula seminalis absent; accessory glands straight, short.

Female. Bursa copulatrix cylindrical; spermatheca stick-shaped; spermathecal duct short; spermathecal gland tubular, long, with larger apex.

1.16. Subfamily Zuphinae

Galerita orientalis Schmidt-Gobel, 1846

(Fig. 42)

Alimentary canal

Alimentary canal 33.0 mm in length, almost 1.6 times as long as body; relative lengths of fore gut, mid gut, and hind gut 30 : 46: 24.

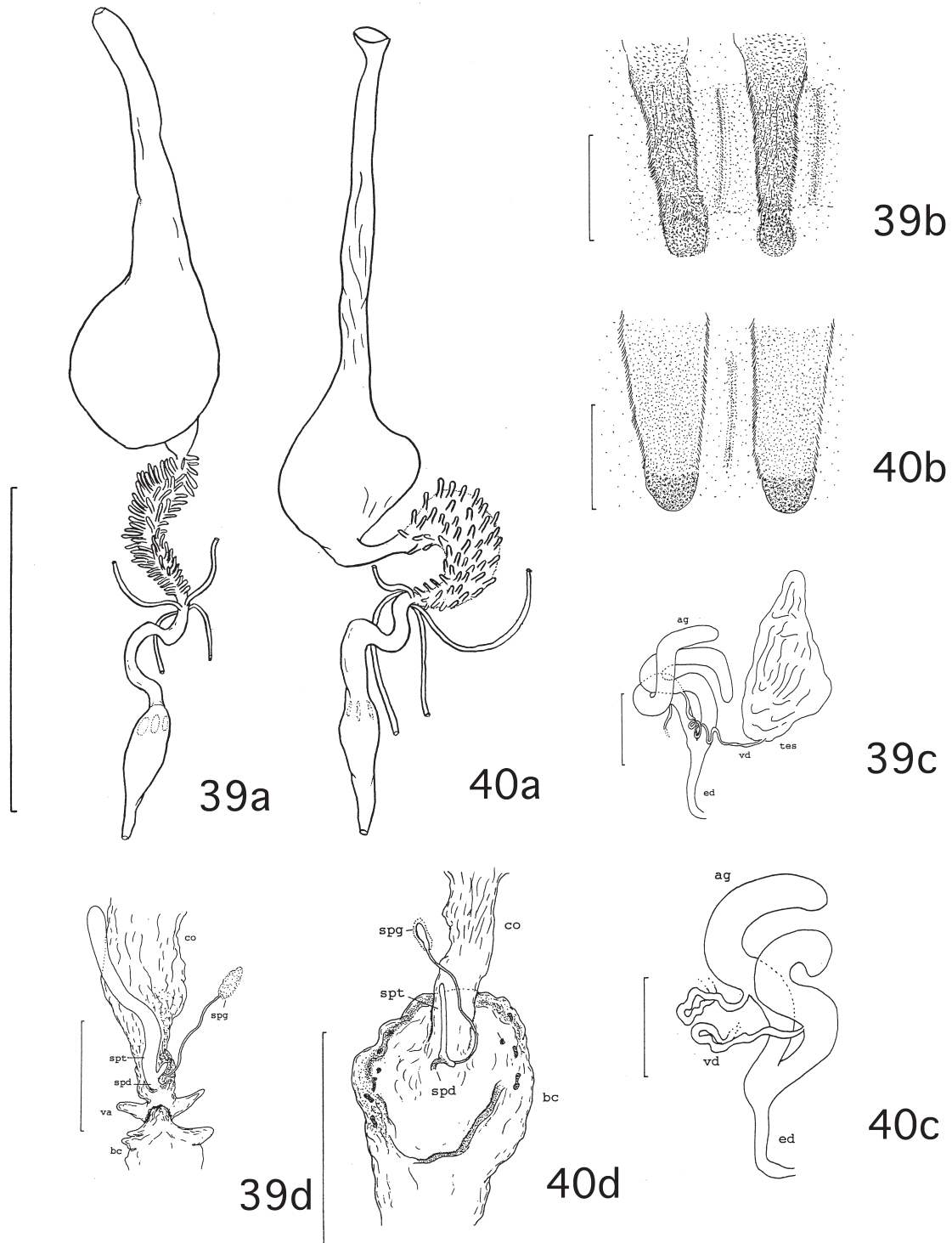
Fore gut with oesophagus straight; crop large, bulbous; proventriculus moderately complicated, its main longitudinal folds with hairs in entire length, knobby posteriorly, intermediate longitudinal folds not haired, not sclerotized, weakly convex.

