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Morphologic studies of the alimentary canal and internal reproductive organs of the Chaetosomatidae and the Cleridae (Coleoptera: Cleroidea) with comparative morphology and taxonomic analyses

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Morphologic studies of the alimentary canal and internal reproductive organs of the Chaetosomatidae and the Cleridae (Coleoptera: Cleroidea) with comparative morphology and taxonomic analyses

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Morphologic studies of the alimentary canal and internal reproductive organs of the Chaetosomatidae and the Cleridae (Coleoptera: Cleroidea) with comparative morphology and taxonomic analyses

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Abstract. Considerations of the alimentary canal, mesodermal reproductive organs, and ventral nervous system and brain are provided. The treatise is based on studies of 301 species, representing 99 genera, 11 subfamilies, and two cleroid families. A comparative morphology summary is provided. Morphological variations of the stomodaeum, ventriculus, malpighian tubules, configuration of the spermathecal capsule, shape of the bursa copulatrix, male accessory glands, and testes provide taxonomically useful characteristics. Provided are 252 illustrations. A new name, *Katachaetosoma*, **nom. nov.**, is proposed to replace the preoccupied name *Chaetosoma* Dejean (Insecta: Coleoptera: Cerambycidae).

Introduction

Morphological variations of the alimentary canal and mesodermal reproductive organs of Chaetosomatidae and the Cleridae present many phylogenetically useful character states [Crowson 1972; Ekis (now Opitz) 1978; Opitz 2003, 2010a]. Such information formed important components of my systematic endeavors begun with my PhD dissertation (Ekis and Gupta 1971). The thesis (Ekis 1972) contains copious heretofore unpublished information about the structures under consideration. Moreover, since the thesis research, hundreds of additional specimens, representing a vast number of checkered beetle species and genera, were acquired, dissected and increments of the information published in various taxonomic treatments. The purpose of this contribution is to make available new information about the digestive and reproductive systems of Chaetosomatidae and Cleridae.

It must be emphasized that the inventory of information presented serves as a beginning, an indication of what mesodermal structures may help to resolve taxa relationships. Except for genera such as *Cymatodera* Gray, *Phyllobaenus* Dejean, *Enoclerus* Gahan, *Trichodes* Herbst, *Eleale* Newman, and *Pelonium* Spinola, only specimens of few species/genus became available in a proper fixative. It is hoped that this treatise will encourage other cleridologists to examine the mesodermal organs as a potential source of taxonomic characteristics. The intent is to thoroughly examine the gestalt of one's research animal for heuristic and lasting proposals of evolutionarily based classifications.

Literature Review

To my knowledge only in Crowson (1972) and Opitz (2010a: 947) does one find information about the internal organs of Chaetosomatidae. However, morphologic studies of Cleridae mesodermal organs began with Dufour (1824) who investigated the alimentary canal of *Trichodes alvearius* (Fabricius) and *T. apiarius* (Linnaeus). Then, Spinola (1844) published a general description of the digestive and internal reproductive organs, and Cholodkovsky (1913) treated the histology of the alimentary canal of *Necrobia ruficollis* (Fabricius). Further, Umeya (1960) figured the digestive tract of *Thanasimus substriatus* (Gebler) and Stammer (1934) described the malpighian tubules of *Clerus* Fabricius. More recently, Ekis and Gupta (1971) described and figured the digestive tract and malpighian tubules of 44 Cleridae species. Crowson (1972) evaluated the contents of this work from a systematic perspective. Then, Opitz (2010a) described and illustrated additional mesodermal information about Chaetosomatidae and Cleridae, with taxonomic coverage involving 11 of the 12 currently recognized subfamilies of Cleridae.

Early studies of clerid mesodermal reproductive organs involve Dufour (1825) who studied the male and female reproductive structures of *Trichodes alvearius* (Fabricius), while Escherich (1893) published about the male organs of *T. apiarius* (Linnaeus). During this period Bordas (1898) studied the male organs of both of these *Trichodes* species. Then, Lesne (1938) discussed the spermathecal capsule and bursa copulatrix of *Pelonium multinotatum* Pic and *P. fasciculatum* (Klug). A comprehensive treatise of the internal reproductive organs of 65 species of *Enoclerus* Gahan was published by Ekis (1978). Further, Opitz (2003) provided an analysis of structure, function, and evolutionary significance of spermatophore-producing organs of diverse checkered beetle genera. Lastly, Opitz (2010a) made use of mesodermal organs in his taxonomic investigations involving the subfamilial and generic levels in the Cleridae. Most recently, Yang, *et al.*, (2011) investigated the female organs of two species of the clerine genus *Tillicera* Spinola.

Materials and Methods

This treatise is based on examination of the internal organs of 301 species, involving 99 genera and 11 out of 12 subfamilies presented in a scheme of higher classification as proposed by Opitz (2010a). Many of the observations were published in taxonomic papers as listed in Opitz (2010a). Specimens were collected by the author or received in various stages of liquid preservation from diverse parts of the world. Beetles that were initially preserved in fluid, but then dry mounted were rehydrated to soften their mesodermal organs. Various fixatives were used to liquid preserve the beetles including Weaver's fixative, Bouin's fixative, Barber's solution, 10% formaldehyde, and 70% ethyl alcohol. Pampel's fluid (glacial acetic acid, 4 parts; 40% formaldehyde, 6 parts; 95% ethyl alcohol, 15 parts; water, 30 parts) proved to be the most useful fixative in quality of organ preservation and in more than 10 years years of useful fixation. Techniques that involve dissection, histological preparations, illustration, and sources for morphological terms are described in Ekis and Gupta (1971), Ekis (1977a) and Opitz (2010a: 36). The species included in this work are presented in a scheme of higher classification as proposed by Opitz (2010a).

Nomenclatural Note

The Chaetosomatidae genus *Katachaetosoma* Opitz, **new replacement name** for *Chaetosoma* Westwood, 1851 (Insecta: Coleoptera: Chaetosomatidae), a junior primary homonym of *Chatosoma* Dejean, 1835 (Insecta: Coleoptera: Cerambycidae), is proposed to include *Chaetosoma scaritides* Westwood and *Chaetosoma colossa* Opitz.

Descriptions

Chaetosomatidae

Somatochaetus quadraticollis Menier and Ekis. Alimentary canal: Stomodaeum very long, as long as length of ventriculus (Fig. 1).

Metaxina ornata Broun. Alimentary canal: As in previous species (Fig. 2). Notes: The extensive length of the stomodaeum is considered herein a primitive characteristic within Cleroidea, one that is also found among species of Thaneroclerinae Chapin and Isoclerinae Kolibáč, the most primitive subfamilies in the Cleridae.

Cleridae

Isoclerinae Kolibáč: *Ababa* Casey, sp. (Brazil). Alimentary canal: As in previous species (Fig 3).

Hydnocerinae Spinola: *Callimerus* Gorham, sp. (South India). Alimentary canal: 6 cryptonephridial malpighian tubules. Reproductive organs: Female-Spermathecal capsule well sclerotized; spermathecal gland attached to middle of capsule; bursa copulatrix not saccular; ovariole comprising 6 follicles (Fig. 4).

Eurymetopum maculatum Blanchard. Reproductive organs: Male-One pair of accessory glands; seminal vesicle well developed; testis comprising 12 follicles (Fig. 5). Female-Spermathecal capsule well sclerotized; spermathecal gland attached to base of capsule; bursa copulatrix not saccular (Fig. 6).

Eurymetopum Blanchard, species a-e (Chile). Species a. Reproductive organs: Male-Two pairs of accessory glands, lateral pair bifurcated distally and much shorter than medial pair; testis comprising 6 follicles (Fig. 7). Species b. Reproductive organs: Male-Two pairs of accessory glands, lateral pair much longer than medial pair (Fig. 8). Species c-e. Female- Spermathecal capsule well sclerotized; spermathecal gland attached to base of capsule; bursa copulatrix not saccular; ovary comprising 6 follicles (Figs. 9-11).

Isohydnocera aegra (Newman). Reproductive organs: Male-One pair of accessory glands, glands swollen at base and particularly long; testis comprising 6 follicles (Fig. 12). Female- Spermathecal capsule well sclerotized; spermathecal gland attached to apex of capsule; bursa copulatrix not saccular (Fig. 13).

Isohydnocera tabida (Leconte). Reproductive organs: Male-As in previous species except testis comprising 12 follicles (Fig. 14). Female- As in previous species, except spermathecal gland notably shorter (Fig. 15).

Isohydnocera Chapin, species a (Arizona), species b (México). Reproductive organs: Males-As in previous species except testis comprising 6 follicles. Species a (Fig. 16). Species b (Fig. 17).

Lemidia nitens (Newman). Reproductive organs: Male- One pair of accessory glands; testis comprising 12 follicles (Fig. 18). Female- Spermathecal capsule well sclerotized; spermathecal gland attached near middle of capsule; bursa copulatrix not saccular (Fig. 19).

Lemidia Spinola, species a-g (Australia). Reproductive organs: Species a. Male- One pair of accessory glands, glands diverticulated at base; testis comprising 12 follicles (Fig. 20). Female- As in previous species (Fig. 25). Species b. Male- One pair of accessory glands, glands particularly long; testis comprising 12 follicles (Fig. 21). Species c-g. Female- As in *L. nitens* (Figs. 22, 23, 24, 26, 27).

Phyllobaenus pallipennis (Say). Reproductive organs: Male- One pair of accessory glands, glands trilobed; seminal vesicle bipartite; vas deferens particularly long; testis comprising 6 follicles (Fig. 28). Female- Spermathecal capsule well sclerotized; spermathecal gland attached to apex of capsule; bursa copulatrix not saccular (Fig. 29).

Phyllobaenus longus (Leconte). Reproductive organs: Male- As in *P. pallipennis* except base of accessory gland highly diverticulated (Fig. 30). Female- As in *P. pallipennis* (Fig. 31).

Phyllobaenus antillae (Wolcott). Reproductive organs: Male- As in *Isohydnocera tabida* except seminal vesicle bipartite and testis comprising 6 follicles (Fig. 32). Female- Female-As in *P. pallipennis* (Fig. 33).

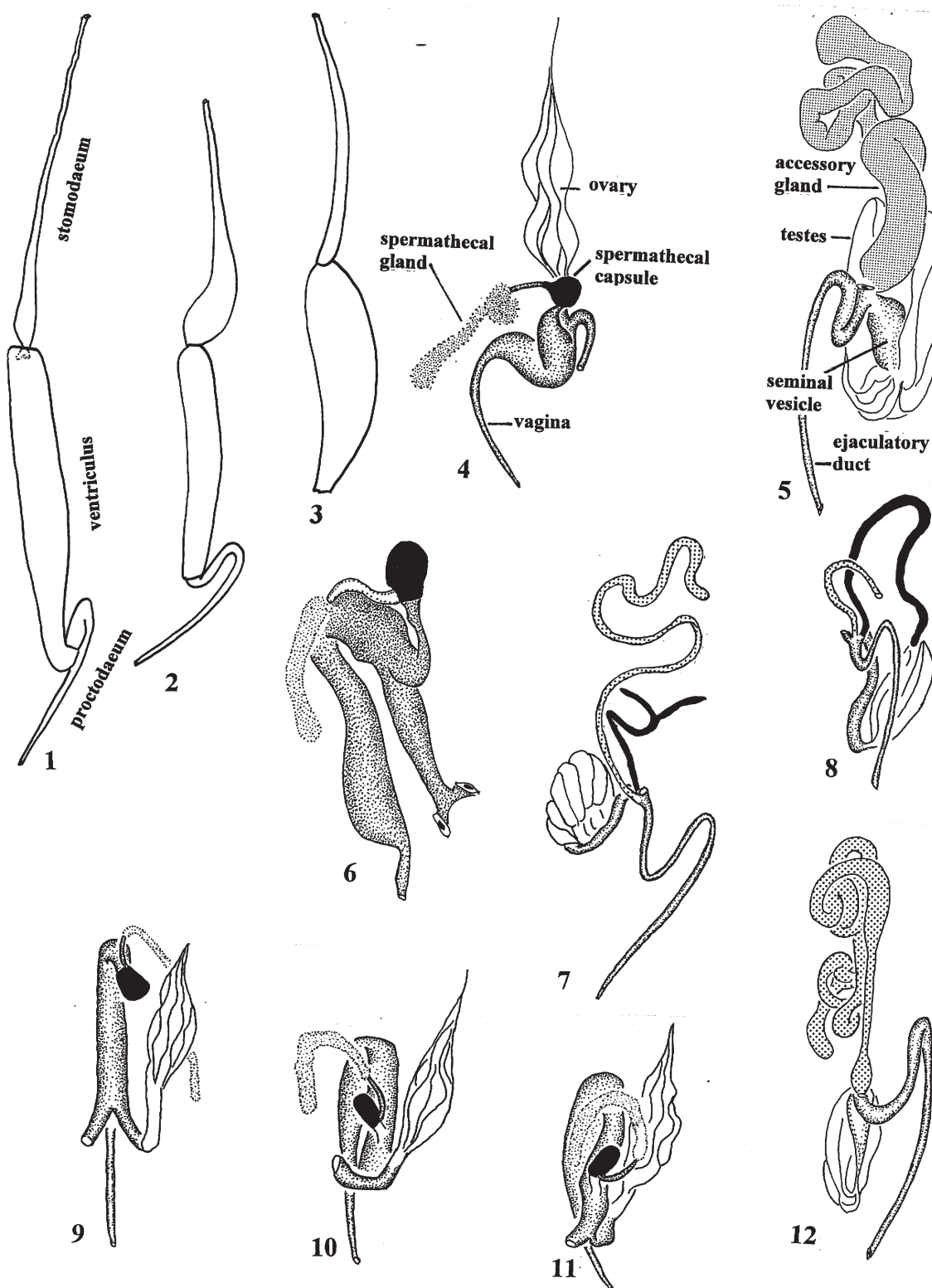
Phyllobaenus Dejean, sp. (Guatemala). Reproductive organs: Male- As in *P. antillae* (Fig. 35). Female- As in *P. pallipennis* (Fig. 36).

Wolcottia sobrina (Fall). Reproductive organs: Male- One pair of accessory glands, glands particularly long, swollen at base; testis multifollicular (Fig. 34). Female- Spermathecal capsule well sclerotized, elongated; spermathecal gland attached to apex of capsule; bursa copulatrix not saccular (Fig. 39).

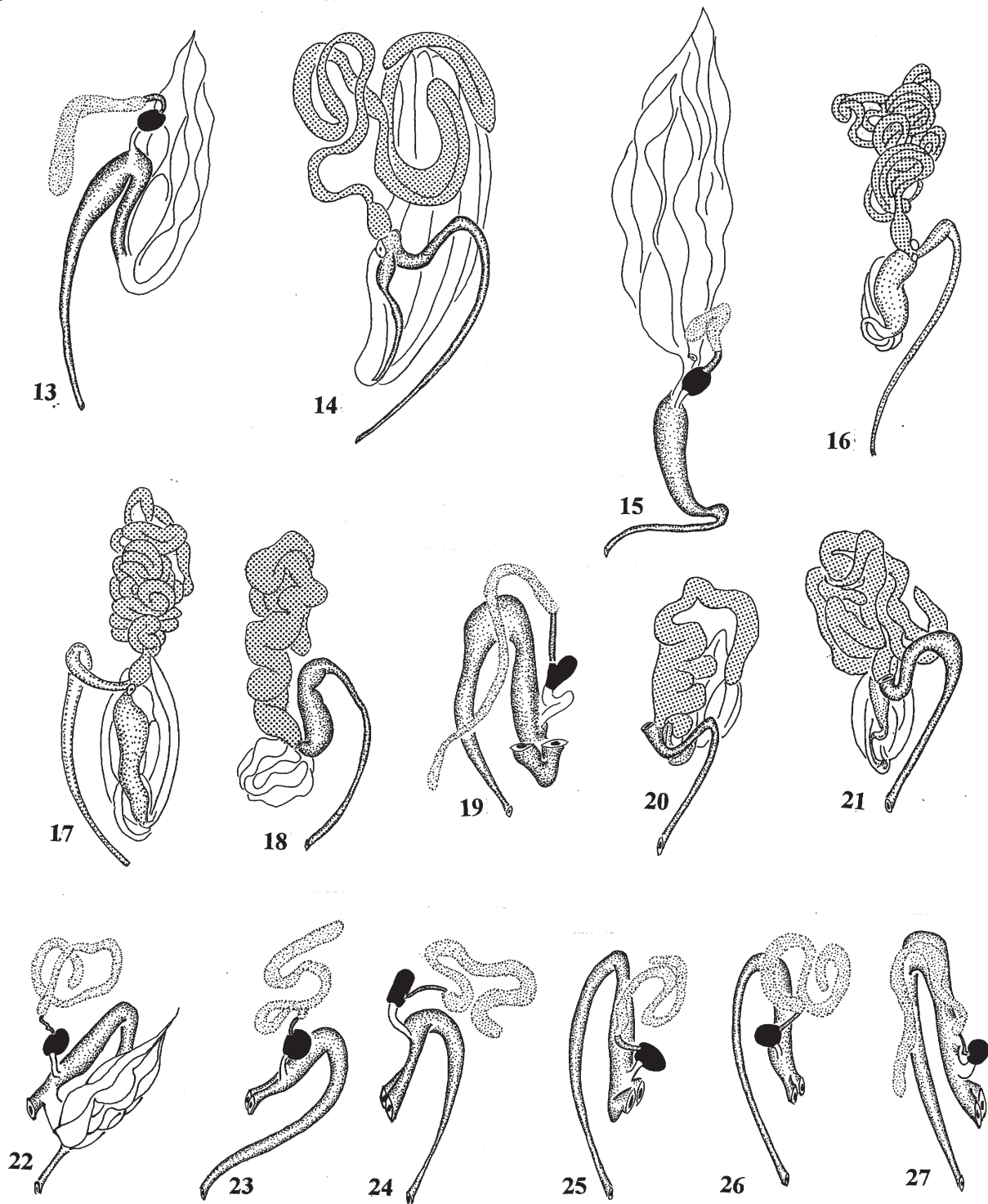
Clerinae Latreille: *Aulicus femoralis* Schaffer. Reproductive organs: Male- Two pairs of accessory glands, both glands biramous, medial pair transformed into spermatophoral gland (Fig. 37).

Aulicus nigriventris Schaeffer. Reproductive organs: Female- Spermathecal capsule not well sclerotized, bipartite; spermathecal gland attached to middle deflexed branch of capsule; bursa copulatrix not saccular; ovary comprising 13 follicles (Fig. 38).

