Arquivos de Zoologia

MUSEU DE ZOOLOGIA DA UNIVERSIDADE DE SÃO PAULO

CONTEÚDO

ISSN 0066-7870

Arq. Zool., S. Paulo	São Paulo	v. 35	n. 3	p. 231-300	1999

Arquivos de Zoologia

MUSEU DE ZOOLOGIA DA UNIVERSIDADE DE SÃO PAULO

ISSN 0066-7870

ARQ. ZOOL. S. PAULO 35(3): 231-300 28.VI.1999

SYSTEMATICS AND BIONOMICS OF CNEOGLOSSIDAE WITH A CLADISTIC ANALYSIS OF BYRRHOIDEA *SENSU* LAWRENCE & NEWTON (1995) (COLEOPTERA, ELATERIFORMIA)

CLEIDE COSTA [1]
SERGIO ANTONIO VANIN [2]
SERGIO IDE [3]

ABSTRACT

A description of a new species of Cneoglossa (C. edsoni *sp. n., type locality: Brazil, São Paulo State, City of São Paulo, Parque Estadual da Cantareira) is presented based on male and female adults, pupae and larvae.The synonymy of* Buckodrillus *Wittmer, 1948, with* Cneoglossa *Guérin-Méneville, 1843, is confirmed and* C. brasiliensis *(Wittmer, 1948), is a new combination. Larvae of* C. edsoni *were collected in submerged rotting brushwood in shallow flowing streams; pupae and adults were obtained from larvae reared in laboratory. Immatures of this genus were unknown up to date. Larval and/or adult features of species belonging to* Anchytarsus *Guérin-Méneville, 1843;* Araeopidius *Cockerell, 1906;* Cladotoma *Westwood, 1837;* Epilichas *White, 1859;* Paralichas *White, 1859; and,* Ptilodactyla, *Illiger, 1807 are described and illustrated. A cladistic analysis, conducted for 32 taxa of selected Byrrhoidea (*sensu *Lawrence & Newton, 1995) and 72 features of adults, larvae and pupae, is also given, in an attempt to clear up the systematic position of the Cneoglossidae. As a result of the analysis, Callirhipidae and Eulichadidae are excluded from Byrrhoidea (*sensu *Lawrence & Newton, 1995) and placed* incertae sedis *within the Elateriformia. The strict consensus cladogram of the 24 most parsimonious trees presented the following relationships: ((Byrrhidae ((Cneoglossidae, Psephenidae) ((Ptilodactylinae (Anchytarsinae, Epilichinae)) (Aploglossinae, Araeopidiinae (Cladotominae, Chelonariidae))))) (Larainae (Elminae (Lutrochidae (Hyphalinae (Limnichinae, Cephalobyrrhinae, Thaumastodinae, Dryopidae, Heteroceridae)))))). The monophyly of this assemblage is supported by three striking synapomorphies, the anterior process of metendosternite shortened, the proximal end of radial cell with acute inner angle, and the wing folding of the dryopoid-type. A sister-group relationship between Cneoglossidae and Psephenidae is indicated by the presence of paired dorsal glandular openings on abdominal tergites of adult, + five homoplasic features. Elmidae, Limnichidae and Ptylodactylidae, as currently defined, are paraphyletic. Ptylodactylidae is monophyletic with the inclusion of Chelonariidae.*

Keywords: Bionomics, Byrrhoidea, Cladistic Analysis, Cneoglossidae, New Species.

---

[1] Museu de Zoologia, Universidade de São Paulo, Caixa Postal 42.694, 04299-970 São Paulo SP, Brazil (e-mail: cleideco@usp.br).

[2] Departamento de Zoologia, Instituto de Biociências, Universidade de São Paulo, Caixa Postal 11.294, 05422-970 São Paulo SP, Brazil (e-mail: savanin@ib.usp.br).

[3] Seção de Entomologia Geral, Divisão de Parasitologia Vegetal, Instituto Biológico, Caixa Postal 12.898 e 12.959, 04010-970 São Paulo SP, Brazil (e-mail: ide@biologico.sp.gov.br).

Recebido para publicação em 13.XI.1996 e aceito em 14.XI.1997.

INTRODUCTION

While collecting water beetles in the neighborhood of the City of São Paulo (Parque Estadual da Cantareira) larvae of a new species of *Cneoglossa* were found in submerged rotting wood in shallow flowing streams. Pupae and adults were obtained from these larvae reared in the laboratory. The discovery of immatures of this rare group of beetles, undescribed up to now, led us to study in more detail the larvae, pupae and adults, to present a description of the new species as complete as possible. Besides, our studies prompted us to carry out a cladistic analysis including Cneoglossidae and its allies.

The Cneoglossidae, monogeneric to *Cneoglossa* Guérin-Méneville, 1843, a Neotropical genus with eight known species distributed from Mexico to Brazil (Rio Grande do Sul), is represented by very small beetles (3-5 mm in lenght) with soft integument, dark elytra, and bicolor pronotum hidding partially the head.

The systematic position of Cneoglossidae has suffered many changes in the last 30 years. The genus *Cneoglossa* was originally described within the Dascillidae; Crowson (1972) transferred it to the Cantharoidea, including it in his new family Cneoglossidae. Brown (1981) enrolled the genus among the Psephenidae. Lawrence (1982) followed Crowson's (*l. c.*) ideas, but later included it in his Psephenoidea (Psephenidae, Callirhipidae, Eulichadidae, Cneoglossidae, Ptilodactylidae and Chelonariidae) (Lawrence, 1988). Lawrence & Britton (1991, 1994), transferred Cneoglossidae to Byrrhoidea + Psephenoidea *sensu* Lawrence (1988).

Lawrence *et al.* (1995) studied the relationships of Decliniidae (Scirtoidea) and presented a cladistic analysis of the Elateriformia + Scirtoidea where they used many characters of Lawrence's (1988) analysis, reformulated some of them and added others. Although the larva of *Cneoglossa* was undescribed at that time they used on their matrix data a few larval characters, concerning the maxilla (galea, lacinia, and palpomeres). They considered Psephenidae as the sister group of Cneoglossidae, including both in their expanded Byrrhoidea. They stated that Byrrhoidea *sensu* Lawrence (1988), with Buprestidae excluded - i. e., Byrrhidae, Dryopidae, Lutrochidae, Limnichidae, Heteroceridae and Elmidae occurred in some cladograms, whereas Psephenoidea (Psephenidae, Callirhipidae, Eulichadidae, Cneoglossidae, Ptilodactylidae and Chelonariidae) was never supported by synapomorphies. Although they did not consider Byrrhoidea, currently defined as a monophyletic assemblage, they recognized the lack of an alternative classification at the moment. However, the authors concluded that their results "could well be artifacts of a poorly chosen character set or a limited set of genera which may not be the most appropriate representatives of their respective family group taxa".

Lawrence & Newton (1995: 780) placed the Cneoglossidae within Byrrhoidea, suggesting a position near Ptilodactylidae or Psephenidae, in a classification where the "higher taxa are listed in a sequence inferred to be from less to more derived, with closely related taxa placed next to one another as far as possible". The sequence of the families of the Byrrhoidea presented by them is: Byrrhidae, Elmidae, Dryopidae, Lutrochidae, Limnichidae, Heteroceridae, Psephenidae, Cneoglossidae, Ptilodactylidae, Chelonariidae, Eulichadidae and Callirhipidae. The first six families plus Buprestidae correspond to the "Byrrhoidea", and the last six to the "Psephenoidea", of Lawrence (1988), where they appear as sister groups in a cladogram produced by using PAUP.

A cladistic analysis of Elateriformia based only on morphological structures of immatures stages has recently been conducted by Beutel (1995). This author emphasized the characters transformation of the head which, according to him, play a predominant role in the evolution, but did not present a new classification of that series.

The knowledge of all these tentatives to clear up the systematic position of Cneoglossidae and its difficulties stimulated us to perform a cladistic analysis of the "expanded" Byrrhoidea *sensu* Lawrence & Newton (1995), employing both immatures and adults characters.

MATERIAL AND METHODS

DEPOSITORIES

The specimens examined are deposited in the following institutions (letters codes according to Arnett *et al.* (1993), except for NHCK): ANIC, Australian Nacional Insect Collection, Division of Entomology, C. S. I. R. O., Canberra (Dr. J. F. Lawrence); BMNH, Department of Entomology, The Natural History Museum, London (Miss C. M. F. von Hayek); MNHN, Entomologie, Muséum National d'Histoire Naturelle, Paris (Dr. N. Berti); MZSP, Museu de Zoologia, Universidade de São Paulo, São Paulo; NHMB, Entomologisches Abteilung, Naturhistorisches Museum, Basel (Dr. M. Brancucci); NHCK, Nodoka Hayashi Collection, Kanagawa (Dr. N. Hayashi); OMNO, Department of Zoology and Oklahoma Museum of Science and History, University of Oklahoma, Norman (Dr. H. P. Brown); UCRC, Entomology Research Museum, Department of Entomology, University of California, Riverside (Dr. S. I. Frommer).

MATERIAL EXAMINED AND DESCRIBED OR REDESCRIBED (see complete list within descriptions)

CNEOGLOSSIDAE. *Cneoglossa edsoni* sp. n. BRAZIL. SÃO PAULO: 6 larvae, 3 pupae, 3 adults (MZSP).

PTILODACTYLIDAE, ARAEOPIDIINAE. *Araeopidius monachus* (LeConte, 1874). CANADA. BRITISH COLUMBIA: 1 adult (UCRC). U. S. A. WASHINGTON: 2 adults (UCRC). OREGON: 1 larva (ANIC).

PTILODACTYLIDAE, CLADOTOMINAE. *Cladotoma ovalis* Westwood, 1837. BRAZIL. MATO GROSSO: 2 adults (MZSP). ESPÍRITO SANTO: 1 adult (MZSP). SÃO PAULO: 3 adults (MZSP). *C. thoracica* Guérin-Méneville, 1837. BRAZIL. PARÁ: 2 adults (MZSP). MATO GROSSO: 1 adult (MZSP). GOIÁS: 1 adult (MZSP). *Paralichas pectinata* (Kiesenwetter, 1874). JAPAN. HYOGO: 2 larvae, 1 adult (NHCK).

PTILODACTYLIDAE, PTILODACTYLINAE. *Ptilodactyla humeralifer* Pic, 1928. BRAZIL. SÃO PAULO: 9 adults (MZSP). *Ptilodactyla* spp. BRAZIL. MINAS GERAIS: 2 adults (MZSP). SÃO PAULO: 43 larvae, 2 pupae, 24 adults (MZSP). RIO DE JANEIRO: 2 adults (MZSP). SANTA CATARINA: 2 adults.

PTILODACTYLIDAE, ANCHYTARSINAE. *Anchytarsus bicolor* (Melsheimer, 1845). COSTA RICA. SAN JOSÉ: 3 larvae, 1 adult (BMNH). *A. palpalis* (Champion, 1897). PANAMA. CANAL ZONE: 1 larva (ANIC). GUATEMALA. ALTA VERAPAZ: 1 adult (ANIC).

PTILODACTYLIDAE, EPILICHINAE. *Epilichas flabellatus* (Kiesenwetter, 1874). JAPAN. TOKYO-TO: 1 adult (MZSP). KANAGAWA-KEN: 5 larvae, 2 adults (NHCK).

OTHER MATERIAL EXAMINED

BYRRHIDAE, BYRRHINAE. *Byrrhus gigas* (Fabricius, 1787). ITALIA. VENETO: Belluno, Cencenighi (M. Alto di Pelsa), 1 adult (MZSP). *B. pilula* (Linnaeus, 1758). EUROPE. 5 adults (MZSP). *Byrrhus* spp. GERMANY. RHEINLAND-PFALZ: Pfalz, Elmstein, 1 adult (MZSP). BAYERN: Ober-Franken, Fichtelgebirge, 3 adults (MZSP). *Lioon* sp. Without collecting data, 3 larvae (MZSP). *Pedilophorus* sp. EUROPE. 2 adults (MZSP).

BYRRHIDAE, SYNCALYPTINAE. *Chaetophora monnei* (Reichardt, 1975). URUGUAY. RIVERA: Sierra de la Aurora, Arroyo de la Aurora, 1 adult, holotype, (MZSP). *C. striata* (Pic, 1922). BRAZIL. PARÁ: Jacareacanga, 9 adults, (MZSP). MATO GROSSO: Jacaré (Parque Nacional do Xingu), 33 adults (MZSP). MATO GROSSO DO SUL: Corumbá, 1 adult paralectotype (MZSP). *C. tesselata* (LeConte, 1850). U.S.A. NEW HAMPSHIRE: Grafton Co., Rumney, 1 adult, (MZSP). PERU. LORETO: Colonia Calleria (15 km. from Ucayali on R. Calleria), 1 adult (MZSP). *Chaetophora* sp. BRAZIL. AMAZONAS: Manaus, 6 adults (MZSP).

CALLIRHIPIDAE. *Callirhipis goryi* Laporte, 1834. BRAZIL. SÃO PAULO: Salesópolis (Estação Biológica de Boracéia), 12 larvae (1♂ dissected), 3 pupae, 12 adults (1 dissected) (MZSP). *C. scapularis* Laporte, 1834. BRAZIL. SÃO PAULO: Salesópolis (Estação Biológica de Boracéia), 1 ♀ (dissected) (MZSP). *Callirhipis* sp. BRAZIL. MATO GROSSO DO SUL: Cassilândia (Fazenda Olho d'Água), 1 larva (MZSP). *Zenoa picea* (Palisot de Beauvois, 1805). U. S. A. OHIO: Franklin Co., Columbus, 4 larvae (MZSP). MISSOURI: Jackson Co., Independence, 1 adult (MZSP); Raytown, 2 adults (MZSP); Saint Louis Co., Saint Louis, 1 adult (MZSP). FLORIDA: Alachua Co., 1 adult (MZSP).

CHELONARIIDAE. *Chelonarium ornatum* Klug, 1825. BRAZIL. MINAS GERAIS: Centralina, 7 adults (2 ♀ dissected) (MZSP). MATO GROSSO DO SUL: Cassilândia (Fazenda Olho d'Água), 1 ♂ (dissected) (MZSP). *Chelonarium* sp. BRAZIL. MATO GROSSO DO

SUL: Costa Rica, 2 larvae (MZSP). SÃO PAULO: Salesópolis (Casa Grande), 1 larva (dissected) (MZSP); São Paulo (Parque Estadual da Cantareira), 2 larvae (MZSP). Without collecting data, DZUSP, 2 larvae (MZSP).

Cneoglossidae. *Cneoglossa brasiliensis* (Wittmer, 1948). Brazil. RIO GRANDE DO SUL: 2 adults (NHMB). *C. elongata* Pic, 1916. Brazil. MINAS GERAIS: 1 adult (MNHN), 1 adult (MZSP). SÃO PAULO: 2 adults (MZSP). *C. gounelli* Pic, 1916. Brazil. MINAS GERAIS: 5 adults (1 MNHN, 4 MZSP). *C. peruviana* Pic, 1916. Peru. 1 adult (MNHN). *C. rufifrons* Pic, 1916. Brazil. CEARÁ: 1 adult (MNHN). *C. rufifrons* var. *testaceicollis* Pic, 1916. Brazil. PERNAMBUCO: 1 adult (MNHN). *Cneoglossa* spp. Brazil. PARÁ: 1 adult (MZSP). MARANHÃO: 1 adult (MZSP). GOIÁS: 2 adults (MZSP). RIO DE JANEIRO: 1 adult (MZSP). SÃO PAULO: 3 adults (MZSP).

Dryopidae. *Dryops vicinus* Grouvelle, 1896. Brazil. ESPÍRITO SANTO, 2 adults (MZSP). *Dryops* spp. Brazil. MINAS GERAIS: Itacarambi (Gruta Olhos d'Água), 1 adult (MZSP). SÃO PAULO: Campos do Jordão (Parque Estadual, Rio Cachoeira), 2 young larvae, 14 mature larvae, 18 adults (MZSP); Iporanga (Fazenda Intervales) (Charco da Pesquisa), 3 adults (MZSP); (Rio do Charco & Riacho da Barra Bonita), 3 young larvae, 2 mature larvae, 1 pupa, 8 adults (MZSP); Ribeirão Grande (Fazenda Intervales, Córrego da Cachoeira), 3 adults (MZSP); São Paulo (Parque Estadual da Cantareira, Carpa), 1 adult (MZSP). *Guaranius* aff. *carlosi* Spangler, 1991. Brazil. SÃO PAULO: São Paulo (Parque Estadual da Cantareira), 1 larva, 1 adult (MZSP). *Helichus productus* LeConte, 1852. U. S. A. ARIZONA: Coconino Co., Grand Canyon (Bt. Angel Trail), 4 adults (MZSP). *Helichus* sp. Brazil. SÃO PAULO, Iporanga (Ribeirão Betari), 3 adults (MZSP). *Onopelmus guarani* Vanin, Ide & Costa, 1997. Brazil. SÃO PAULO: São Paulo (Parque Estadual da Cantareira), 4 larvae (2 dissected); 1 pupa; 1 ♂, 4 ♀ (1 ♀, dissected), paratypes (MZSP); 1 ♂, holotype (dissected) (MZSP).

Elmidae, ELMINAE. *Cylloepus* sp. Bolivia. 2 adults (MZSP). *Elmis maugei* Mueller, 1806. Europe. 1 adult (MZSP). *Elsianus* sp. Brazil. SÃO PAULO: Salesópolis (Estação Biológica de Boracéia), 6 larvae, 4 adults (MZSP); *Heterelmis* spp. Brazil. SÃO PAULO: Campos do Jordão (Parque do Estado), 1 larva (MZSP); Iporanga (Ribeirão Betari), 78 larvae, 4 adults (MZSP). *Hintonelmis opis* Hinton, 1971. Brazil. AMAZONAS: Rio Cauaburi, 1 adult (MZSP). *Hintonelmis* sp. Brazil. AMAPÁ: Serra Lombard (Limão), 4 adults (MZSP). *Limnius ovalis* LeConte, 1863. U. S. A. NEW YORK: Tompkins Co., Freeville, 4 adults (MZSP). *Neoelmis maculata* Hinton, 1940. Brazil. AMAZONAS: Rio Cauaburi, 7 adults (MZSP). *N. reichardtii* Hinton, 1972. Brazil. SANTA CATARINA: Nova Teutônia, 10 adults (1 holotype, 9 paratypes) (MZSP). *Stenelmis* sp. 4 larvae (MZSP). *Tyletelmis mila* Hinton, 1972. Brazil. RONDÔNIA: Porto Velho, 10 adults (MZSP).

Elmidae, LARAINAE. *Hexanchorus caraibus* (Coquerel, 1851). Martinique. SW of St. Joseph, Rivière Monsieur, 1 larva, 2 adults (MZSP). *H. thermarius* (Coquerel, 1851). Brazil. ESPÍRITO SANTO, 2 adults (MZSP). *Hexanchorus* spp. Brazil. SÃO PAULO: Iporanga (Ribeirão Betari), 76 larvae (MZSP). *Phanocerus clavicornis* Sharp, 1882. Puerto Rico. PR 119, km. 15.5, Rio Cañas, 1 larva, 2 adults (MZSP). *Phanocerus* spp. Brazil. SÃO PAULO: Campos do Jordão (Parque do Estado), 3 larvae, 22 adults (MZSP); Iporanga (Ribeirão Betari), 3 larvae (MZSP). *Potamophilus cinereus* (Blanchard, 1837). Brazil. MINAS GERAIS: Buritis (Ribeirão Confins), 3 adults (MZSP). ESPÍRITO SANTO: 2 adults (MZSP). Bolivia. SANTA CRUZ: Sara (Nueva Moka), 2 adults (MZSP).

Eulichadidae. *Eulichas* spp. Malaysia. Gomback River (= near Kuala Lumpur) (M. A. Jäch, pers.com.), 7 larvae (1 dissected) (BMNH). SARAWAK: Mount Dulit (4,000 ft., moss forest), 1 adult (BMNH). SABAK: Mount Kinabalu, 1 adult (BMNH). PAHANG: Cameron Highland (19 mile point), 15 adults (2 ♂, 1 ♀ dissected) (MZSP). *Stenocolus scutelaris* LeConte, 1853. U. S. A. CALIFORNIA: Colusa Co., Ladoga, 1 adult (UCRC); Tulare Co., Sequoia National Forest (7 mi. NE Lake Kaweak), 1 adult (UCRC).

Heteroceridae, HETEROCERINAE. *Centuriatus auromicans* (Kiesenwetter, 1851). U. S. A. TEXAS: Paladuro Co., 3 adults (MZSP). *Efflagitatus freudei* Pacheco, 1973. Brazil. SÃO PAULO: Guarujá (Praia de Pernambuco), 292 mature larvae (5 dissected), 74 pupae, 342 adults (MZSP). RIO GRANDE DO SUL: Rio Grande (Praia do Cassino) (25 km Sul), 4 mature larvae, 18 adults (MZSP); (28 km Sul), 62 mature larvae, (2 dissected), 6 pupae, 183 adults (1 ♂ dissected) (MZSP); (15 & 28 km Sul), 161 adults (2 ♂, 2 ♀ dissected) (MZSP). *Heterocerus* sp. U. S. A. CALIFORNIA: Del Norte Co., C. 6 mi. Smith River, 1 larva (MZSP). *Neoheterocerus pallidus* (Say, 1823). U. S. A. ILLINOIS: Jackson Co., Grand Tower, 8 adults (MZSP). *Tropicus imperator* Pacheco, 1965. BRAZIL. MATO GROSSO DO SUL: Porto Murtinho (Rio Caraguatá, 400 m), 5 adults, paratypes (MZSP). *T. ladonnae* Ivie & Stribling, 1984. TRINIDAD AND TOBAGO. TRINIDAD: Espagnole River & Princess Margaret Highway, 100 adults, paratypes (MZSP).

LIMNICHIDAE, LIMNICHINAE. *Physemus levis* Wooldridge, 1984. TRINIDAD AND TOBAGO. TRINIDAD: M. Espagnole River & Princess Margaret Highway, 10 adults, paratypes (MZSP).

LUTROCHIDAE. *Lutrochus geniculatus* Chevrolat, 1864. CUBA. 1 adult (MZSP). *L. germari* Grouvelle, 1889. BRAZIL. SÃO PAULO: Campos do Jordão (Parque do Estado), 4 adults (MZSP); 1 larva (MZSP); (Parque do Estado, Rio Cachoeira), 4 larvae, 4 adults (1 ♂ dissected) (MZSP); 4 larvae, 1 adult (MZSP); Iporanga (Fazenda Intervales, Córrego da Barra Bonita & Riacho do Charco), 26 larvae (2 dissected), 2 pupae (1 associated with larval exuvia), 7 adults (1 ♂ dissected) (MZSP); Iporanga (Fazenda Intervales) (Rios Lageado & Carmo), 3 adults (MZSP); (Córrego da Cachoeira), 1 adult (MZSP); 16 adults (1 ♂, 1 ♀ dissected) (MZSP); (Ribeirão Água Comprida & Córrego da Bocaina), 2 larvae, 3 adults (MZSP); Salesópolis (Estação Biológica de Boracéia), 1 larva (MZSP); (Estação Biológica de Boracéia, Ribeirão Venerando), 2 adults (1 ♂ dissected) (MZSP); 15 larvae, 2 adults (MZSP); 2 larvae (MZSP); São Paulo (Pico do Jaraguá), 5 larvae (MZSP); (Parque Estadual da Cantareira), 2 larvae, 5 adults (1 ♂, 1 ♀ dissected) (MZSP); 13 larvae (2 dissected) (MZSP); 16 larvae, 10 adults (2 ♀ dissected) (MZSP); 10 larvae, 1 adult (MZSP); 3 adults (MZSP). PARANÁ: Londrina, 2 adults (MZSP). *L. luteus* LeConte, 1852. U. S. A. TEXAS: Bosque Co., Morgan, 1 larva, 2 adults (MZSP). *L.* aff. *montanus* Grouvelle, 1896. BRAZIL. SANTA CATARINA: Anita Garibaldi, 1 adult, (MZSP); 1 adult (MZSP); 8 adults (1 ♂ dissected) (MZSP). RIO GRANDE DO SUL: Pelotas (Cascata), 1 adult (MZSP).

PSEPHENIDAE, EUBRIANACINAE. *Eubrianax edwardsii* (LeConte, 1874). U.S.A. CALIFORNIA: Tehama/Shasta Co., Cottonwood Creek (Platina), 3 adults (1 ♂ dissected) (OMNO); Tulare Co., Sequoia National Park (Dorst Creek), 3 larvae (OMNO).

PSEPHENIDAE, EUBRIINAE. *Ectopria thoracica* (Melsheimer, 1845). U. S. A. ALABAMA: Jefferson Co., Birmingham, 2 ♂, 1 ♀ (dissected) (OMNO); Shades Creek, 4 larvae (OMNO).