Mid gut straight to middle, then curved to right and forms one dextral coil at posterior part; crypts stick-shaped, dense.

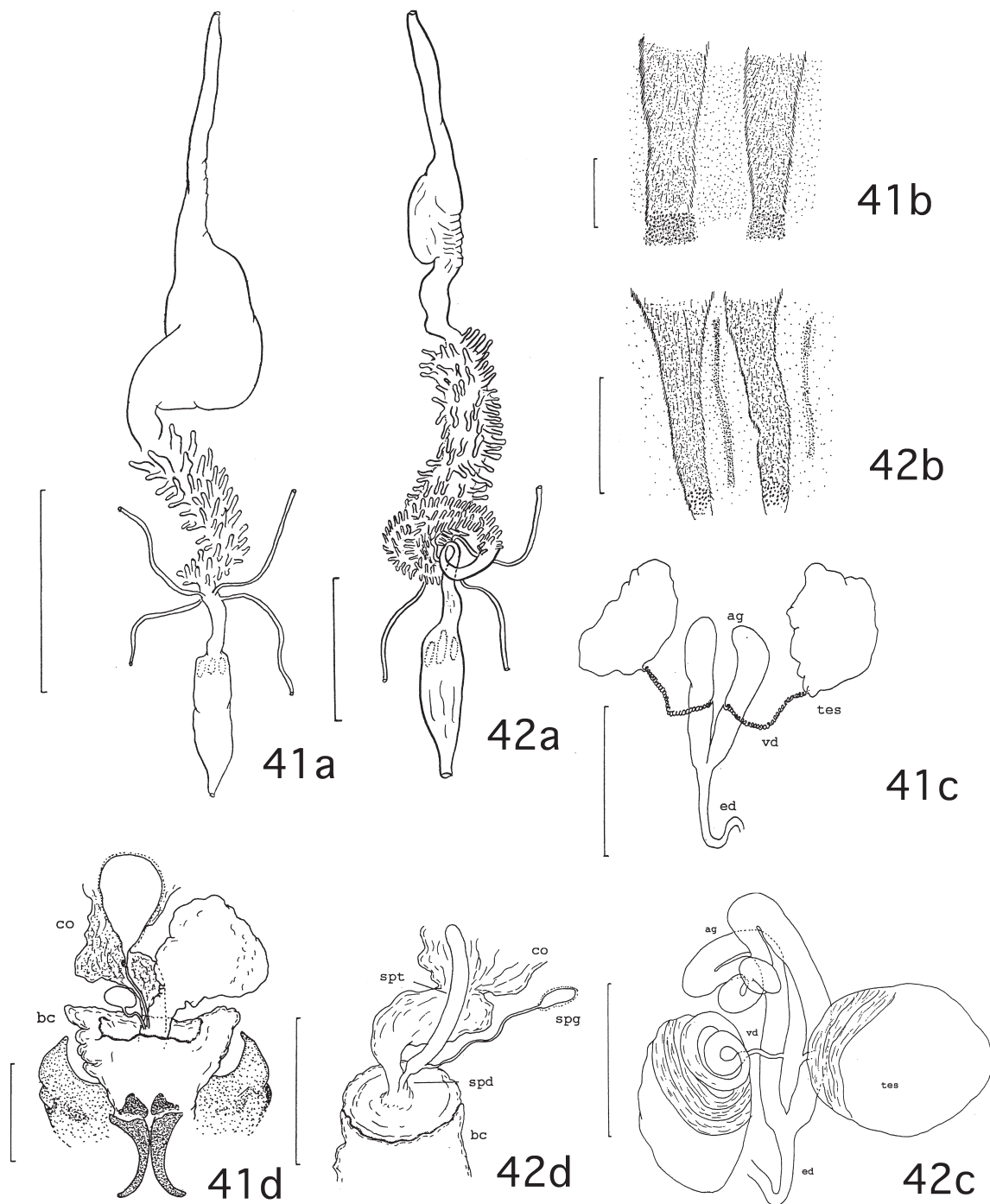
Hind gut with ileum curved to right and forms one dextral coil; rectum medium in size; rectal glands elliptical, lying in one ring around anterior part of rectum.