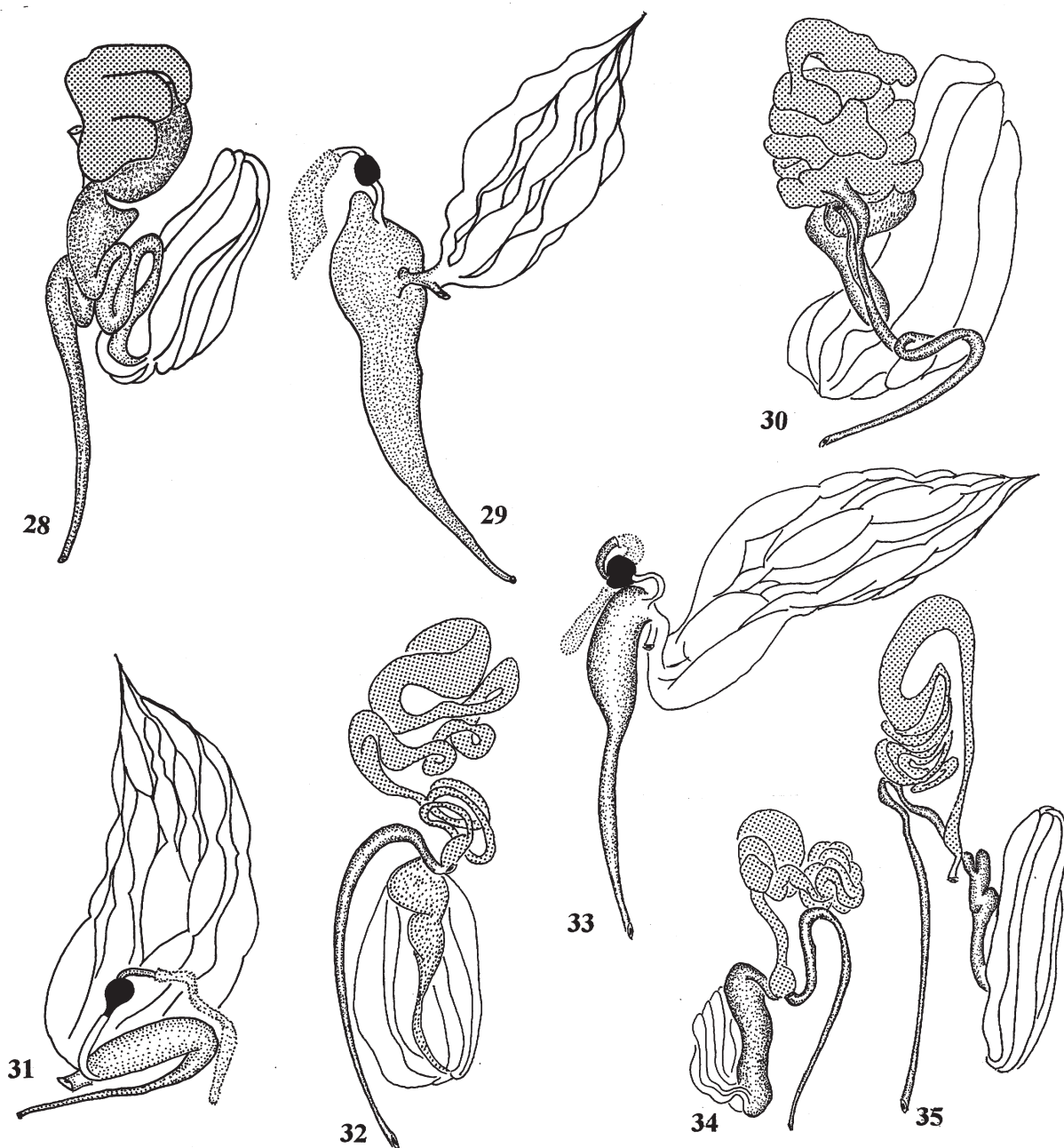
Axina conspicua Schenkling. Alimentary canal: With 6 cryptonephridial malpighian tubules. Reproductive organs: Male- Two pairs of biramous accessory glands, medial gland much shorter than lateral glands, inner branch of medial gland with central longitudinal dark streak (Fig. 40). Female- Spermathecal capsule slightly sclerotized; spermathecal gland attached to middle of capsule; bursa copulatrix saccular (Fig. 41).



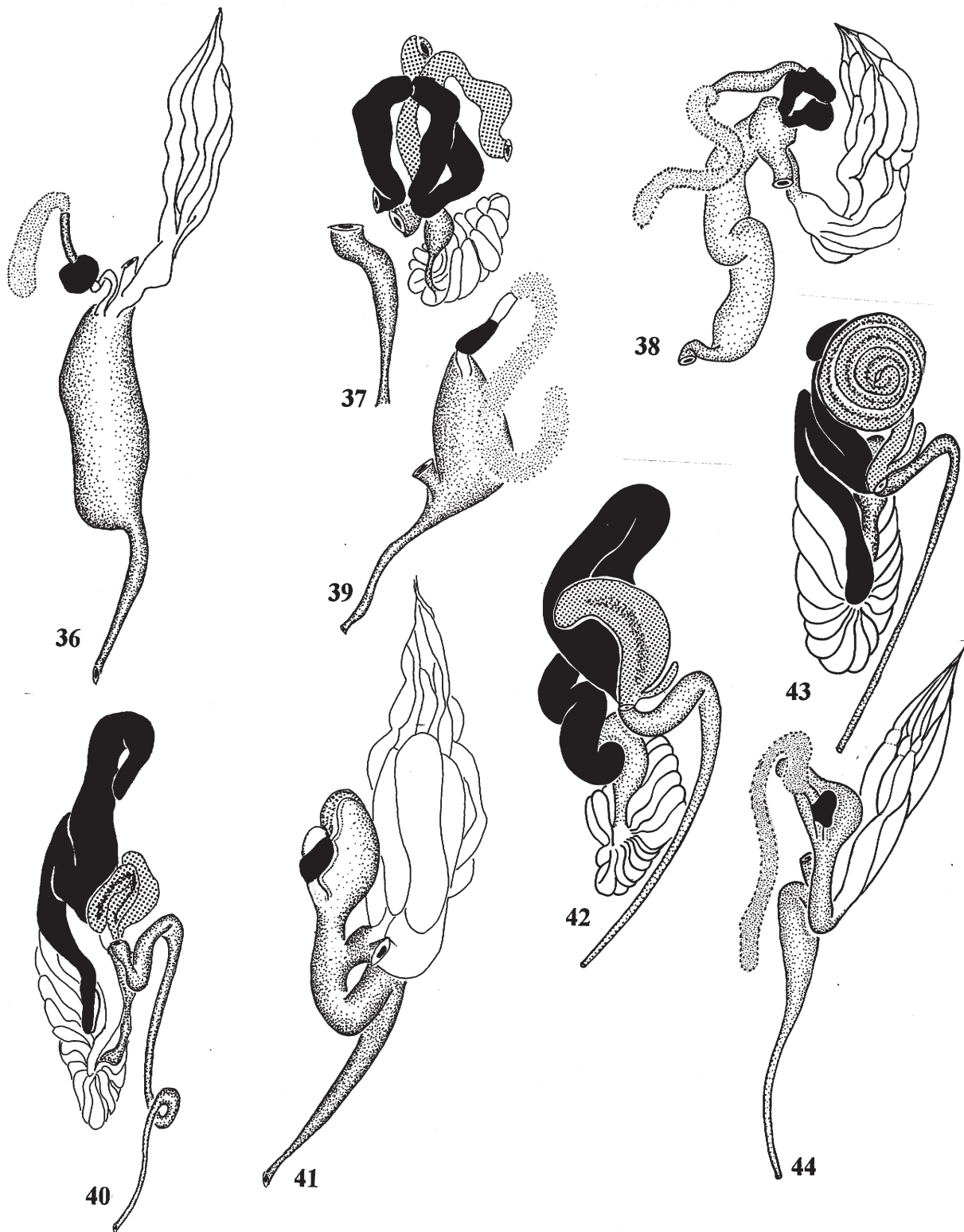
Figures 1–12. Alimentary canals and reproductive organs. 1–3. Alimentary canals. 1) *Somatochaetus quadraticollis*. 2) *Metaxina ornata*. 3) *Ababa* sp. 4–12. Reproductive organs. 4) *Callimerus* sp., female. 5–6. *Eurymetopum maculatum*, 5) male, 6) female. 7–12. *Eurymetopum* spp., 7) sp. a., male. 8) sp. b., male. 9) sp. c., female. 10) sp. d., female. 11) sp. e., female. 12). *Isohydnocera aegra*, male.



Figures 13–27. Reproductive organs. 13) *Isohydncera aegra*, female. 14–15 *Isohydncera tabida*, 14) male, 15) female. 16–17. *Isohydncera*, males. 16) sp. a. 17) sp. b. 18–19. *Lemidia nitens*, 18) male, 19) female. 20–27. *Lemidia* spp. 20) sp. a. male. 21) sp. b, male. 22–27, females. 22) sp.c, 23) sp. d, 24) sp. e. 25) sp. a, female. 26) sp. f, 27) sp. g.



Figures 28–35. Reproductive organs. 28–29. *Phyllobaenus pallipennis*. 28) male. 29) female. 30–31. *Phyllobaenus longus*. 30) male. 31) female. 32–33. *Phyllobaenus antillae*. 32) male. 33) female. 34) *Wolcottia sobrina*, male. 35) *Phyllobaenus* sp., male.



Figures 36–44. Reproductive organs. 36) *Phyllobaenus* sp., female. 37) *Aulicus femoralis*, male. 38) *Aulicus nigriventris*, female. 39) *Wolcottia sobrina*, female. 40–41. *Axina conspicua*. 40) male. 41) female. 42) *Axina bifasciata*, male. 43) *Axina plagiata*, male. 44) *Axina parcepunctata*, female.

Axina bifasciata (Chevrolat). Reproductive organs: Male. With two pairs of biramous accessory glands, medial pair much shorter than lateral pair, inner branch of medial branch with central longitudinal dark streak; testis comprising 44 follicles (Fig. 42).

Axina parcepunctata Schenkling. Reproductive organs. Females- Spermathecal capsule slightly sclerotized; spermathecal gland attached to middle of capsule (Fig. 44).

Axina plagiata Schenkling. Reproductive organs: Male- With 2 pairs of biramous accessory glands, inner branch of medial gland highly coiled distally and with central longitudinal dark streak; testis comprising 49 follicles (Fig. 43).

Caestron concinnus (Gorham). Reproductive Organs: Male- Two pairs of accessory glands, both glands with basal diverticulum, inner chamber of medial gland with central longitudinal dark streak; testis comprising 11 follicles (Fig. 45). Female- Spermathecal capsule slightly sclerotized; spermathecal gland attached to basal region of capsule; spermathecal duct exceptionally long; bursa copulatrix saccular (Fig. 46).

Caestron contractus (Gorham). Reproductive Organs: Female- As in previous species (Fig. 47). Notes: The extraordinarily long spermathecal duct may be apotypic for *Caestron* Spinola.

Calendyma chilensis (Castelnau). Alimentary canal: Stomodaeum with well- developed proventriculus; ventricular papillae well developed; with 6 cryptonephridial malpighian tubules; proctodaeum well developed (Fig. 48). Reproductive organs: Female- Spermathecal capsule slightly sclerotized, capsule elongated and tapered; spermathecal gland attached to apex of capsule; spermathecal duct extraordinarily long; with large saccular bursa copulatrix (Fig. 49).

Cardiostychus gabonicus (Thomson). Alimentary canal: As in previous species (Fig. 50). Reproductive organs: Male- Two pairs of very long accessory glands, medial gland biramous, lateral gland uniramous; testis comprising 20 follicles (Fig. 51). Female- Spermathecal capsule well sclerotized; spermathecal gland attached to base of capsule; bursa copulatrix saccular (Fig. 52).

Cardiostychus Quedenfeldt, sp. a (Democratic Republic of the Congo). Reproductive organs: Male- Two pairs of accessory glands, medial gland biramous, lateral gland not branched (Fig. 53). Female- Spermathecal capsule well sclerotized; spermathecal gland attached to base of capsule; bursa copulatrix saccular (Fig. 54).

Chiloclerus mimus Solervicens. Alimentary canal: Stomodaeum with well- developed proventriculus; ventricular papillae well developed; 6 cryptonephridial malpighian tubules; proctodaeum well developed (Fig. 55). Reproductive organs: Male- Two pairs of accessory glands, medial pair transformed into spermatophoral glands, lateral pair biramous; testis comprising more than 70 follicles (Fig. 56).

Clerus mutillarius (Fabricius). Alimentary canal: Stomodaeum with well- developed proventriculus; ventricular papillae well developed; 6 cryptonephridial malpighian tubules; proctodaeum well developed (Fig. 57). Reproductive organs: Male- Two pairs of accessory glands, medial pair not branched, lateral pair biramous; testis comprising 26 follicles (Fig. 59). Female- Spermathecal gland well sclerotized; spermathecal gland attached to base of capsule; bursa copulatrix saccular (Fig. 58).

Eleale Newman, species a-h (Australia). Reproductive organs. Species a. Male- Two pairs of accessory glands, medial pair not branched, diverticulated at base, lateral pair biramous; testis comprising 32 follicles (Fig. 60). Species b. Male- Two pairs of accessory glands, lateral pair not branched, medial pair extraordinarily long, biramous and diverticulated at base; testis small and spheroid (Fig. 61). Species c. Male- Two pairs of accessory glands, medial pair not branched, medial gland biramous; testis comprising 15 follicles (Fig. 62). Female- Spermathecal gland well sclerotized; spermathecal gland attached to base of capsule; bursa copulatrix not saccular (Fig. 67). Species d. Male- Two pairs of accessory glands, medial pair not branched, diverticulated at base, lateral glands biramous (Fig. 63). Female- Spermathecal gland well sclerotized; spermathecal gland attached to base of capsule; bursa copulatrix not saccular (Fig. 66). Species e. Male- Two pairs of accessory glands, medial pair not branched, diverticulated at base, lateral pair biramous; testis multifollicular (Fig. 64). Species f-h. Females- Spermathecal capsule well sclerotized; bursa copulatrix not saccular (sp. f, Fig. 65; sp. g, Fig. 68; sp. h, 69).

Epiclines basalis Blanchard. Reproductive organs: Male- Two pairs of accessory glands, medial gland not branched, highly diverticulated at base, lateral gland biramous; testis multifollicular (Figs. 70, 72). Female- Spermathecal capsule well sclerotized, annulated; spermathecal gland attached near apex of capsule; bursa copulatrix saccular (Fig. 71).

Eunatalis Schenkling, species a-b (Australia). Species a. Alimentary canal: Stomodaeum with well-

developed proventriculus; ventricular papillae well developed; 6 cryptonephridial malpighian tubules; proctodaeum well developed (Fig. 73). Reproductive organs: Male- Two pairs of uniramous accessory glands; testis multifollicular (Fig. 74). Female- Spermathecal capsule feebly sclerotized; spermathecal gland attached to apex of capsule; bursa copulatrix saccular, long and slender (Fig. 75). Species b. Reproductive organs. Male- Two pairs of uniramous accessory glands (Fig. 77). Female- Spermathecal capsule feebly sclerotized, exceptionally elongated; spermathecal gland attached near middle of capsule; bursa copulatrix saccular, long and slender (Fig. 76). Notes: The long narrow condition of the bursa copulatrix may be taxonomically significant in *Eunatalis* Schenkling.

Metademiis Schenkling, species a (Australia). Reproductive organs: Female- Spermathecal capsule not well sclerotized; spermathecal gland attached near middle of capsule; bursa copulatrix saccular (Fig. 78).

Neoscrobiger patricius (Klug). Alimentary canal: Stomodaeum short, with well- developed proventriculus; ventricular papillae well developed; 6 cryptonephridial malpighian tubules; proctodaeum well developed (Fig. 83). Reproductive organs: Male- Two pairs of accessory glands, medial gland with spheroid lobe at base, lateral pair not branched; testis multifollicular (Fig. 81). Female- Spermathecal capsule not well sclerotized, bifid; spermathecal gland attached to base of inner chamber; bursa copulatrix saccular and twisted at extremity (Fig. 82).

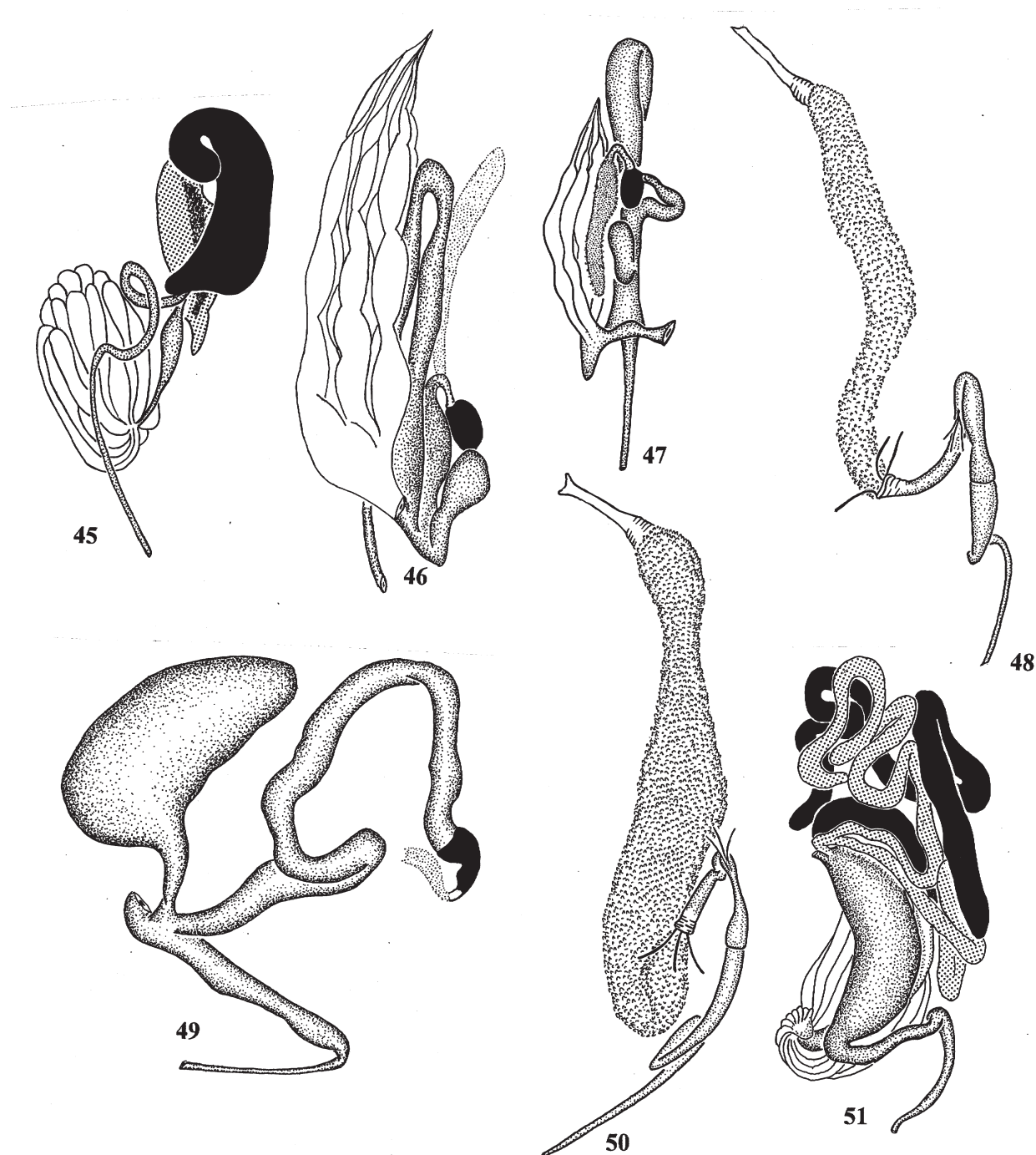
Omadius semicarinatus Chevrolat. Reproductive organs. Male- Two pairs of accessory glands, medial pair not branched, lateral pair with basal vesicle; testis multifollicular (Fig. 79). Female- Spermathecal capsule well sclerotized, sinuous; spermathecal gland attached to base of capsule (Fig. 80).