PSEPHENIDAE, PSEPHENINAE. *Psephenus herricki* (DeKay, 1844). U. S. A. PENNSYLVANIA: 2 adults (MZSP). *Psephenus* sp. BRAZIL. SÃO PAULO: Campos do Jordão (Parque Estadual), 1987, 42 larvae (MZSP); 1 ♂ (dissected) (MZSP); Santa Isabel, 1 ♀ (dissected) (MZSP); São Paulo (Pirituba, Pico do Jaraguá), 18 larvae (3 dissected), 7 adults (1 ♂ dissected) (MZSP).

PSEPHENIDAE, PSEPHENOIDINAE. *Psephenoides gahani* Champion, 1920. INDIA. UTTAR PRADESH: Kumaon (W. Almora), 1 ♂, paratype (BMNH); Haldwani (Nandhaur R.), 2 larvae; 22 adults (2 ♂, 1 ♀ dissected) (BMNH). *Psephenoides* sp. PHILIPPINES. BENGUET: Tuba, 2 larvae (OMNO).

CHARACTERS TAKEN FROM LITERATURE

Many data on morphology, biology, systematics and distribution of adults and immatures, and on taxa that were not available for study were obtained from literature. Special mention merit the works of Crowson (1938, 1944) on Coleoptera metendosternite; Stribling (1986) on Ptilodactylidae adults; and Johnson (1987) on Byrrhidae larvae. The general larval characters to families and subfamilies were obtained from Costa *et al.* (1988) and Lawrence *et al.* (1993).

CLADISTIC ANALYSIS

The methodology employed for proposing the hypotheses of relationships was phylogenetic systematics (Hennig, 1966; Nelson & Platnick, 1981; Wiley, 1981; Forey *et al.* 1992). Transformation series were coded in discrete binary and multistate characters. When the multistate characters could be ordered by morphological continuity, which implied in a logical linear sequence of intermediate states, they were treated as additive; otherwise, they were treated as non-additive (unordered), which results in the equal cost of only one step for the transformation between any of its states. Transformation series were polarized through the out-group comparison method (Watrous & Wheeler, 1981; Maddison *et al.*, 1984; Nixon & Carpenter, 1993). As operational outgroups, the following taxa were employed: Elateroidea, Buprestoidea, Dascilloidea, Scirtoidea and Scarabaeiformia. The available phylogenies presented by Lawrence (1988) and Lawrence *et al.* (1995) served as a base for the selection of the outgroups. In the preliminary analysis, only taxa of the family level were treated as terminals. However, some of such terminals were polymorphic, and they were broken up into subunits that were monomorphic for each character employed in the analysis. So, the terminal units were based on an unique combination of character states. This splitting also decreased the number of missing entries due to terminal polymorphism, a procedure that may cause problems during parsimony analysis (Nixon & Davis, 1991). Autapomorphies for the terminals were included in the analysis, because of the informative value they may have in future studies (Yeates, 1992). Parsimony analysis were performed with the computer program Hennig 86, v. 1.5 (Farris, 1988), employing the mh*, bb* algorithms. Clados, v. 1.2 (Nixon, 1992) computer program was used for tree manipulations and tracing character evolution.

SYSTEMATICS

HISTORICAL REVIEW OF THE GENUS *CNEOGLOSSA*

FIRST PERIOD: 1843-1897. Guérin-Méneville (1843b) characterized shortly the genus *Cneoglossa* in a identification key including it in "Malacodermes Dascillites" but did not enrolled any species in it. Blanchard (1845) keyed the genus *Cneoglossa* close to *Anchytarse* Guérin-Menéville, 1843 in the tribe "Lampyriens", family "Cébrionides", group "Atopites". Guérin-Méneville (1849) described *C. collaris* from Colombia which was considered the type-species of the genus *Cneoglossa* by monotypy. Lacordaire (1857) redescribed the genus and *C. collaris* keeping its systematic position within the "Dascyllides". Champion (1897) described two more species: *C. lampyroides*, from Mexico and Nicaragua, *C. brevis* from Panama, proposed its systematic position within the Dascillidae, Dascillinae, Cneoglossini.

SECOND PERIOD: 1914-1972. Pic *in* Schenkling (1914) and Blackwelder (1944) in their catalogues, sustained the systematic position proposed by Champion (1897). The number of species was raised to seven by adding four species described by Pic (1916): *C. elongata* and *C. gounellei*, both from Brazil, Minas Gerais; *C. peruviana* from Peru and *C. rufifrons* with a variety *testaceicollis* both from Northeastern Brazil. Wittmer (1948) described the genus *Buckodrilus*, monotypic to *B. brasiliensis* from Brazil, Rio Grande do Sul (Porto Alegre) within the Drilidae (Cantharoidea). Costa Lima (1953) transcribed part of a personal letter received from Wittmer were this author confimed the synonymy of *Buckodrilus* to *Cneoglossa*. Crowson (1955) changed the systematic position of *Cneoglossa* including it in his Dryopoidea, Ptilodactylidae. Arnett (1968) adopted again Champion's (*l. c.*) position. Crowson (1972) described the family Cneoglossidae, monogeneric to *Cneoglossa* and transfered it to the Cantharoidea.

THIRD PERIOD: 1988-1995. During this period several phylogenetical papers were published, which included *Cneoglossa*: Lawrence (1988), studying a new Australian family from the Elateriformia series, proposed a new classification of this series and suggested the placement of Cneoglossidae within his Psephenoidea, close to Psephenidae, Callirhipidae, Eulichadidae, Ptilodactylidae and Chelonariidae. Lawrence & Britton (1991, 1994), considered the genus in the Byrrhoidea + Psephenoidea of Lawrence (1988). Lawrence *et al.* (1995) suggested *Cneoglossa* as sister group of Psephenidae. Lawrence & Newton (1995) suggested a position near Ptilodactylidae or Psephenidae within the Byrrhoidea.

Cneoglossidae Champion, 1897

Malacodermes, Dascillites Guérin-Méneville, 1843b: 193.

Lampyriens, Cébrionides, Atopites Blanchard, 1845: 57.

Dascillides Lacordaire, 1857: 264.
Dascillidae, Dascillinae, Cneoglossini Champion, 1897: 594; Pic, 1914: 8; Blackwelder, 1944: 266.
Dascilliformia, Dryopoidea, Ptilodactylidae, Cneoglossini Crowson, 1955: 170.
Elateriformia, Cantharoidea, Cneoglossidae Crowson, 1972: 43; 1981: 696; Lawrence, 1982: 510, 511; 1991: 422; Costa *et al.*, 1988: 25, 157.
Dryopoidea, Psephenidae, Eubriinae Brown, 1981: 143.
Elateriformia, Psephenoidea, Cneoglossidae Lawrence, 1988: 43.
Elateriformia, Byrrhoidea, Cneoglossidae Lawrence & Britton, 1991: 564; 1994: 36, 37; Lawrence & Newton, 1995: 783, 784, 846.
Elateriformia Lawrence *et al.*, 1995: 387, 389, 393, 407.

Cneoglossa Guérin-Méneville, 1843
(Fig. 1-53)

Cneoglossa Guérin-Méneville, 1843b: 194 (type species: *Cneoglossa collaris* Guérin-Méneville, 1849: 1); Blanchard, 1845: 57; Lacordaire, 1857: 264; Champion, 1897: 594; Wittmer *in* Costa Lima, 1953: 160; Lawrence, 1988: 15, 22, 42; Lawrence *et. al.*, 1995: 393, 395, 396, 403-405, 407.
Buckodrillus Wittmer, 1948: 215 (type species: *Buckodrillus brasiliensis* Wittmer, 1948: 216, monotypy); Wittmer *in* Costa Lima, 1953: 160.

REDESCRIPTION. ADULT (Fig. 28-53). Body (Fig. 28) elongate, lampyriform, weakly sclerotized; without hydrofuge hairs.

Head deeply retracted into prothorax (Fig. 28). Transverse occipital ridge present. Median endocarina absent. Eyes (Fig. 28) large, protuberant; hemispherical; without interfacetal setae; ommatidia exocone. Interocular distance wider than diameter of eye. Antennae (Fig. 29) 11-segmented. Fronto-clypeal suture absent. Labrum transverse. Mandibles (Fig. 30) symmetrical; very small; foliaceus; short and broad; with rounded apex; mola absent. Maxillae (Fig. 32-33a): palp 4-segmented, elongate, apical segment subulate; galea 1-segmented; lacinia reduced. Labium (Fig. 31, 34) with mentum sub-trapezoidal; labial palpi 3-segmented; ligula broad, transverse.

Thorax. Prothorax transverse, narrower anteriorly; notum (Fig. 28) bicolor, with anterior margin more or less straight, not produced forward, sides arcuate, borders explanate, lateral carina complete, posterior margin lacking crenulations, notal projection very short and angulate or absent; postcoxal extension of hypomeron (Fig. 36) absent; anterior edge of sternum (Fig. 36) not produced, in front of coxae (Fig. 36) short, sub-equal in length to sternal process; coxal cavities (Fig. 36) broadly open externally and internally; trochantin well developed, exposed, freely moveable. Conection between prosternal and mesosternal cavity (Fig. 36, 39) absent. Scutellum (Fig. 28) triangular. Elytra (Fig. 28): each elytron with ten elytral striae formed by more or less regular rows of punctures; 2 additional shorter basal striae placed between striae I and II; scutellary striole absent; epipleura well developed. Membranous wing (Fig. 43): wing folding dryopoid-type; radial cell elongate, strongly oblique, acute internally; proximal end forming acute inner angle; r4 crossvein weak, distal part arising from radial cell; proximal r-m (r4) crossvein between rs and m absent; 1st cubito-anal cell present; 2nd cubito-anal cell absent; medial field (posterior to MP_{1+2}) containing four veins in the maingroup (not including AP_{3+4}): MP_3, MP_4, CuA_2 and AA_{3+4}. Mesosternum (Fig. 39) transverse; sternal process present; coxal cavities (Fig. 39) very reduced, internally well separated, laterally closed by episternum and epimeron; coxae narrowly separated by intercoxal process, long and slender, rounded at apex; episterna (Fig. 39) sub-triangular; epimeron (Fig. 39) quadrangular. Metasternum (Fig. 39) with longitudinal suture present; transverse suture absent; exposed portion of episternum (Fig. 39) broad, narrowing posteriorly; epimeron (Fig. 39) triangular; suture between sternum and epimeron well distinct; coxal plates (Fig. 39) poorly developed, very oblique; trochantin not distinct; endosternite (Fig. 38): furca with long narrow stalk as long as sternum, crux region with short anterior arms, lateral margins of ventrolateral processes projected forward under arm bases, anterior tendons short, almost contiguous at base, anterior process short or absent. Legs (Fig. 40-42, 44) not fossorial; unequal, increasing gradually in length from front to posterior pair; mesocoxae narrowly separated, metacoxae large and contiguous; metatrochanter larger than meso- and protrochanters, strongly oblique and produced along inner edge of femur; femora compressed; tibial apex bearing two distinct normal spurs on all legs (Fig. 44); tarsal formula (Fig. 42) 5-5-5, tarsomeres simple and elongate without membranous lobes or setose pads beneath, claws (Fig. 40) stout bearing a strong teeth at base; empodium highly reduced.

Abdomen (Fig. 37) convex; with five visible ventrites; the first 3 of which connate but separate by distinct sutures; 1st ventrite deeply excavate for reception of metacoxae, without intercoxal process, but with a distinct, flattened, elongate-oval carina; all ventrites bearing sensory elements (backward curled setae); with paired dorsal openings on abdominal tergites; spiracles on 8th segment absent. Male 9th tergite entire; 9th and 10th tergites not fused. Female 8th sternite with spiculum ventrale, with 1-paired projection.

Aedeagus (Fig. 45-48) of trilobed type, symmetrical; phallobase slightly transverse or moderately elongate; parameres free, not setose, sub-equal in length as phallobase, or slightly shorter; penis not longitudinally divided at midline nor at apex, with dorsal and ventral lobes. Female genitalia (Fig. 49-53): coxites divided; stylus well developed. Ovipositor moderately sclerotyzed.

REMARKS. All the borrowed type specimens, except for *C. brasiliensis*, were stuck on small rectangular cards and some of them were badly preserved; for that reason it was impossible to dissect them and the external morphological characters did not show many interspecific differences.

It is possible to note three main types of male antennae: i) dentate in *C. edsoni*, *C. elongata*, *C. peruviana*, and *C. collaris*; ii) strongly dentate in *C. brasiliensis*, *C. gounellei*, *C. lampyroides*, and *C. brevis*; and iii) pectinate in *C. rufifrons*.

The anterior margin of pronotum is sligthly truncate in all species except for *C. elongata* in which it is rounded.

The pronotum with the anterior lateral margins transparent yellow and a median longitudinal dark spot which may be of the following types: i) narrow and straight in *C. edsoni* and *C. lampyroides*; ii) large and straight in *C. brasiliensis* and *C. gounellei*; iii) large with irregular limits in *C. rufifrons* and *C. peruviana*; and iv) rounded in *C. elongata*. One badly preserved specimen, labelled as *C. rufifrons* var. *testaceicollis* seems to be devoid of dark spot.

The colour pattern of the elytra may be: i) only the lateral borders of elytra marginated by a narrow and yellow stripe in *C. brasiliensis*; ii) elytra dark with narrow lateral yellow stripes in *C. gounellei*; ii) the same pattern but adding yellow apices in *C. elongata*; and iii) unicolor dark elytra in all the remainder species.

MATERIAL EXAMINED. *Cneoglossa brasiliensis* (Wittmer, 1949). BRAZIL. RIO GRANDE DO SUL: Porto Alegre, 15.x.1941, 1 adult, type, ex-coll. W. Wittmer (NHMB); 28.ix.1949, in *Miconia hyematis*, 1 adult, ex-coll. W. Wittmer (NHMB). *C. edsoni* sp. n., the material examined is enrolled in the description of species. *C. elongata* Pic, 1916. BRAZIL. MINAS GERAIS: Chapada Diamantina, 1 ♀ labelled as type, ex-coll. M. Pic (MNHN); Serra do Caraça, 27.xi-05.xii.1972, Exp. MZSP coll., 1 ♀ (dissected) (MZSP). SÃO PAULO: Caraguatatuba (Reserva Florestal, 40 m), 22.v-01.vi.1962, Exp. MZSP coll., 1 adult (MZSP); Iporanga (Fazenda Intervales, Gruta do Moquem), 28.ii.1990, E. Trajano coll., 1 adult (MZSP). *C. gounellei* Pic, 1916. BRAZIL. MINAS GERAIS: Campos de Diamantina, 1 ♂ labelled as type, ex-coll. M. Pic (MNHN); Mar de Espanha, 27-28.ii.1962, J. Bechyné coll., 3 adults (1 ♂, dissected) (MZSP); Serra do Caraça, 27.xi-05.xii.1972, Exp. MZSP coll., 1 ♀ (dissected) (MZSP). *C. peruviana* Pic, 1916. PERU. 1 ♂ labelled as type, ex-coll. M. Pic (MNHN). *C. rufifrons* Pic, 1916. BRAZIL. CEARÁ: Serra de Baturité, i.1895, Gounelle coll., 1 ♂ labelled as type, ex-coll. M. Pic (MNHN). *C. rufifrons* var. *testaceicollis* Pic, 1916. BRAZIL. PERNAMBUCO: Pery Pery, i.1895, Gounelle coll., 1 adult labelled as type, ex-coll. M. Pic (MNHN). *Cneoglossa* spp. (probably new species). BRAZIL. PARÁ: Santa Isabel do Pará, 30.xii.1962, J. Bechyné coll., 1 adult (MZSP). MARANHÃO: Igarapé Gurupi-Uma, Aldeia Araçu (50 km. E Canindé), v.1963, B. Malkin coll., 1 adult (MZSP). GOIÁS: Dianópolis, 11-14.i.1962, J. Bechyné coll., 2 adults (MZSP). RIO DE JANEIRO: Rio de Janeiro (Corcovado), x.1961, M. Alvarenga coll., 1 adult, ex-coll. M. Alvarenga (MZSP). SÃO PAULO: Itu (Fazenda Pau d'Alho), 01-05.xi.1961, U. R. Martins coll., 3 adults (MZSP).

SPECIES INCLUDED:

1. *Cneoglossa brasiliensis* (Wittmer, 1948: 216), **comb. n.** (*Buckodrillus*, type locality:

Brazil, Rio Grande do Sul, Porto Alegre); Costa Lima, 1953: 160.
2. *C. brevis* Champion, 1897: 595 (type locality: Panama).
3. *C. collaris* Guérin-Méneville, 1849: 1 (type locality: Colombia).
4. *C. edsoni* sp. n. (type locality: Brazil, São Paulo, São Paulo, Parque Estadual da Cantareira).
5. *C. elongata* Pic, 1916: 8 (type locality: Brazil, Minas Gerais, Chapada Diamantina).
6. *C. gounellei* Pic, 1916: 8 (type locality: Brazil, Minas Gerais, Campos de Diamantina).
7. *C. lampyroides* Champion, 1897: 595 (type locality not stated, syntypes from Mexico and Nicaragua).
8. *C. peruviana* Pic, 1916: 7 (type locality: Peru).
9. *C. rufifrons* Pic, 1916: 8 (type locality: Brazil, Ceará, Serra de Baturité).
   C. rufifrons var. *testaceicollis* Pic, 1916: 8 (type locality: Brazil, Pernambuco, Pery Pery).

Cneoglossa edsoni sp. n.

(Fig. 1-44, 47-53)

TYPE MATERIAL. HOLOTYPE, adult. "BRASIL. SÃO PAULO: São Paulo (Parque Estadual da Cantareira), 16.xii.1992, Exp. MZSP col." (MZSP). PARATYPES. Same data as holotype, 3 mature larvae, 2 pupae (associated with last larval instar exuviae) (MZSP); 06.i.1993, 1 pupa (associated with last larval instar exuvia) (MZSP); 20.x.1994, 1 ♀ (reared from larva, associated with last larval instar exuvia) (MZSP). Ilha dos Búzios, 16.x-04.xi.1963, Exp. MZSP col., 1 ♂ (adult) (MZSP).

Other material examined (not paratypes, some specimens dismembered in ethanol and/or slide mounted). Same data as holotype, 2 mature larvae, 1 ♀ (associated with pupal and last larval instar exuviae) (MZSP); 06.i.1993, 1 larva (MZSP). BRAZIL. SÃO PAULO: Campos do Jordão (Parque do Estado), 06.x.1993, 1 pharate adult (broken at middle) (MZSP).

ETYMOLOGY. We take the pleasure to name this species after our colleague Édson Possidônio Teixeira from the Instituto Florestal, São Paulo.

DESCRIPTION. ADULT (Fig. 28-35, 47-53). Length: 4.5 mm; width: 1.9 mm. Dark-brown, almost black; yellow lateral strips with transparent margins on pronotum, legs yellow with distal region of femur and posterior half of tibia darker.

Antennae (Fig. 29) serrate in both sexes (segments 3rd to 10th), bearing sensory elements, represented by backwards curled setae, present on segments 3rd to 11th. Labrum: anterior margins slightly concave. Mandibles (Fig. 30): prostheca represented by a membranous, hyaline and setose narrow lobe; outer margin and apex setose. Maxillae (Fig. 32-33a): palp with apical segment tapering toward apex in distal 1/4, basal 3/4 obliquely beveled with an irregular row of short and curved setae, apex with a peg (Fig. 33a); galea bilobed, outer lobe much smaller than inner lobe, both clothed with compound setae formed by one spatulate and one rod-like seta (Fig. 32); lacinia with outer margin setose, apex obtuse and with dense brush of curved hairs. Labium (Fig. 31, 34) with mentum densely setose, lateral margin sinuous, anterior and posterior margins curved; labial palp: apical segment (Fig. 31) slightly expanded, bilobed, inner lobe much more reduced than outer lobe, both bearing sensorial papillae at tip; ligula with anterior margin slightly concave, drawn into two slender and cylindrical processes about as long as ligula length, anterior margin and processes bearing compound setae similar to those present on galea and lacinia. Hypopharyngeal (Fig. 35) and epipharyngeal surfaces clothed with distally inclined setae.

Prothorax. Notum (Fig. 28) with posterior margin sinuous, posterior angles somewhat produced and acute. Legs (Fig. 40-42, 44): procoxae conical and projecting, narrowly separate by very short sternal process, acute at apex; sensory elements represented by backwards curled setae (Fig. 41), present on femora and tibiae (Fig. 42). Scutellum (Fig. 28) about as long as wide. Elytra (Fig. 28) elongate-oval, densely pubescent, apices conjointly rounded, combined width at base slightly larger than basal width of prothorax; punctures of striae fine, rounded, contiguous or separate by a distance of 1-3 diameters of one puncture; epipleura wider at base and tapering posteriorly. Membranous wing (Fig. 43) broad, about 2.2x as long as wide. Mesosternum (Fig. 39) very short; sternal process narrow and rounded at apex. Metasternum (Fig. 39) slightly wider than long, strongly convex; longitudinal suture as long as sternal length.

Aedeagus (Fig. 47, 48): parameres with

pointed apex, penis about 2/3 as long as parameres. Female terminalia (Fig. 50): 8th sternite with spiculum ventrale well developed. Genitalia (Fig. 49, 51-53): ovipositor (Fig. 52, 53) moderately elongate, stylus with apical setose tuft; baculi less elongate; bursa copulatrix (Fig. 49, 51) well developed, with two spiniform sclerites (Fig. 51) and a band of microtrichia.

MATURE LARVA (Fig. 1-24). Length: 14.9 mm; width: 1.7 mm. Elongate; subcylindrical; setose mainly on dorsal side, setae long and translucid; white-cream or slightly yellow, head and thorax brown (Fig. 1, 2).

Head (Fig. 7-9). Anterior region densely setose dorsally and ventrally; posterior region glabrous and lighter than the anterior one (Fig. 7, 8); prognathous with ventral mouthparts retracted. Epicranial suture (Fig. 7): coronal suture short; frontal suture V-shaped, attaining the antennal bases. Stemmata (Fig. 7, 8): a pair of large stemmata next to antenna; area adjacent to stemmata light. Antennae (Fig. 3, 4) 3-segmented; moderately long about 0.4x length of head capsule at midline; cylindrical; scape about 1.8x as long as pedicel; pedicel narrower than scape, with some sensilla and apical setae; sensory appendix elongate, as long as flagellum (Fig. 3); flagellum with some rounded subapical sensilla and one elongate apical sensillum. Clypeus (Fig. 7) narrow; transverse. Labrum (Fig. 13) transverse, roughly hexagonal; anterior margin irregulary undulate; anterior and posterior regions less pigmented; mesoanterior region with a transverse setose band. Epipharynx (Fig. 15): anterior margin with five pairs of stout setae (3 pairs long, two pairs short), and a transverse setose band; three pairs of sensilla on submarginal region; lateral margins bearing fine setae; lateral regions with two groups of submarginal setae; central region with two longitudinal and dense bands of setae; tormae longitudinal. Mandibles (Fig. 17, 18) symmetrical; well developed; apices tridentate; mesal region with two ribs; prostheca formed by two parallel fringes of hairs, some setae very long; mola absent; external side with a basal group of setae. Maxillae (Fig. 14, 16) completely separated from labium by large maxillary articulating area; cardines separated, well developed, with some marginal setae; stipes elongate, with a lateral group of long setae next to palp base; galea and lacinia distinct; lacinia with stout apicoventral setae, thin setae on latero-dorsal side; galea with tuft of stout setae on ventral side; palp 4-segmented; 1st segment shorter and larger, bearing long setae around distal margin; 2nd segment almost as long as 3rd and 4th segments together, with some sensilla; 4th segment short and narrow. Maxillary articulating area, membranous, concealed by expanded mentum. Labium (Fig. 10, 12): ligula (Fig. 10) bilobate. setose, some setae stout and pedunculate; prementum with two triangular, sclerotized, and setose areas; mentum undivided, broad, anterior region largely membranous, lateral margins rounded and setose, posterior region with two groups of long setae; postmentum elliptical, with a pair of sensilla next to anterior margin: palp (Fig. 10) 3-segmented, segments with similar length; 1st segment bearing many long setae. Hypopharynx (Fig. 11) setose on palp base and on middle anterior region; anterior margin with median group of sensilla; two groups of spines next to lateral margins; two large apodemes contiguous to lateral margins. Gula (Fig. 9) membranous; elongate; longitudinal; anterior region slightly enlarged and with three rounded less sclerotized areas. Ventral epicranial ridge present.

Thorax. Dorsal side (Fig. 1) densely setose; with transverse glabrous band on each segment; more sclerotized than abdomen. Ventral side (Fig. 2) with soft integument; almost entirely glabrous. Prothorax slightly longer than large; dorsal side (Fig. 1) with large anterior setose band and a narrower posterior one; sternum (Fig. 2) divided, with two anterior setose tufts. Meso- and metathorax transverse; dorsal side with an anterior setose line and a posterior setose band. Spiracle (Fig. 5) on lateroanterior region of mesothorax; biforous; scar narrow. Legs (Fig. 21-24) short; robust; diminishing in size from anterior to posterior; coxa conical, with few setae; trochanter elongate, triangular, larger than femur, with many scale-like setae and long setae; femur triangular, scale-like setae on basal region; tibia narrower than femur, with scale-like seta next to tarsungulus; tarsungulus robust, unisetose.