Reproductive organ

Male. Testis ovoid; vas deferens spiraled, vesicula



Figs. 39-40. Alimentary canal and reproductive organ of *Lebidia octoguttata* (Fig. 39), and *Lebidia bifeneistrata* (Fig. 40). a, alimentary canal; b, proventriculus; c, male reproductive organ; d, female reproductive organ. Scales; 5.0mm for 39a; 0.2mm for 39b; 1.0mm for 39c-d; 1.3mm for 40a; 0.1mm for 40b; 0.5mm for 40c-d.



Figs. 41-42. Alimentary canal and reproductive organ of *Apristus cuprascens* (Fig. 41), and *Galerita orientalis* (Fig. 42). a, alimentary canal; b, proventriculus; c, male reproductive organ; d, female reproductive organ. Scales; 0.5mm for 41a, 41c and 42b; 0.1mm for 41b; 0.3mm for 41d; 5.0mm for 42a; 2.0mm for 42c; 0.1mm for 42d.

seminalis absent; accessory glands straight, folded several times toward apex, contiguous to each other.

Female. Bursa copulatrix cylindrical; spermatheca bipartite, with a basal bulb and an apical bulbs with tubular, ovoid apex; spermathecal duct short; spermathecal gland tubular, medium in size, with larger apex, derived from basal part of spermathecal apical bulb.

Planetes puncticeps Andrewes, 1919
(Fig. 43)

Alimentary canal

Alimentary canal 16.5 mm in length, almost 1.4 times as long as body; relative lengths of fore gut, mid gut, and hind gut 39 : 24: 37.

Fore gut with oesophagus straight; crop large, bulbous; proventriculus moderately complicated, its main longitudinal folds with hairs in entire length, while intermediate longitudinal undeveloped, not haired, not sclerotized.

Mid gut curved to right and forms one dextral coil posteriorly; crypts rod-shaped, dense.

Hind gut with ileum curved to right and forms one dextral coil; rectum medium in size; rectal glands elliptical, lying in one ring around anterior part of rectum.

Reproductive organ

Male. Testis ovoid; vas deferens spiraled, vesicula seminalis absent; accessory glands straight, folded several times toward apex, contiguous to each other.

Female. Bursa copulatrix cylindrical; spermatheca with wrinkled basal part and ovoid apex; spermathecal duct medium in size; spermathecal gland tubular, medium in size, with larger apex, derived from basal part of spermatheca; common oviduct swollen at basal part.

1.17. Subfamily Brachiniinae

Pheropsophus jessoensis Morawitz, 1862
(Fig. 44)

Alimentary canal

Alimentary canal 26.0 mm in length, almost 1.5 times as long as body; relative lengths of fore gut, mid gut, and hind gut 44 : 23: 33.

Fore gut with oesophagus straight; crop large, bulbous; proventriculus simple, its main longitudinal folds with hairs in entire length, while intermediate longitudinal folds not haired, weakly convex, not sclerotized.

Mid gut gently curved to right side; crypts uniformly arranged, rod-shaped, dense.

Hind gut with ileum meandering to form S-shape; rectum medium in size; rectal glands elliptical, lying in one ring around anterior part of rectum.

Reproductive organ

Male. Testis subglobular; vas deferens sinuate, long, derived from basal one third of accessory gland, vesicula seminalis absent; accessory glands long, narrow.

Female. Bursa copulatrix cylindrical, sclerotized; spermatheca equally and deeply bilobed, heart-shaped; spermathecal duct short; spermathecal gland tubular, small, with larger apex, derived from one of bilobed spermatheca; vagina visible beyond bursa copulatrix.

Pheropsophus javanus (Dejean, 1825)
(Fig. 45)

Alimentary canal

Alimentary canal 35.5 mm in length, almost 1.9 times as long as body; relative lengths of fore gut, mid gut, and hind gut 37 : 33: 30.

Fore gut with oesophagus straight; crop large, bulbous; proventriculus simple, its main longitudinal folds with hairs in entire length, with scale-like ctenidia posteriorly, not sclerotized, while intermediate longitudinal folds not haired, weakly convex, not sclerotized.

Mid gut gently curved to right side and forms one dextral coil; crypts uniformly arranged, stick-shaped, dense.

Hind gut with ileum meandering to left side to form S-shape; rectum medium in size; rectal glands elliptical, lying in one ring around anterior part of rectum.