Omadius Castelnau, species a-p (New Guinea). Species a. Reproductive organs: Two pairs of accessory glands, medial pair biramous, much longer than biramous lateral gland; testis multifollicular (Fig. 84). Species b. Male- Two pairs of accessory glands, medial pair biramous, much longer than uniramous lateral gland; testis comprising 12 follicles (Fig. 85). Species c. Male- Two pairs of accessory glands, medial pair biramous, dorsal branch very short, lateral glands uniramous (Fig. 86). Species d. Male- Two pairs of accessory glands, medial pair biramous and much longer than uniramous lateral pair; testis comprising 18 follicles (Fig. 87). Species e. Male- Two pairs of accessory glands, medial pair biramous and much longer than uniramous lateral pair; testis comprising 12 follicles (Fig. 88). Species f. Male- Two pairs of accessory glands, medial pair biramous; testis comprising 8 follicles (Fig. 89). Species g-i. Males- Two pairs of accessory glands, medial pair biramous and much longer than uniramous lateral pair; testis comprising 12 follicles (species g Fig. 90, species i Fig. 92). Species h. Male- Testis comprising 7 follicles (Fig. 91). Female-Spermathecal capsule well sclerotized; spermathecal gland attached near apex of capsule; bursa copulatrix not saccular (Fig. 95). Species j. Male- Two pairs of uniramous accessory glands, lateral pair vesicular; testis comprising 12 follicles (Fig. 93). Female- Spermathecal capsule well sclerotized, elongated; spermathecal gland attached to middle of capsule; bursa copulatrix not saccular (Fig. 94). Species k. Female- Spermathecal capsule well sclerotized; spermathecal gland attached to middle of capsule; bursa copulatrix highly reduced (Fig. 96). Species l-o. Females- Spermathecal capsule well sclerotized; spermathecal gland attached to base of capsule; bursa copulatrix saccular (species l Fig. 97, species m Fig. 98, species n Fig. 99, species o Fig. 100). Species p. Female-Spermathecal capsule well sclerotized; spermathecal gland attached to base of capsule; bursa copulatrix highly reduced (Fig. 101).

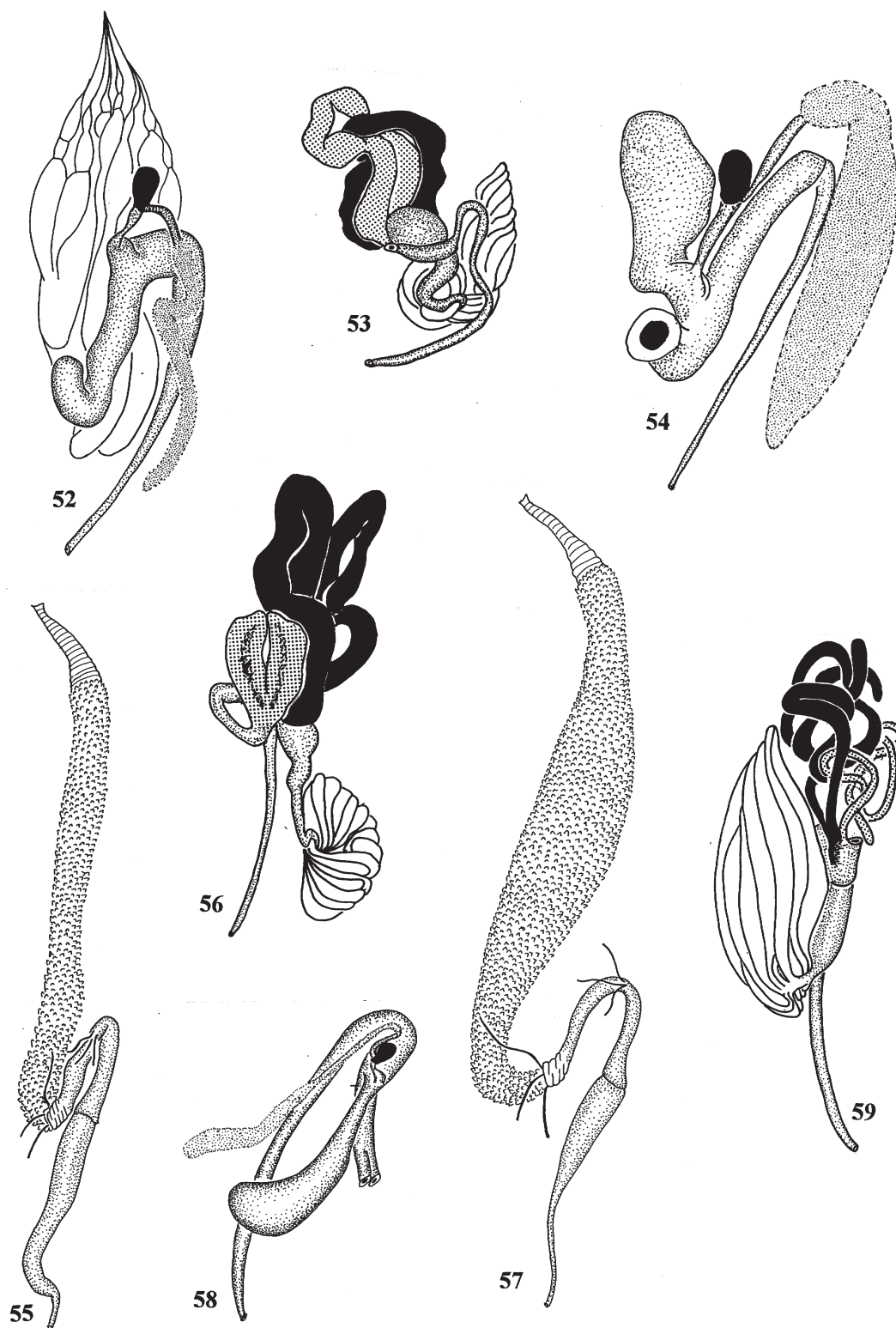
Opilo taeniatus (Klug). Reproductive organs: Male- Two pairs of biramous accessory glands, inner branch of medial glands with central longitudinal dark streak; testis comprising 11 follicles (Figs. 102, 104, 105). Female- Spermathecal capsule bifid, not well sclerotized; spermathecal gland attached at middle of secondary chamber; bursa copulatrix not saccular (Fig. 103).

Phloeocopus Spinola, species. (Democratic Republic of the Congo). Alimentary canal: Stomodaeum with well-developed proventriculus; ventricular papillae well developed; 6 cryptonephridial malpighian tubules (Fig. 106). Reproductive organs: Male- Two pairs of biramous accessory glands, inner branch of medial pair with central longitudinal dark streak; testis multifollicular (Fig. 107). Female- Spermathecal capsule feebly sclerotized; spermathecal gland particularly long and attached to middle of capsule; bursa copulatrix saccular and small, spinous plates near bursa and median oviduct (Figs. 108, 109).

Phlogistus imperialis (Gorham). Reproductive organs: Female- Spermathecal gland bifid, not well sclerotized; spermathecal gland attached to secondary chamber; bursa copulatrix not saccular (Fig. 110).



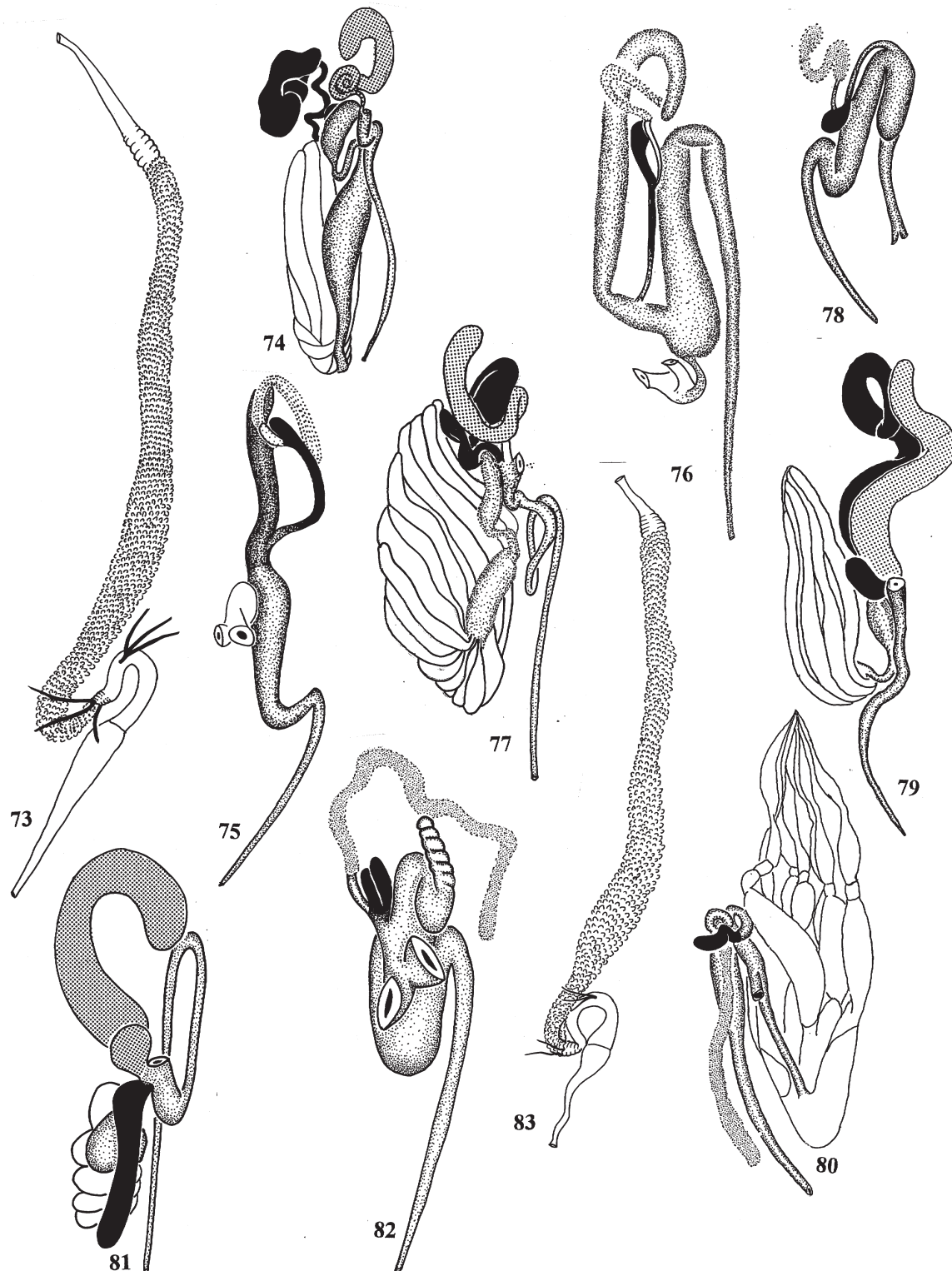
Figures 45–51. Reproductive organs and alimentary canals. 45–47, 49, 51. Reproductive organs. 45–46. *Caeston concinus*. 45) male. 46) female. 47) *Caeston contractus*, female. 48–49. *Calendyma chilensis*. 48) Alimentary canal. 49) Reproductive organs, female. 50–51. *Cardiostychus gabonicus*. 50) Alimentary canal. 51) reproductive organs, male.



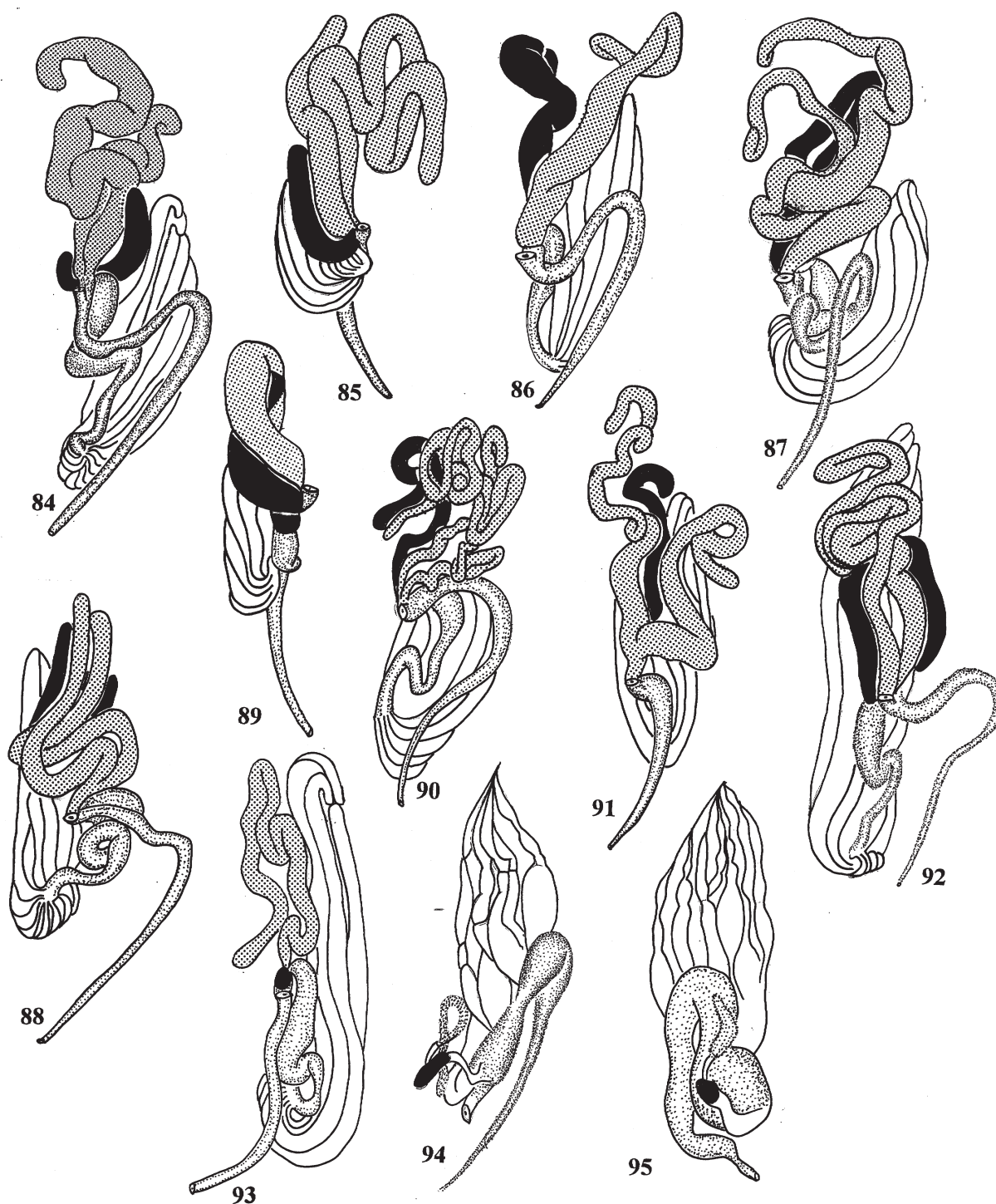
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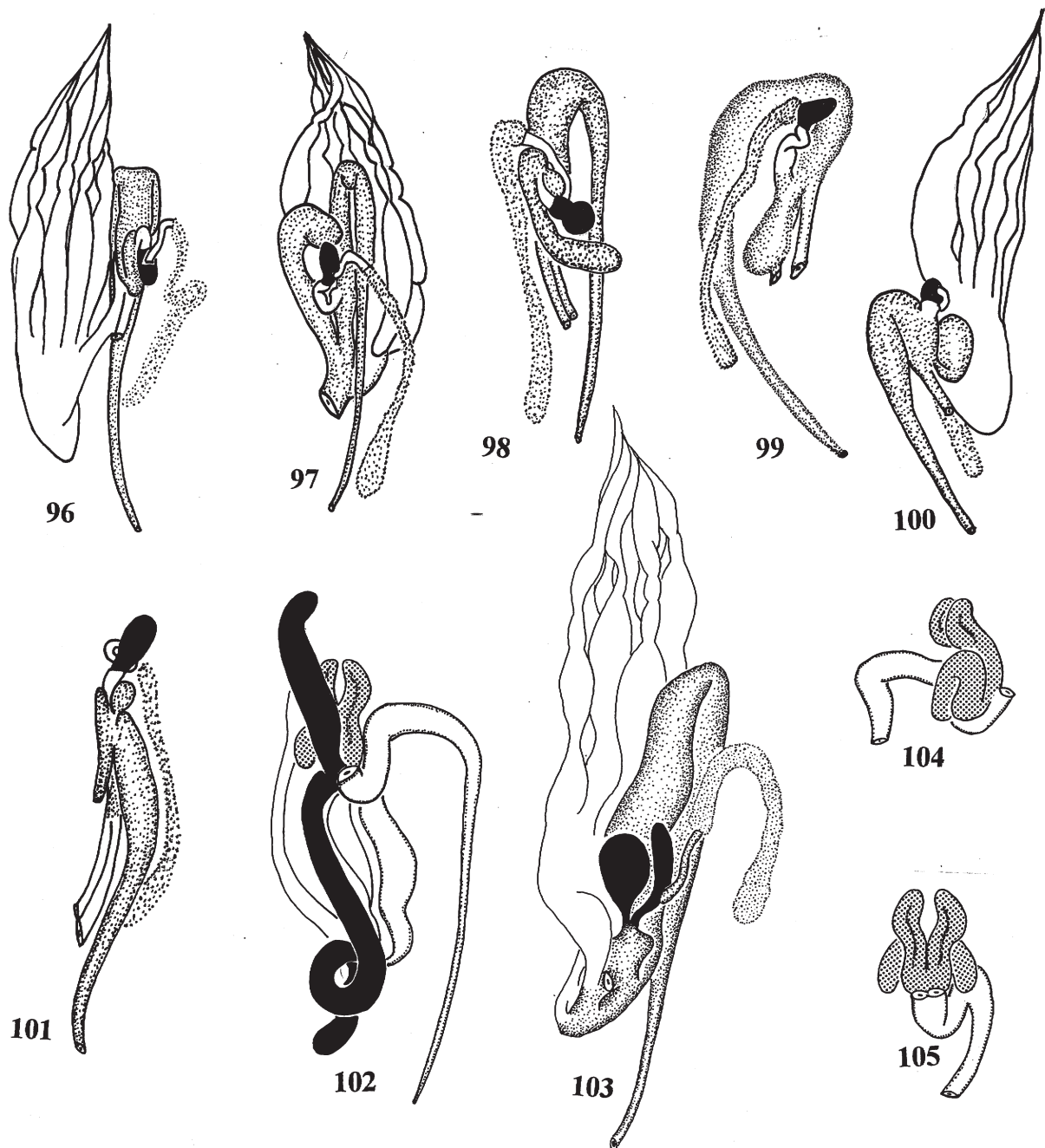
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Figures 73–83. Alimentary canals and reproductive organs. 73–75. *Eunatalis* sp. a. 73) Alimentary canal. 74) Reproductive organs, male. 75) Reproductive organs, female. 76–77. *Eunatalis* sp. b. 76) Reproductive organs, female. 77) Reproductive organs, male. 78) *Metademius* reproductive organs, female. 79–80. *Omadius semicarinatus*. 79) Reproductive organs, male. 80) Reproductive organs, female. 81–83. *Neoscrobiger patricius*. 81) Reproductive organs, male. 82) Reproductive organs, female. 83) Alimentary canal.



Figures 84–95. *Omadius* reproductive organs. 84–93. Males. 84) sp. a. 85) sp. b. 86) sp. c. 87) sp. d. 88) sp. e. 89) sp. f. 90) sp. g. 91) sp. h. 92) sp. i. 93) sp. j. 94–95. Females. 94) sp. j. 95) sp. h.



Figures 96–105. Reproductive organs. **96–101.** *Omadius* females. **96)** sp. k. **97)** sp. l. **98)** sp. m **99)** sp. n. **100)** sp. o. **101)** sp. p. **102–105.** *Opilo taeniatus* **102)** male. **103)** female. **104–105)** Males.

Priocera castanea (Newman). Reproductive organs: Male- Two pairs of accessory glands, medial gland biramous, lateral gland vesicular; testis multifollicular (Fig. 111). Female- Spermathecal capsule partially sclerotized; spermathecal gland attached to apex of capsule; bursa copulatrix saccular (Fig. 112).