Abdomen. Dorsal side (Fig. 1) less setose than thorax. Ventral side (Fig. 2, 19) glabrous, except by 9th and 10th segments; integument less sclerotized. 1st-9th segments with an anterior setose line. 8th segment with spiracles on pleura. 9th segment (Fig. 2, 19) with rounded posterior margin; dorsal side setose on anterior and lateral regions; ventral side (Fig. 19) setose at apex; urogomphi absent. 10th segment (Fig. 19, 20) ventrally oriented; not visible from above; with paired pygopods (Fig. 20) bearing 10-12 hooks; osmoregulatory organs present as one conical membranous papilla plus two small papillae associated with each pygopod. Spiracles (Fig. 6) bifourous; on pleura of 1st-8th segments. Sternum enlarged.

PUPA (Fig. 25-27). Length: 12.6 mm; width: 1.8 mm. White-cream, adecticous, exarate, without gin-traps.

Head. Not visible from above; setose on anterior region. Antenna with a terminal pointed projection.

Thorax. Dorsal side finely hairy; metapterothecae glabrous. Pronotum roughly trapezoidal; anterior region with a pair of soft, large projections; posterior angles shortly projected.

Abdomen. 1st-6th segments tranverse; narrowed basally. 1st segment setose on dorsal side. 2nd-6th segments with a pair of lateral tubercles; a spinose tranverse line on posterior region. 8th segment narrower and shorter than the anterior ones. 9th segment short, with lateral margins convergent posteriad; urogomphi elongate, apices sharp.

BIONOMICS. Larvae of *Cneoglossa edsoni* sp. n., were collected in a small shallow stream, with moderate to fast running water and muddy or sandy bottoms depending on the declivity of hill sides. The water was clear, slightly acid (pH 6.0-6.2). The cneoglossid larvae were found inside submerged rooting brushwood, together with some larvae of Lutrochidae (*Lutrochus germari*) and Elmidae (*Elsianus* sp.).

In 16.xii.1992 seven last instar larvae were collected, brought to laboratory and mantained in plastic vials with water and pieces of brushwood. Pupae and adults were obtained in January, 1993. Although the authors had tried to find more specimens in subsequent trips to the same site, only one additional larva was collected in 20.x.1994.

REMARKS. *Cneoglossa edsoni* sp. n., is easily distinguished from the other species of the genus by the following: general form broader (about 2.3x as long as wide), not so elongate; elytral margins not parallel-sided but sligthly curved; elytra finely punctured, with striae not well impressed; and apex of the scutelum sligthly rounded.

REDESCRIPTIONS OF LARVAE AND ADULTS OF THE PTILODACTYLID GENERA STUDIED

During the last ten years, all papers dealing with the Ptilodactylidae pointed out the need of more studies of the members of this family to clarify its classification. For that reason we considered opportune to redescribe all the genera studied in the present analysis.

Araeopidius Cockerell, 1906

(Fig. 54-78)

Araeopus LeConte, 1874: 56 *non* Spinola (1839); Horn, 1880: 88. LeConte, & Horn, 1883:170.

Araeopidius Cockerell, 1906: 241 (type species: *Araeopus monachus* LeConte, 1874); Arnett, 1968: 443, 444; Hlavac, 1975: 182; Lawrence & Newton 1982: 278; 1995: 847; White *et al.*, 1984: 363, 405; Stribling, 1986: 232; Lawrence, 1988: 14, 18, 19, 23, 42; 1991: 157, 168, 170, 391, 393, 394; Lawrence & Stribling, 1992: 25, 26; Beutel, 1995: 145-148, 157-159, 163, 164, 166, 167; Lawrence *et al.*, 1995: 393.

ADULT (Fig. 67-78). Without hydrofuge tomentum. Head. Transverse occipital ridge present. Mandibles (Fig. 71) well developed; not foliaceus; apex unidentate; prostheca and mola present. Maxillae (Fig. 72): galea and lacinia distinct; with spatulate setae; galea bilobate; palp 4-segmented, apical segment slightly expanded and truncate at apex. Labium (Fig. 73): ligula 2-lobate with two lobules each one; mentum subtrapezoidal; palp 3-segmented.

Thorax. Prothorax: notum with lateral carinae absent, posterior edge without crenulations, notal projection elongate; anterior edge of sternum (mentonière) not produced forward; trochantin exposed. Conection between prosternal process and mesosternal cavity present. Membranous wing (Fig. 68): folding of dryopoid-type; proximal end of radial cell straight or obtuse internally; anal cell present; five veins posterior to cubitus, but not including 4th anal. Metathorax: sternal transverse suture absent; anterior process of endosternite short; coxal plates poorly developed. Legs not fossorial; mesocoxae narrowly separated; tibial spurs present, normal on all legs; tarsi 5-5-5, without membranous appendages on two or more segments; 4th tarsal segment not expanded and lobed beneath, not reduced; empodium highly reduced; claws not cleft or toothed.

Abdomen. Paired dorsal openings on tergites absent. Intercoxal process of 1st ventrite well developed. Spiracles on 8th segment reduced, non-functional or absent.

Male terminalia (Fig. 69, 70): 9th tergite (Fig. 69) entire; 9th and 10th tergites (Fig. 69) non-fused; 9th sternite (Fig. 70), elongate. Aedeagus (Fig. 67): basal piece symmetrical; penis with apex longitudinally divided, with distinct dorsal and ventral lobes. Female terminalia (Fig. 74-78): 8th tergite (Fig. 75) hexagonal, base larger than apex, covered with very short setae, some apical setae longer; 8th sternite (Fig. 76) with short and wide spiculum ventrale, with one pair of small lateral projections. Genitalia: stylus (Fig. 77) highly reduced; coxite divided (Fig. 74); ovipositor (Fig. 74) moderately sclerotized; bursa copulatrix (Fig. 74, 78) with two spinose regions and a pair of apical sclerites (Fig. 78).

LARVA (Fig. 54-66). Body (Fig. 54-56) subcylindrical; integument rugose, covered by short setae; two pairs of transverse depressions and a basal submarginal fringe on each segment.

Head. Ventral epicranial ridge absent. Stemmata present. Antennae very short. Labrum (Fig. 59) transverse; roughly rectangular. Epipharynx (Fig. 61): lateral margins bearing large setae; two pairs of stout and short setae on median region; sensories on median and basal regions. Mandibles (Fig. 60, 62): apex tridentate; with a ventro-mesal fringe. Maxilla (Fig. 63, 65) cardines well separated; with separated galea and lacinia; palp 4-segmented. Maxillary articulating area absent (Fig. 65). Maxillolabial sutures complete (Fig. 65). Labium (Fig. 65): postmentum slightly expanded laterally; mentum not divided; labial palp 2-segmented. Hypopharynx (Fig. 63).

Thorax. Mesonotum on laterals with a pair of rounded plastrons (Fig. 64) around the spiracles. Legs (Fig. 57, 58) short and robust; tarsungulus with one seta.

Abdomen. A pair of trilobate plastrons (Fig. 66) around spiracles of 1st-7th segments. Spiracles of 8th segment (Fig. 55, 56) placed on tergal protuberances. 9th segment not opercular; not reduced; dorsally orientated, without urogomphi. 10th segment (Fig. 56) visible; forming operculum; not reduced. Ventral and anal gills absent. Paired eversible glands absent. Pleurites absent. Sternites (Fig. 56) extremelly narrowed, on 1st-7th segments.

MATERIAL EXAMINED. *Araeopidius monachus* (LeConte, 1874). CANADA. BRITISH COLUMBIA: Fauquier, 19.vi.1944, W. Coleorave coll., 1 ♀ (adult, dissected), ex-coll. G. P. Mackenzie (UCRC). U. S. A. WASHINGTON: Yakima Co., Mount Adams, (Klickitat River, 3000 ft), 21.vi.1935, J. Wilcox coll., 1 adult (UCRC); Signal Peak?, 21.vi.1935, S. E. Crumb coll., 1 adult, ex-coll. G. P. Mackenzie (UCRC); OREGON: Hood River Co., Bill Williams Creek, G. Ulrich, 1 larva (dissected) (ANIC).

Cladotoma Westwood, 1837
(Fig. 79-89)

Cladotoma Westwood, 1837: 254 (type species: *Cladotoma ovalis* Westwood, 1837); Guérin-Méneville, 1843a: 1; 1843b: 194; Blanchard, 1845: 56; Lacordaire, 1857: 276; Champion, 1897: 626; Pic, 1914: 45; Blackwelder, 1944: 268; Stribling, 1986: 232; Lawrence, 1988: 14, 17; Lawrence & Stribling, 1992: 21, 26; Lawrence & Newton, 1995: 847.

ADULT (Fig. 79-89). Hydrofuge tomentum absent. Head. Transverse occipital ridge present. Mandibles (Fig. 84) well developed; not foliaceous; bidentate, apex unidentate and one subapical tooth; mola absent. Maxillae (Fig. 79, 79a): galea and lacinia present; galea bilobate, with a lateral filiform process, bearing lanceolate setae (Fig. 79a); lacinia filiform apicad; palp 4-segmented, 4th palpomere subtriangular. Labium (Fig. 81): ligula with two pairs of filiform appendix; palp 3-segmented.

Thorax. Prothorax: notum with lateral carinae complete, posterior edge crenulate, notal projection very short and angulate; anterior edge of sternum (mentonière) not produced forward; trochantin exposed. Conection between prosternal process and mesosternal cavity present. Membranous wing (Fig. 85): folding of dryopoid-type; proximal end of radial cell with acute inner angle; anal cell present; five veins posterior to cubitus, but not including 4th anal.

Metathorax: sternal transverse suture absent; anterior process of endosternite short or absent; coxal plates well developed. Legs not fossorial; mesocoxae narrowly to moderately separated; tibial spurs normal on all legs; tarsi pentamerous, with membranous appendages on two or more segments; 4th tarsal segment expanded and lobed beneath, highly reduced; empodium well developed; claws not cleft or toothed.

Abdomen. Paired dorsal openings on abdominal tergites absent. Intercoxal process of 1st ventrite well developed. Spiracles on 8th segment reduced, non-functional or absent. Male terminalia (Fig. 82, 83): 9th tergite (Fig. 83) entire; 9th and 10th tergites (Fig. 83) non-fused; 9th sternite (Fig. 82) elongate. Aedeagus (Fig. 80): basal piece symmetrical; penis with apex not longitudinally divided, with distinct dorsal and ventral lobes. Female terminalia (Fig. 87, 88): 8th tergite (Fig. 87) setose, with pointed apex; 8th sternite (Fig. 88) with short and wide spiculum ventrale, with 1 pair of lateral projections. Genitalia (Fig. 86, 89): stylus absent; coxite undivided; ovipositor heavily sclerotized, cuneiform.

MATERIAL EXAMINED. *Cladotoma ovalis* Westwood, 1837. BRAZIL. MATO GROSSO: Xingu, xi.1961, Alvarenga & Werner colls., 2 ♂ (adults) (MZSP). ESPÍRITO SANTO: Linhares (Parque Sooretama), i.1970, M. Morais, 1 ♂ (adult, dissected) (MZSP). SÃO PAULO: Cubatão, 20.xi.1935, 1 ♀ (adult, dissected) (MZSP); Itu (Fazenda Pau d'Alho), 01-08.i.1970, U. Martins coll., 1 ♂ (adult) (MZSP); Piraju, xii.1965, M. Carrera coll., 1 ♀ (adult) (MZSP). *C. thoracica* Guérin-Méneville, 1837. BRAZIL. PARÁ: Cachimbo, x.1955, F. S. Pereira coll., 1 ♂ (adult) (MZSP); Canindé (Rio Gurupi), 27.ii.1966, Malkin coll., 1 ♂ (adult) (MZSP). MATO GROSSO: Rosário do Oeste, 1 ♂ (adult), ex-coll. Dirings (MZSP). GOIÁS: Jataí (Fazenda Aceiro), x.1962, Exp. DZSP coll., 1 ♀ (adult, dissected) (MZSP).

Paralichas White, 1859
(Fig. 90-115)

Paralichas White, 1859: 287 (type species: *Paralichas guerini* White, 1859); Pic, 1914: 9; Nakane, 1948: 5, 1956: 52; Hayashi, 1986: plate 28; Lawrence, 1988: 14, 17, 19; Lawrence & Stribling, 1992: 21, 25, 26; Lawrence & Newton, 1995: 847.

Eucteis Guérin-Méneville, 1861: 539 (type species: *Eucteis bimaculata* Guérin-Méneville, 1861); Fairmaire, 1886: 335; Lewis, 1895: 99.

ADULT (Fig. 110-115). Hydrofuge tomentum absent. Head. Transverse occipital ridge present. Mandibles (Fig. 113) well developed; not foliaceus; bidentate with one apical and one subapical teeth; mola absent. Maxillae (Fig. 110): galea and lacinia separated; galea lobated; palp 4-segmented, 4th palpomere subtriangular. Labium (Fig. 112): ligula 2-lobate, each lobe bearing lobules; palp 3-segmented.

Thorax. Prothorax: notum with lateral carinae complete, posterior edge crenulate, notal projection very short and angulate; anterior edge of sternum (mentonière) not produced forward; trochantin exposed. Conection between prosternal process and mesosternal cavity present. Membranous wing (Fig. 111): folding dryopoid-type; proximal end of radial cell with acute inner angle; anal cell present; five veins posterior to cubitus, but not including 4th anal. Metathorax: sternal transverse suture vestigial; anterior process of endosternite short or absent; coxal plates well developed. Legs not fossorial; mesocoxae narrowly to moderately separated; tibial spurs normal on all legs; tarsi pentamerous, with membranous appendages on two or more segments; 4th tarsal segment expanded and lobed beneath, highly reduced; empodium well developed; claws not cleft or toothed.

Abdomen. Paired dorsal openings on abdominal tergites absent. Intercoxal process of 1st ventrite well developed. Spiracles on 8th segment reduced, non-functional or absent.

Male terminalia: 9th tergite entire; 9th and 10th tergites non-fused; 9th sternite elongate (Fig. 115). Aedeagus (Fig. 114): basal piece symmetrical; parameres short; penis with apex not longitudinally divided, with distinct dorsal and ventral lobes. Female terminalia: 8th sternite with spiculum ventrale, with 1-2 paired projections. Genitalia: stylus absent; coxite undivided; ovipositor heavily sclerotized, cuneiform.

LARVA (Fig. 90-109). Body (Fig. 90, 94, 95) shape subcylindrical; integument strongly sclerotized and punctate; segments with basal submarginal fringe.

Head (Fig. 96, 98) partially inserted into prothorax. Ventral epicranial ridge present. Stemmata present. Antennae (Fig. 99) very short.

Labrum (Fig. 103) transverse; anterior region setose. Epipharynx (Fig. 105) with marginal stout setae; lateral areas densely setose. Mandibles (Fig. 97, 100) stout; apex tridentate; one subapical dorsal tooth; prostheca formed by a large tuft of hairs and an inarticulated asetose process. Maxillae (Fig. 101, 102): cardines well separated; with separated galea and lacinia; palp 4-segmented. Maxillary articulating area present. Maxillolabial sutures complete (Fig. 101). Labium (Fig. 101): postmentum slightly expanded laterally; mentum not divided; palp 2-segmented.

Thorax. Prothorax with notum longer than ventral side; longer than meso- and metathorax (Fig. 90, 95). Spiracles (Fig. 106) lateral on mesonotum. Legs (Fig. 107, 108) robust; tarsungulus with one seta.

Abdomen. 8th segment elongate, tappering posteriad; spiracles (Fig. 91-93) placed on apex of a tube. 9th segment (Fig. 109) not opercular; reduced to a narrow band; ventrally placed; without urogomphi. 10th (Fig. 109) segment visible; not reduced; forming operculum, without opercular hooks. Ventral and anal gills absent. Paired eversible glands absent. Pleurites (Fig. 94) present on 1st-7th segments. Sternites (Fig. 94) narrow on 1st-7th segments. Osmoregulatory organs absent.

MATERIAL EXAMINED. *Paralichas pectinata* (Kiesenwetter, 1874). JAPAN. HYOGO: Tsunagun (Igawa), 09.ii.1972, N. Furukawa coll., 2 larvae (1 dissected), 1 ♂ (adult, dissected) (NHCK).

Ptilodactyla Illiger, 1807
(Fig. 116-121)

Ptilodactyla Illiger, 1807: 342 (type species: *Ptilodactyla elaterina* Illiger, 1807); Latreille, 1829: 462; Laporte, 1836: 21; 1840: 258; Blanchard, 1845: 57; Lacordaire, 1857: 279; LeConte, 1861: 179; Chenu, 1870: 16; Kirsch, 1874: 371; Horn, 1880: 90; LeConte & Horn, 1883: 171; Champion, 1897: 627; Blatchley, 1910: 690; Pic, 1914: 47-50; Blackwelder, 1944: 268-270; Legros, 1947: 96, Nakane, 1956: 51; Arnett, 1968: 460, 461; Delève, 1972: 264; Hayashi, 1986: plate 29; Lawrence, 1982: 506; 1988: 14, 42; 1991: 157, 172, 176, 391-394; Stribling, 1986: 232; Costa *et al.*, 1988: 132, 133, plate 47; Lawrence & Stribling, 1992: 19, 25, 26; Beutel, 1995: 147, 148, 150, 151, 162-164; Lawrence & Newton, 1995: 847; Downie & Arnett, 1996: 719, 720.

Hypselothorax Kirsch, 1866: 188.

Ptylodactyla Laporte, 1836: 21.

ADULT (Fig. 116-121). Hydrofuge tomentum absent. Head. Transverse occipital ridge present. Mandibles well developed; not foliaceus; apex with more than one tooth or lobe; mola present. Maxillae: apical segment of maxillary palp cylindrical or subulate.

Thorax. Prothorax: notum with lateral carinae incomplete or absent; posterior edge crenulate; notal projection elongate; anterior edge of sternum (mentonière) not produced forward; trochantin completely concealed. Conection between prosternal process and mesosternal cavity present. Membranous wing: wing folding dryopoid-type; proximal end of radial cell with acute inner angle; anal cell absent; three or less veins posterior to cubitus, but not including 4th anal. Metathorax: sternal transverse suture absent or vestigial; anterior process of endosternite short or absent; coxal plates well developed. Legs not fossorial; mesocoxae narrowly to moderately separated; tibial spurs present, enlarged on at least one pair of legs; tarsi pentamerous, with membranous appendages on two or more segments; 4th tarsal segment expanded and lobed beneath, not or slightly reduced; empodium highly reduced; tarsal claws cleft or toothed.

Abdomen. Paired dorsal openings on abdominal tergites absent. Intercoxal process of 1st ventrite well developed. Spiracles on 8th segment reduced, non-functional or absent.

Male terminalia (Fig. 117, 118): 9th tergite entire (Fig. 117); 9th and 10th tergites non-fused (Fig. 117); 9th sternite elongate (Fig. 118). Aedeagus (Fig. 116): basal piece symmetrical; penis with apex not longitudinally divided, with a single lobe. Female terminalia (Fig. 119): 8th sternite with spiculum ventrale, with 1-2 paired projections. Genitalia: style absent (Fig. 121); ovipositor (Fig. 120) moderately sclerotized; coxite undivided (Fig. 121).

LARVAE AND PUPAE. Larvae and pupae are described in Costa *et al.* (1988: 132, 133, pl. 47).

MATERIAL EXAMINED. *Ptilodactyla humeralifer* Pic, 1928. BRAZIL. SÃO PAULO: Salesópolis (Estação Biológica de Boracéia), 03-08.iii.1962, Lenko & Reichardt colls., 1 ♂ (adult) (MZSP); 19.ii.1963, L. Silva & H. Reichardt colls., 1 ♂ (adult) (MZSP); 25.ii.1963, F. Werner & H. Reichardt colls., 1 ♂ (adult) (MZSP); 21.i.1966, Reichardt coll., 1 ♂ (adult) (MZSP); 03-08.i.1974, Vanin & Leme colls., 1 ♂ (adult) (MZSP); 20.xii.1982, C. Costa coll., 1 ♀ (adult, reared from larva) (MZSP), 30.xii.1982, C. Costa coll., 1 ♂ (adult) (MZSP); Santo André (Estação Biológica de Paranapiacaba) 19.ii.1961, Reichardt & Werner colls., 1 ♂ (adult) (MZSP); 24.ix.1961, Reichardt & Werner colls., 1 ♂ (adult) (MZSP). *Ptilodactyla* spp. BRAZIL. MINAS GERAIS: Vila Monte Verde, 27.xi.1969, J. Halik coll., 1 ♂ (adult), ex-coll. J. Halik (MZSP); 26.xii.1970, J. Halik coll., 1 ♂ (adult), ex-coll. J. Halik (MZSP). SÃO PAULO: Atibaia, 26.x.1970, E. Halik, 1 ♀ (adult), ex-coll. J. Halik (MZSP); Botucatu, 16-18.i.1980, Exp. MZUSP coll., 1 ♀ (adult) (MZSP); (Parque das Cascatas), 16.x.1980, 1 ♂ (adult) (MZSP); Caraguatatuba, 23.xi.1976, C. T. Seixas F°. coll., 1 ♀ (adult) (MZSP); Salesópolis (Estação Biológica de Boracéia), 20-22.iv.1982, Exp. MZUSP coll., 6 mature larvae, 2 pupae (reared from larva), 2 ♀ (adults, reared from larvae) (MZSP); 20.xii.1982, C. Costa coll., 1 ♂ (adult, reared from pupa) (MZSP); 11-13.iv.1983, Exp. MZUSP coll., 1 young larva, 18 mature larvae 3 ♂, 5 ♀ (adults, 1 ♂ and 1 ♀ dissected) (MZSP); 30.vi-01.vii.1983, Exp. MZUSP coll., 1 ♂, 1 ♀ (adults) (MZSP); 22-25.viii.1983, Exp. DZUSP coll., 1 ♀ (adult) (MZSP); 16.ix.1983, Exp. MZUSP coll., 1 ♂ (adult) (MZSP); 21.x.1983, C. Costa coll., 3 ♀ (adults) (MZSP); 13.xii.1984, Exp. MZUSP coll., 1 ♂ (adult, dissected) (MZSP); São Paulo (Água Funda), 13.viii.1965, C. Costa coll., 1 ♀ (adult) (MZSP); (Parque Estadual da Cantareira, Carpa), 06.i.1993, Exp. MZUSP coll., 4 young larvae, 14 mature larvae (MZSP). RIO DE JANEIRO: Nova Friburgo, 05-09.i.1981, Exp. MZSP coll., 2 ♂ (adults) (MZSP). SANTA CATARINA: Timbó, xi.1962, 1 ♂, 1 ♀ (adults), ex-coll. Dirings (MZSP).

Anchytarsus Guérin-Méneville, 1843
(Fig. 122-142)

Anchytarsus Guérin-Méneville, 1843b: 194 (type species: *Atopa bicolor* Melsheimer, 1845: 221); Blanchard, 1845: 56; Guérin-Méneville, 1849: 1; Lacordaire, 1857: 264; LeConte, 1853: 229; 1861: 179; 1866: 50; Horn, 1880: 86; 1881: 87; LeConte & Horn, 1883: 170; Champion, 1897: 593; Blatchley, 1910: 689; Pic, 1914: 8; Bertrand, 1935: 138; 1939: 307; 1956: 275; 1966: 143; 1972: 391; Blackwelder, 1944: 266; Arnett, 1968: 443; Spangler, 1966: 397; 1981: 208; 1982: 386; 1983: 161; Brown, 1972: 24; 1975: 149; Hlavac, 1975: 182; Doyen & Ulrich, 1978: 229; White, 1980: 94; Stribling, 1986: 219-233; Lawrence, 1988: 14; 1991: 170, 391, 392, 394; White *et al.*, 1984: 405, 408, 435; Lawrence & Stribling, 1992: 25; Beutel, 1995: 147; Lawrence & Newton, 1995: 846; Downie & Arnett, 1996: 719.

Tetraglossa Champion, 1897: 593 (type species: *Tetraglossa palpalis* Champion, 1897); Pic, 1914: 8; Blackwelder, 1944: 266; Bertrand, 1956: 278; 1972: 393; Brown, 1975: 150; Spangler, 1983: 161-175; Stribling, 1986: 220; Beutel, 1995: 161.

ADULT (Fig. 136-142). Hydrofuge tomentum absent. Head. Transverse occipital ridge present. Mandibles well developed; not foliaceus; apex with more than one tooth or lobe; mola present. Maxillae: 4th segment of palp cylindrical or subulate.