Reproductive organ

Male. Testis subglobular; vas deferens sinuate, long, vesicula seminalis absent; accessory glands long, narrow, contiguous to each other.

Female. Bursa copulatrix cylindrical, sclerotized at dorsal surface; spermatheca weakly bilobed; spermathecal duct short; spermathecal gland tubular, small, with larger and ovoid apex, derived from one of bilobed spermatheca; vagina visible beyond bursa copulatrix.

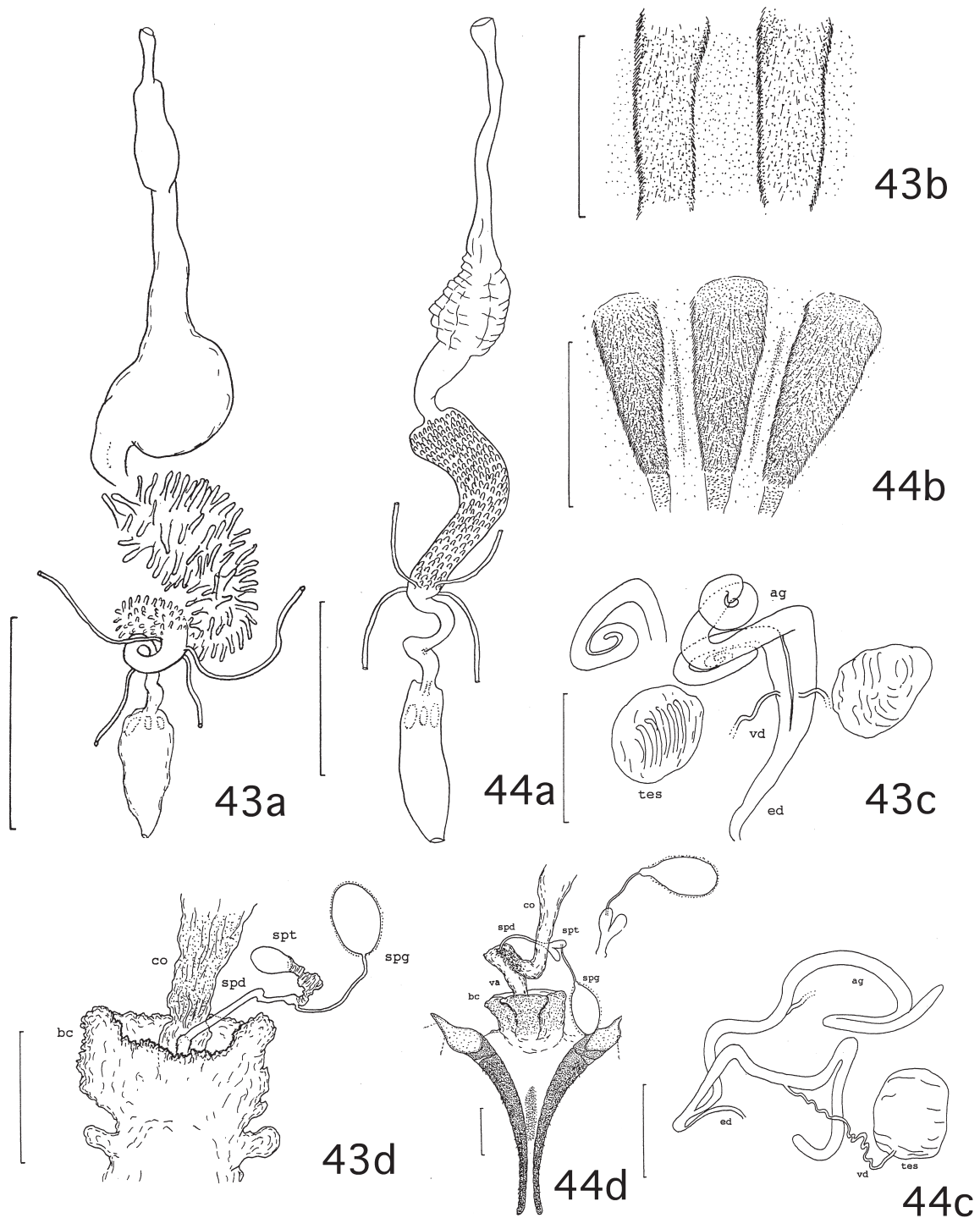
Brachinus scotomedes Redtenbacher, 1868
(Fig. 46)