Priocera hypocrita Chevrolat. Reproductive organs: Male- medial glands biramous, lateral glands vesicular, round; testis comprising 25 follicles (Fig. 113). Female- Spermathecal capsule partially sclerotized; spermathecal gland attached to apex of capsule; bursa copulatrix saccular (Fig. 114).

Priocera variegata Kirby. Reproductive organs: Female- Spermathecal capsule partially sclerotized, annulated; spermathecal gland attached to apex of capsule; bursa copulatrix not saccular (Fig. 116).

Priocera Kirby, species. (Brazil). Alimentary canal: Ventricular papillae well developed; 6 cryptonephridial malpighian tubules. Reproductive organs: Female- Spermathecal capsule partially sclerotized; spermathecal gland attached to apex of capsule; bursa copulatrix saccular (Fig. 115). Notes. The condition of having the spermathecal capsule partially sclerotized may have phylogenetic significance in the genus. There is some question regarding the extent of sclerotization of the capsule in *P. variegata*.

Stigmatium gilberti White. Reproductive organs: Female- Spermathecal capsule well sclerotized; spermathecal gland attached to base of capsule; spermathecal duct with small papilla at base; bursa copulatrix saccular (Fig. 118).

Stigmatium Gray, species (Australia). Reproductive organs: Female-As in previous species, except spermathecal duct without basal papilla (Fig. 117).

Thanasimus dubius (Fabricius). Reproductive organs: Male- Two pairs of accessory glands, medial pair biramous, lateral pair not branched; testis comprising 12 follicles (Fig. 119). Female- Spermathecal capsule well sclerotized; spermathecal gland attached to base of capsule; bursa copulatrix reduced to two small chambers; ovary comprising 12 follicles (Fig. 120).

Thanasimus formicarius Linnaeus. Reproductive organs: Male- Two pairs of accessory glands, medial pair biramous, lateral pair not branched; testis comprising 12 follicles (Fig. 121, 122). Female- Spermathecal capsule well sclerotized; spermathecal gland attached to base of capsule; bursa copulatrix reduced to two small chambers (Fig. 123).

Thanasimus ceylonicus Kraatz. Reproductive organs: Male- Two pairs of accessory glands, both glands biramous; testis comprising 12 follicles (Figs. 124, 125).

Thanasimus rufipes (Brahm). Reproductive organs: Male- Two pairs of accessory glands, medial pair with small basal branch (Figs. 126, 127).

Notes: The characteristic of having the bursa copulatrix modified into two small chambers may have phylogenetic significance within the genus.

Trichodes alvearius (Fabricius). Reproductive organs: Male- Two pairs of biramous accessory glands, medial pair short and transformed into spermatophoral gland, lateral pair very long; testis multifollicular (Fig. 128). Female- Spermathecal capsule bifid, not well sclerotized; spermathecal gland attached to secondary chamber; bursa copulatrix modified into spermatophoral chamber-note spermatophore Fig. 129- (Fig. 130).

Trichodes apiarius (Linnaeus). Reproductive organs: Male- As in previous species (Fig. 131). Female- As in previous species (Fig. 132).

Trichodes nutalli (Kirby). Reproductive organs: Female- As in previous species except spermathecal gland shorter (Fig. 133). Notes: I examined the reproductive organs of the following *Trichodes* Herbst species and found essentially the same design in structure as those I described in the abovementioned species: *T. bibalteatus* Leconte, *T. crabroniformis* (Fabricius), *T. favarius* Illiger, *T. flavocinctus* Spinola, *T. horni* Wolcott, *T. leucopsideus* (Olivier), *T. octopunctatus* (Fabricius), *T. oregonensis* Barr, *T. oresterus* Wolcott, *T. punctatus* Fischer, *T. quadriguttatus* Adams, and *T. umbellatarum* (Olivier). Notes: Opitz (2003) found the modification of male accessory glands into spermatophoral glands and the bifurcation of the spermathecal capsule phylogenetically significant among various Nearctic and Palaearctic genera.

Trogodendron fasciculatum (Schreibers). Alimentary canal: Stomodaeum with well-developed proventriculus; ventricular papillae well developed, 6 cryptonephridial malpighian tubules; proctodaeum well developed (Fig. 136). Reproductive organs: Male- Two pairs of accessory glands, medial glands much longer than lateral glands; testis multifollicular (Figs. 134, 135). Female- Spermathecal capsule bifid, poorly sclerotized; spermathecal gland attached to secondary chamber; bursa copulatrix not saccular (Fig. 137).

Tillinae Leach: *Callotillus elegans* Erichson. Reproductive organs: Male- Two pairs of accessory glands, medial pair uniramous and with central longitudinal dark streak, lateral pair diverticulated at base; testis comprising 1 follicle (Fig. 138).

Cladiscus obeliscus Lewis. Reproductive organs: Male Two pairs of accessory glands, medial pair lobed basally not branched and with central longitudinal dark streak, lateral branch biramous; testis comprising 6 follicles (Fig. 139).

Cladiscus sanguinicollis (Spinola). Reproductive organs: Female- Spermathecal capsule well sclerotized; spermathecal gland short, attached to apex of capsule; bursa copulatrix saccular; ovary comprising 6 follicles (Fig. 140).

Cladiscus Chevrolat, species (Japan). Reproductive organs: Female- Spermathecal capsule well sclerotized, wrinkled; spermathecal gland attached to apex of capsule; bursa copulatrix saccular (Fig. 141).

Cymatoderella collaris (Spinola). Alimentary canal: Stomodaeum with proventriculus not well defined externally; ventricular papillae well developed; 6 cryptonephridial malpighian tubules; proctodaeum well developed (Fig. 145). Reproductive organs: Male- Two pairs of accessory glands, medial pair not branched, lateral pair biramous; testis comprising 1 follicle (Fig. 142).

Cylidrus abdominalis Klug. Alimentary canal: Stomodaeum long, with proventriculus not well defined externally; ventricular papillae well defined; 4 cryptonephridial malpighian tubules; proctodaeum well developed (Fig. 146). Reproductive organs: Male- One pair of accessory glands; vas deferens particularly elongated; testis comprising 6 follicles (Fig. 143). Female- Spermathecal capsule bifid, not well sclerotized; spermathecal gland attached to secondary chamber; bursa copulatrix not saccular (Fig. 144).

Cymatodera aegra Wolcott. Reproductive organs: Female- Spermathecal capsule bifid, curvate; spermathecal gland attached to base of capsule; bursa copulatrix not saccular, bursal plate as in Fig. 148 (Fig. 147).

Cymatodera undata Spinola. Reproductive organs: Male- Two pairs of accessory glands, medial gland not branched, with central longitudinal dark streak, lateral pair branched; testis comprising 1 very long follicle (Fig. 149). Female- Spermathecal capsule slightly bifid; spermathecal gland attached to base of capsule; bursa copulatrix not saccular; bursal plate as in Fig. 150 (Fig. 151).

Cymatodera antennata Schaeffer. Reproductive organs: Male- Two pairs of accessory glands, medial pair not branched, with central longitudinal dark streak, lateral pair branched; testis comprising 1 follicle (Fig. 154). Female- Spermathecal gland partially divided; spermathecal gland attached to base of capsule; bursa copulatrix not saccular; bursal plate as in Fig. 152 (Fig. 153).

Cymatodera bicolor (Say). Reproductive organs: Female- Spermathecal capsule bifid, poorly sclerotized; spermathecal gland attached to base of capsule; bursa copulatrix not saccular; bursal plate present (Fig. 158).

Cymatodera californica Horn. Reproductive organs: Female- spermathecal capsule bifid; spermathecal gland attached to base of capsule; bursa copulatrix not saccular; bursal plate as in Fig. 159 (Fig. 160).

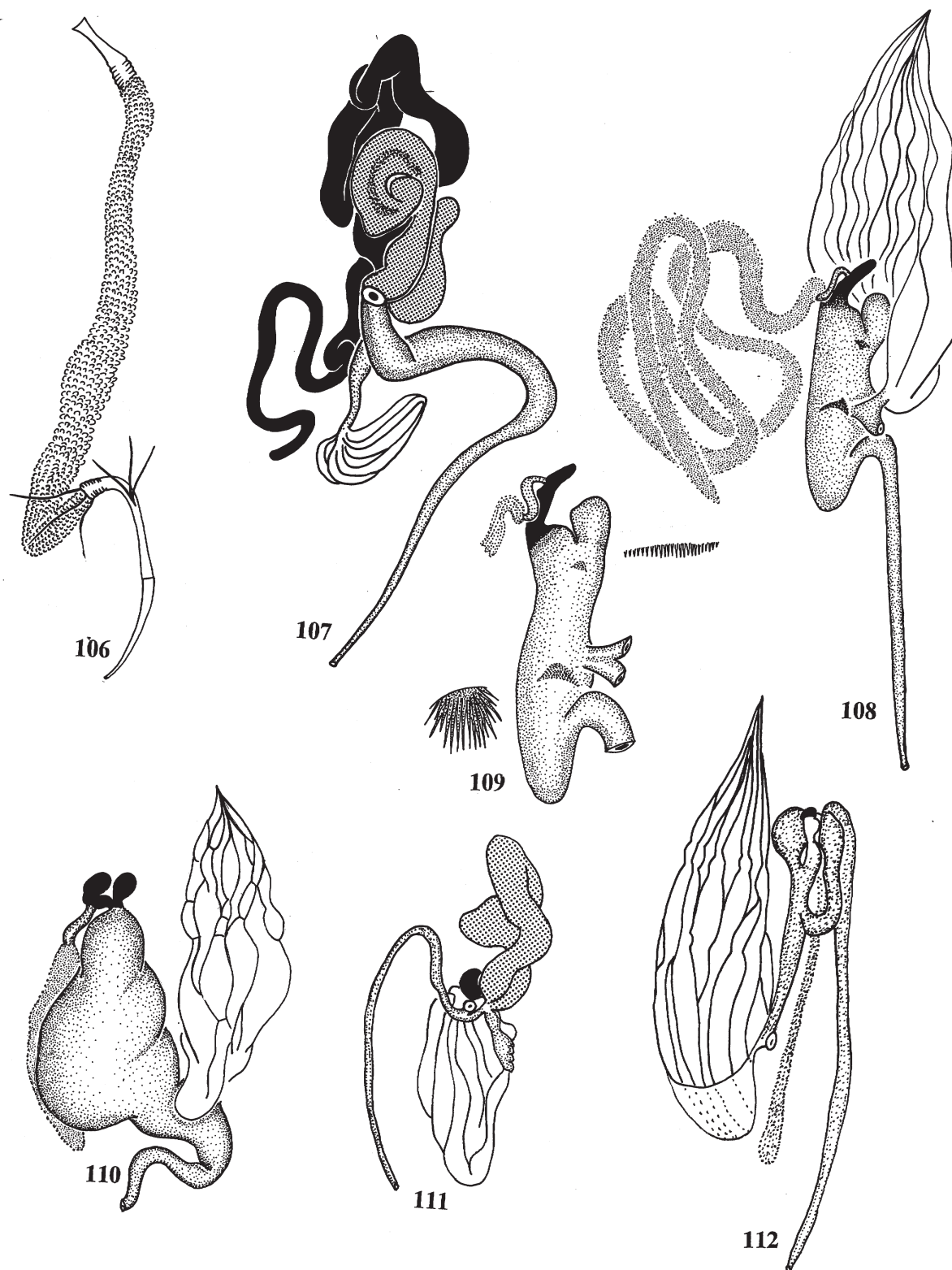
Cymatodera dietrichi Barr. Reproductive organs: Male- Two pairs of accessory glands, medial pair not branched, with central longitudinal dark streak, lateral gland bilobed and very long; testis comprising 1 long follicle (Fig. 155). Female- Spermathecal capsule feeble incised, poorly sclerotized; spermathecal gland attached to base of capsule; bursa copulatrix not saccular; bursal plate as in Fig. 156 (Fig. 157).

Cymatodera fuchsii Schaeffer. Reproductive organs: Female- Spermathecal capsule feebly incised, poorly sclerotized; spermathecal gland attached to base of capsule; bursa copulatrix not saccular; bursal plate as in Fig. 161 (Fig. 162).

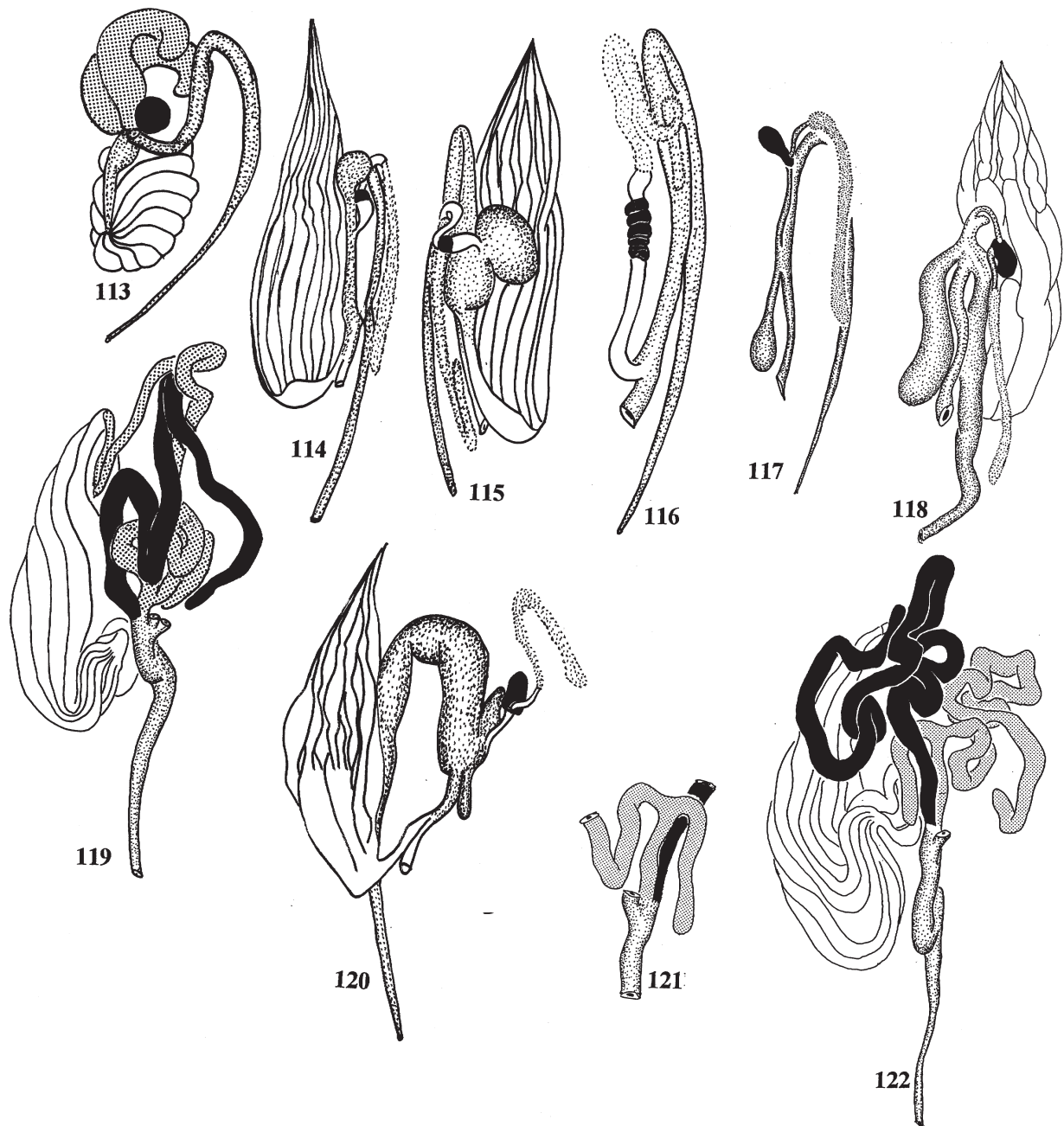
Cymatodera horni Wolcott. Reproductive organs: Male- Two pairs of accessory glands, medial pair not branched, with central longitudinal dark streak, lateral gland bilobed and very long; testis comprising 1 follicle (Fig. 163). Female- Spermathecal capsule feebly incised, poorly sclerotized; spermathecal gland attached to base of capsule; bursa copulatrix not saccular; bursal plate present (Fig. 164).

Cymatodera inornata (Say). Reproductive organs: Male- Two pairs of accessory glands, medial pair not branched, with central longitudinal dark streak, lateral gland bilobed and very long; testis comprising 1 follicle (Fig. 165).

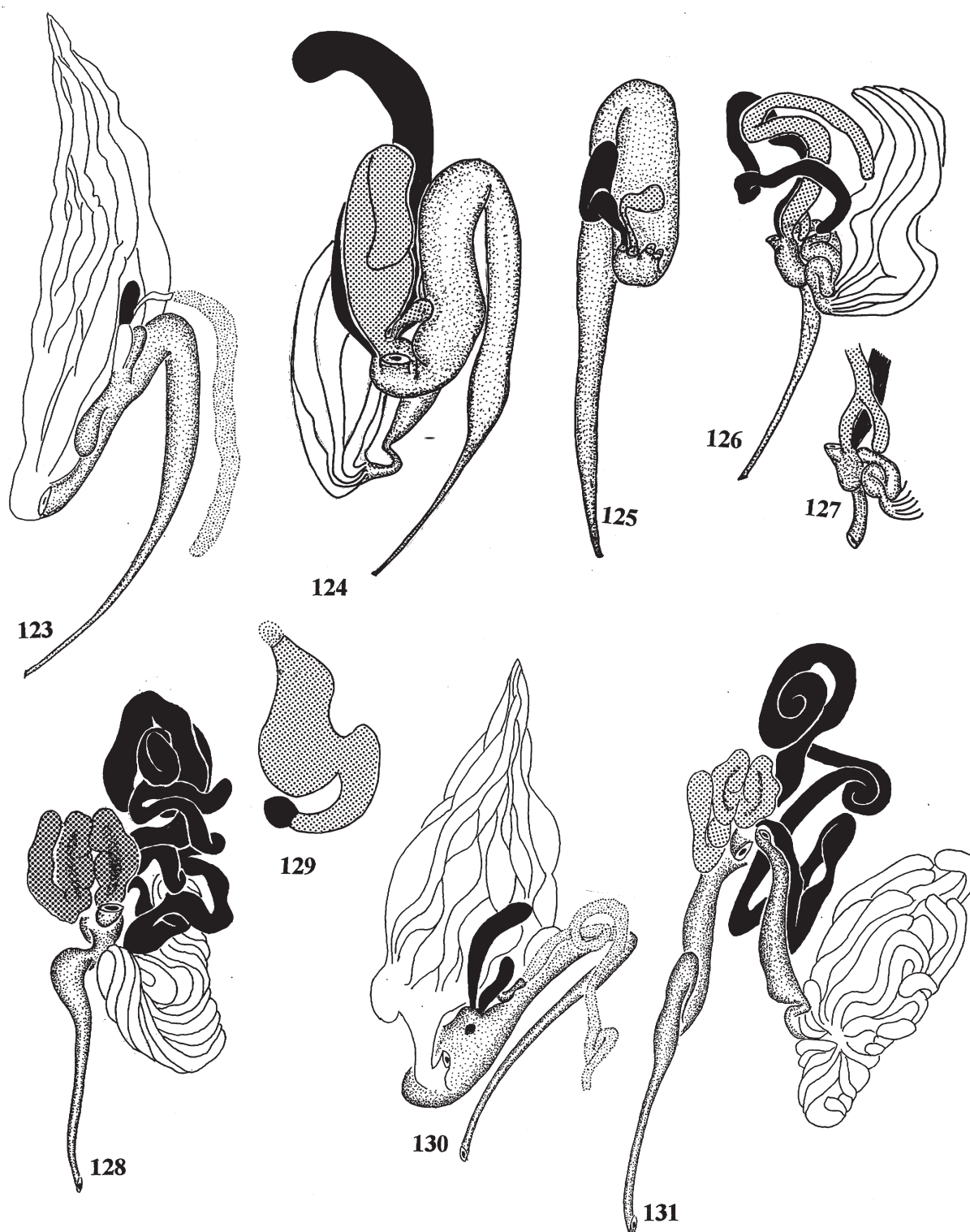
Cymatodera latefascia Schaeffer. Reproductive organs: Male- Two pairs of accessory glands, medial