Thorax. Prothorax: notum with lateral carinae incomplete or absent, posterior edge crenulate, notal projection elongate; anterior edge of sternum (mentonière) not produced forward; trochantin exposed. Conection between prosternal process and mesosternal cavity present. Membranous wing (Fig. 136): folding dryopoid-type; proximal end of radial cell with acute inner angle; anal cell present; five veins posterior to cubitus, but not including 4th anal. Metathorax: sternal transverse suture absent or vestigial; anterior process of metendosternite short or absent; coxal plates well developed. Legs not fossorial; mesocoxae narrowly to moderately separated; tibial spurs present, normal on all legs; tarsi pentamerous, without membranous appendages on two or more segments; 4th tarsal segment not expanded and lobed beneath, not or slightly reduced; empodium highly reduced; tarsal claws not cleft or toothed.

Abdomen. Paired dorsal openings on abdominal tergites absent. Intercoxal process of 1st ventrite well developed. Spiracles on 8th segment reduced, non-functional or absent.

Male terminalia (Fig. 139, 141): 9th tergite (Fig. 141) entire; 9th and 10th tergites (Fig. 141) non-fused; 9th sternite oval (Fig. 139). Aedeagus (Fig. 142): basal piece symmetrical; penis with apex not longitudinally divided, with distinct dorsal and ventral lobes. Female terminalia (Fig. 137, 138): 8th tergite (Fig. 137); 8th sternite (Fig 138) with spiculum ventrale, with 1-2 paired projections. Genitalia (Fig. 140): style highly reduced; coxite divided; ovipositor moderately sclerotized.

LARVA. (Fig. 122-135). Body (Fig. 122, 123) subcylindrical; integument densely punctate on head and pronotum, less punctate on remaing segments.

Head (Fig. 126). Ventral epicranial ridge present. Antennae (Fig. 126) almost as long as the cephalic capsule on lateral view. Stemmata (Fig. 126) present. Labrum (Fig. 129) transverse; setose and punctate anteriad. Epipharynx (Fig. 130) setose laterally. Mandibles (Fig. 128, 131): apex tridentate; two subapical teeth (one dorsal, one ventral); prostheca formed by two parallel fringes of hairs. Maxillae (Fig. 132, 135) with separated galea and lacinia; palp 4-segmented; cardines well separated. Maxillary articulating area present. Maxillolabial sutures complete. Labium (Fig. 134): postmentum expanded concealing maxillary articulating area; mentum divided into 3 parts by longitudinal sutures; labial palp 3-segmented. Hypopharynx (Fig. 133) U-shaped; densely setose; with a pair of large sensilla near an anterior cluster of small ones.

Legs (Fig. 124, 125): tarsungulus with one seta.

Abdomen. Spiracles of 8th segment placed on pleura. 9th segment (Fig. 127) not opercular; not reduced; dorsally oriented; without urogomphi. 10th segment (Fig. 127) visible; not forming operculum; not reduced; bearing paired pygopodium with apical hooks and osmoregulatory organs. Abdominal and anal gills absent. Paired eversible glands absent. Pleurites present on 1st-8th segments. Sternites (Fig. 123) enlarged.

PUPA. Gin-traps present.

MATERIAL EXAMINED. *Anchytarsus bicolor* (Melsheimer, 1845). Without precise collecting data, 1 ♂ (adult, dissected) (BMNH). COSTA RICA. SAN JOSÉ: San José, 11.ii.1934, Maria Aguilar coll., 3 mature larvae, ex-coll. Emden (BMNH). *A. palpalis* (Champion, 1897). GUATEMALA. ALTA VERAPAZ: Trece Aguas, Cacao, 30.iii, Schwarz & Barber colls., 1 ♀ (adult, dissected) (ANIC); PANAMA. CANAL ZONE: Barro Colorado Island, 26.ii.1975, J. F. Lawrence coll., 1 mature larva (dissected) (ANIC).

Epilichas White, 1859
(Fig. 143-179)

Epilichas White, 1859: 290 (type species: *Epilichas candezei* White, 1859); Pic, 1914: 9, 10; Nakane, 1948: 5; Crowson, 1955: 50; Hayashi, 1986: plate 28; Lawrence. 1987: 360; Lawrence & Stribling, 1992: 25; Lawrence & Newton, 1995: 847.

ADULT (Fig. 164-179). Hydrofuge tomentum absent. Head. Transverse occipital ridge present. Mandibles (Fig. 166) well developed; not foliaceus; apex unidentate; prostheca present; mola absent. Maxillae (Fig. 164, 165): galea and lacinia distinct; lacinia short; galea bilobed; palp 4-segmented, apical segment securiform. Labium (Fig. 167): ligula bilobate with two lobule each lobe; palp 3-segmented.

Thorax. Prothorax: notum with lateral carinae incomplete or absent, posterior edge crenulate, notal projection elongate; anterior edge of sternum (mentonière) not produced forward; trochantin exposed. Conection between prosternal process and mesosternal cavity present. Membranous wing (Fig. 171): folding of dryopoid-type; proximal end of radial cell with acute inner angle; anal cell absent; five veins posterior to cubitus, but not including 4th anal. Metathorax: sternal transverse suture absent or vestigial; anterior process of endosternite short or absent; coxal plates well developed. Legs (Fig. 168, 169) not fossorial; mesocoxae narrowly to moderately separated; tibial spurs present, normal on all legs; tarsi (Fig. 169) pentamerous, with membranous appendages on two or more segments; 4th tarsal segment expanded and lobed beneath, not or slightly reduced; empodium highly reduced; claws not cleft or toothed.

Abdomen. Paired dorsal openings on abdominal tergites absent. Intercoxal process of 1st ventrite well developed. Spiracles on 8th segment reduced, non-functional or absent.

Male terminalia (Fig. 172, 173): 9th tergite

(Fig. 172) entire; 9th and 10th tergites (Fig. 172) non-fused; 9th sternite elongate (Fig. 173). Aedeagus (Fig. 170): basal piece symmetrical; penis with apex not longitudinally divided, with distinct dorsal and ventral lobes. Female terminalia (Fig. 174, 177): 8th tergite (Fig. 177); 8th sternite (Fig. 174) with spiculum ventrale, with 1-2 paired projections. Genitalia (Fig. 175, 176, 178, 179): style (Fig. 178) highly reduced; coxite (Fig. 176, 179) divided; ovipositor (Fig. 175) moderately sclerotized.

LARVA (Fig. 143-163). Body (Fig. 143-145) subcylindrical; not punctate; setose dorsaly and ventraly.

Head (Fig. 158-160) with lateral setae. Ventral epicranial ridge present (Fig. 159). Stemmata present. Antennae (Fig. 148, 149) almost as long as the cephalic capsule on lateral view. Labrum (Fig. 147) transverse; setose on anterior region. Epipharynx (Fig. 146) setose on median region. Mandibles (Fig. 150, 152): wide; apex with three short teeth; prostheca formed by two parallel fringes of hairs. Maxilla (Fig. 153, 155, 157): cardines well separated; with separated galea and lacinia; galea 2-segmented, apical segment (Fig. 155) with flat teeth; palp 4-segmented. Maxillary articulating area present. Maxillolabial sutures complete. Labium (Fig. 156): postmentum expanded concealing maxillary articulating area; mentum divided into three parts by longitudinal sutures; labial palp 3-segmented. Hypopharynx (Fig. 154) with a pair of lateral setose bands and a pair of sensilla on anterior region.

Thorax. Spiracles (Fig. 151) on mesothorax. Legs (Fig. 161, 163): tarsungulus with one seta.

Abdomen. Spiracles of 8th segment placed on pleura. 9th segment (Fig. 162) not opercular; not reduced; dorsally orientated; without urogomphi. 10th segment (Fig. 162) visible; not forming operculum; not reduced; bearing paired pygopodium with apical hooks, and osmoregulatory organs. Abdominal and anal gills absent. Paired eversible glands absent. Abdominal pleurites absent. Sternites (Fig. 145) narrow.

PUPA. With gin-traps.

MATERIAL EXAMINED. *Epilichas flabellatus* (Kiesenwetter, 1874). JAPAN. TOKYO-TO: Hikawa, 05.vii.1958, N. Inahara coll., 1 ♂ (adult, dissected) (MZSP). KANAGAWA-KEN: Kawasaki (Higashitakane), 11.v.1985, N. Hayashi coll. 1 ♂ (adult), 1 ♀ (adult), 1 mature larva (dissected) (NHCK); (Ikuta-Ryokuchi), 16.vi.1988, N. Hayashi coll., 2 young larvae, 1 mature larva, 1 ♀ (adult) (NHCK).

BRIEF HISTORICAL REVIEW OF CALLIRHIPIDAE AND EULICHADIDAE

The systematic position of Callirhipidae and Eulichadidae is not well defined yet and is in need of more accurate studies. We consider usefull to present a few comments on the History of both families.

Pic (1914) included *Eulichas* Jacobs.,1913 and *Stenocolus* LeC.,1853 in the Dascillinae, Dascillidae. Pic (1925) considered some genera, now included in Callirhipidae, as a tribe of Rhipiceridae. Forbes (1926) was the first to correlate Eulichadidae (as Lichadidae) with the Callirhipidae (genera *Zenoa* and *Callirhipis*) based on the similarities on the wing venation and folding. Böving & Craighead (1930-1931), based on larvae, considered Callirhipidae in the Elateroidea together with Rhipiceridae and Sandalidae.

Crowson (1955), in his work on the classification of Coleoptera, established a new superfamily, Rhipiceroidea and redefined Dascilloidea. In the former he included Rhipiceridae and Callirhipidae, giving as characteristic of the group: "strongly flabellate antennae, with their insertions rather close together on a protuberance of the front of the head; and, presence of a nasale-like projection between the mandibles instead of a normal free labrum". In the Dascilloidea, he included four families, Clambidae, Eucinetidae, Helodidae and Dascillidae. About Callirhipidae, Crowson (*l. c.*) stated: "Many features of this family are suggestive of a relationship to Ptilodactylidae, for example the occurrence of a distinct scutellary striole in the elytra (where these are striate), the marked "hooding" of the prothorax over the head, the metendosternite which in *Callirhipis* closely resembles that of *Eulichas*, the wing-venation and folding, and the crenulate hind margin of the pronotum in a few species; it should not be forgotten that *Eulichas* has the same large and plurisetose empodium as the Rhipiceroids". Refering to *Eulichas*, Crowson (*l. c.*) said: "some features of *Eulichas*, notably the empodium, the wing-venetion and the metendosternite, are suggestive of affinities to the Rhipiceroidea".

Crowson (1960) established a new superfamily, Eucinetoidea, for Clambidae, Eucinetidae and Helodidae, leaving Dascillidae as the only representative of the Dascilloidea. Posteriorly Crowson (1971) based mainly on adult characters presented a new definition to the Dascilloidea to include Dascillidae, Rhipiceridae and Karumiidae. In 1973, this author established the new superfamily Artematopoidea, to include Artematopidae, Brachypsectridae, and Callirhipidae, this last one transferred from his Rhipiceroidea.

Kasap & Crowson (1975), stated that "the sternal musculature of *Eulichas* is similar to that of *Byrrhocryptus* and *Callirhipis*; the position of Eulichadidae, as indicated by the abdominal skeleton and musculature is somewhat ambiguous. On one hand, there are clear resemblances to Ptilodactylidae and Psephenidae, on the other, almost equally marked ones, to the Callirhipidae, with which Forbes (1926) associated *Eulichas* on the basis of wing venation and folding. In the case of Ptilodactylidae, structural similarities to Eulichadidae may be correlated with considerable similarities in habits, whereas, available data indicate very different habits in Eulichadidae and Callirhipidae. Whether a structural similarity, which can be correlated with similar habits, provides a stronger or weaker evidence for phylogenetic relationship than one which is not so correlated, is a disputable point. It is very desirable that further informations should be obtained on the soft parts of Eulichadidae, Ptilodactylidae, Callirhipidae, etc. such information might contribute much to a solution of some of the major problems considered here". About Callirhipidae, they stated that: "We find no clear positive feature in abdominal structure to associate Artematopidae with Callirhipidae, but also no cogent evidence against such a grouping".

Crowson (1978) included Eulichadidae in the Dryopoidea pointing out "the small familia Eulichadidae has a number of exceptional features. Some of them are apparently plesiomorphic, e. g., the adult wing-venation and folding of the "serricorn" type of Forbes (1926), and the male paraprocta not fused medially in front of the proctiger. Others are possibly apomorphic, e. g., the elongate sclerotized ovipositor (with articulated gonapophyses) of the adult, the plurisetose ungues and large second pair of thoracic spiracula of the larva. They together suggest that it may be a sister-group to the rest of the superfamily. The large and apparently functional second pair of thoracic spiracula are exceptional for larval Coleoptera generally". Crowson (1981) considered Callirhipidae within the Artematopoidea.

Lawrence & Newton (1982), included Callirhipidae and Eulichadidae in the Dryopoidea, saying: "Although Callirhipidae have been included in Artematopoidea, partly based on the absence of a mandibular mola and presence of eighth abdominal spiracles in the adult, the prothoracic structure is very similar to that in various Ptilodactylidae, the metendosternite and wing are like those in Eulichadidae, and the ovipositor resembles those in both families". Also they stated that: "Eulichadid adults are similar to Ptilodactylidae in having a mandibular mola and specialized ovipositor and in lacking functional eighth spiracles".

Lawrence (1988), considered that "the large number of apparent synapomorphies shared by Callirhipidae and Eulichadidae prompted Lawrence & Newton (1982) to transfer Callirhipidae to an enlarged and redefined Dryopoidea", his Psephenoidea. Lawrence & Britton (1991, 1994), and Lawrence *et al.* (1995), considered both families on their expanded Byrrhoidea; and in this last study they stated that Eulichadidae and Callirhipidae usually cluster with ptilodactylids and Chelonariidae at the base of the Elateroidea (including Cantharoidea + Artematopoidea).

CLADISTIC ANALYSIS

DESCRIPTION AND DISCUSSION OF CHARACTERS

In the following list, 1-43 refer to adult characters (male and/or female), 44-71 to larval characters, and 72 to a pupal character. The sequence roughly follows the main body regions, from anterior to posterior. Most of the characters analyzed are those traditionally employed in the Elateriformia classification. When the character was previously used by Crowson (1971, 1978), Lawrence (1988, 1991), Lawrence & Stribling (1992) or Lawrence *et al.* (1995), the name of these authors appears parenthesized after the short character description. In most cases, we agreed with the character polarization employed by those authors, but in some instances we made changes or formulated a new interpretation. In such cases, the author's name is followed by the notation "modified". Characters not employed before appear without specific references. The abbreviation "na" means that the multistate character was considered nonadditive (unordered). The ci (consistency index) for each character is presented, as well as the ri (retention index) when estimable. Whenever necessary, a more detailed discussion about the interpretation of the character polarization is presented.

ADULT CHARACTERS

1. Transverse occipital ridge (Lawrence, 1988; Lawrence *et al.*, 1995) (ci = 33, ri = 83).

0. absent
1. present

This character was defined by Lawrence & Britton (1991) as a carina "which fits against the anterior edge of the pronotum".

In the Elateroidea both states are present but in the Buprestoidea the transverse occipital ridge is absent and this condition is considered plesiomorphic. The apomorphic condition appears in Byrrhidae, Ptilodactylidae, Cneoglossidae, and Eubriinae (Psephenidae). Both states occur in the Dryopidae.

2. Mandibles (Lawrence, 1988; Lawrence *et al.*, 1995) (ci = 50, ri = 80).

0. well developed
1. very small (reduced)

In the Elateroidea (except Brachypsectridae) and Buprestoidea the mandibles are well developed, condition considered plesiomorphic. The reduced mandibles represent the apomorphic condition and appears in Cneoglossidae, Chelonariidae, and Psephenidae. Crowson (1995) stated that in Psephenidae the mouthparts are reduced and probably non-functional.

3. Apex of mandibles (na) (Lawrence, 1988; Lawrence *et al.*, 1995 - modified) (ci = 25, ri = 33).

0. with more than one tooth or lobe
1. unidentate
2. rounded

Lawrence (1988) considered the rounded and the unidentate apices to be a single state, but we prefer to separate them, in a nonadditive series, due to the difficulties in the polarization.

Both unidentate apex and apex with more than one tooth or lobe are present in the Elateroidea and in Lutrochidae whereas in the Buprestoidea only the 1st condition occurs.

4. Mandibular mola (Lawrence, 1988; Lawrence *et al.*, 1995) (ci = 33, ri = 71)

0. present
1. absent

The mandibular mola is absent in the Elateroidea, Buprestoidea and Dascilloidea. In the Scirtoidea both states occur and in the Scarabaeiformia it is present. Mola present was considered plesiomorphic. The apomorphic condition appears in the Cneoglossidae, Chelonariidae, Psephenidae, Epilichinae (Ptilodactylidae), and Callirhipidae.

Crowson (1978) considered the absence of the mandibular mola in Byrrhidae, Chelonariidae and Psephenidae as an apomorphic condition.

5. Mandibles (ci = 50, ri = 0).

0. not foliaceous
1. foliaceous

The foliaceus type of the mandibles occurs only in Cneoglossidae and Chelonariidae.

6. Apical segment of maxillary palp (Lawrence, 1988; Lawrence *et al.*, 1995) (ci = 18, ri = 50).

0. cylindrical or subulate
1. slightly expanded and truncate at apex
2. securiform or subtriangular

In the Elateroidea the first two conditions occur; the plesiomorphic condition appears in the Buprestoidea. In the Byrrhoidea the condition 1 of the transformation series appears in Larainae (Elmidae); Psephenoidinae, Eubriacinae (Psephenidae); and, in Aploglossinae, Araeopidiinae (Ptilodactylidae). The fully apomorphic condition is present in the Amphicyrtinae (Byrrhidae); Lutrochidae; Psepheninae (Psephenidae); Cladotominae, Epilichinae (Ptilodactylidae); and Chelonariidae.

7. Lateral pronotal carinae (Lawrence, 1988; Lawrence *et al.*, 1995) (ci = 33, ri = 66).

0. complete
1. incomplete or absent

Both conditions are present in the Elateroidea, Buprestoidea and Dascilloidea, but in the Scirtoidea the lateral pronotal carina is complete, condition considered plesiomorphic. In the Byrrhoidea the apomorphic condition occurs in Heteroceridae, Ptilidactylidae (except for Cladotominae), and in Callirhipidae.

8. Conection between prosternal process and mesosternal cavity (Lawrence, 1988 - modified) (ci = 20, ri = 42).

0. present
1. absent

Hlavac (1975) considered three major zones of contact in the pro-mesothoracic joint, one of them formed by "the prosternal projection against a cavity or groove on the mesosternum", and it is with this sense that we define this character. Crowson (1971) and Lawrence (1988) considered the Callirhipidae as possessing a groove on the mesosternum but the genera we studied evidenced the contrary. The mesosternal cavity is present in Archostemata, Adephaga, Myxophaga and most Polyphaga. The presence of this condition and the consequent lodging of the prosternal process is independently acquired by several polyphagan lineages. The apomorphic condition appears in Byrrhidae, Heteroceridae, Eubrianacinae (Psephenidae), Cneoglossidae, and Callirhipidae.

9. Posterior edge of pronotum (Lawrence, 1988; Lawrence *et al.*, 1995) (ci = 33, ri = 66).

0. without crenulations
1. crenulate

In the Elateroidea (except for a few Elateridae) and in the Eucinetoidea the posterior edge of pronotum is without crenulations, condition considered plesiomorphic. The apomorphic condition is found in the Ptilodactylidae (except in Araeopidiinae), in the Chelonariidae, in the Eubriinae (Psephenidae) and in the Eulichadidae. Lawrence (1988) considered the lack of crenulations in some Ptilodactylidae and in the Psephenidae as a secondary loss. The same author (Lawrence *et. al.*, 1995) reported the presence of crenulations in Callirhipidae. However, all the species of *Callirhipis* and *Zenoa* studied by us lack crenulations.

10. Anterior edge of prosternum ("mentonière") (Lawrence, 1988; Lawrence *et al.*, 1995) (ci = 50, ri = 91).

0. not produced forward
1. produced forward

Both conditions appear in the Elateroidea but in the Buprestoidea, Dascilloidea and Scirtoidea the anterior edge of prosternum is not produced forward, condition considered plesiomorfic. In the Byrrhoidea the apomophic conditon appears in Eubriinae (Psephenidae), Elminae (Elmidae), Dryopidae, Limnichidae, and Heteroceridae.

11. Pronotal projection (Lawrence, 1988; Lawrence *et al.*, 1995) (ci = 20, ri = 50).

0. elongate
1. very short and angulate or absent

In the Elateroidea both conditions are present; in the Buprestoidea and Scirtoidea the pronotal projection is very short. Lawrence (1988) considered the short condition as apomorphic and we accept here that procedure. The apomorphic condition occurs in Cladotominae (Ptilodactylidae), Cneoglossidae, Chelonariidae, Eubriacinae (Psephenidae), Byrrhidae, Elmidae, Dryopidae, Lutrochidae, Limnichidae, and Heteroceridae.

12. Protrochantin (Lawrence, 1988; Lawrence *et al.*, 1995 - modified) (ci = 50, ri = 50).

0. exposed
1. completely concealed

Lawrence (1988) considered a transformation series formed by the protrochantin exposed (0); partly exposed (1) and completely concealed (2). However, we have been unable to distinguish between the conditions exposed and partly exposed, at least in the specimens examined; thus, we decided to recognize only two well defined states.

In the Elateroidea both conditions occur; in the Buprestoidea the protrochantin is exposed, condition considered plesiomorphic. The protrochantin completely concealed occurs only in the Ptilodactylinae

(Ptilodactylidae) and in Elminae (Elmidae).

13. Mesocoxae (Lawrence, 1988) (ci = 33, ri = 81).

0. narrowly to moderately separated
1. widely separated

Both conditions appear in the Elateroidea; the widely separated mesocoxae occurs in the Buprestoidea but, in the Dascilloidea and Scirtoidea the mesocoxae are narrowly separated, condition considered plesiomorphic. The apomorphic condition appears in the Byrrhidae, Elminae (Elmidae), Dryopidae, Lutrochidae, Limnichidae, Heteroceridae, and Chelonariidae.

14. Metasternal transverse suture (Lawrence, 1988; Lawrence *et al.*, 1995) (ci = 50, ri = 92).

0. well developed, usually extending across at least half the metasternal width
1. absent or vestigial

Crowson (1971) cited this suture as "distinguinshable for a short distance near the middle in Callirhipidae and *Eulichas*" and, in 1978, he considered the absence of this suture as a synapomorphic condition of Byrrhidae, Ptilodactylidae, and Chelonariidae.

In the Elateroidea the metasternal transverse suture is absent but in the Buprestoidea, Dascilloidea and Scirtoidea it is well developed, condition regarded as plesiomorphic. The apomorphic condition occurs in Byrrhidae, Psephenidae (except for Psephenoidinae), Cneoglossidae, Ptilodactylidae, Chelonariidae, Eulichadidae, and Callirhipidae.

15. Metacoxal plates (Lawrence, 1988) (ci = 40, ri = 62).

0. well developed
1. poorly developed
2. absent

All conditions occur in the Elateroidea; in the Buprestoidea they are poorly or well developed, but in the Scirtoidea they are well developed, condition regarded as plesiomorphic. The intermediate apomorphic condition appears in Araeopidiinae and Aploglossinae (Ptilodactylidae), Cneoglossidae, Psephenidae (except for Eubrianacinae), and Heteroceridae. The fully apomorphic condition occurs only in Eubrianacinae (Psephenidae).

16. Anterior process of metendosternite (Lawrence, 1988; Lawrence *et al.*, 1995) (ci = 100).

0. long and narrow
1. short or absent

In the Elateroidea, Buprestoidea and Dascilloidea both conditions appear, in the Scirtoidea the anterior process of the metendosternite is short or absent, and in Scarabaeiformia it is long. Lawrence (1988) considered the condition short or absent as apomorphic, and his opinion, which was followed herein, is a synapomorphy to Byrrhoidea (*sensu* Lawrence & Newton, 1995), excluding Callirhipidae and Eulichadidae .

17. Legs (ci = 100, ri = 100).

0. normal
1. fossorial

The fossorial legs are associated with burrowing habits that "is not common in adult beetles", according to Crowson (1981), and constitutes an autapomorphic condition to Heteroceridae.

18. Tibial spurs (Lawrence, 1988) (ci = 100).

0. present
1. absent

Both conditions appear in the Elateroidea; in the Buprestoidea the tibial spurs are present and was regarded as plesiomorphic. The apomorphic condition is an autapomorphy to Chelonariidae.

According to Crowson (1981), "the loss of the spurs is a characteristic of many groups of Coleoptera and is polyphiletic, but it is not certain that it is always irreversible it is inconceivable that an ordinary apical tibial spine could be developed into an effective replacement for a lost tibial spur"; he stated also that "there is some evidence that tibial spurs may serve as detectors of vibrations in the substrate; in many groups, especially among the species living on plant foliage, the spurs tend to be reduced or lost altogether".