Alimentary canal

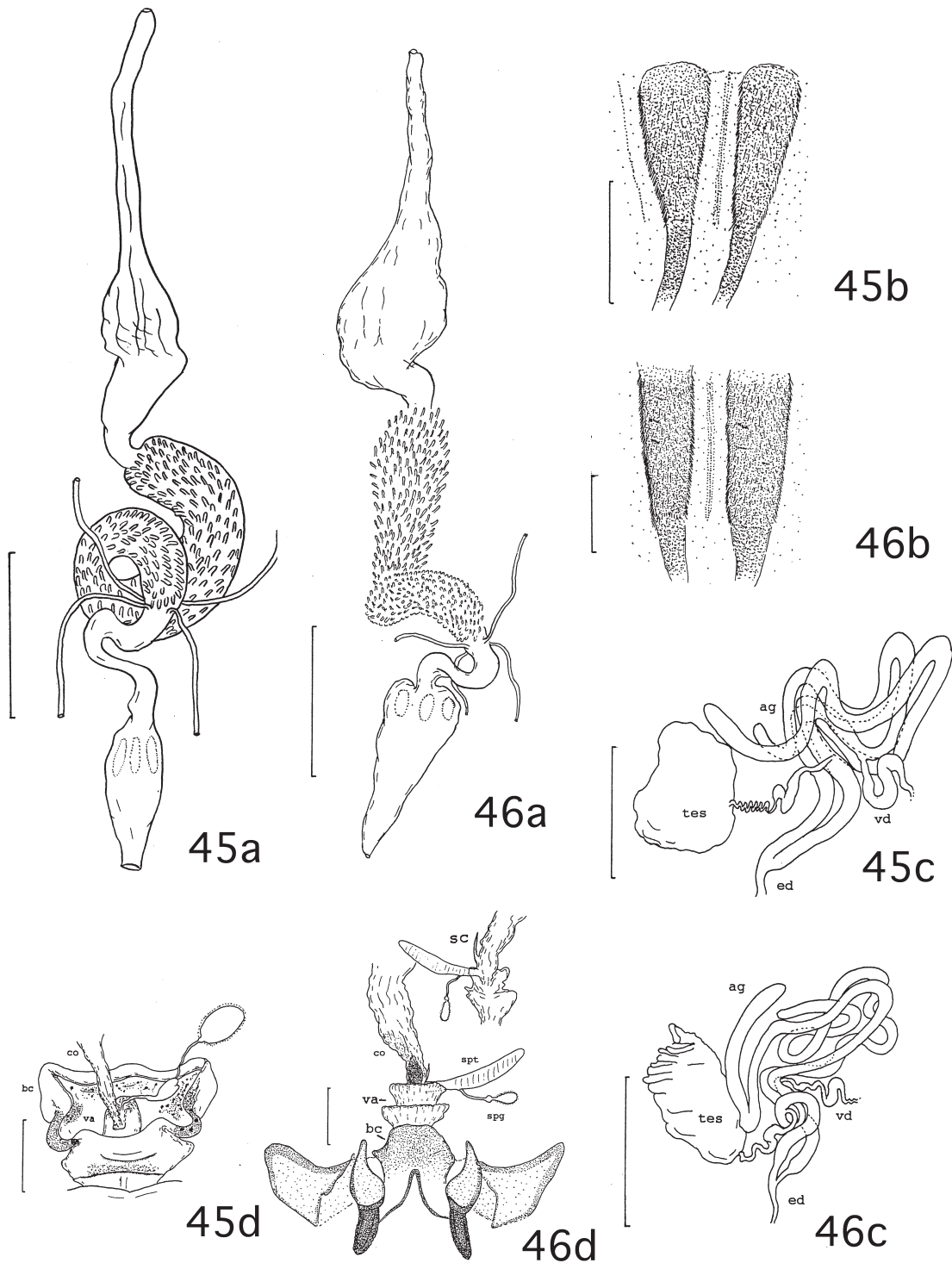
Alimentary canal 30.0 mm in length, almost 2.0 times as long as body; relative lengths of fore gut, mid gut, and hind gut 40 : 40: 20.

Fore gut with oesophagus straight; crop large, bulbous; proventriculus simple, its main longitudinal folds with hairs in entire length, with scale-like ctenidia posteriorly, not sclerotized, while intermediate longitudinal folds not haired, weakly convex, not sclerotized.