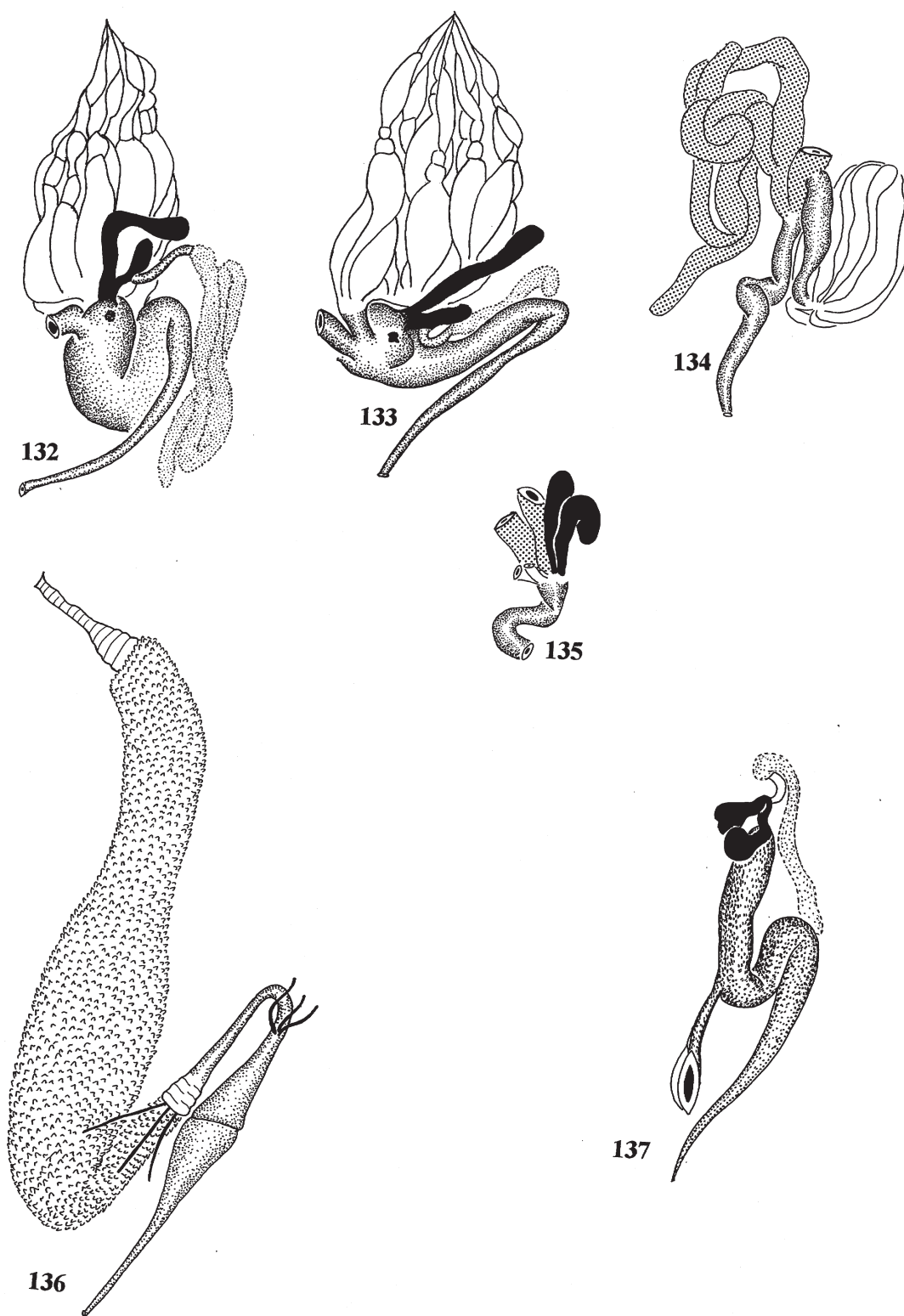
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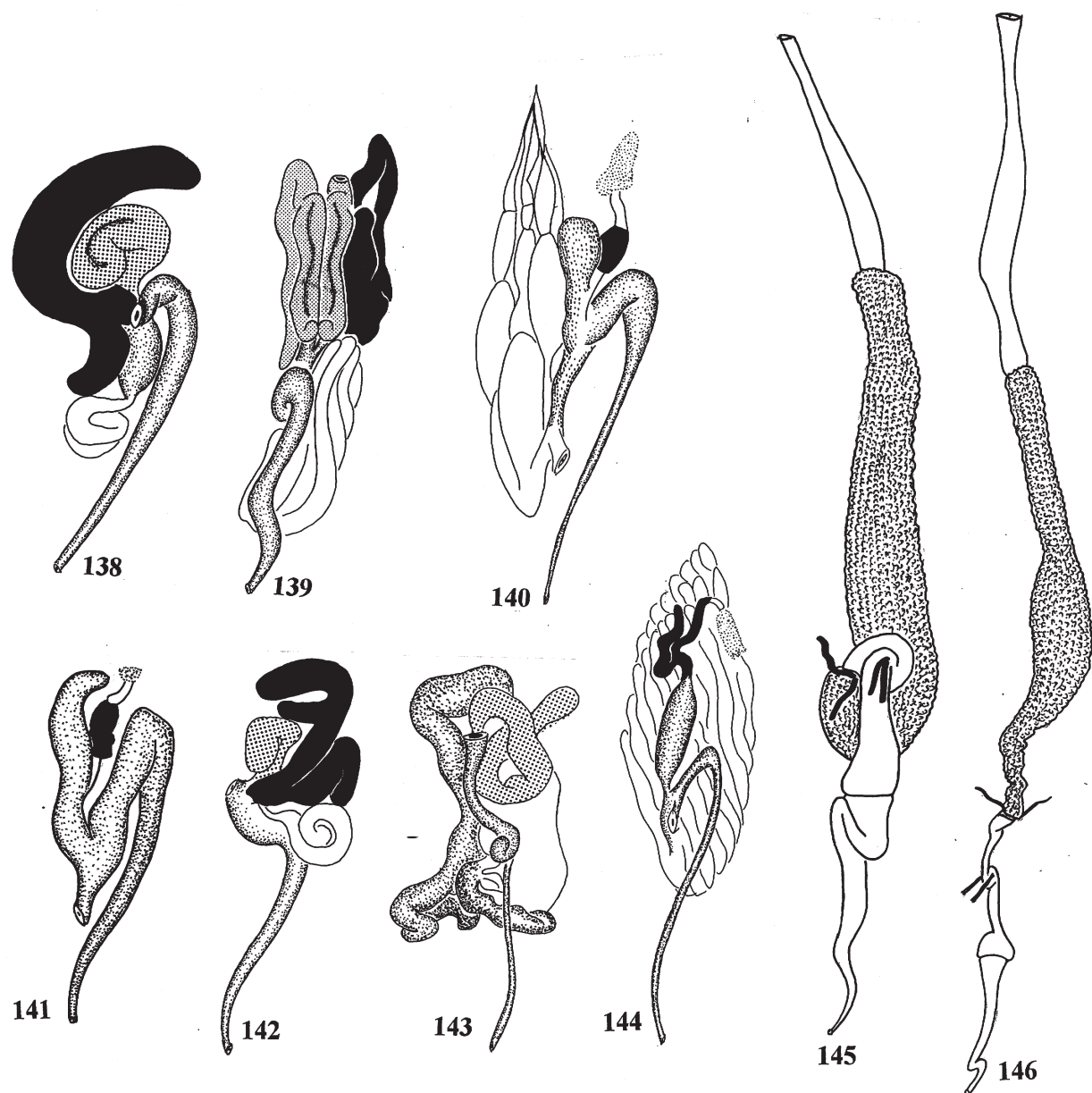
Figures 113–122. Reproductive organs. 113–114. *Priocera hypocrita*. 113) Male. 114) female. 115–118. Females. 115) *Priocera* sp. 116) *Priocera variegata*. 117) *Stigmatium* sp. 118) *Stigmatium gilberti*. 119–120. *Thanasimus dubius*. 119) male. 120) female. 121–122) *Thanasimus formicarius* males.



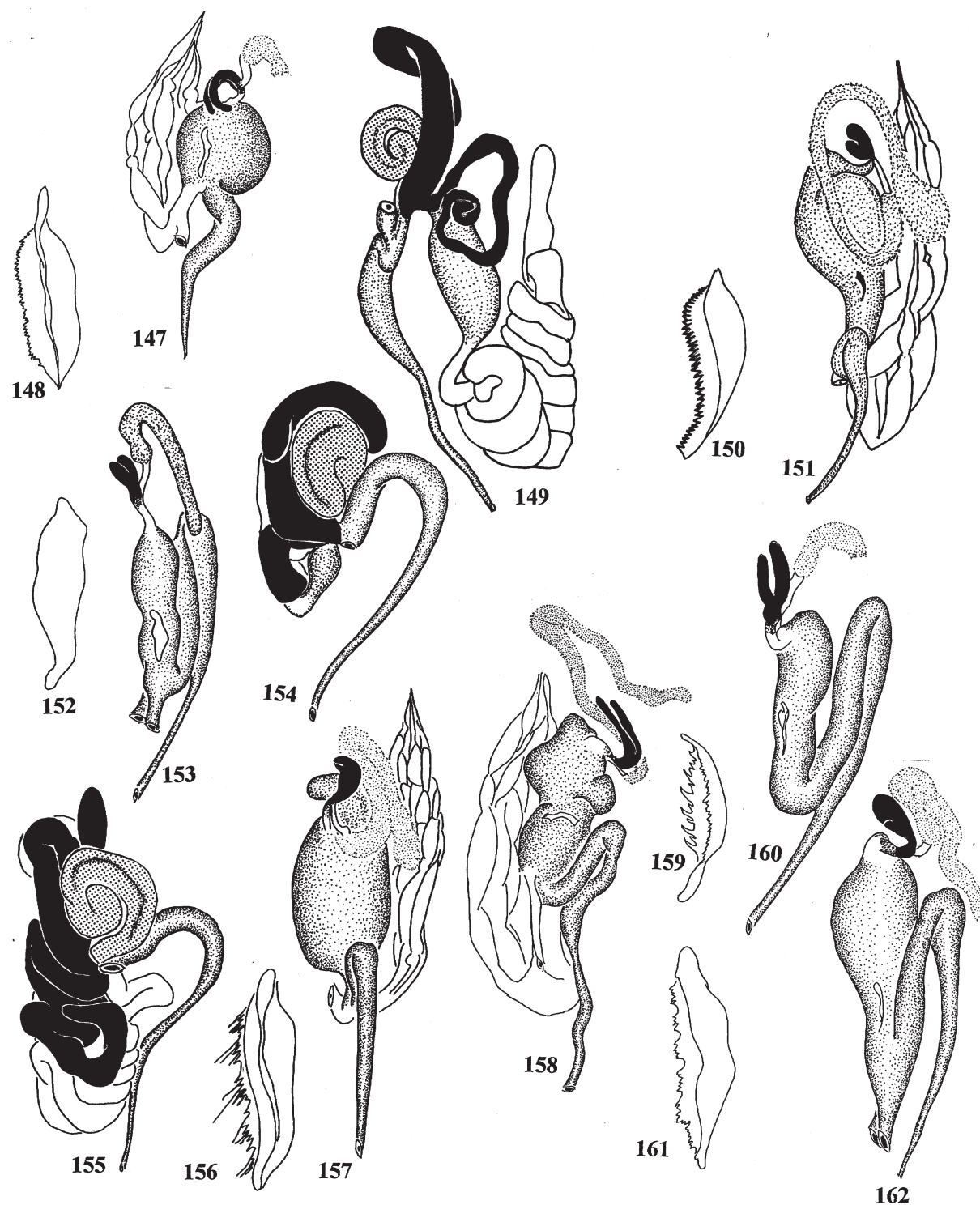
Figures 123–131. Reproductive organs. 123) *Thanasimus formicarius* female. 124–125 *Thanasimus ceylonicus*. 124) male. 125) female. 126–127) *Thanasimus rufipes* males. 128–130. *Trichodes alvearius*. 128) male. 129) spermatophore. 130) female. 131). *Trichodes apiarius*, male.



Figures 132–137. Reproductive organs and alimentary canal. **132)** *Trichodes apiarius*, female reproductive organs. **133)** *Trichodes nutalli*, female reproductive organs. **134–137.** *Trogodendron fasciculatum*. **134–135)** Male reproductive organs. **136)** Alimentary canal. **137)** Female reproductive organs.



Figures 138–146. Reproductive organs and alimentary canals. **138)** *Callotillus elegans* male reproductive organs. **139)** *Cladiscus obeliscus* male reproductive organs. **140)** *Cladiscus sanguinicollis* female reproductive organs. **141)** *Cladiscus* sp., female reproductive organs. **142)** *Cymatoderella collaris* male reproductive organs. **143–144.** *Cylidrus abdominalis*. **143)** male reproductive organs. **144)** female reproductive organs. **145)** alimentary canal of *Cymatoderella collaris*. **146)** alimentary canal of *Cylidrus abdominalis*.



Figures 147–162. Reproductive organs. 147–148. *Cymatodera aegra*. 147) female. 148) bursal plate. 149–151. *Cymatodera undata*. 149) male. 150) bursal plate. 151) female. 152–154. *Cymatodera antennata*. 152) bursal plate. 153) female. 154) male. 155–157. *Cymatodera dietrichi*. 155) male. 156) bursal plate. 157) female. 158) *Cymatodera bicolor* female. 159–160. *Cymatodera californica*. 159) bursal plate. 160) female. 161–162. *Cymatodera fuchsii*. 161) bursal plate. 162) female.

pair not branched, with central longitudinal dark streak, lateral gland bilobed and very long; testis comprising 1 follicle (Fig. 166). Female- Spermathecal capsule bifid, poorly sclerotized; spermathecal gland attached to base of capsule; bursa copulatrix not saccular; bursal plate as in Fig. 168 (Fig. 167).

Cymatodera oblita Horn. Reproductive organs: Female- Spermathecal capsule feebly incised, poorly sclerotized; spermathecal gland attached to middle of capsule; bursa copulatrix not saccular; bursal plate present (Fig. 169).

Cymatodera tricolor Skinner. Reproductive organs: Female- Spermathecal capsule bifid, poorly sclerotized; spermathecal gland attached to middle of capsule; bursa copulatrix not saccular; bursal plate present (Fig. 170).

Cymatodera serena Barr. Reproductive organs: Female- Spermathecal capsule feebly incised, poorly sclerotized; spermathecal gland attached to base of capsule; bursa copulatrix not saccular; bursal plate as in Fig. 172 (Fig. 171).

Cymatodera tutoides Barr. Reproductive organs: Male- Two pairs of accessory glands, medial pair not branched, with central longitudinal dark streak, lateral gland bilobed and very long; testis comprising 1 follicle (Fig. 173).

Cymatodera undulata (Say). Reproductive organs: Male- Two pairs of accessory glands, medial pair not branched, with central longitudinal dark streak, lateral gland bilobed and very long; testis comprising 1 follicle (Fig. 175). Female- Spermathecal capsule slightly bifid, poorly sclerotized; spermathecal gland attached to base of capsule; bursa copulatrix not saccular; bursal plate as in Fig. 176 (Fig. 174).

Lecontella cancellata (Leconte). Reproductive organs: Male- Two pairs of accessory glands, medial pair not branched, with central longitudinal dark streak, lateral gland bilobed; testis comprising 1 follicle (Fig. 178). Female- Spermathecal capsule very narrow and elongated, poorly sclerotized; spermathecal gland attached to base of capsule; bursa copulatrix saccular; bursal plate as in Fig. 181 (Fig. 184).

Lecontella gnara Wolcott. Reproductive organs: Female- Spermathecal capsule very narrow and elongated, poorly sclerotized; spermathecal gland particularly large, attached to base of capsule; bursa copulatrix saccular; bursal plate present (Fig. 179).

Monophylla terminata (Say). Reproductive organs: Male- Two pairs of accessory glands, medial pair not branched, with central longitudinal dark streak, lateral gland bilobed; testis comprising 1 follicle (Fig. 183). Female- Spermathecal capsule not distinguishable; spermathecal gland well defined; bursal plate as in Fig. 180 (Fig. 177).

Monophylla californica (Fall). Reproductive organs: Male- Two pairs of accessory glands, medial pair not branched, with central longitudinal dark streak, lateral gland bilobed; testis comprising 1 follicle (Fig. 182). Female- Spermathecal capsule not distinguishable; spermathecal gland well defined; bursal plate present (Fig. 185).

Onychotillus vittatus Chapin. Alimentary canal: Stomodaeum long, with proventriculus not well defined externally; ventricular papillae well defined; 4 cryptonephridial malpighian tubules; proctodaeum well developed (Fig. 186). Reproductive organs: Male- Two pairs of accessory glands, medial pair not branched, with central longitudinal dark streak, lateral gland bilobed; testis comprising 1 follicle (Fig. 187). Female- Spermathecal capsule bifid; spermathecal gland attached to base of capsule; bursal plate as in Fig. 189 (Fig. 188).

Orthocladiscus dispar (Gorham). Reproductive organs: Male- Two pairs of accessory glands, medial pair branched, with central longitudinal dark streak, lateral gland not branched; testis comprising 6 follicles (Fig. 190).

Pallenis Castelnau (Madagascar). Species. Reproductive organs: Female- Spermathecal capsule poorly sclerotized; spermathecal gland attached to base of capsule; bursa copulatrix saccular; bursal plate present (Fig. 191).

Tillus elongatus (Linnaeus). Alimentary canal: Stomodaeum long, with proventriculus not well defined externally; ventricular papillae well defined; 6 cryptonephridial malpighian tubules; proctodaeum well developed (Fig. 194). Reproductive organs: Male- Two pairs of accessory glands, medial pair not branched, with central longitudinal dark streak, lateral gland bilobed; testis comprising 1 follicle (Fig. 192). Female- Spermathecal capsule long and narrow; spermathecal gland attached to base of capsule; bursal plate present (Fig. 193).

Tillus notatus Klug. Reproductive organs: Female- Spermathecal capsule long and narrow; spermathecal gland attached to base of capsule; bursal plate present (Fig. 195).

Tillus Olivier (Africa). Species a. Reproductive organs: Male- Two pairs of accessory glands, medial pair not branched, with central longitudinal dark streak, lateral gland bilobed; testis comprising 1 follicle (Fig. 196).

Tillus Olivier (Africa). Species b. Reproductive organs: Male- Two pairs of accessory glands, medial pair not branched, with central longitudinal dark streak, lateral gland bilobed; testis comprising one follicle (Fig. 197).

Tilloidea unifasciata (Fabricius). Reproductive organs: Male- Two pairs of accessory glands, medial pair not branched, with central longitudinal dark streak, lateral gland bilobed; testis comprising 1 follicle (Fig. 198). Female- Spermathecal capsule long, narrow and bifid; spermathecal gland attached to base of capsule; bursa copulatrix not saccular, bursal plate as in Fig. 200 (Fig. 199).