19. Tibial spurs (Lawrence, 1988) (ci = 100).

0. normal on all legs
1. enlarged on at least one pair of legs

All Elateroidea (except for a few Cebrionidae) have tibial spurs normal on all legs and this condition was considered plesiomorphic. The apomorphic condition is an autapomorphy to Ptilodactylinae (Ptilodactylidae).

20. Tarsi (ci = 100, ri = 100).

0. pentamerous
1. tetramerous

According to Crowson (1981), "the 5-segmented condition is undoubtedly primitive". The 4-segmented condition is an autapomorphy to Heteroceridae.

21. Tarsi (Lawrence, 1988) (ci = 33, ri = 50).

0. without membranous appendages on two or more segments
1. with membranous appendages on two or more segments

Both states appear in the Elateroidea and Dascilloidea; in the Buprestoidea the membranous appendages are present but the Eucinetoidea present no appendages. The absence is considered the plesiomorphic condition. In the Byrrhoidea the apomorphic condition occurs in Ptilodactylidae (except for Anchytarsinae and Araeopidiinae) and in Chelonariidae.

22. 4th tarsal segment (Lawrence, 1988) (ci = 33, r = 0).

0. not expanded and lobed beneath
1. expanded and lobed beneath

In the Elateroidea both states appear; in the Buprestoidea and Dascilloidea the 4th tarsal segment is simple, condition regarded as plesiomorphic. The apomorphic condition is found in Epilichinae, Cladotominae, and Ptilodactylinae (Ptilodactylidae).

23. 4th tarsal segment (Lawrence,1988) (ci = 33, ri = 33).

0. not or slightly reduced
1. highly reduced

In the Elateroidea (except for a few Elateridae) and Buprestoidea the 4th tarsal segment is not or is slightly reduced, condition considered as plesiomorphic. The apomorphic condition is found in Cladotominae and Aploglossinae (Ptilodactylidae), Amphicyrtinae (Byrrhidae), and Chelonariidae.

24. Empodium (Lawrence, 1988) (ci = 33, ri = 77).

0. well developed
1. highly reduced

In the Elateroidea (except for Artematopidae and Throscidae) the empodium is well developed. Both conditions occur in Buprestoidea, Dascilloidea and Scirtoidea. In Scarabaeiformia the empodium is well developed. Thus, the reduction must be considered the apomomorphic condition, which occurs in Ptilodactylidae (except for Cladotominae); Cneoglossidae; Chelonariidae; Eubriinae and Psepheninae (Psephenidae).

25. Tarsal claws (Lawrence, 1988) (ci = 33, r = 0).

0. not cleft or toothed
1. cleft or toothed

In the Elateroidea (except for a few Elateridae) the tarsal claws are not cleft or toothed; in the Buprestoidea and Dascilloidea both states occur but, in the Scirtoidea the tarsal claws are simple, not cleft, condition considered plesiomorphic. The apomorphic condition is found in Ptilodactylinae (Ptilodactylidae), Cneoglossidae, and Chelonariidae.

26. Radial cell (Crowson, 1978, Lawrence, 1988) (ci = 100, ri = 100).

0. present
1. absent

These authors considered the absence of the radial cell as a synapomorphic condition to Heteroceridae, Limnichidae, and Dryopidae.

27. Proximal end of radial cell (Lawrence, 1988) (ci = 25, ri = 25).

0. straight or obtuse inner angle
1. acute inner angle

In the Elateroidea and Buprestoidea the proximal end of radial cell is straight or obtuse, condition considered plesiomorphic. The apomorphic condition appears in Byrrhidae, Larainae *pars* (Elmidae), Ptilodactylidae (except for Araeopidiinae), Cneoglossidae, Chelonariidae, and Psephenidae (except for Psepheninae).

28. Anal cell (Lawrence, 1988) (ci = 14, ri = 25).

0. present
1. absent

Both states occur in the Elateroidea and Buprestoidea; Dascilloidea presents anal cell, condition considered plesiomorphic. The apomorphic condition is found in Byrrhidae, Limnichidae, Heteroceridae, Psephenidae, Epilichinae and Ptilodactylinae (Ptilodactylidae), and Chelonariidae.

29. Wing folding (Lawrence, 1988) (ci = 100).

0. dascilloid-type
1. elateroid-type
2. dryopoid-type

Lawrence (1988) considered the dascilloid-type as plesiomorphic because it could be found in groups called "primitives" within the Elateriformia as Dascillidae and Artematopidae and other polyphagan groups. The elateroid-type is found in Callirhipidae and Eulichadidae and the dryopoid-type in all remainder Byrrhoidea.

30. Paired dorsal openings on abdominal tergites (ci = 100, ri = 100).

0. absent
1. present

The presence of paired dorsal openings on abdominal tergites constitutes an apomorphic condition found in Psephenidae and Cneoglossidae. Crowson (1995) recorded paired dorsal openings as presumably defensive glands in Psephenidae, Scirtidae and in many Buprestidae, explaining that "defensive glands opening under the elytra would probably be aimed at predators liable to attack the beetle in flight, i. e., against birds, and are likely to be developed in beetles which fly readily".

31. Intercoxal process of 1st ventrite (Lawrence, 1988; Lawrence *et al.*, 1995) (ci = 100).

0. well developed
1. highly reduced or absent

In Elateroidea (except for a few Cebrionidae) the intercoxal process of the first ventrite is well developed and this state was regarded as plesiomorphic. The reduction of this process is an autapomorphy to Cneoglossidae.

32 Spiracles on 8th segment (Lawrence, 1988; Lawrence *et al.*, 1995) (ci = 50, ri = 92).

0. well developed, functional
1. reduced, non-functional or absent

Crowson (1978), stated that "In Dryopoidea, the presence of functional spiracula on adult 8th abdominal segment appears to be completely correlated with a certainly apomorphic abdominal character, the specialization or reduction of the ovipositor with complete loss of the articulated gonapophyses" and also that in the Elateriformia there is an strict relation between the absence of this character and the habit of depositing eggs in very wet situations, as is the condition of Eulichadidae, Ptilodactylidae, Chelonariidae, Psephenidae, and Elmidae. Again according to this author, in the "Dryopid-Limnichid-Heterocerid line, there may have been an initial change in the oviposition habits, the ovipositor becoming adapted to cutting holes in the stems of emergent plants and depositing eggs in them. Of course the spiracles 8 are well developed in this last group". Crowson (1995), refering to this character, stated again "this is probably basically adapted to the habit of oviposition in water with the extrusion of the ovipositor, abdominal segment 8 is liable to be submerged with the danger of water entering the tracheal system through the 8th abdominal spiracles".

In the Elateroidea the spiracles on 8th segment are well developed and functional (plesiomorphic condition). The apomorphic condition occurs in Elminae (Elmidae); Psephenidae, Cneoglossidae, Ptilodactylidae, Chelonariidae, and Eulichadidae.

33. 9th male tergite (Lawrence, 1988; Lawrence *et al.*, 1995) (ci = 100).

0. entire
1. longitudinally divided forming two hemitergites

In Elateroidea (except for a few Artematopidae and Eucnemidae) and Dascilloidea the 9th male tergite is entire, condition considered plesiomorphic. The apomorphic condition appears only in Eulichadidae.

34. 9th and 10th male tergites (Lawrence, 1988 - modified) (ci = 100).

0. not-fused together
1. fused together

The 9th and 10th male tergites fused together is an autapomorphy to Chelonariidae.

35. Basal piece of aedeagus (Crowson, 1978) (ci = 100, ri = 100).

0. symmetrical base
1. asymmetrical base

Lawrence (1988) considered not only the basal piece as symmetric or asymmetric but the whole aedeagus, and considered Byrrhidae (*pars*) as having asymmetric aedeagus. We prefer to follow Crowson (1978) who stated that "the original apomorphisms of the Elmid-Dryopid line include the asymmetrical base of the basal piece". The apomorphic condition appears in Elmidae, Dryopidae, Lutrochidae, Limnichidae, and Heteroceridae.

36. Penis (Lawrence, 1988; Lawrence *et al.*, 1995 - modified) (ci = 100).

0. with apex not longitudinally divided
1. with apex longitudinally divided

In the Elateroidea and Buprestoidea the apex of the penis is not longitudinally divided, plesiomorphic condition. The apomorphic condition occurs in Byrrhinae (Byrrhidae); Epilichinae and Araeopidiinae (Ptilodactylidae); Eulichadidae, and Callirhipidae.

37. Penis (Lawrence, 1988; Lawrence *et al.*, 1995 - modified) (ci = 25, ri = 72).

0. with a single lobe
1. with distinct dorsal and ventral lobes, sometimes the ventral lobe is a rod-like sclerotisation.

In the Elateroidea both conditions occur; in the Buprestoidea the median lobe has a single lobe, condition considered as plesiomorphic.The apomorphic condition appears in the Dryopidae, Chelonariidae, Psephenidae, Ptilodactylidae (except for Ptilodactylinae), Eulichadidae and Callirhipidae.

38. Stylus (Lawrence, 1988) (ci = 33, ri = 80).

0. well developed
1. highly reduced
2. absent

The three conditions occur in the Elateroidea and Buprestoidea; in the Dascilloidea the styli are well developed, condition considered as plesiomorphic. The intermediate state appears in the Anchytarsinae, Epilichinae, Araeopidiinae (Ptilodactylidae), and in the Eulichadidae. The fully apomorphic condition occurs in the Dryopidae, Lutrochidae, Limnichinae and Thaumastodinae (Limnichidae), Heteroceridae, Cladotominae, Ptilodactylinae (Ptilodactylidae), Chelonariidae, and Callirhipidae.

39. Coxite (Lawrence, 1988; Lawrence *et al.*, 1995) (ci = 33, ri = 83).

0. divided
1. undivided

Both conditions occur in the Elateroidea; in Buprestoidea the coxite is not divided, but in the Dascilloidea they are divided, condition considered as plesiomorphic. The apomorphic condition appears in the Dryopidae, Lutrochidae, Limnichidae, Heteroceridae, Ptilodactylinae, Cladotominae (Ptilodactylidae), Chelonariidae, Eulichadidae, and Callirhipidae.

40. Ovipositor (ci = 33, ri = 71).

0. moderately sclerotized
1. heavily sclerotized, cuneiform

The apomorphic condition occurs in Dryopidae, Lutrochidae, Thaumastodinae, Limnichinae (Limnichidae), Cladotominae (Ptilodactylidae), Chelonariidae, and Callirhipidae.

41. 8th female sternite (Lawrence, 1988; Lawrence *et al.*, 1995 - modified) (ci = 33, ri = 75).

0. with ventral spiculum
1. without ventral spiculum

In the Elateroidea the 8th female sternite present a ventral spiculum, condition considered as plesiomorphic. Lawrence (1988) considered as plesiomorphic the absence of a ventral spiculum. However, the ventral spiculum is an esclerotized structure present in the forms with a well developed ovipositor. Its absence is correlated with ovipositor reduced or absent. The apomorphic state occurs in Byrrhidae, Heteroceridae, Psephenidae whose females lay their eggs under submersed stones.

42. 8th female sternite (Lawrence, 1988; Lawrence *et al.*, 1995) (ci = 50, ri = 85).

0. without paired antero-lateral projections
1. with paired 1-2 projections

In the Elateroidea and Buprestoidea the 8th female sternite is devoid of antero-lateral projections, condition considered as plesiomorphic. The apomorphic condition occurs in Cneoglossidae, Ptilodactylidae, Chelonariidae, Eulichadidae, and Callirhipidae.

43. Hydrofuge tomentum (Crowson, 1978) (ci = 50, ri = 90).

0. absent
1. present

Crowson (1978) considered the presence of hydrofuge pubescence an especialization "enabling the adults to move freely into water". The apomorphic condition appears in Elmidae; Dryopidae; Lutrochidae; Limnichidae; Heteroceridae; and Psephenidae.

LARVAL CHARACTERS

44. Ventral epicranial ridge (Lawrence, 1988; Lawrence *et al.*, 1995) (ci = 33, ri = 66).

0. absent
1. present

Both states occur in the Elateroidea; in the Buprestoidea, Dascilloidea and Scirtoidea this carina is absent, condition considered as plesiomorphic. The apomorphic condition appears in all families except for Elminae (Elmidae) and Psephenidae.

45. Stemmata (Lawrence, 1988) (ci = 100).

0. present
1. absent

In Coleoptera, the presence of stemmata is the plesiomorphic condition. Stemmata absent is an autapomorphy of Callirhipidae.

46. Prostheca type 1 (articulated process at base and setose at apex) (ci = 50, ri = 50).

0. absent
1. present

47. Prostheca type 2 (2 parallel fringes of hairs) (ci = 50, ri = 50).

0. absent
1. present

48. Prostheca type 3 (na) (ci = 66, ri = 60).

0. absent
1. asetose process
2. setose process
3. setose process and fringe of hairs
4. inarticulated asetose process and fringe of hairs

46-48. The prostheca corresponds to various types of diferent structures located in the mesal area of the mandibles: fixed or articulated process; membranous or sligthtly sclerotized; fringe-like or lobe-like, etc.

We identified three main types of prostheca within the Byrrhoidea, being formed by: a) an articulated process at base and setose at apex; b) two parallel fringes of hairs; and, c) a setose process with a fringe of hairs.

There are no clues about the homologies of these three different types of prostheca, and they are considered as distinct characters. The absence of the prostheca was considered plesiomorphic in the three cases. Although four states are easily distinguished in the prostheca of type 3, it is not possible to polarize the character, which is considered nonadditive.

49. Antennae (Lawrence, 1988; Lawrence *et al.*, 1995) (ci = 33, ri = 81).

0. moderately long
1. very short

Both states occur in the Elateroidea; in the Dascilloidea the antennae are reduced and in the Scirtoidea they are elongate; this last state was considered as plesiomorphic. The apomorphic condition occurs in the Dryopidae, Limnichidae, Heteroceridae, Araeopidiinae, Cladotominae (Ptilodactylidae), Chelonariidae, Eubriinae (Psephenidae), and Callirhipidae .

50. Maxilla (Lawrence, 1988; Lawrence *et al.*, 1995) (ci = 100).

0. with separated galea and lacinia

1. with single mala

In the Elateroidea both states occur; in the Dascilloidea and Scirtoidea the galea and lacinia are separated, condition considered as plesiomorphic. The presence of the mala constitute an autapomorphy to Callirhipidae.

51. Maxillary articulating area (Lawrence, 1988; Lawrence *et al.*, 1995 modified) (ci = 50, ri = 90).

0. present
1. absent

According to Crowson (1995), "a general feature of predaceous larva is reduction or loss of the molar part in the mandibles, frequently accompanied by reduction or loss of the maxillary articulating area and reduction of the cardo".

The apomorphic condition appears in Elmidae; Dryopidae; Lutrochidae; Limnichidae; Heteroceridae; Araeopidiinae (Ptilodactylidae); Chelonariidae; and Callirhipidae.

52. Maxillolabial sutures (Lawrence, 1988; Lawrence *et al.*, 1995) (ci = 33, ri = 50).

0. complete
1. incomplete

Both states are found in the Elateroidea and Dascilloidea; the Buprestoidea and Scirtoidea present a complete maxillolabial suture, condition considered as plesiomorphic. The incomplete maxillolabial suture is found in Dryopidae, Lutrochidae, and Chelonariidae. Lawrence (1988) considered Callirhipidae with an incomplete suture but the material we studied did not show this condition.

53. Cardines (Lawrence, 1988; Lawrence *et al.*, 1995 - modified) (ci = 40, ri = 40).

0. well separated
1. approximate and contiguous
2. fused together

Lawrence (1988) considered only two states in the transformation series of this character, but we preferred to recognize three different states. However, this procedure did not affect the results of the analysis, because the changes appeared independently in four lineages. The intermediate apomorphic condition occurred in Limnichidae and Callirhipidae. The extreme apomorphic, represented by the cardines fused together, occurred in Lutrochidae and Chelonariidae.

54. Postmentum (ci =50, ri = 87).

0. not expanded
1. slightly expanded laterally
2. expanded concealing maxillary articulating area

The condition that appears in the ground plan of Coleoptera is the postmentum with parallel sides, not expanded, considered the plesiomorphic condition. Within the Byrrhoidea, we postulated a transformation series, with an intermediate apomorphic condition represented by the slightly laterally expanded postmentum, that occurs in the Araeopidiinae and Cladotominae (Ptilodactylidae), and the fully apomorphic state represented by the expanded prementum concealing the maxillary articulating area, presented by the remainder Ptilodactylidae, Cneoglossidae, and Psephenidae.

55. Mentum (Lawrence & Stribling, 1992; Lawrence *et al.*,1995) (ci = 100, ri = 100).

0. not divided
1. divided into three parts by longitudinal sutures

The mentum with longitudinal sutures represents the apomorphic condition present in the Epilichinae and Anchytarsinae (Ptilodactylidae). In the remainder Coleoptera the mentum is not divided (plesiomorphic condition).

56. Tarsungular setae (Lawrence, 1988; Lawrence *et al.*, 1995 - modified) (ci = 100).

0. present
1. absent

The presence of setae on tarsungulus is the plesiomorphic condition in Coleoptera larvae. The apomorphic condition is an autapomorphy to Callirhipidae. Lawrence (1988) recognized a multistate character, considering the number of setae (two, one, or none), but we preferred to consider only the presence or absence of these setae.

57. 10th Segment (ci = 100).

0. visible
1. concealed, not visible

The 10th segment concealed, not visible is an autapomorphy to Callirhipidae.

58. Pygopodium of the 10th segment (ci = 100).

0. absent
1. with a single pygopodium
2. paired pygopodia

In the Buprestoidea, Dascilloidea and Scirtoidea, the pygopodium is absent, condition considered plesiomorphic. In the Byrrhoidea, single pygopodium occurs in Limnichidae and Heteroceridae; paired pygopodia, appears in Byrrhidae, Ptilodactylinae, Epilichinae, Anchytarsinae (Ptilodactylidae); Cneoglossidae; and Eulichadidae.

59. Vertical operculum formed by 9th segment (ci = 100).

0. absent
1. present

In the Elateroidea and Dascilloidea this operculum is absent, condition considered plesiomorphic. It is an autapomorphy to Callirhipidae.

60. Operculum formed by 10th segment (Lawrence, 1988) (ci = 20, ri = 63).

0. absent
1. present

In the Elateroidea and Dascilloidea the 10th segment does not form an operculum. The apomorphic condition occurs in Araeopidiinae, Cladotominae (Ptilodactylidae); Elmidae; Dryopidae; Lutrochidae; and Chelonariidae.

61. 10th abdominal segment (ci = 100, ri= 100).

0. not reduced
1. reduced to a narrow band
2. absent

The intermediate apomorphic condition occurs in Psepheninae and Eubrianacinae (Psephenidae) and the fully apomorphic condition in Psephenoidinae and Eubriinae (Psephenidae), and Callirhipidae.

62. 9th abdominal segment (ci = 100).

0. not reduced and dorsally oriented
1. reduced and ventrally placed

The 9th abdominal segment reduced and ventrally placed constitutes an autapomorphy to Cladotominae (Ptilodactylidae).

63. 9th abdominal segment (ci = 100).

0. without urogomphi
1. with a pair of fixed urogomphi

The 9th abdominal segment with a pair of fixed urogomphi constitutes an autapomorphy to Eulichadidae.

64. Abdominal gills (Lawrence, 1988) (ci = 50, ri = 0).

0. absent
1. present

In the Elateroidea and Dascilloidea the abdominal gills are absent, condition considered as plesiomorphic. In the Byrrhoidea, gills occur (apomorphic condition) in the Eubrianacinae, Psepheninae (Psephenidae); and Eulichadidae.

65. Anal gills (Lawrence, 1988) (ci = 25, ri = 62).

0. absent
1. present

In the Elateroidea and Dascilloidea the anal gills are absent (plesiomorphic condition). In the Byrrhoidea this kind of gills occurs in Psephenoidinae, Eubriinae (Psephenidae); Elmidae; Lutrochidae; and Hyphalinae (Limnichidae).

66. Opercular hooks (Lawrence, 1988 - modified) (ci = 50, ri = 90).

0. absent
1. present

Lawrence (1988) considered the presence of paired hooks on segment 10, but we preferred to consider these hooks to be associated with an operculum formed by segment 10. The apomorphic condition appears in Dryopidae, Lutrochidae, Elmidae, and Limnichidae; in the last family the operculum is not well developed.

67. Abdominal spiracles on 8th segment (ci = 42, ri = 20).

0. placed on pleura
1. placed on terga
2. placed on tergal protuberances
3. placed on apex of a tube

In the Elateroidea and Buprestoidea the 8th spiracles are placed laterally, on pleura, condition considered plesiomorphic. The change to the tergal region is considered apomorphic, and can be ordered in a series of transformation. In Dryopidae and Psepheninae (Psephenidae) the spiracles are placed on tergum, in the Araeopidiinae (Ptilodactylidae) on tergal protuberances, and in Cladotominae (Ptilodactylidae) on the apex of a more or less developed tube, occurring a concomitant reduction of the 9th segment.

68. Paired eversible glands (ci = 100).

0. absent
1. present

The presence of these glands is an autapomorphy to Ptilodactylinae (Ptilodactylidae).

69. Body shape (ci = 100, ri = 100).

0. subcylindrical
1. flattened

The flattened body shape is an autapomorphy to Psephenidae, and seems to represent an especialization to life in fast-running streams.

70. Abdominal sternites (na) (ci = 100, ri = 100).

0. with tergum and sternum not fused on 1st- 8th segments
1. with tergum and sternum fused on 8th segment
2. with tergum and sternum fused on 7th- 8th segments
3. with tergum and sternum fused on 4/5th- 8th segments
4. with tergum and sternum fused on 1st- 8th segments

In Coleoptera, the plesiomorphic condition is represented by the tergum and sternum of abdominal segments not fused. In Byrrhoidea, different apomorphic states can be distinguished, in a series considered nonadditive. In Chelonariidae, Cladotominae and Araeopidiinae (Ptilodactylidae), only the 8th segment forms a ring; in Dryopidae the 7th- 8th segments forms a complete ring; in Lutrochidae, 4/5th- 8th segments have tergum and sternum fused; and in Callirhipidae there are no sutures separating tergum, pleuron and sternum on 1st- 8th segments.

71. Osmoregulatory organs (ci = 50, ri = 50).

0. absent
1. present

The presence of the osmoregulatory organs is an apomorphic condition to Epilichinae, Anchytarsinae (Ptilodactylidae); and Cneoglossidae.

PUPAL CHARACTER

72. Pupa (ci = 25, ri = 50).

0. without gin-traps
1. with gin-traps

In Elateroidea, dorsal gin-traps are absent, condition considered plesiomorphic. Gin-traps occur in pupae of Dryopidae, Limnichinae (Limnichidae), Epilichinae (Ptylodactylidae), Ptilodactylinae (Ptylodactylidae), Anchytarsinae (Ptilodactylidae), and Eubriinae (Psephenidae).

RESULTS OF CLADISTIC ANALYSIS

The 72 characters described and discussed above were coded for each terminal taxon and presented in the data matrix (Tab. 1). The matrix was analyzed with Hennig86 computer software (Farris, 1988), employing the algorithms mh*, bb*. Different analyses were performed, considering adults only, immatures only, adults and immatures together, and including and excluding Callirhipidae and Eulichadidae. This last procedure was needed due to the conflicting opinions on the phylogenetic relationships of Callirhipidae and Eulichadidae proposed by different authors (v. g. Crowson, 1981; Lawrence, 1988; Lawrence & Newton, 1982, 1995).

When the 72 characters are considered and the taxa Eulichadidae and Callirhipidae are included in the analysis (32 terminal taxa) and adults and immatures characters are considered together, 24 equally parsimonious cladograms are found, with a length of 213 steps. The strict consensus cladogram (CI = 41, RI = 71) is presented in Fig. 181. Eulichadidae and Callirhipidae appear as the sister group of the remainder Byrrhoidea *sensu* Lawrence & Newton (1995), but the whole group does not share an exclusive synapomorphy. The synapomorphies indicated in branch 1 (Fig. 181), metasternal transverse suture absent or vestigial (14.1), wing folding elateroid-type (29.1), presence of ventral epicranial ridge (44.1), and presence of pygopodium on 10th segment (58.1), also occur in other Elateriformia. Thus the monophyly of Byrrhoidea *sensu* Lawrence & Newton (1995) cannot be maintained when other Elateriformia are included in the analysis. The inclusion of Callirhipidae and Eulichadidae in the analysis helped to test the monophyly of the ingroup (Nixon & Carpenter, 1993). The monophyly of the assemblage represented by the remainder taxa of Byrrhoidea (*sensu* Lawrence & Newton, 1995), excluding Eulichadidae and Callirhipidae, is well supported by three striking synapomorphies, the anterior process of metendosternite shortened (16.1), the proximal end of the radial cell with acute inner angle (27.1), and the wing folding of the dryopoid-type (29.2). The last two features are autapomorphies of the group.