Mid gut straight at anterior part, then forms one dextral coil at posterior part, lying from 1st to 4th abdominal segments; crypts stick-shaped, dense.



Figs. 43-44. Alimentary canal and reproductive organ of *Planetes puncticeps* (Fig. 43), and *Pheropsophus jessoensis* (Fig. 44). a, alimentary canal; b, proventriculus; c, male reproductive organ; d, female reproductive organ. Scales; 3.0mm for 43a and 44c; 0.5mm for 43b, 43d and 44d; 2.0mm for 43c; 5.0mm for 44a; 1.0mm for 44b.



Figs. 45-46. Alimentary canal and reproductive organ of *Pheropsophus javanus* (Fig. 45), and *Brachinus scotomedes* (Fig. 46). a, alimentary canal; b, proventriculus; c, male reproductive organ; d, female reproductive organ. Scales; 5.0mm for 45a and 46a; 1.0mm for 45b; 4.0mm for 45c; 1.0mm for 45d; 0.5mm for 46b and 46d; 2.5mm for 46c.

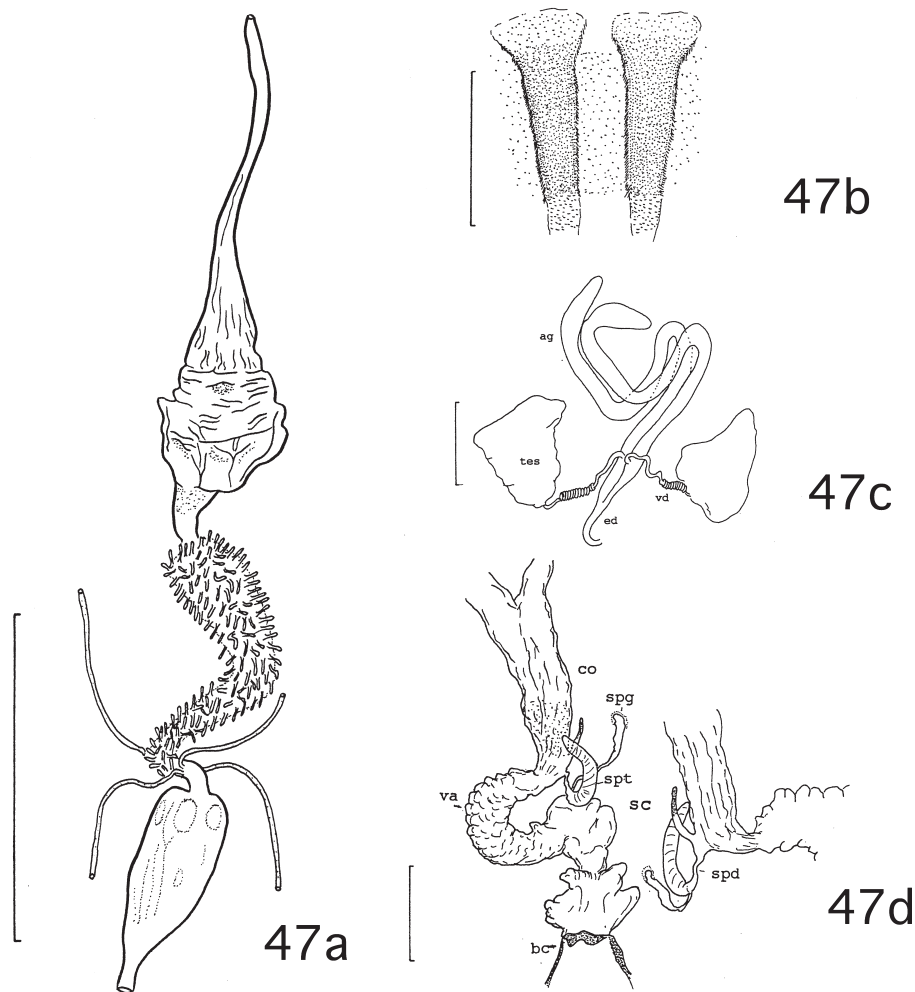


Fig. 47. Alimentary canal and reproductive organ of *Brachinus stenoderus*. a, alimentary canal; b, proventriculus; c, male reproductive organ; d, female reproductive organ. Scales; 5.0mm for 47a; 0.5mm for 47b; 1.0mm for 47c; 0.5mm for 47d.