Epiphloeinae Kuwert: *Iontoclerus sericeus* (Klug). Reproductive organs: Male- Two pairs of accessory glands, neither gland branched; testis multifollicular (Fig. 201). Female- Spermathecal capsule poorly sclerotized; spermathecal gland attached to distal third of capsule; bursa copulatrix saccular (Fig. 202).

Peloniinae Opitz: *Chariessa dichroa* (Leconte). Reproductive organs: Male- Two pairs of accessory glands, neither gland branched; seminal vesicle bulbous; testis multifollicular (Fig. 204). Female- Spermathecal capsule well sclerotized; spermathecal gland attached to base of capsule; bursa copulatrix saccular (Fig. 203).

Chariessa pilosa (Forster). Reproductive organs: Male- Two pairs of accessory glands, neither gland branched; testis multifollicular (Fig. 205). Female- Spermathecal capsule well sclerotized, wrinkled; spermathecal gland attached to base of capsule; bursa copulatrix saccular (Fig. 206).

Chariessa vestita (Chevrolat). Reproductive organs: Male- Two pairs of accessory glands, glands particularly long and unbranched; testis multifollicular (Fig. 207).

Pelonium alcicorne Klug. Reproductive organs: Female- Spermathecal capsule well sclerotized, wrinkled; spermathecal gland attached to base of capsule; bursa copulatrix saccular (Fig. 208).

Pelonium amabile Spinola. Reproductive organs: Male- Two pairs of accessory glands, glands unbranched; testis multifollicular (Fig. 209).

Pelonium auripenne (Hope). Reproductive organs: Male- Two pairs of accessory glands, glands unbranched; testis multifollicular (Fig. 210). Female- Spermathecal capsule well sclerotized, wrinkled; spermathecal gland attached to base of capsule; bursa copulatrix saccular, bursal plate present (Fig. 211).

Pelonium badeni Gorham. Reproductive organs: Male- Two pairs of accessory glands, glands unbranched; testis multifollicular (Fig. 212).

Pelonium fasciculatum Klug. Reproductive organs: Male- Two pairs of accessory glands, glands unbranched; testis multifollicular (Fig. 213). Female- Spermathecal capsule well sclerotized, wrinkled; spermathecal gland attached to base of capsule; bursa copulatrix saccular, bursal plate present (Fig. 214).

Pelonium disconotatum Pic. Reproductive organs: Male- Two pairs of accessory glands, medial pair particularly long, glands unbranched; testis multifollicular (Fig. 215).

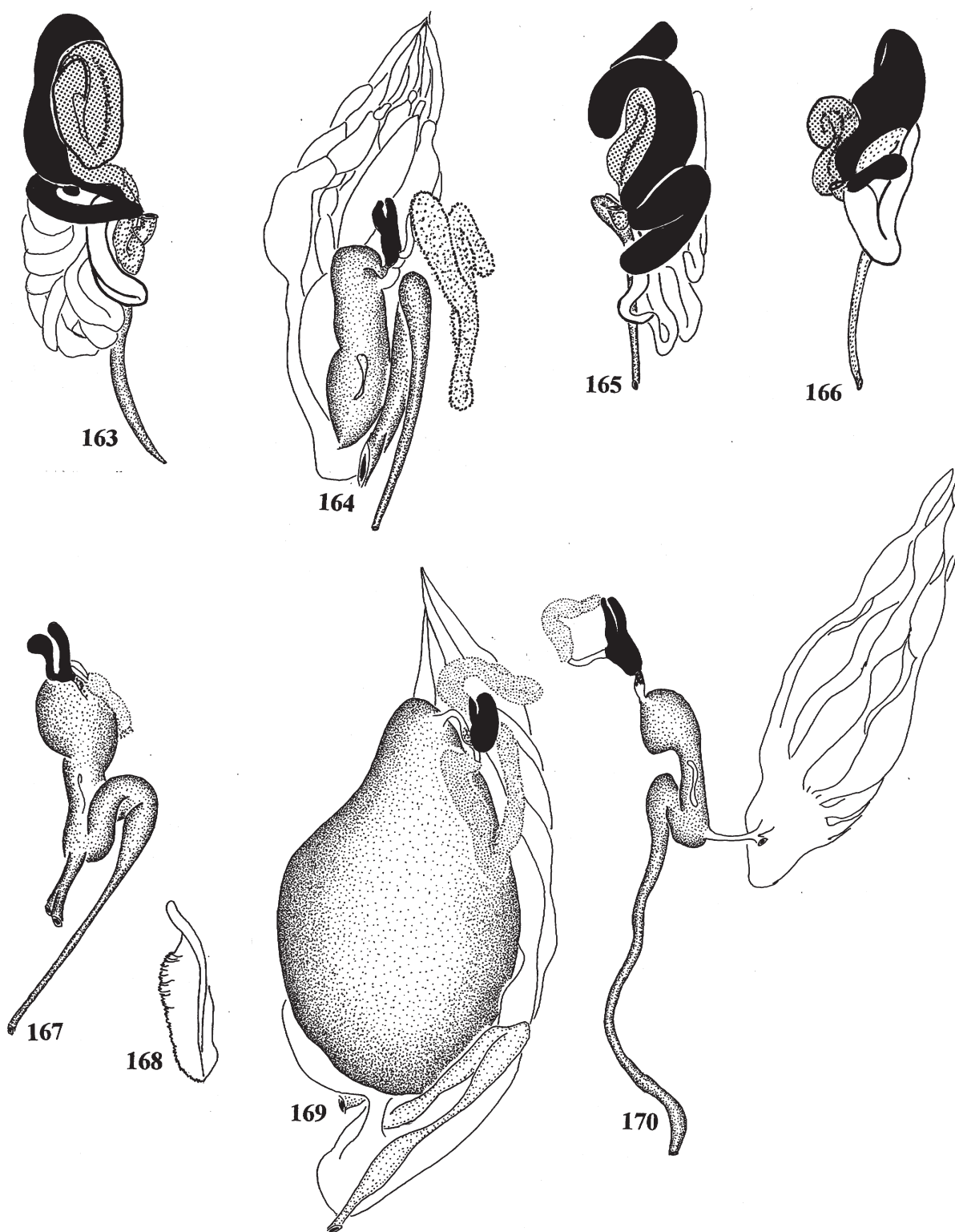
Pelonium leucophaeum Klug. Reproductive organs: Female- Spermathecal capsule well sclerotized; spermathecal gland attached to base of capsule; bursa copulatrix saccular (Fig. 216).

Pelonium lituratum Kirby. Reproductive organs: Female- Spermathecal capsule well sclerotized; spermathecal gland attached to base of capsule; bursa copulatrix saccular (Fig. 217). Nervous organs: Ventral nerve chord and brain as in Fig. 219.

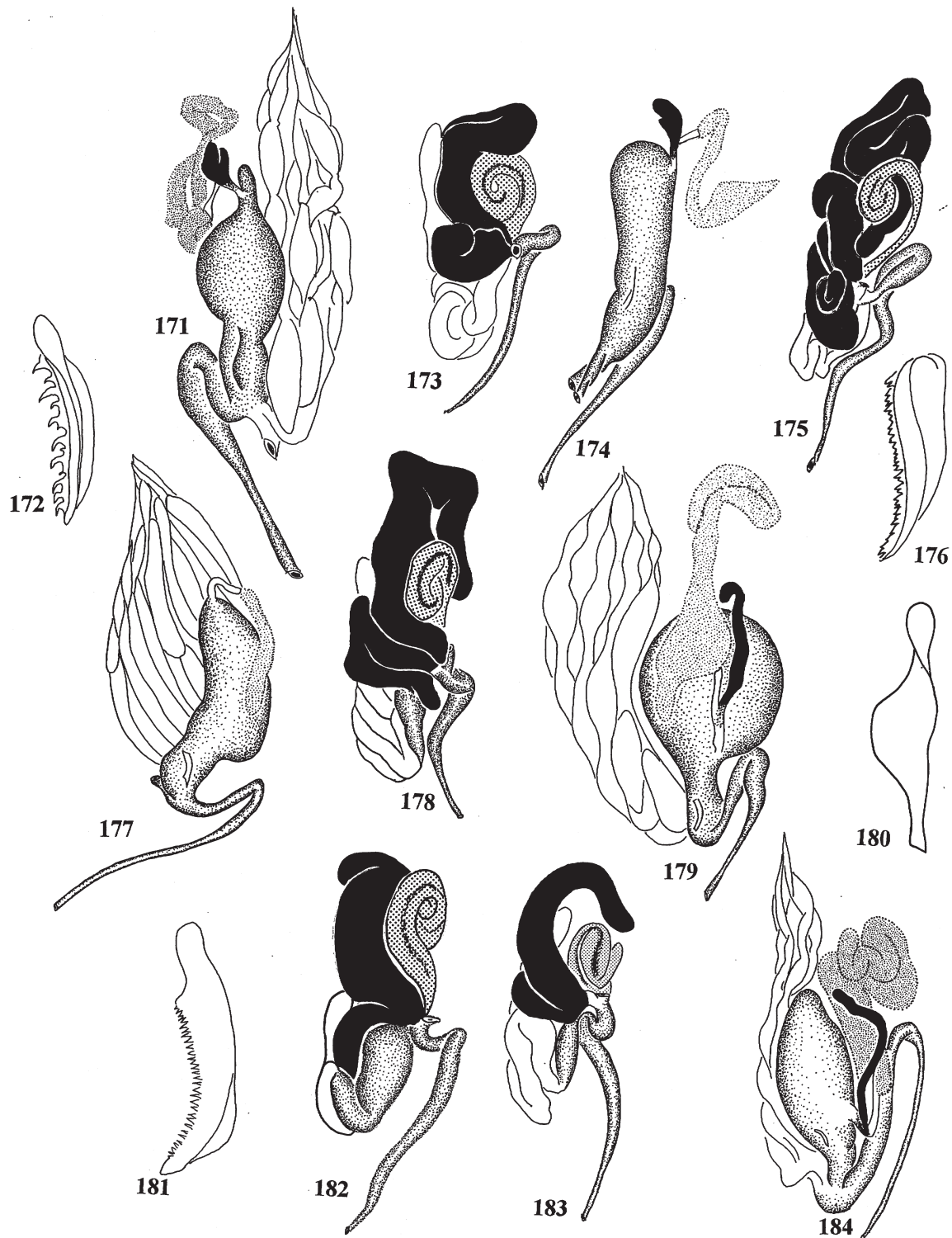
Pelonium nigroclavatum Chevrolat. Reproductive organs: Female- Spermathecal capsule well sclerotized; spermathecal gland attached to base of capsule; bursa copulatrix saccular (Fig. 218).

Pelonium peninsulare Schaeffer. Reproductive organs: Male- Two pairs of accessory glands, glands unbranched; testis multifollicular (Fig. 220). Female- Spermathecal capsule well sclerotized; spermathecal gland attached to base of capsule; bursa copulatrix saccular (Fig. 221).

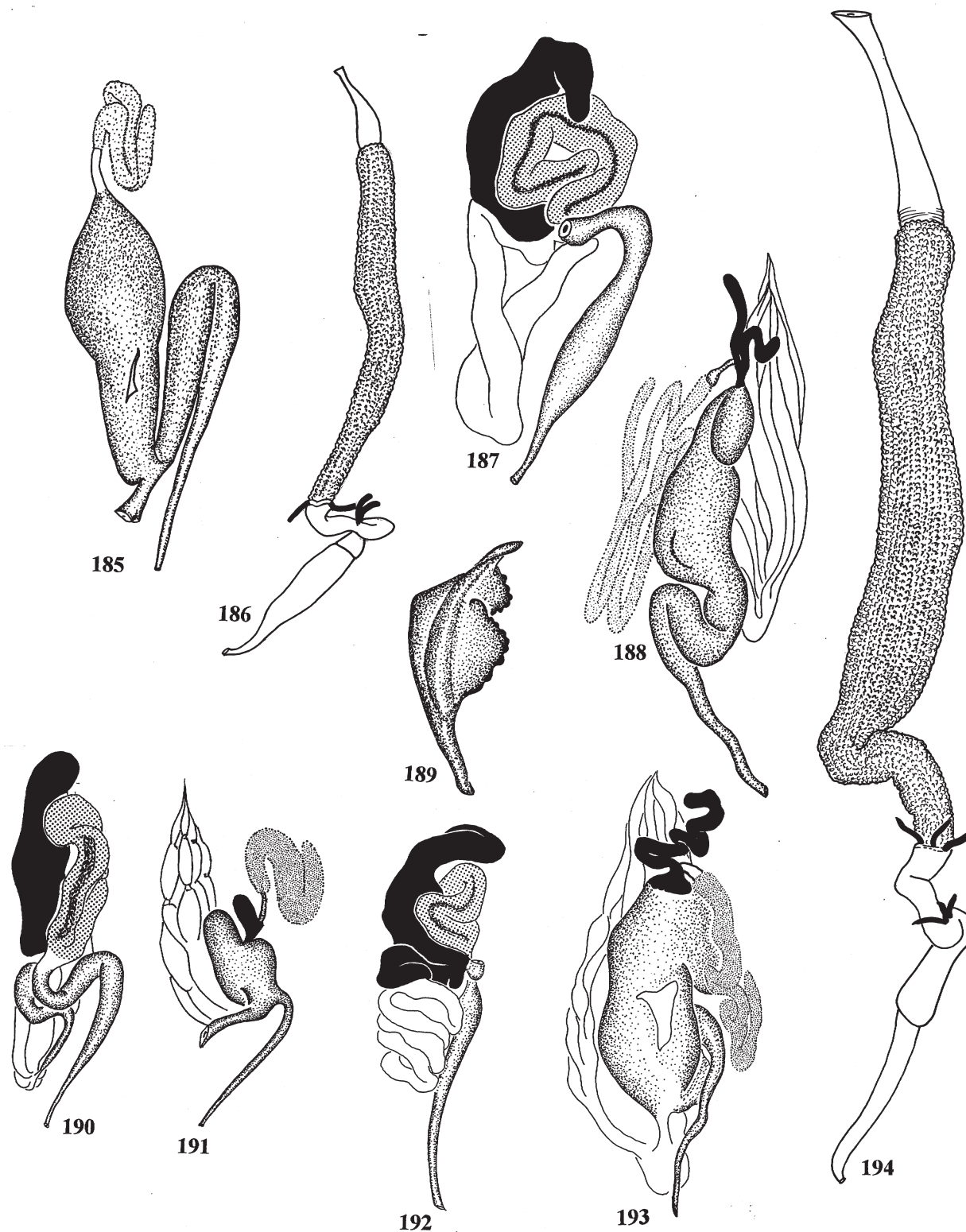
Pelonium placidum Schenkling. Reproductive organs: Female- Spermathecal capsule well sclerotized; spermathecal gland attached to base of capsule; bursa copulatrix saccular (Fig. 222).



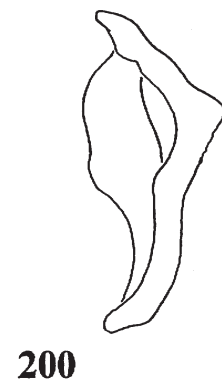
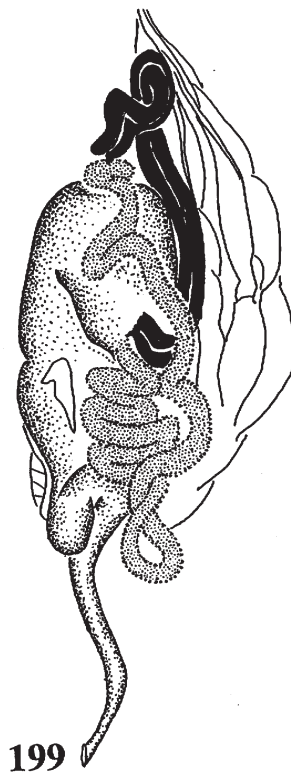
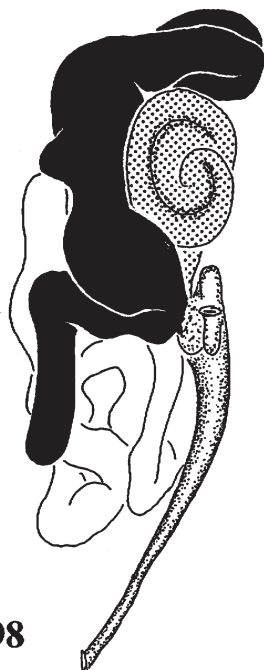
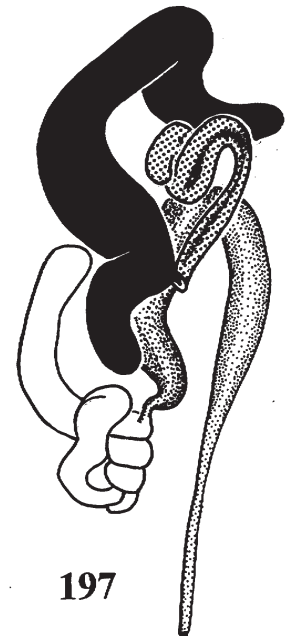
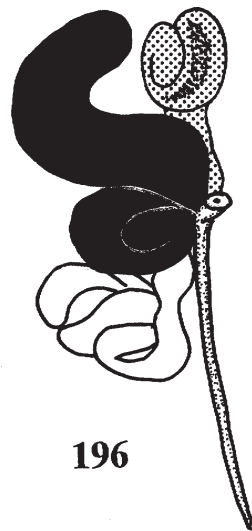
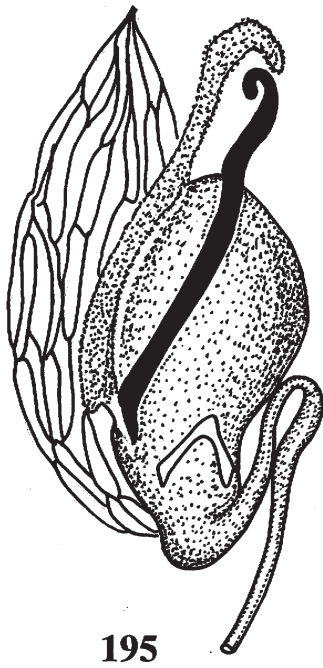
Figures 163–170. Reproductive organs. 163–164. *Cymatodera horni*. 163) male. 164) female. 165) *Cymatodera inornata*, male. 166–168. *Cymatodera latefasciata*. 166) male. 167) female. 168) bursal plate. 169) *Cymatodera oblita*, female. 170) *Cymatodera tricolor*, female.