When Eulichadidae and Callirhipidae are excluded from the analysis (30 terminal taxa), and adult and immature characters are considered together, 24 cladograms are found, with a length of 186 steps. The strict consensus cladogram (CI = 43, RI = 73) is presented in Fig. 180. The topologies of the cladograms of Fig. 180 and 181 are very similar, differing mainly in relation to the relative position of Byrrhidae. The monophyly of Cneoglossidae + Psephenidae + "Ptilodactylidae" + Chelonariidae + "Elmidae" + Lutrochidae + "Limnichidae" + Heteroceridae + Dryopidae is strongly supported by the shortening of the anterior process of metendosternite (16.1), and the presence of wing folding of dryopoid-type (29.2). Cneoglossidae appears as the sister-group of the Psephenidae, and the monophyly of the group is supported by the presence of paired glandular openings on abdominal tergites of adults (30.1), + five homoplasic features (2.1, 3.2, 4.1, 15.1, and 54.2). Ptilodactylidae is paraphyletic, but can be considered monophyletic with the inclusion of Chelonariidae. The monophyly of this group is indicated by the presence of tarsi with membranous appendages on two or more segments (21.1), female styli highly reduced (38.1), + three homoplasic characteristics (7.1, 15.1, and 42.1). The monophyly of Cneoglossidae + Psephenidae + "Ptilodactylidae" + Chelonariidae is well supported by the reduction of the empodium (24.1), postmentum expanded laterally (54.1), + two homoplasic characteristics. A sister-group relationship between this group and Byrrhidae is supported by the absence of the metasternal suture (14.1), 10th larval segment with a paired pygopodium (58.1), + four homoplasic features. The remainder terminals, which comprise Elmidae + Lutrochidae + "Limnichidae" + Heteroceridae + Dryopidae, seem to constuitute a monophyletic assemblage, sharing the asymmetrical base of the basal piece of aedeagus (35.1), presence of paired hooks on 10th larval segment (66.1), + six homoplasic characteristics. Dryopidae and Heteroceridae resulted as monophyletic groups, but their relationships with the "Limnichidae" remains unsolved. "Limnichidae", as currently defined, resulted paraphyletic. The monophyly of the whole group ("Limnichidae" + Heteroceridae + Dryopidae) is indicated by the absence of the radial cell, what is in agreement with Crowson (1978) and Lawrence (1988). The monophyly of Lutrochidae is indicated by the abdomen of larvae with tergum and sternum fused on 4/5th- 8th segments (70.3), + five homoplasic features. "Elmidae" resulted paraphyletic, Elminae forming a monophyletic unit with Lutrochidae + "Limnichidae" + Heteroceridae + Dryopidae, weakly supported by three homoplasic characteristics: the anterior edge of prosternum produced forward (10.1), the absence of anal cell (28.1), and the presence of a ventral epicranial ridge in the larvae (44.1).

When Eulichadidae, Callirhipidae, and Aploglossinae (larva unknown) are excluded, and only larval characters are considered in the analysis (29 characters, 29 taxa), 3157 equally parsimonious cladograms are obtained, with a length of 57 steps. The strict consensus cladogram (CI = 57, RI = 79), is presented in Fig. 183. The monophyly of the group cannot be sustained by any synapomorphy. The small numbers of larval characters employed in the analysis, and the high percentage of homoplasies, resulted in a brush-like cladogram. The only informative clade is Psephenidae, characterized by prostheca with an asetose process (48.1) and flattened body (69.1); Cneoglossidae appears in an assemblage with Anchytarsinae and Epilichinae.

When Eulichadidae and Callirhipidae are excluded and only adult characters are considered in the analysis (43 characters, 30 taxa), 357 equally parsimonious cladograms are obtained, with a length of 114 steps. The strict consensus cladogram (Fig. 182) (CI = 41, RI = 75), is very similar to that of Fig. 180, when adult and immatures characters are analyzed together. The main observed difference is a basal tricotomy, with three monophyletic groups: Byrrhidae, Cneoglossidae + Psephenidae + "Ptilodactylidae" + Chelonariidae, and "Elmidae" + Lutrochidae + "Limnichidae" + Dryopidae + Heteroceridae. This last grouping is less resolved as when compared with the cladogram of Fig. 180, when the larval characters are included in the analysis.

DISCUSSION AND CONCLUSIONS

We agree with Hennig (1966) that holomorphological studies provide better support to phylogenetic hypothesis. Thus we prefer the cladogram which combines adults and immatures features as the final result of our analyses. The cladogram of Fig. 180 represents the most parsimonious hypothesis on basis of the adult and larval characters studied.

The monophyly of Byrrhoidea (*sensu* Lawrence & Newton, 1995) cannot be indicated by any synapomorphy so far. However, excluding Eulichadidae and Callirhipidae, the monophyly of the remainder taxa (Fig. 180) is supported by three striking synapomorphies: the anterior process of metendosternite shortened (16.1), the proximal end of the radial cell with acute inner angle (27.1), and the wing folding of the dryopoid-type (29.2).

Callirhipidae and Eulichadidae possibly share several apomorphic conditions, as the lacking of the metasternal transverse suture (14.1), and reduction of spiracles on 8th segment (32.1). However, these conditions are homoplasic and occur in different taxa of the expanded Byrrhoidea, or even in the Elateriformia. Moreover, the conspicuous elateroid pattern of wing folding (29.1) led us to set Callirhipidae and Eulichadidae as *incertae sedis* within the Elateriformia.

A sister-group relationship between Cneoglossidae and Psephenidae is supported by an adult feature, the presence of paired glandular openings on abdominal tergites (30.1). A similar relationship was evidenced by Lawrence *et al.* (1995).

Three Byrrhoidea families, as currently defined, resulted paraphyletic from our analysis: Elmidae, Limnichidae and Ptilodactylidae.

Our data on Limnichidae are mainly based on literature, and a more accurate study must be done. Hyphalinae resulted as the sister-group of the remainder Limnichidae + Heteroceridae + Dryopidae. The paraphyly of Limnichidae was pointed out by Beutel (1995), who commented on the controversial phylogenetic affinities of *Hyphalus* Britton, 1971, and suggested a relationship between Heteroceridae and Limnichidae (excluding *Hyphalus*).

Ptylodactylidae can be considered monophyletic with the inclusion of a single terminal, Chelonariidae. Chelonariidae is a very specialized group, presenting many homoplasic synapomorphies and two conspicuous autapomorphies, the absence of tibial spurs (18.1), and the 9th and 10th male tergites fused (34.1). Anchytarsinae and Epilichinae were evidenced as sister-groups. Although these taxa were synonymized by Lawrence & Newton (1995), they may be considered two distinct groups; the former can be characterized by two reversals: loss of membranous appendages on two or more segments (21.0), and absence of anal cell (28.0); the latter can be characterized by four homoplasies: unidentate apex of mandible (3.1), absence of mandibular mola (4.1), apical segment of palp securiform or subtriangular (6.2), and the fourth tarsal segment expanded and lobed beneath (22.1).

Some of the characteristics considered by Beutel (1995) as synapomorphies of some groups, e. g., larval operculum (*Araeopidius* + Cladotominae + Chelonariidae + Psephenidae + Elmidae + Lutrochidae + Dryopidae), and larval anal gills (Psephenidae + Elmidae + Lutrochidae), turned out to be noteworthy homoplasies in our analysis (Fig. 183). These highly adaptative structures presented by aquatic larvae probably evolved independently in different lineages, subject to convergent adaptation to life in fast-running water. However, the larvae of Psephenidae share a very flattened body (69.1), a synapomorphy that is an evident adaptation to the lotic environment.

Table 1. Data matrix for Byrrhoidea *sensu* Lawrence & Newton (1995). (0), plesiomorphic; (1), (2), (3), (4), apomorphic states; (?), missing data; (x), character not applicable to the taxon in question. Characters numbered as in the text

		1		2		3		4		5		6		7	
	12345	67890	12345	67890	12345	67890	12345	67890	12345	67890	12345	67890	12345	67890	12
Hypothetical ancestor	00000	00000	00000	00000	00000	00000	00000	00000	00000	00000	00000	00000	00000	00000	00
Eulichadidae	00100	00010	00010	00000	00000	00010	01100	11110	01010	10000	00000	00200	00110	00000	0?
Callirhipidae	00110	01100	00010	00000	00000	00010	00000	11211	01011	00011	00100	11x1x	x0000	00004	00
Cneoglossidae	11211	00100	10011	10000	00011	01121	11000	01000	01010	01000	00020	00200	00000	00000	10
Psephenidae, Eubriinae	11210	00011	00011	10000	00010	01121	01000	01000	10100	00110	00020	00x01	00001	00010	01
Psephenidae, Psephenoidinae	01110	10000	00001	10000	00010	01121	01000	01000	10100	00100	00020	00x00	20001	00010	00
Psephenidae, Eubrianacinae	01210	10100	10012	10000	00000	01121	01000	01000	10100	00200	00020	00000	10010	00010	00
Psephenidae, Psepheninae	01110	20000	00011	10000	00010	00121	01000	01000	10100	00300	00020	00000	10010	01010	00
Ptilodactylidae, Ptilodactylinae	10000	01010	01010	10010	11011	01120	01000	00210	01010	10000	00020	00200	00000	00100	01
Ptilodactylidae, Anchytarsinae	10000	01010	00010	10000	00010	01020	01000	01100	01010	01000	00021	00200	00000	00000	11
Ptilodactylidae, Epilichinae	10110	21010	00010	10000	11010	01120	01000	01100	01010	01000	00021	00200	00000	00000	11
Ptilodactylidae, Aploglossinae	10000	11010	00011	10000	10110	01?20	010?0	01000	010??	?????	?????	?????	?????	?????	??
Ptilodactylidae, Araeopidiinae	10100	11000	00011	10000	00010	00020	01000	11100	01010	00010	00010	00x01	00000	02001	0?
Ptilodactylidae, Cladotominae	10010	20010	10010	10000	11100	01020	01000	01211	01010	00410	00010	00x01	01000	03001	0?
Chelonariidae	11211	20010	10110	101x0	10111	01120	01010	01211	01010	00010	11200	00x01	00000	00001	00
Byrrhidae, Byrrhinae	10000	00100	10110	10000	00000	01120	00000	00?0?	10010	00000	00000	00200	00000	00000	0?
Byrrhidae, Syncalyptinae	10000	00100	10110	10000	00000	01120	000?0	00?0?	10010	00000	00000	00200	00000	00000	0?
Byrrhidae, Amphicyrtinae	10000	20100	10110	10000	00100	01120	000?0	00000	10010	00000	00000	00200	00000	00000	0?
Elmidae, Larainae/1	00000	10000	10100	10000	00000	0x020	00001	00000	00100	10000	10000	00x01	00001	10000	0?
Elmidae, Larainae/2	00000	10000	10100	10000	00000	01020	00001	00000	00100	10000	10000	00x01	00001	10000	0?
Elmidae, Elminae/1	00000	00001	11100	10000	00000	0x120	01001	00000	00110	00300	10000	00x01	00001	10000	0?
Elmidae, Elminae/2	00000	00001	11100	10000	00000	0x120	01001	00000	00110	00300	10000	00x01	00001	10000	0?
Lutrochidae/1	00000	20001	10100	10000	00000	00020	00001	00211	00110	00200	11200	00x01	00001	10003	00
Lutrochidae/2	00100	20001	10100	10000	00000	00020	00001	00211	00110	00200	11200	00x01	00001	10003	00
Limnichidae, Hyphalinae	00000	?0001	10100	10000	00000	1x120	000?1	0??1?	00110	00010	?0?00	00100	00001	10000	0?
Limnichidae, Limnichinae	00000	00001	10100	10000	00000	1x120	000?1	0?211	00110	00010	10100	00100	00000	10000	01
Limnichidae, Cephalobyrrhinae	00000	?0001	10100	10000	00000	1x120	000?1	0??1?	00110	???10	?0?00	00?00	00000	10000	0?
Limnichidae, Thaumastodinae	00000	00001	10100	10000	00000	1x120	00001	00211	00110	???10	?0?00	00?00	00000	10000	0?
Dryopidae/1	00000	00001	10100	10000	00000	1x020	00001	01211	00110	00010	11000	00x01	00000	11002	01
Dryopidae/2	10000	00001	10100	10000	00000	1x120	00001	01211	00110	00010	11000	00x01	00000	11002	01
Heteroceridae, Elythomerinae	00100	01101	10101	11001	00000	1x120	000?1	0?210	10110	???10	10000	00?00	00000	00000	0?
Heteroceridae, Heterocerinae	00100	01101	10101	11001	00000	1x120	00001	01210	10110	00010	10000	00100	00000	00000	00

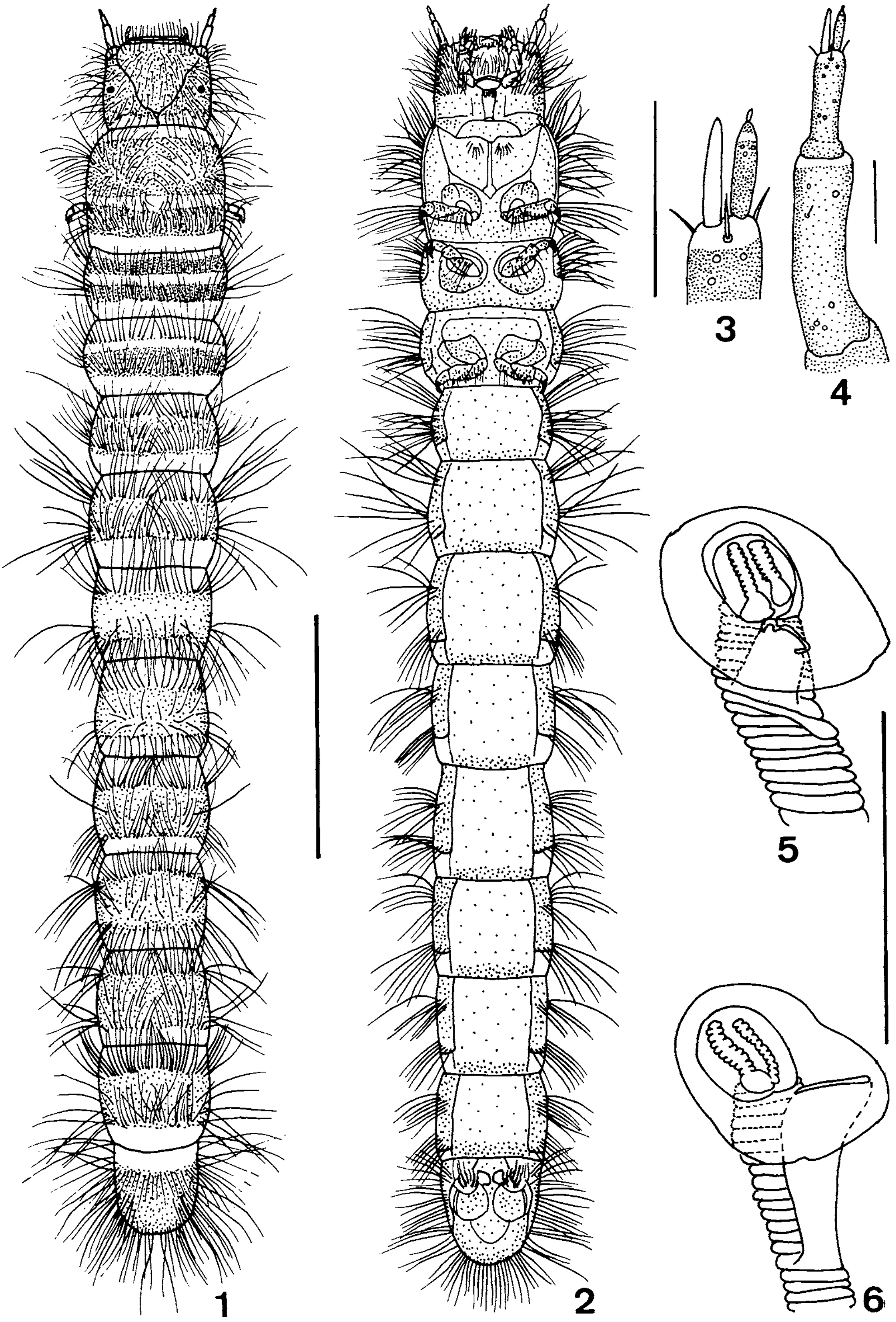


Fig. 1-6. *Cneoglossa edsoni* sp. n. Paratype. Mature larva: 1, 2, general (dorsal, ventral); 3, 4, antenna (apex, general); 5, 6, spiracles (thoracic, abdominal). Scale: Fig. 1, 2 = 3 mm; 3; 4; 5, 6 = 0.1 mm.

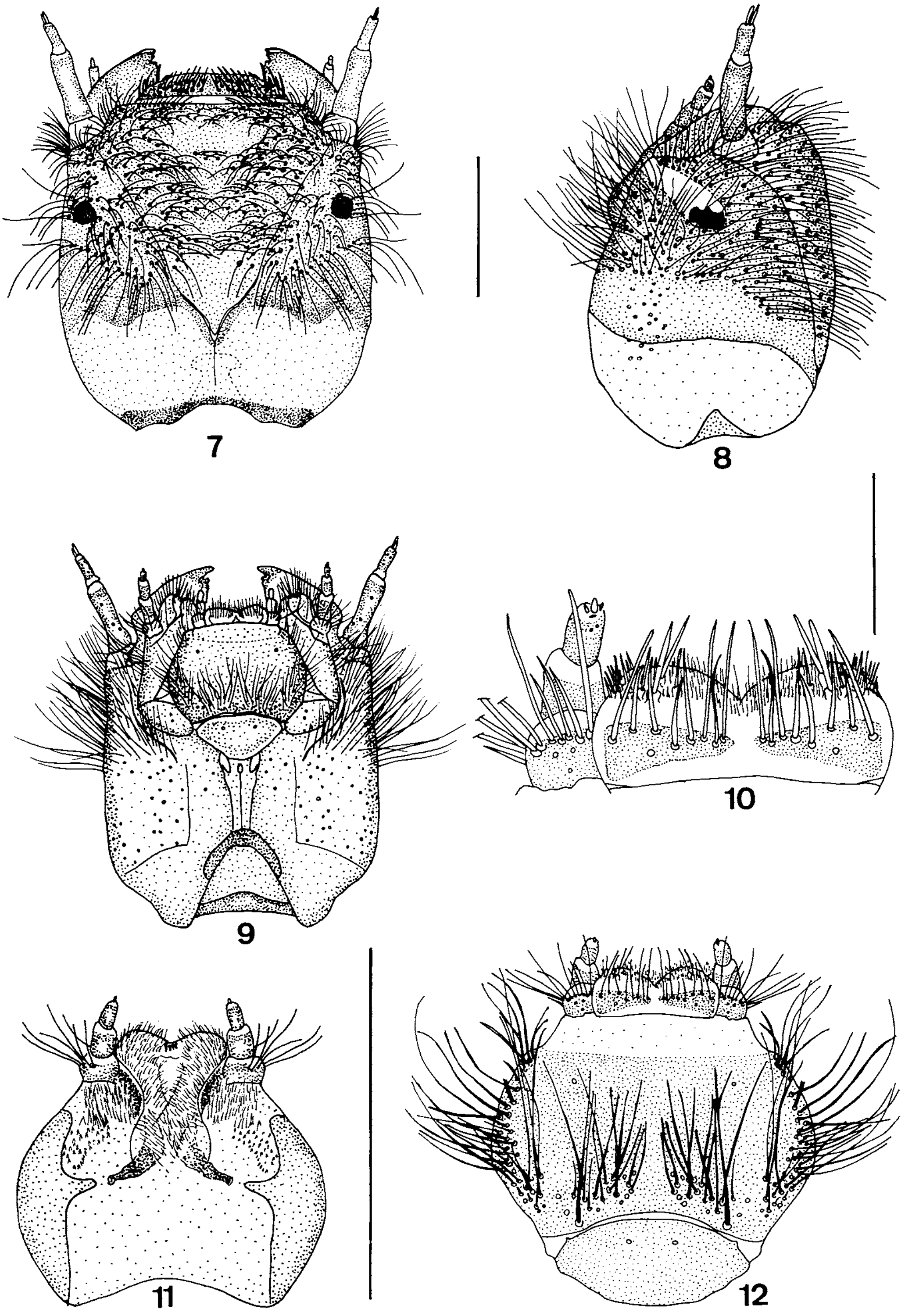


Fig. 7-12. *Cneoglossa edsoni* sp. n. Mature larva: 7-9, head, general (dorsal, lateral, ventral); 10, labial palp and ligula; 11, hypopharynx; 12, labium. Scale: Fig. 7-9; 11, 12 = 0.5 mm; 10 = 0.1 mm.

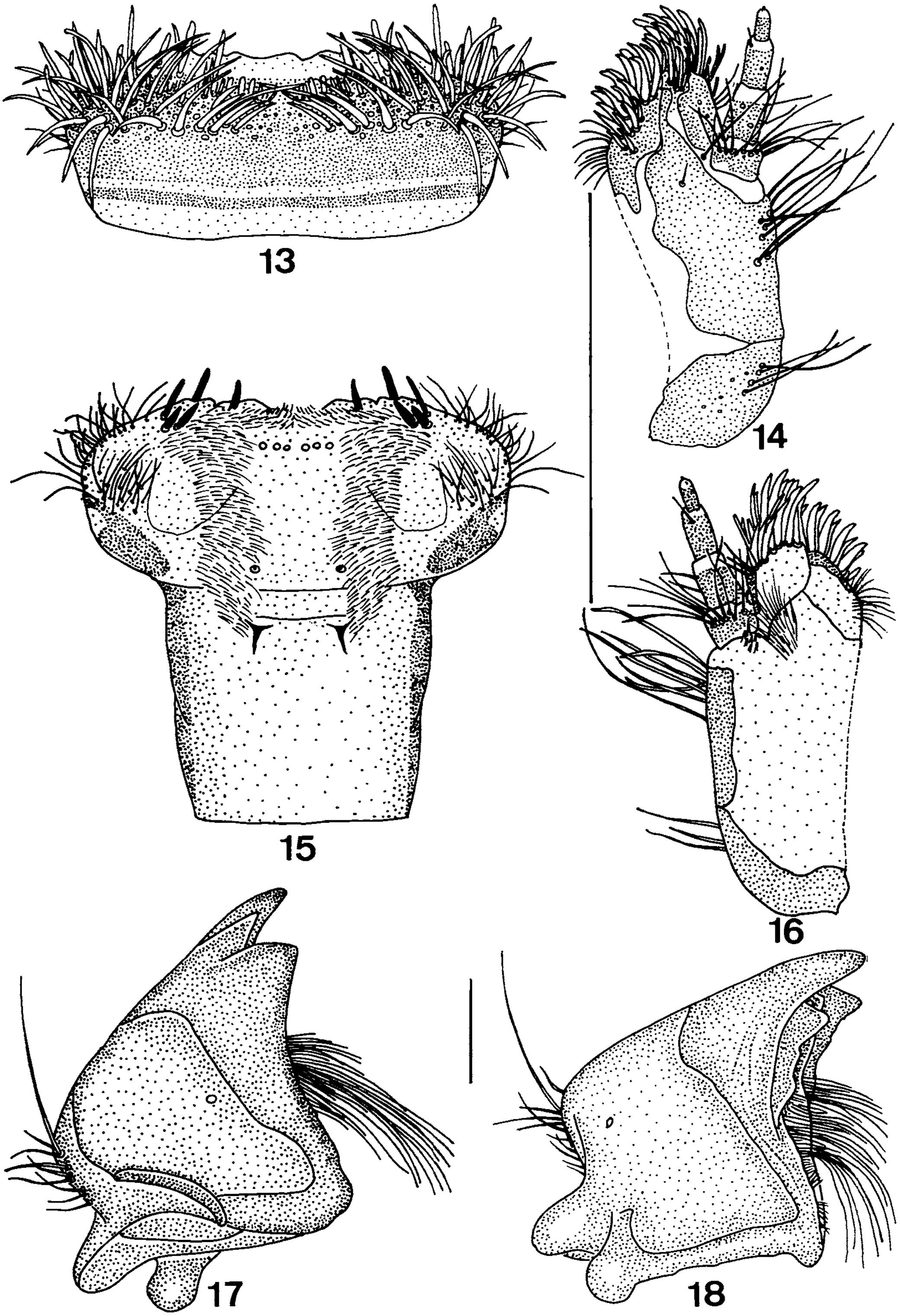


Fig. 13-18. *Cneoglossa edsoni* sp. n. Mature larva: 13, labrum; 14, 16, left maxilla (ventral, dorsal); 15, epipharynx; 17, 18, mandibles (left dorsal, right ventral). Scale: Fig. 13-16 = 0.5 mm; 17, 18 = 0.1 mm.