Hind gut with ileum curved to right side; rectum medium in size; rectal glands elliptical, lying in one ring around anterior part of rectum.

Reproductive organ

Male. Testis ovoid; vas deferens sinuate, vesicula seminalis absent; accessory glands long, narrow, contiguous to each other.

Female. Bursa copulatrix cylindrical, sclerotized; spermatheca stick-shaped; spermathecal duct short; spermathecal gland tubular, small, with slightly larger apex, derived from base of spermatheca; common oviduct with small sclerite at basal part; vagina visible beyond bursa copulatrix.

***Brachinus stenoderus* Bates, 1873.**

(Fig. 47)

Alimentary canal

Alimentary canal 18.0 mm in length, almost 1.8 times as long as body; relative lengths of fore gut, mid gut, and hind gut 45 : 33: 22.

Fore gut with oesophagus straight; crop large, bulbous; proventriculus simple, main longitudinal folds with hairs at lateral margins, with scale-like ctenidia posteriorly, not sclerotized, while intermediate longitudinal folds undeveloped, not haired, not sclerotized.

Mid gut gently curved to right side, gradually narrowing posteriorly, lying from 1st to 4th abdominal segments; crypts rod-shaped, dense.

Hind gut with ileum straight and short; rectum medium in size; rectal glands elliptical, lying in one ring around anterior part of rectum.

Reproductive organ

Male. Testis triangular; vas deferens spiraled from middle to testis, long, vesicula seminalis absent; accessory glands narrow, contiguous to each other.

Female. Bursa copulatrix cylindrical, sclerotized; spermatheca stick-shaped; spermathecal duct short; spermathecal gland tubular, small, weakly dilated apically, derived from base of spermatheca; common oviduct with small sclerite; vagina elongate, visible beyond bursa copulatrix.

Discussion

The anatomical data presented here suggest phylogenetic consequences as follows:

Phylogenetic relationships of subfamily Elaphrinae

Goulet (1983) proposed that elaphrines were related to broscines. This is not supported by the thoracic (Beutel, 1992) and the female genital structures (Liebherr & Will, 1999). From the result of the present study also is not supported.

Phylogenetic relationships of tribe Morionini

Relationship of the tribe Morionini of the subfamily Pterostichinae among the terrestrial Caraboidea has been discussed. Close relation of it to Scaritini was suggested by larval characters (van Emden, 1953; Lindroth, 1969), whereas it was also proposed to be close to Pterostichini on some characters of the adults (Jeannel, 1942; Moore, 1965; Kryzhanovsky, 1976; Straneo, 1979; Erwin, 1985; Habu, 1985). On the other hand a molecular data support inclusion of morionines within Harpalinae (Maddison *et al.*, 1999), and in no analyses with *Scarites* included were Morionini related to it (Ober, 2002). From the result of the present study the tribe Morionini should be regarded as a tribe of Pterostichinae by the character states, absence of the vesicula seminalis and presence of the spermathecal gland etc.

Phylogenetic relationships of subfamily Odacanthinae

The spermathecal duct joined common oviduct by a U-shaped sclerite is autapomorphic in this taxon. However monophyly of Odacanthinae is doubtful.

Phylogenetic relationships of subfamily Brachininae

Brachininae has been treated as an independent family by its unique bombardier habit or a subfamily within the Carabidae according to the different evaluations of the nocturnal taxa (Crowson, 1955; Uéno *et al.*, 1984). Phylogenetic placement of Brachininae has been

controversial. Brachininae is monophyletic and possibly related to higher carabids such as Harpalinae (Erwin, 1970). Liebherr and Will (1998) suggested a phylogenetic placement of Brachininae near Harpalinae based on the female reproductive tract characters. Character states of the larval head (Beutel, 1995), the adult thorax (Beutel, 1992), and the male aedeagus (Jeannel, 1942, 1949), and 18S rDNA (Maddison *et al.*, 1999) argue for placement of Brachininae near Harpalinae. Results of the present observations may suggest arrangement of it as a subfamily of the Carabidae *s. lato* rather than an independent family.

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List of abbreviations in figures

ag	accessory gland	bc	bursa copulatrix
co	common oviduct	ed	ejaculatory duct
sc	sclerite	spt	spermatheca
tes	testis	va	vagina
vd	vas deferens	vs	vesicular seminalis