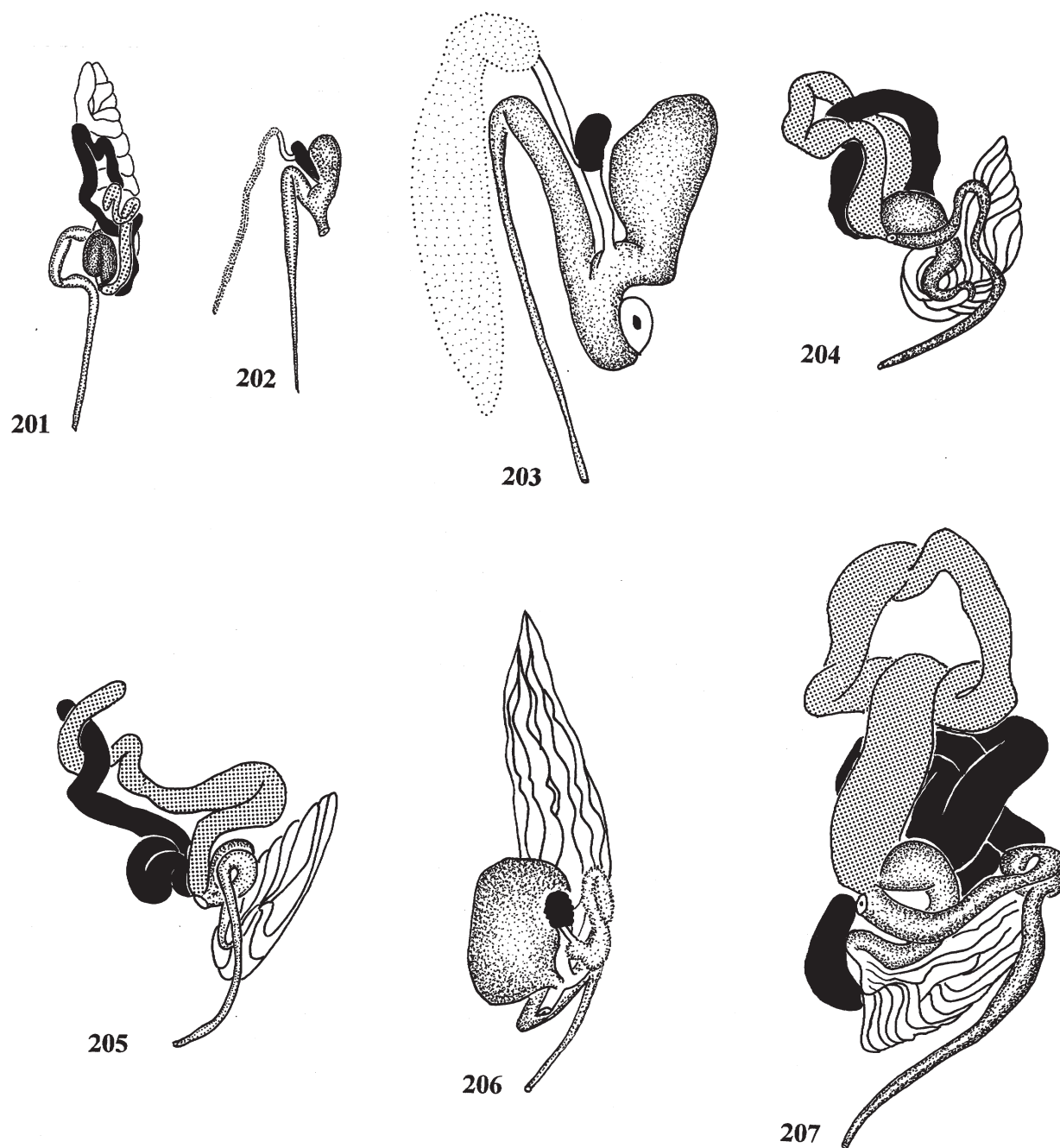
Figures 171–184. Reproductive organs. 171–172. *Cymatodera serena*. 171) female. 172) bursal plate. 173) *Cymatodera tutoides*, male. 174–176. *Cymatodera undulata*. 174) female. 175) male. 176) bursal plate. 177) *Monophylla terminata*, female. 178) *Lecontella cancellata*, male. 179) *Lecontella gnara*, female. 180–81. Bursal plates. 180) *Monophylla terminata*. 181) *Lecontella cancellata*. 182–183. Males. 182) *Monophylla californica*. 183) *Monophylla terminata*. 184) *Lecontella cancellata*.



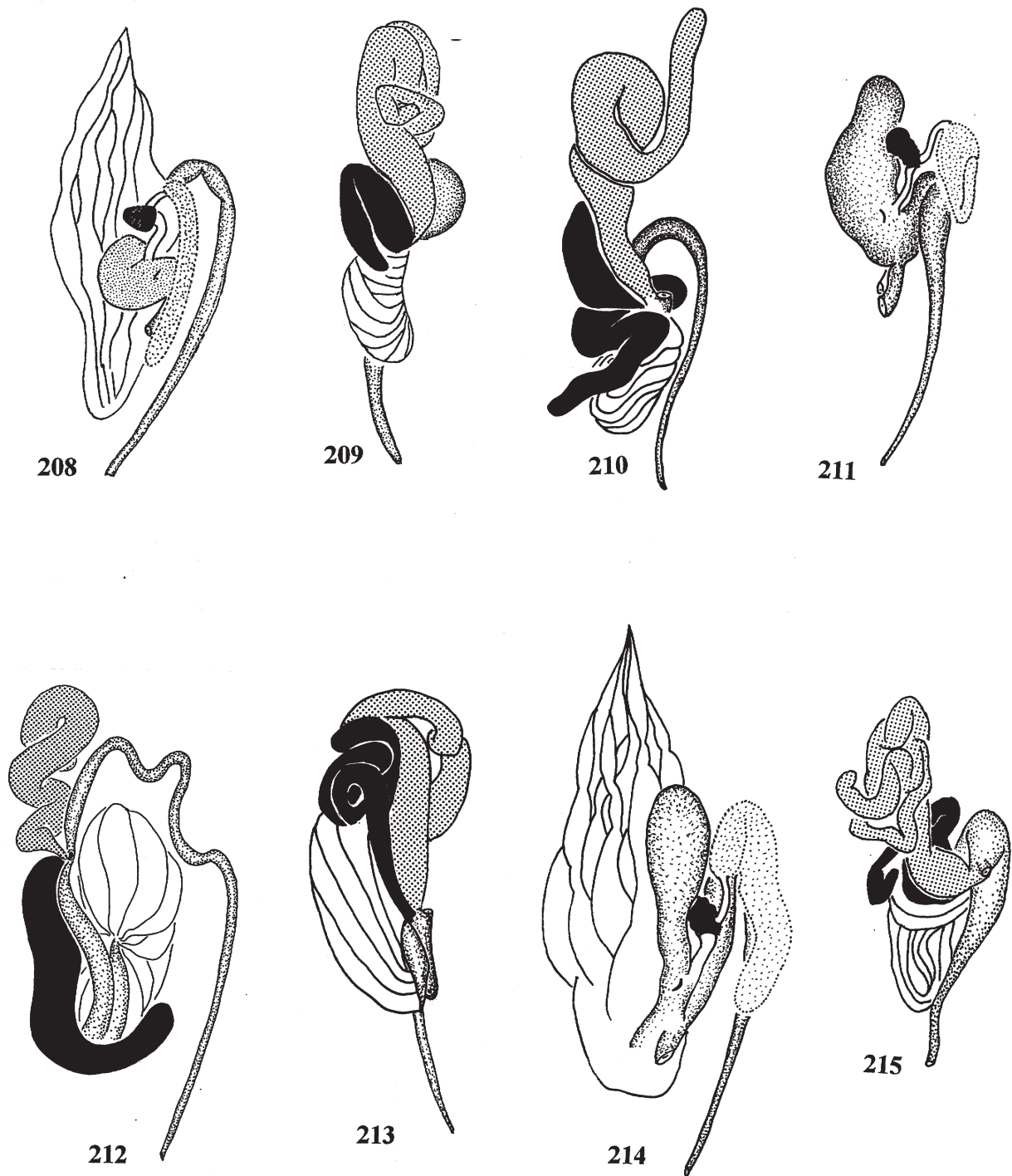
Figures 185–194. Reproductive organs and alimentary canals. 185. *Monophylla californica*, reproductive organs, female.. 186–189. *Onichotillus vittatus*. 186) alimentary canal. 187) reproductive organs, male. 188) reproductive organs, female. 189) bursal plate. 190) *Orthocladiscus dispar*, reproductive organs, male. 191) *Pallenis* sp. reproductive organs, female. 192–194. *Tillus elongatus*. 192) reproductive organs, male. 193) reproductive organs, female. 194) alimentary canal.



Figures 195–200. Reproductive organs. 195. *Tillus notatus*, female. 196–197. Males. 196) *Tillus* sp. a. 197) *Tillus* sp. b. 198–200. *Tilloidea unifasciata*. 198) male. 199) female. 200) bursal plate.



Figures 201–207. Reproductive organs. 201–202. *Iontoclerus sericeus*. 201) male. 202) female. 203–204. *Chariessa dichroa*. 203) female. 204) male. 205–206. *Chariessa pilosa*. 205) male. 206) female. 207) *Chariessa vestita*, male.



Figures 208–215. Reproductive organs. 208) *Pelonium alcicorne*, female. 209) *Pelonium amabile*, male. 210–211. *Pelonium auripenne*. 210) male. 211) female. 212) *Pelonium badeni*, male. 213–214. *Pelonium fasciculatum*. 213) male. 214) female. 215) *Pelonium disconotatum*, male.

Pelonium posticum Klug. Reproductive organs: Male- Two pairs of accessory glands, glands unbranched; testis multifollicular (Fig. 223).

Pelonium quadriplagiatum Kuwert. Reproductive organs: Male- Two pairs of accessory glands, glands unbranched; testis multifollicular (Fig. 224). Female- Spermathecal capsule well sclerotized; spermathecal gland attached to base of capsule; bursa copulatrix saccular (Fig. 225).

Pelonium semirufum Gorham. Reproductive organs: Male- Two pairs of accessory glands, glands unbranched; testis multifollicular (Fig. 226). Female- Spermathecal capsule well sclerotized; spermathecal gland attached to base of capsule; bursa copulatrix saccular (Fig. 227).

Pelonium viridipenne Kirby. Reproductive organs: Male- Two pairs of accessory glands, glands unbranched; seminal vesicle saccular; testis multifollicular (Figs. 229, 230). Female- Spermathecal capsule well sclerotized, wrinkled; spermathecal gland attached to middle of capsule; bursa copulatrix saccular, but very small (Fig. 228).

Pelonium Spinola, species a-c (Brazil). Reproductive organs: Male- Two pairs of accessory glands, glands unbranched; testis multifollicular (Fig. 231). Female- Spermathecal capsule well sclerotized; spermathecal gland attached to base of capsule; bursa copulatrix saccular (Fig. 232). Species b. Reproductive organs: Male- Two pairs of accessory glands, glands unbranched; seminal vesicle saccular; testis multifollicular (Fig. 233). Species c. Reproductive organs: Male- Two pairs of accessory glands, glands unbranched; seminal vesicle saccular; testis multifollicular (Fig. 234).

Tarsosteninae Jacquelin du Val: *Tarsostenodes leucogramma* Elston. Reproductive organs: Male- Two pairs of accessory glands, glands unbranched; testis comprising 6 follicles (Fig. 235).

Blackburniella hilaris (Westwood). Reproductive organs: Female- Spermathecal capsule well sclerotized; spermathecal gland attached to apex of capsule; bursa copulatrix saccular (Fig. 236).

Parapylus sedlaceki (Kolibáč). Reproductive organs: Female- Spermathecal capsule well sclerotized; spermathecal gland attached near base of capsule; bursa copulatrix saccular, bursal plate present (Fig. 237).

Tarsostennus carus (Newman). Reproductive organs: Male- One pair of accessory glands, gland unbranched; seminal vesicle bulbous; testis comprising 6 follicles (Fig. 239). Female- Spermathecal capsule well sclerotized; spermathecal gland attached near middle of capsule; bursa copulatrix saccular (Fig. 238).

Tarsostenodes guttulus (White). Reproductive organs: Female- Spermathecal capsule well sclerotized; spermathecal gland attached near base of capsule; bursa copulatrix saccular (Fig. 240).

Korynetinae Laporte: *Dolichopsis haplocnemodes* Gorham. Reproductive organs: Female- Spermathecal capsule well sclerotized; spermathecal gland attached to apex of capsule; bursa copulatrix saccular (Fig. 241).

Comparative morphology and taxonomic significance of variations

This discussion concerns general descriptions of the alimentary canal and mesodermal reproductive organs. It is not possible to make any comments about the central nervous system and brain, which has not been extensively studied in the Cleridae. Opitz illustrated the ventral nerve cord and brain of *Aphelocerus coactus* Opitz (Opitz, 2005: 22) and *Necrobia violacea* Linnaeus (Opitz, 2011b: 51). This work also includes opinions about the taxonomic significance of some of the differences noted in the alimentary canal and mesodermal reproductive organs. The comparative and taxonomic discussion includes information gleaned from previously published works as noted in Opitz (2010a).

General morphology- Alimentary canal. The gross morphology of the alimentary canal consists of a stomodaeum, ventriculus, cryptonephridial malpighian tubules, and proctodaeum (Fig. 242). The stomodaeum includes a distinct pharynx (Fig. 243), a well-developed esophagus (Fig. 244), and a usually muscular proventriculus (Fig. 245). The pharyngeal intima exhibits several folds that eventually

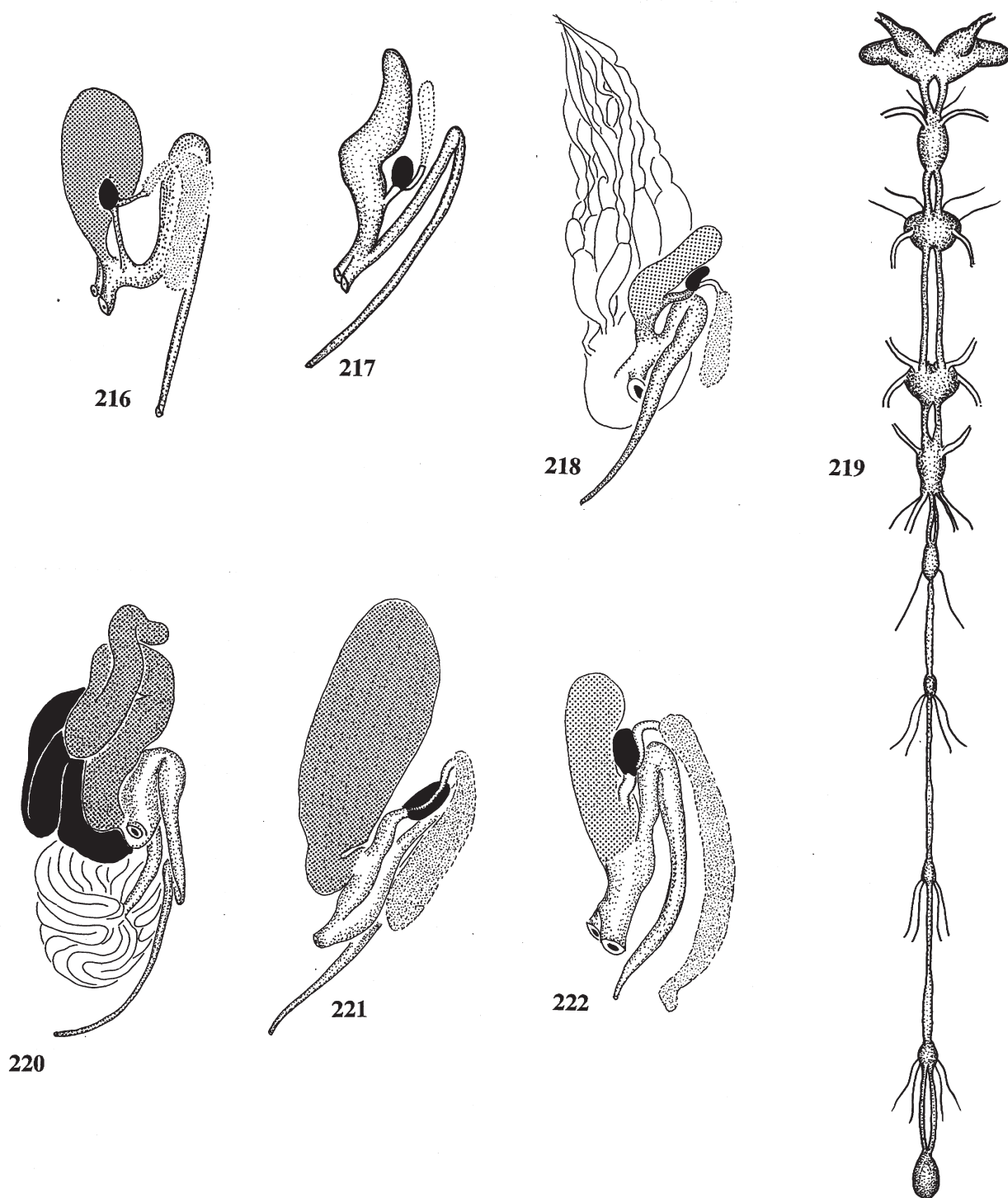
transform into a distinct number of primary and secondary folds in the proventriculus. Intimal spines are numerous in the pharynx, scarce in the anterior region of the esophagus, long and stout and posterior region of the esophagus and anterior region of the stomodaeum. The stomodaeal valve (Fig. 246) consists of lobes that vary in size, shape, and number, but their position in the valve is constant among the taxa examined.

The ventriculus (Fig. 247) is well developed and may be smooth, papillose, or with small transverse wrinkles. Between the ventriculus and the proctodaeum there are the malpighian tubules which attach to the posterior region of the ileum. In the proctodaeum, the pylorus is short and muscular and is marked anteriorly by a 6-lobed pyloric valve (Fig. 248). The anterior intestine is divided into a well-defined ileum and a distally broadened colon. The posterior intestine is composed of a well-developed rectal sac and an elongate rectum proper, which is twice as long in the female as in the male (a morphological development to enable the female to extend her lengthy ovipositor out of the abdomen). The proctodaeal intima shows numerous small folds in the pylorus and 6 larger folds in the colon (Fig. 249). The folds terminate in the region of the rectal valve. The rectal intima exhibits small folds anteriorly and long slender folds posteriorly (Fig. 250). Information about the alimentary canal of the Cleridae, as part of taxonomic revisions, was published recently by Ekis (1977b) and Opitz (2003, 2004, 2005, 2006, 2007, 2008, 2009a, 2009b, 2010b, 2011a, 2011b, 2012).