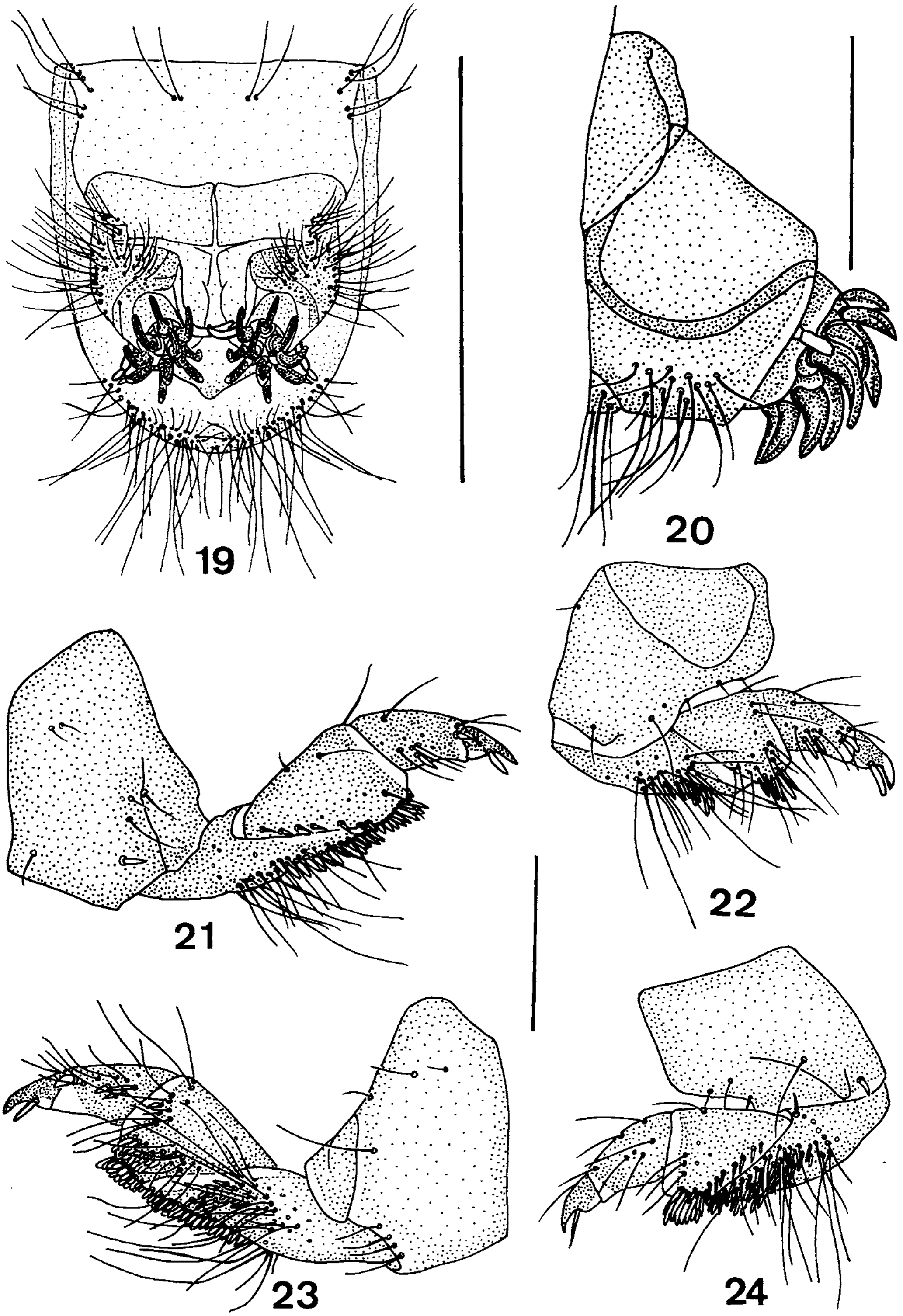


Fig. 19-24. *Cneoglossa edsoni* sp. n. Mature larva: 19, 9th and 10th segments (ventral); 20, pygopod (lateral); 21, 23, anterior leg (internal, external); 22, 24, posterior leg (internal, external). Scale: Fig. 19; 20; 21-24 = 0.5 mm.

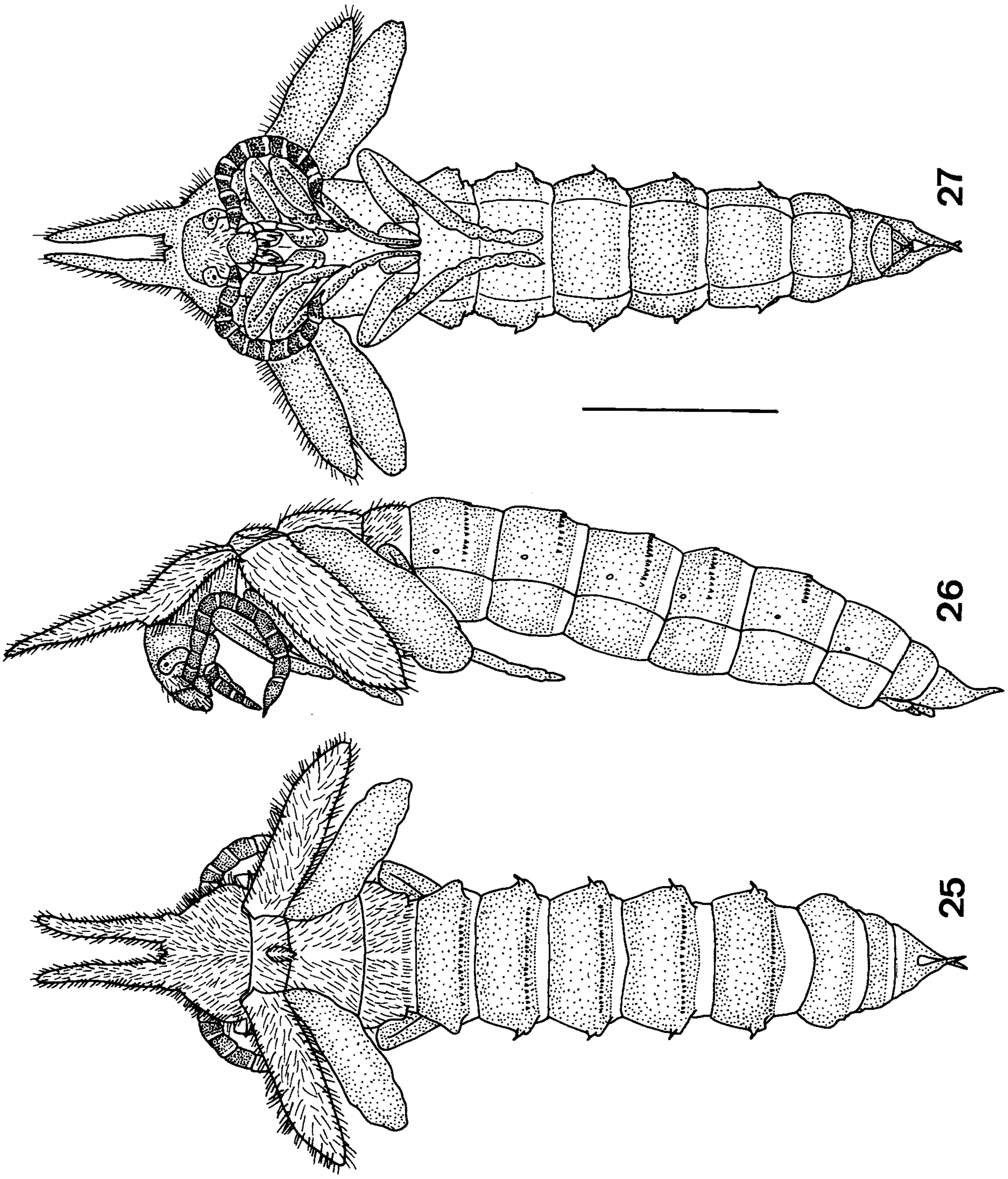


Fig. 25-27. *Cneoglossa edsoni* sp. n. Paratype. Pupa: general (dorsal, lateral, ventral). Scale = 3 mm.

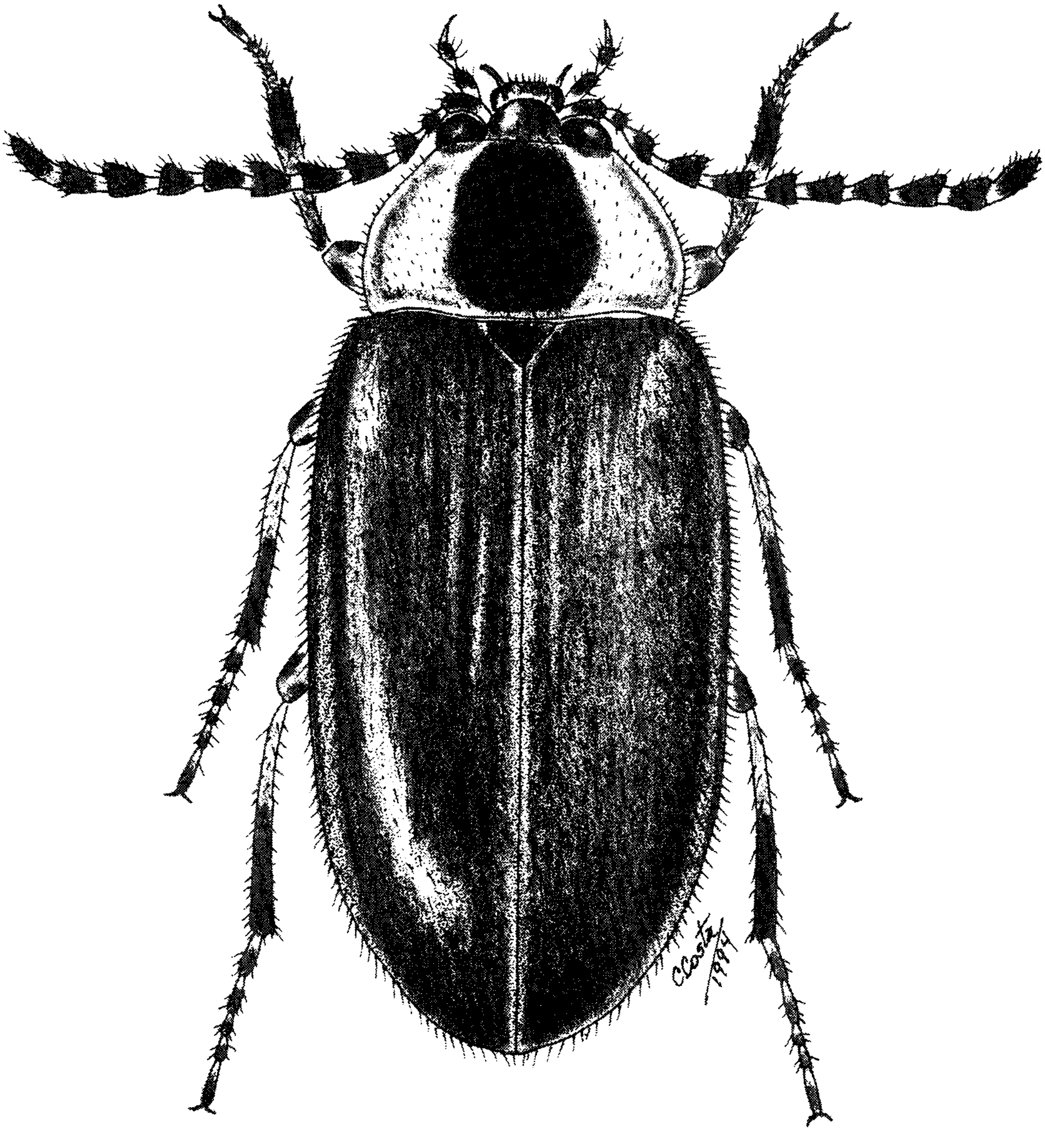


Fig. 28. *Cneoglossa edsoni* sp. n. Paratype. ♂ Adult: general (dorsal). Length 4.5 mm.

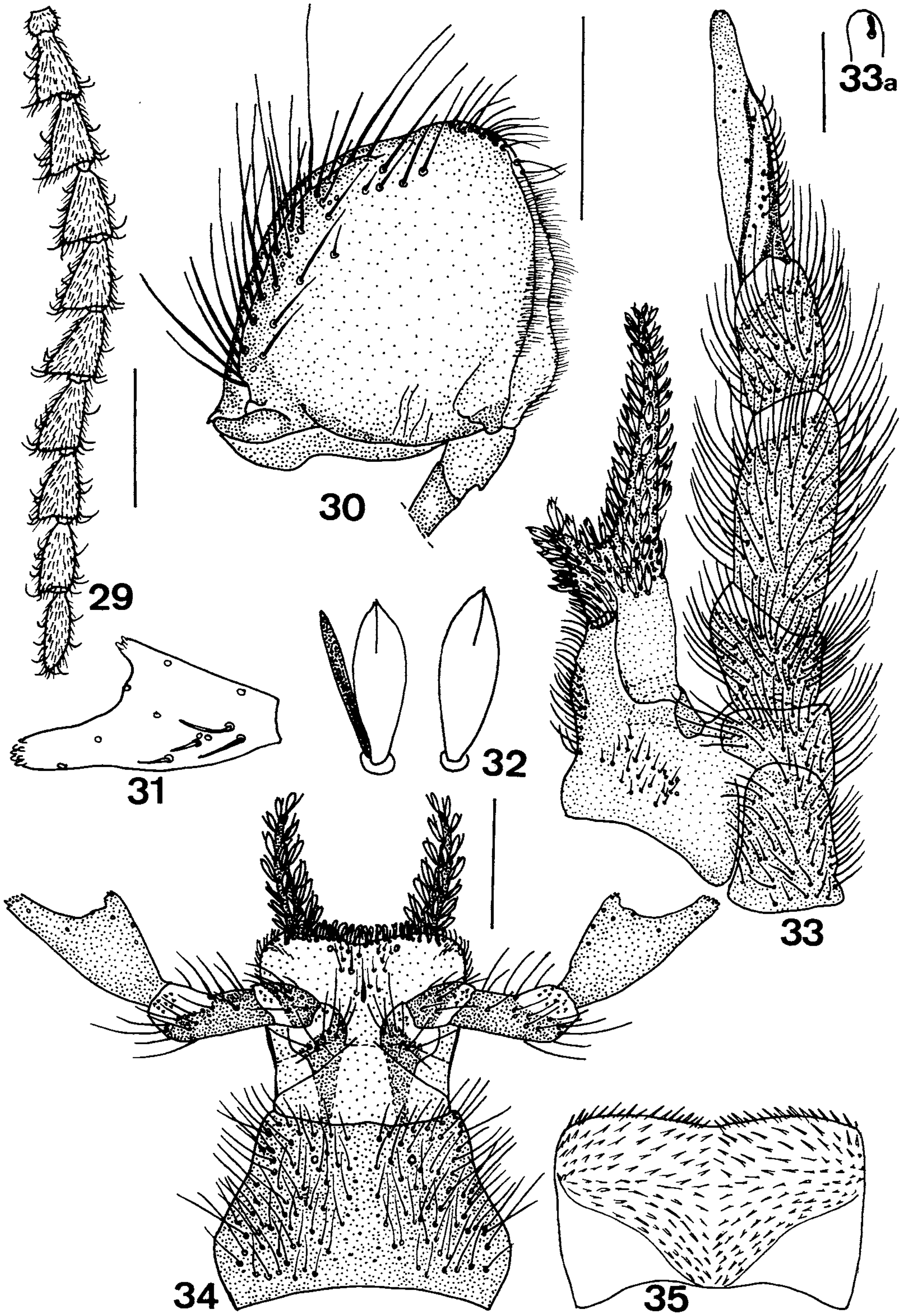


Fig. 29-35. *Cneoglossa edsoni* sp. n. ♂ : 29, antenna (segments 2-11); 30, left mandible (dorsal); 31, 34, labium (3rd palpomere, anterior region); 32, 33, 33a, left maxilla (lacinial setae, general ventral, peg); 35, hypopharynx. Scale: Fig. 29 = 0.5 mm; 30, 31, 35; 33, 34 = 0.1 mm; 33a = 0.05 mm; 32, schematic, without scale.

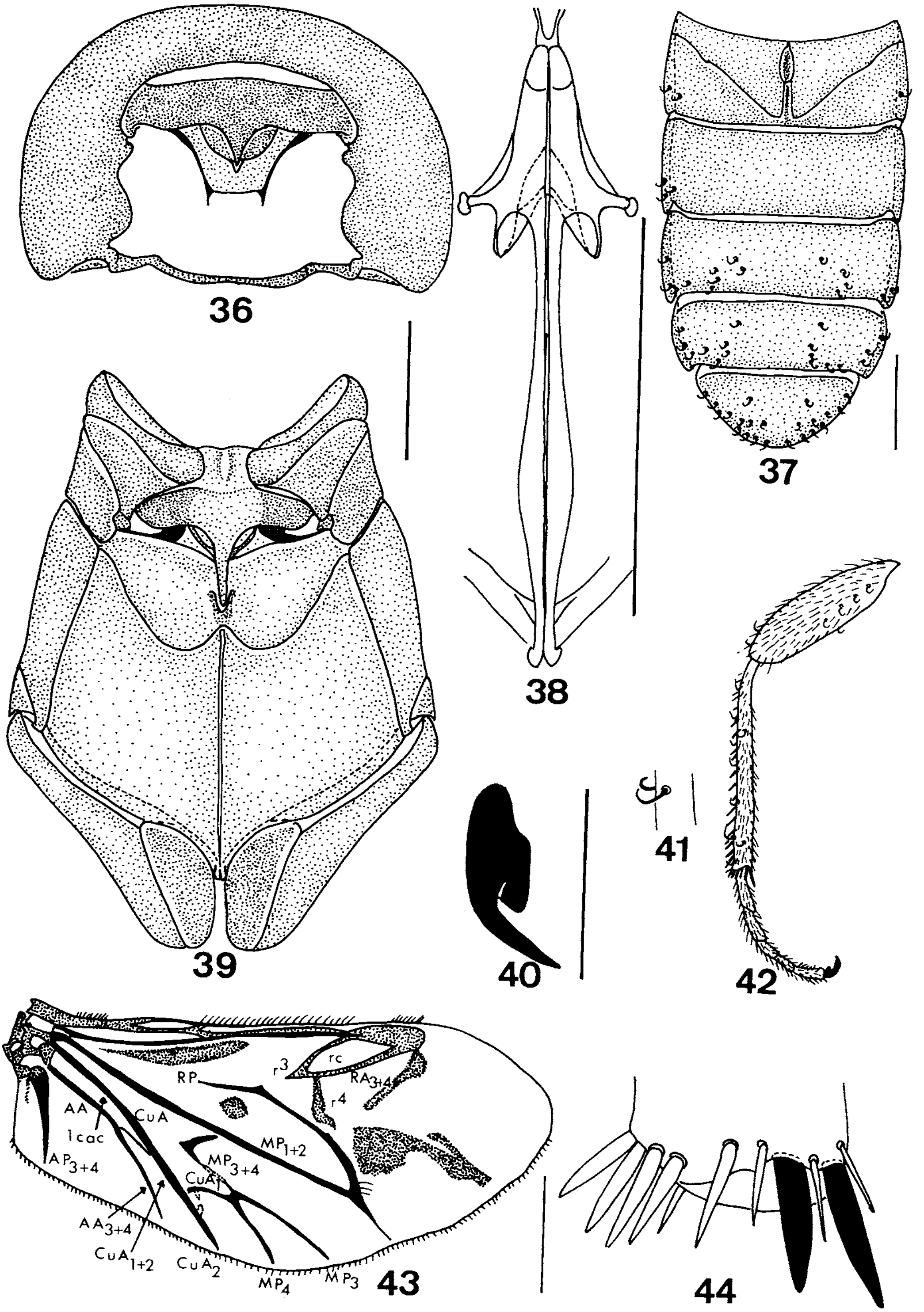


Fig. 36-44. *Cneoglossa elongata* Pic. ♀: 36, prothorax (ventral); 37, abdomen (ventral); 38, metendosternite; 39, meso- and metathorax (ventral); 40-42, 44, leg (claw, curled setae, general, tibial apex); 43, membranous wing. Scale: Fig. 36, 39; 37; 38 = 0.5 mm; 40, 44 = 0.1 mm; 42, 43 = 1 mm; 41, schematic, without scale.

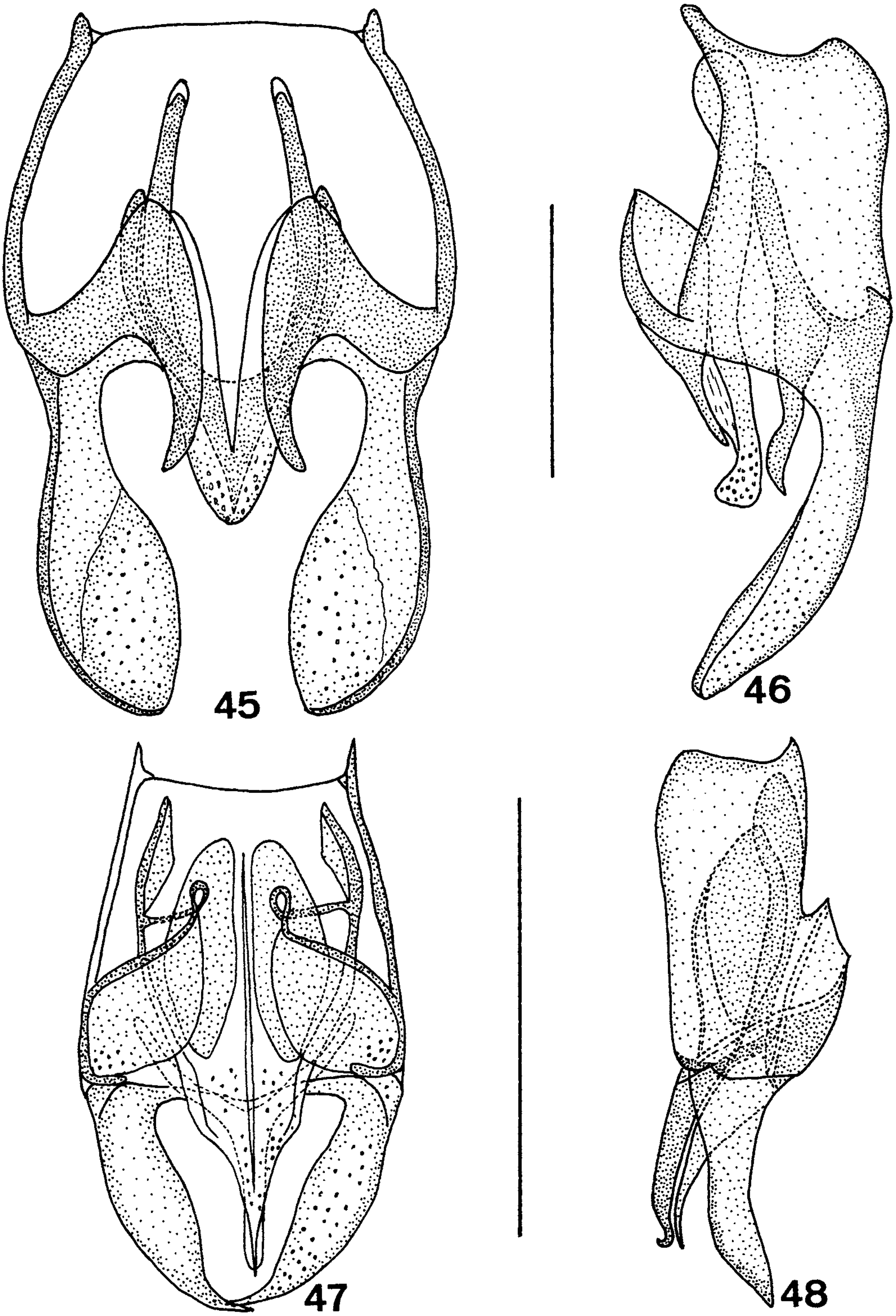


Fig. 45-48. 45, 46. *Cneoglossa elongata* Pic. ♂ : aedeagus (dorsal, lateral). 47, 48. *C. edsoni* sp. n. Holotype. ♂: aedeagus (dorsal, lateral). Scale: Fig. 45, 46, = 0.2 mm; 47, 48 = 0.5 mm.