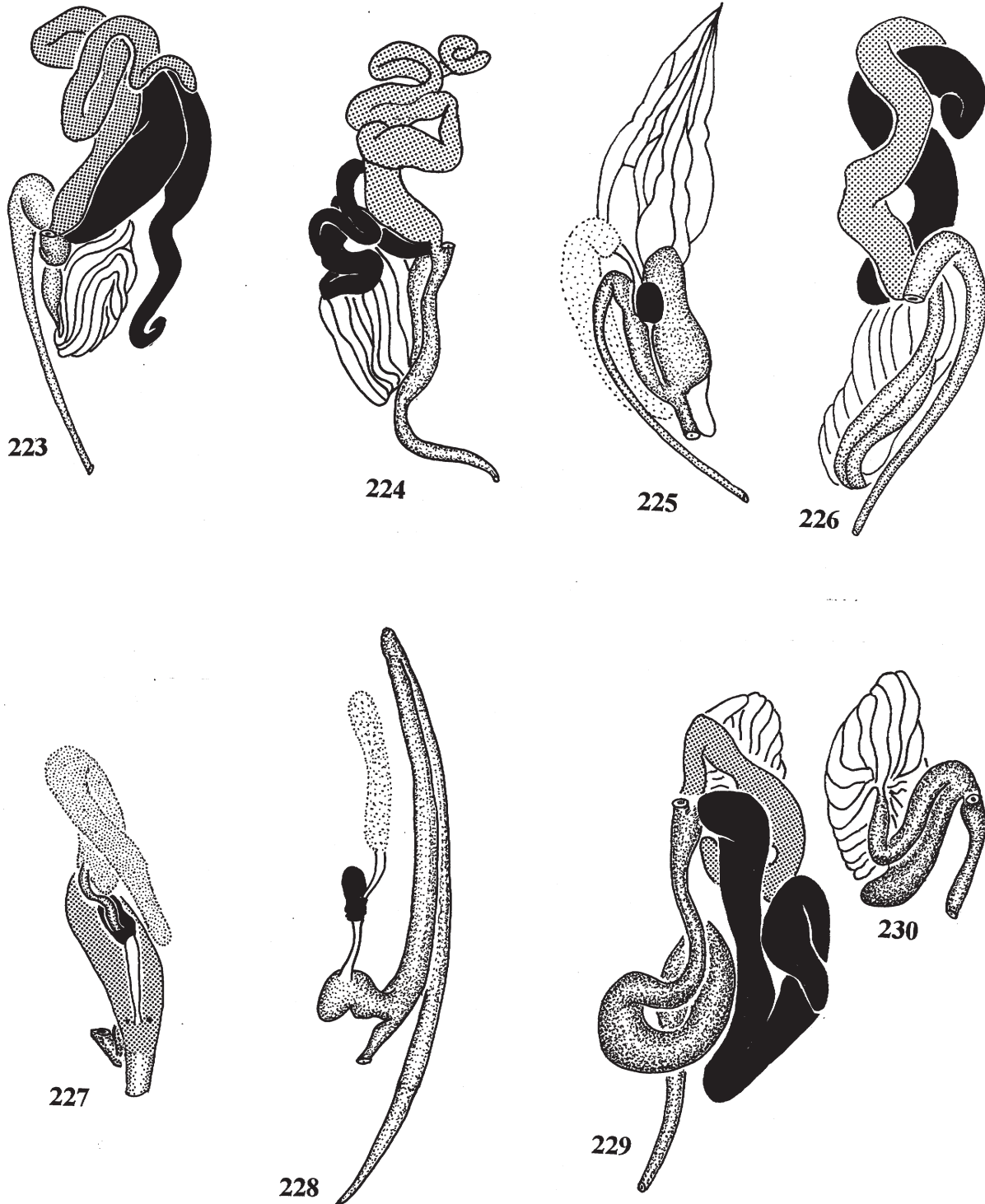
General morphology-Reproductive organs. When fully developed, the male reproductive organs consist of a pair of testes, vas deferens, seminal vesicle, usually two pairs of accessory glands, and the ejaculatory duct (Fig. 252). The number of testicular follicles per testis varies as does the number of accessory glands and shape of seminal vesicle. The term multifollicular is used to indicate that the testis has more than one follicle; this to distinguish from the singular follicle testis as found in most Tillinae. The female organs (Fig. 251) consist of a pair of ovarioles, lateral oviduct, medial oviduct, bursa copulatrix, spermathecal capsule, spermathecal gland, and the vagina. In some species the base of the bursa copulatrix shows a bursal plate (Fig. 148). There is substantial variation in the number of follicles that constitute the ovary, shape and composition of the spermathecal capsule, attachment site of the spermathecal gland to the capsule, length of the spermathecal gland, and in the presence or absence of a saccular bursa copulatrix.

Taxonomic implications-Alimentary canal. A very long stomodaeum occurs in *Somatochaetus* Menier and Ekis, *Metaxina* Broun, and *Katachaetosoma* Opitz, of Chaetosomatidae, and *Thaneroclerus* of Thaneroclerinae, and *Ababa* Casey of Isoclerinae, of the Cleridae. The elongated condition of the stomodaeum was considered a primitive characteristic by Crowson (1972: 340) and Opitz (2010a: 116). All other Cleridae studied to date show a reduced foregut, presumably a manifestation of the loss of the crop (Crowson, 1972: 340). The number of stomodaeal lobes that comprises the stomodaeal valve varies at subfamily level. Primitively there are 8 lobes in Thaneroclerinae and Tillinae whereas the derived condition, involving less than 8 folds, is found in the other subfamilies (Opitz, 2010a: 98). The development of the ventricular papillae varies at subfamily level. They are primitively poorly developed in the Thaneroclerinae, Isoclerinae, Epiphloeinae, Enopliinae, Peloniinae, Tarsosteninae, and Neorthopleurinae. Their well-developed, derived, state is found in the Tillinae, Clerinae, Hydnocerinae, and Korynetinae. Presence of 6 malpighian tubules is the primitive condition found in most of Tillinae, Clerinae, Hydnocerinae, and Korynetinae, whereas in the Thaneroclerinae, Isoclerinae, Neorthopleurinae, Epiphloeinae, Peloniinae, Enopliinae, Tarsosteninae, there are 4 tubules, which reflects the derived condition for this character.

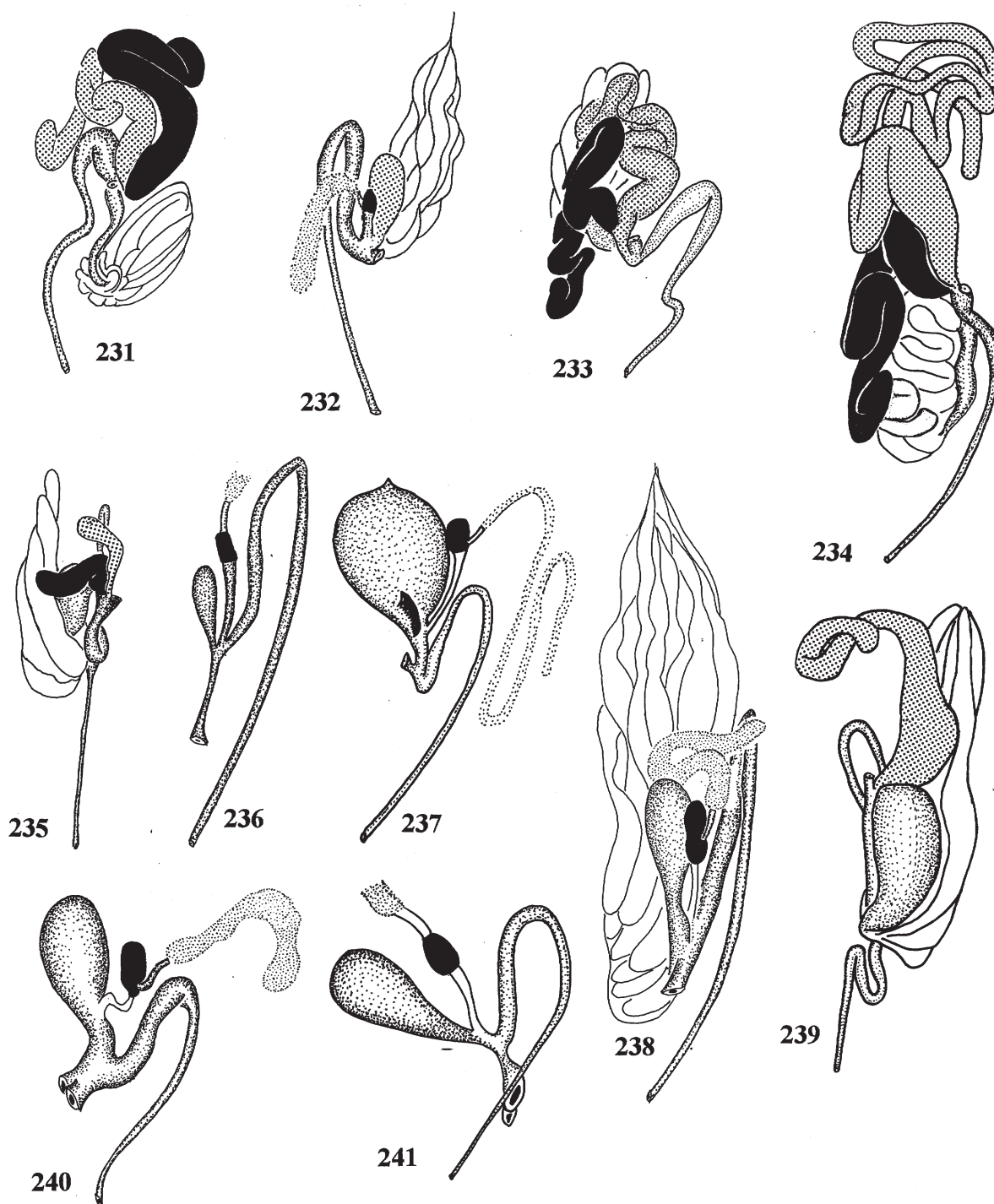
Taxonomic implications-Reproductive organs. Some characteristics of the male and female mesodermal reproductive organs are particularly taxonomically useful at the generic and species-group levels (Opitz 2010a: 51). In nearly every species of Tillinae examined, the testis is comprising one follicle and the median accessory gland exhibits a central longitudinal dark streak (Fig. 154). A similar dark streak is found in the spermatophoral accessory glands of antophilic species of Clerinae (Opitz, 2003). The spermathecal capsule is bifid and the bursa copulatrix is not saccular in tilline females (Fig. 158). Also, at the base of the bursa there is a bursal plate whose configuration is significant at the species level (Fig. 159). In the Hydnocerinae, the males of *Isohydnocera* Chapin and *Phyllobaenus* Dejean are



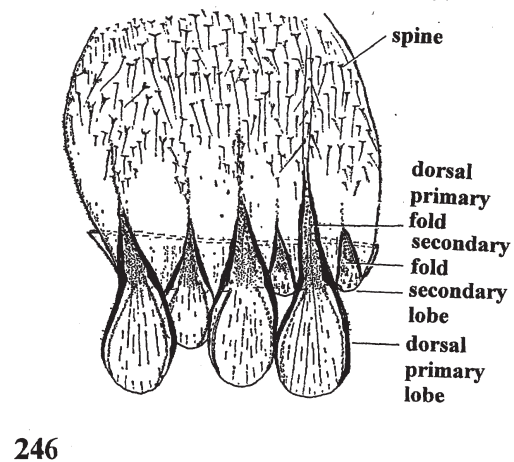
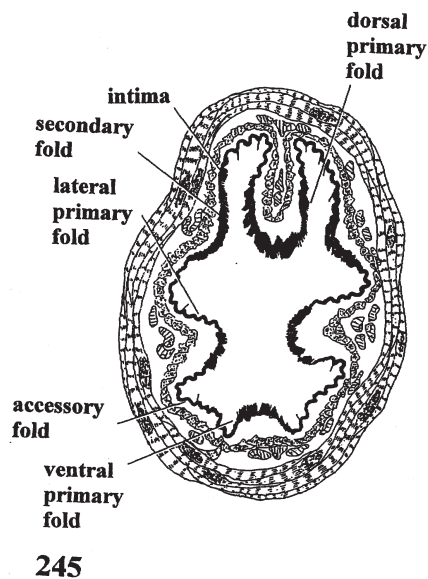
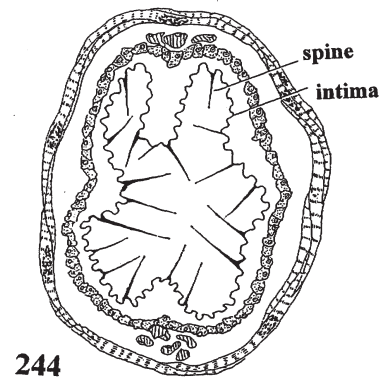
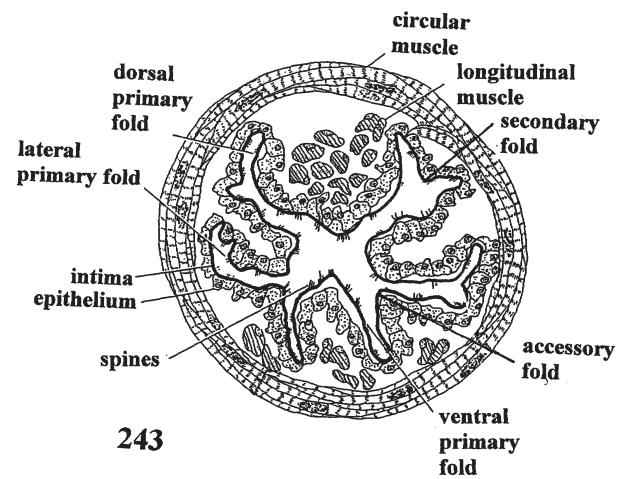
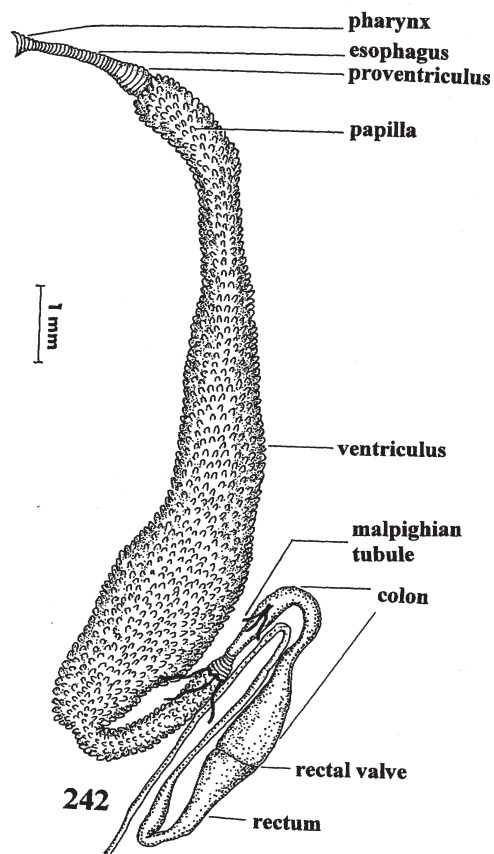
Figures 216–222. Reproductive organs, ventral nerve cord, and brain. **216)** *Pelonium leucophaeum*, reproductive organs, female. **217)** *Pelonium lituratum*, reproductive organs, female. **218)** *Pelonium nigroclavatum*, reproductive organs, female. **219)** *Pelonium lituratum*, ventral nerve cord and brain. **220–221.** *Pelonium peninsulare*. **220)** reproductive organs, male. **221)** reproductive organs, female. **222)** *Pelonium placidum*, reproductive organs, female.



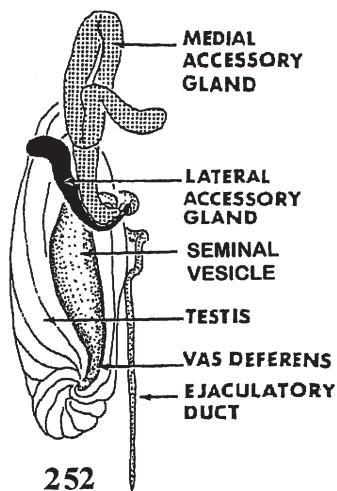
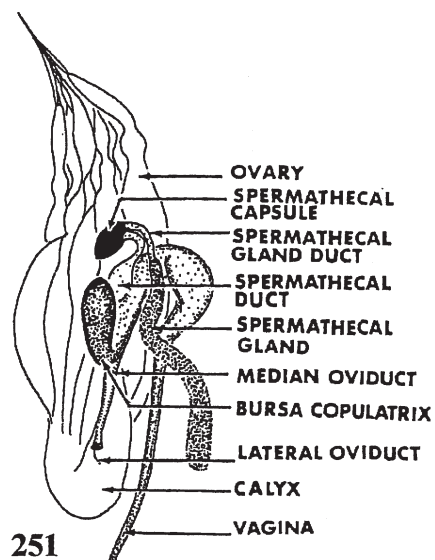
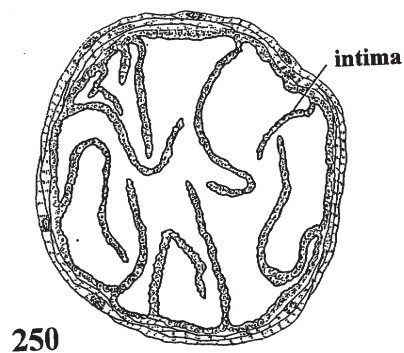
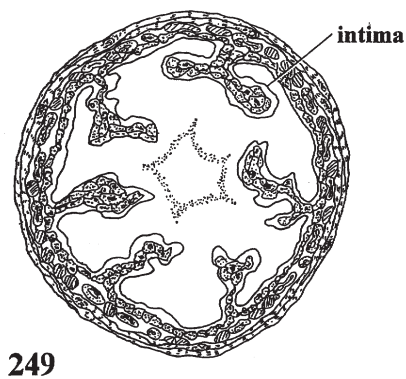
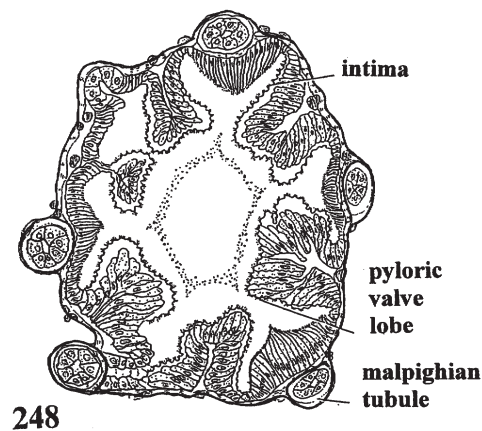
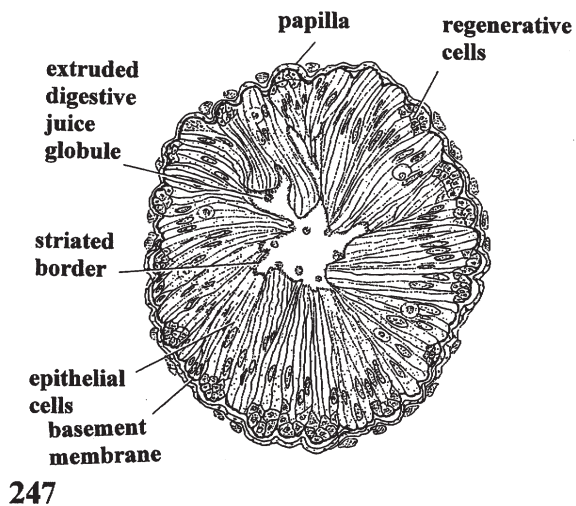
Figures 223–230. Reproductive organs. 223. *Pelonium posticum*, male. 224–225. *Pelonium quadriplagiatum*. 224) male. 225) female. 226–227. *Pelonium semirufum*. 226) male. 227) female. 228–230. *Pelonium viridipenne*. 228) female. 229) male. 230) male.



Figures 231–241. Reproductive organs. **231–234.** *Pelonium* spp. a-c. **231)** sp. a, male. **232)** sp. a, female. **233)** sp. b, male. **234)** sp. c, male. **235.** *Tarsostenodes leucogramma*, male. **236–237.** Females. **236)** *Blackburniella hilaris*. **237)** *Parapylus sedlaceki*. **238–239.** *Tarsostenus carus*. **238)** female. **239)** male. **240)** *Tarsostenodes guttulus*, female. **241)** *Dolichopsis haplocnemodes*, female.



Figures 242–246. Alimentary canal, *Enoclerus quadrisignatus*. 242) alimentary canal. 243) pharynx. 244) esophagus. 245) proventriculus. 246) stomodaeal valve.



Figures 247–252. Alimentary canal and reproductive organs. 247) ventriculus. 248) pyloric valve. 249) colon. 250) rectum. 251–252. Reproductive organs. 251) female. 252) male.

characterized by having only one pair of accessory glands (Fig. 12) that are extraordinarily long (Fig. 12), and in most species of *Phyllobaenus* Dejean the spermathecal capsule is round and heavily sclerotized (Fig. 29). A sacculus bursa copulatrix is not present in all hydnoecine examined. In the Clerinae genus *Enoclerus* Gahan the mode of bifurcation of the medial accessory glands are taxonomically significant at species-group levels. In various species of subfamily Peloniinae the spermathecal capsule is transversally wrinkled (Fig. 206). A bursal plate is found in the Peloniinae genus *Pelonium* Spinola. The spermathecal gland is extraordinarily long and the bursal plate is present in the Korynetinae genus *Parapylus* Blackburn. Information about the mesodermal reproductive organs of the Cleridae, as part of taxonomic revisions, was published recently by Ekis (1977a, 1977b), Ekis (1978), Opitz (1998, 2003, 2004, 2005, 2006, 2007, 2008, 2009a, 2009b, 2009c, 2010a, 2010b, 2010c, 2011a, 2011b, and 2012), and Yang, *et. al.* (2011).

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