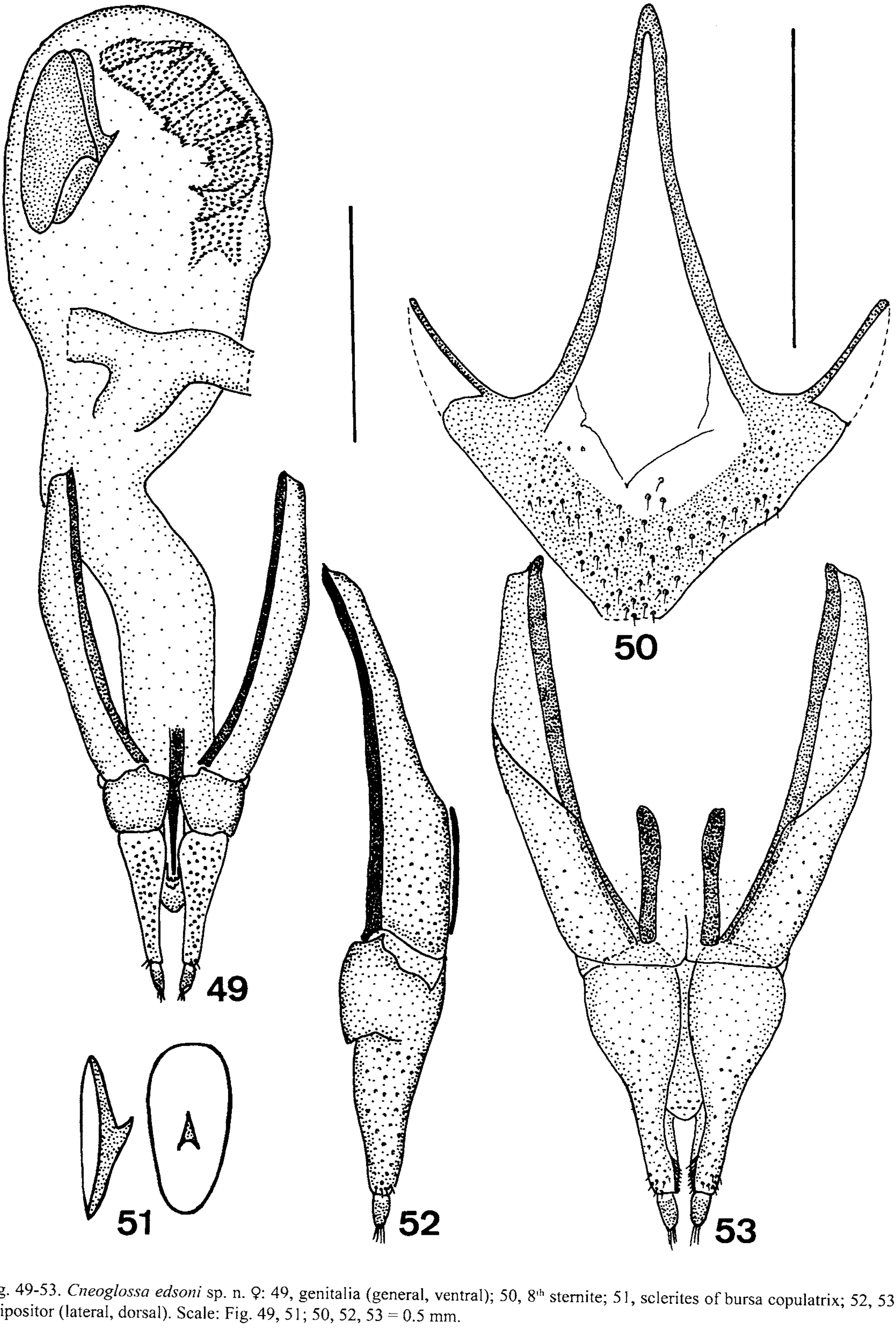


Fig. 49-53. *Cneoglossa edsoni* sp. n. ♀: 49, genitalia (general, ventral); 50, 8th sternite; 51, sclerites of bursa copulatrix; 52, 53, ovipositor (lateral, dorsal). Scale: Fig. 49, 51; 50, 52, 53 = 0.5 mm.

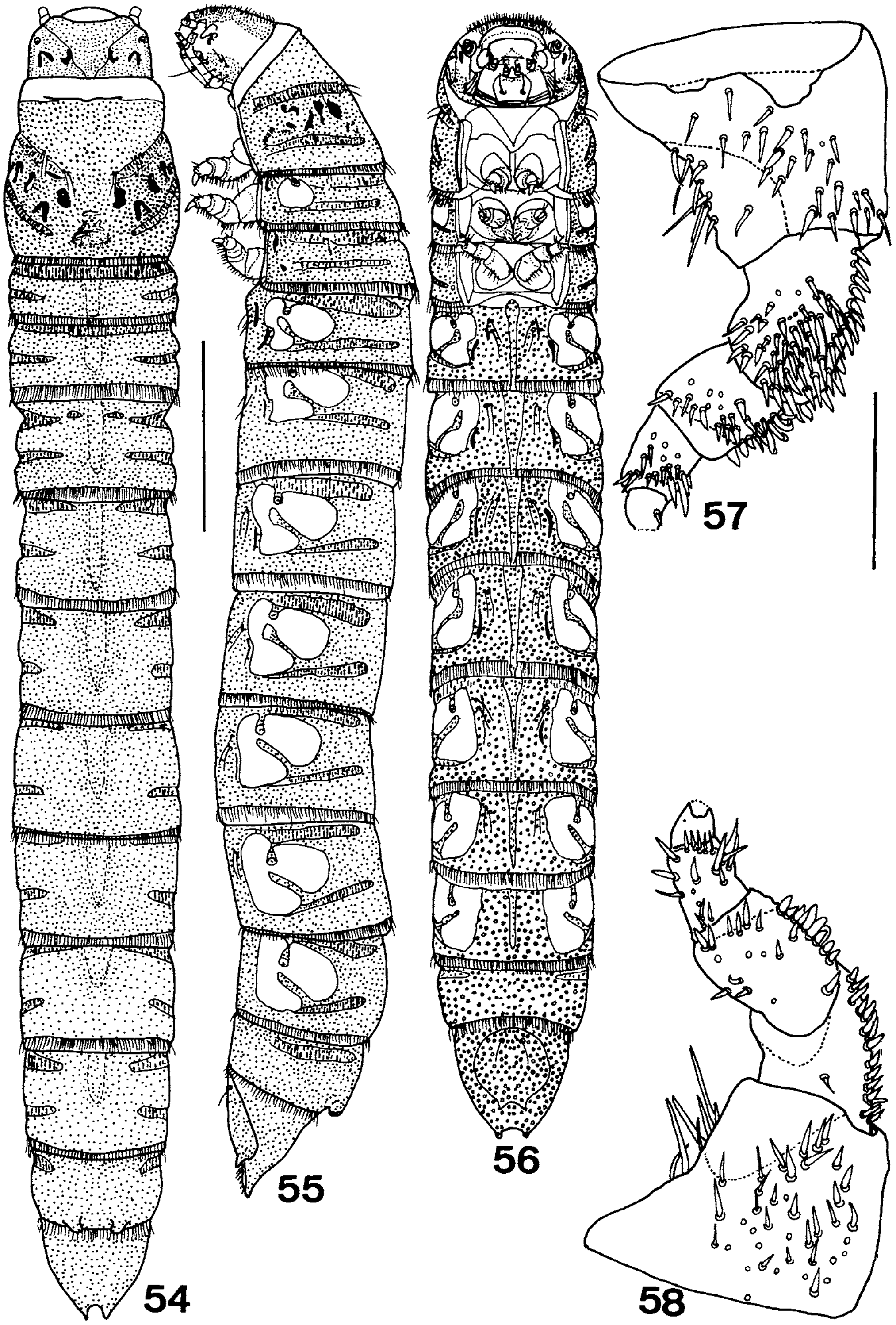


Fig. 54-58. *Araeopidius monachus* (LeConte). Mature larva: 54-56, general (dorsal, lateral, ventral); 57, 58, anterior leg (internal, external). Scale: Fig. 54-56 = 3 mm; 57, 58 = 0.5 mm.

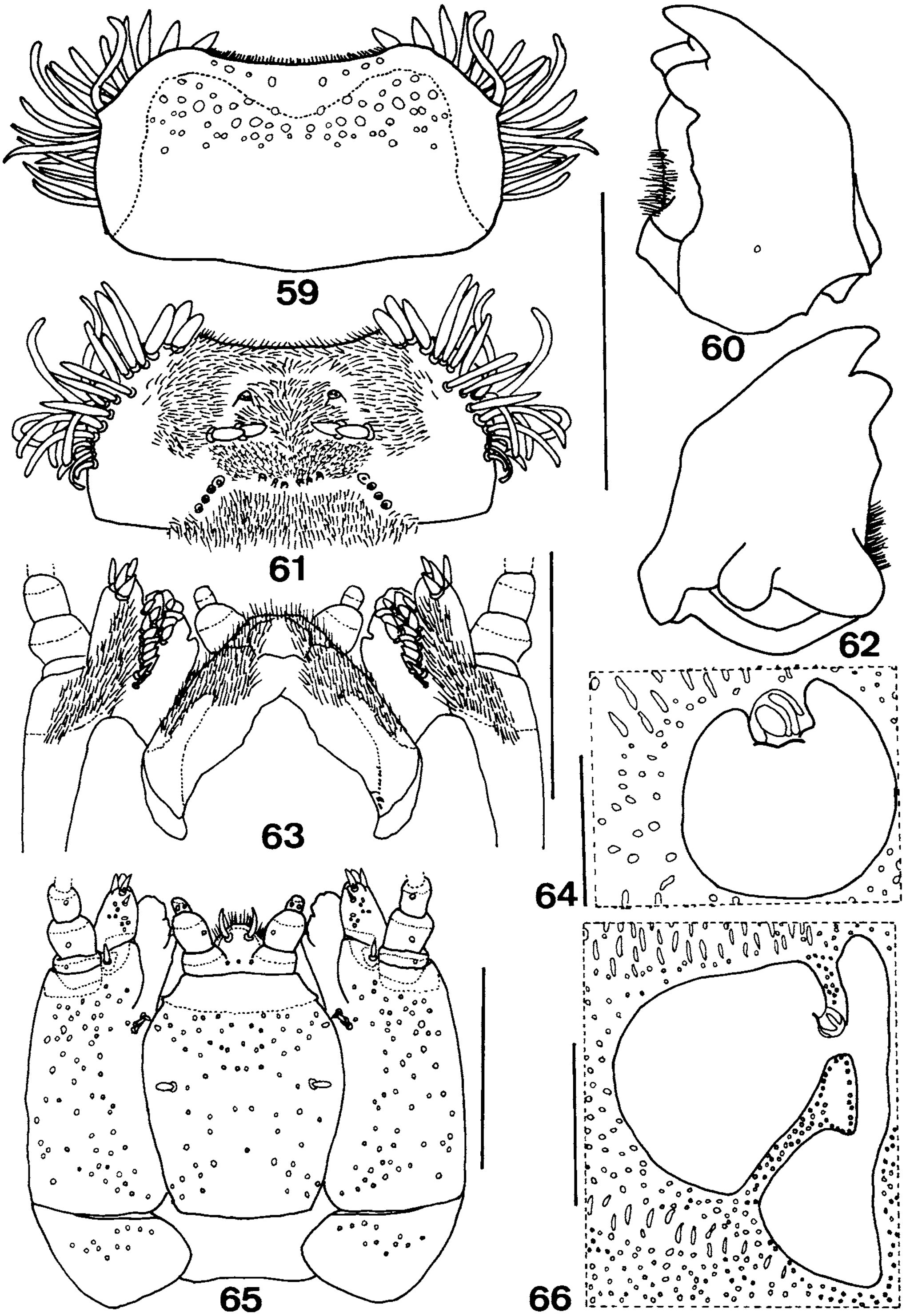


Fig. 59-66. *Araeopidius monachus* (LeConte). Mature larva: 59, labrum; 60, 62, right mandible (dorsal, ventral); 61, epipharynx; 63, maxillae (dorsal) and hypopharynx; 64, 66, plastrons and spiracles (thoracic, abdominal); 65, maxillae (ventral) and labium. Scale: Fig. 59-62; 63; 65; 66 = 0.5 mm; 64 = 0.3 mm.

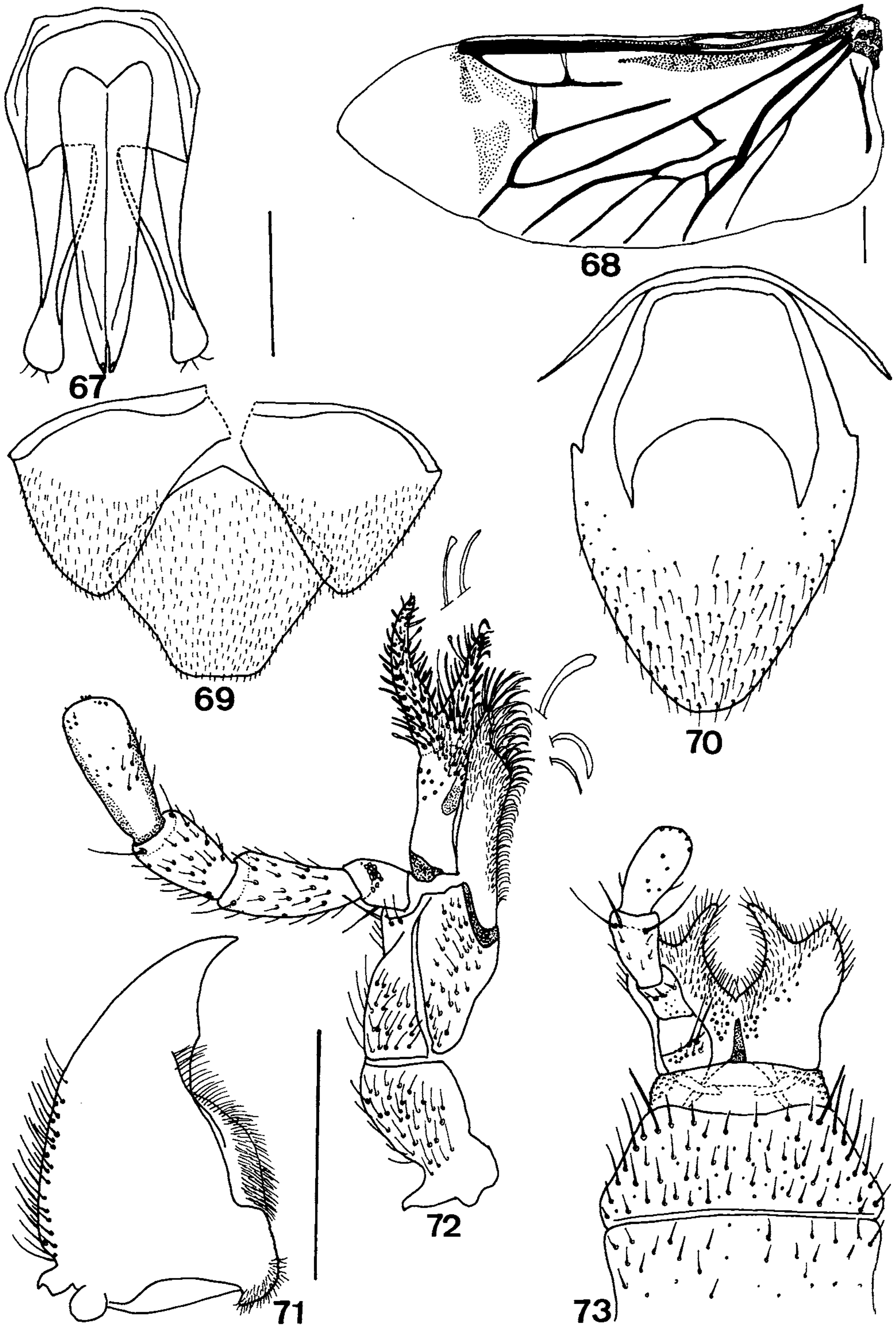


Fig. 67-73. *Araeopidius monachus* (LeConte). ♂: 67, aedeagus (ventral); 68, membranous wing; 69, 9th and 10th tergites; 70, 9th sternite; 71, right mandible (ventral); 72, right maxilla (general ventral, setae of galea and lacinia); 73, labium. Scale: Fig. 67, 69, 70; 71-73 = 0.5 mm; 68 = 1 mm.

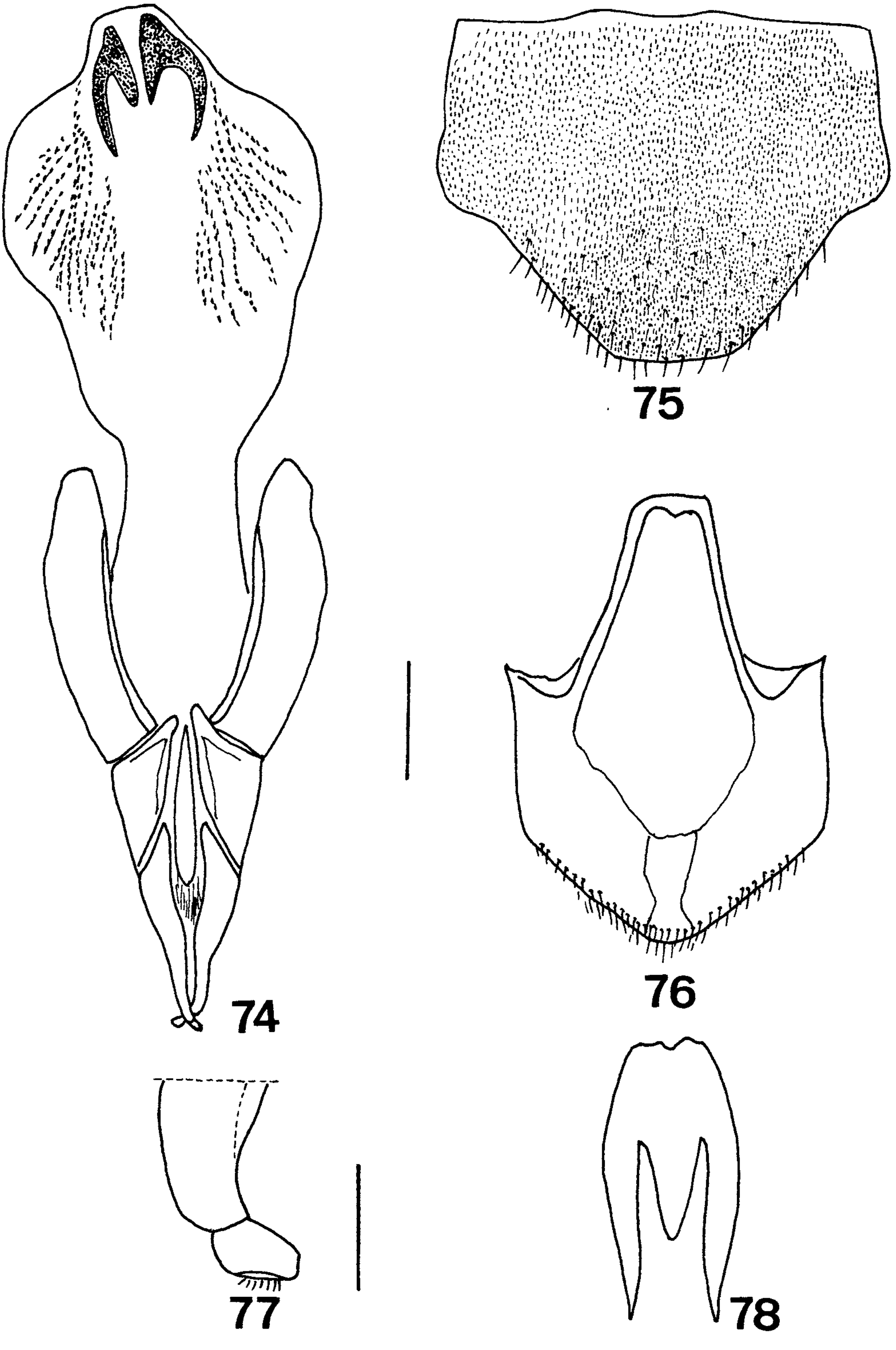


Fig. 74-78. *Araeopidius monachus* (LeConte). ♀: 74, genitalia (general); 75, 8th tergite; 76, 8th.sternite; 77, style; 78, sclerite of bursa copulatrix. Scale: Fig. 74-76, 78 = 0.5 mm; 77 = 0.1 mm.

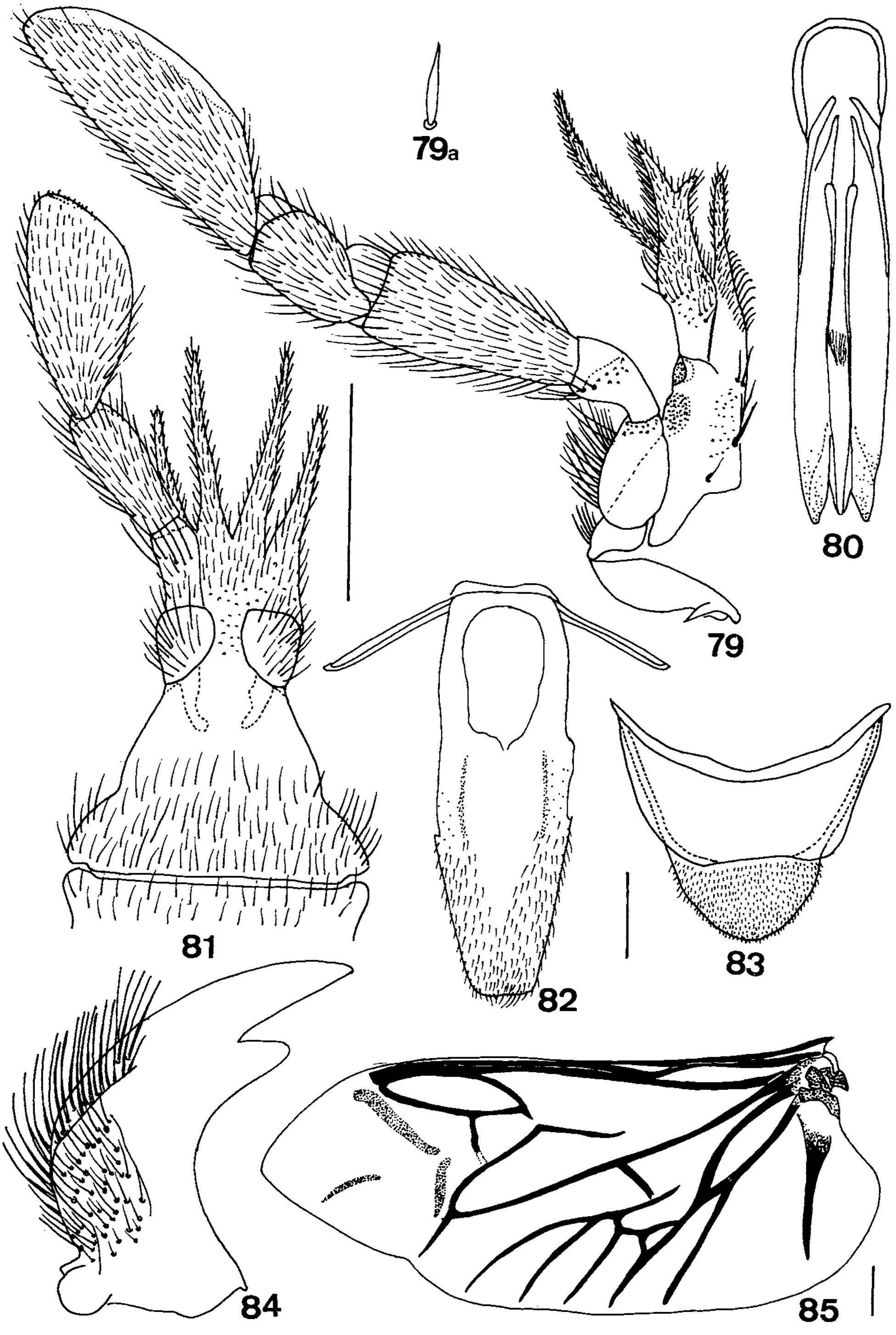
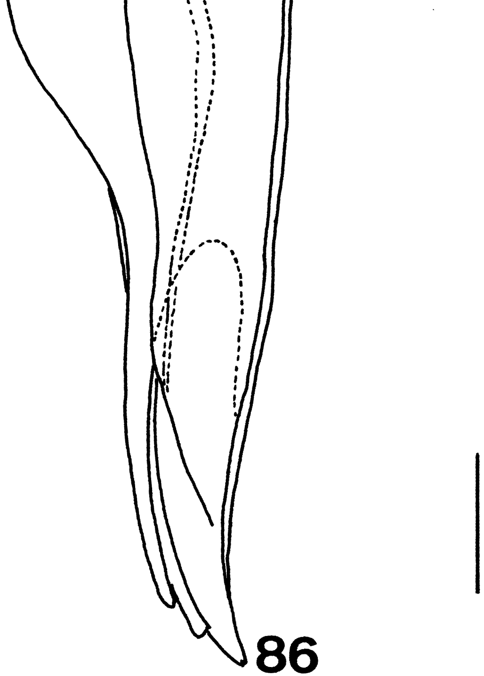
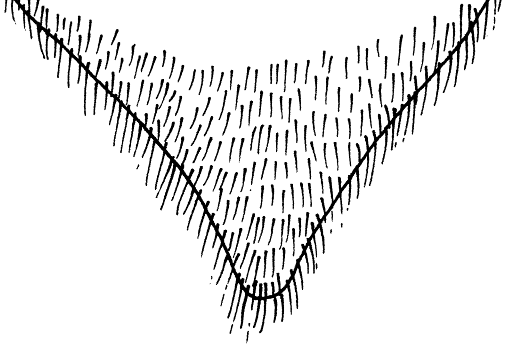


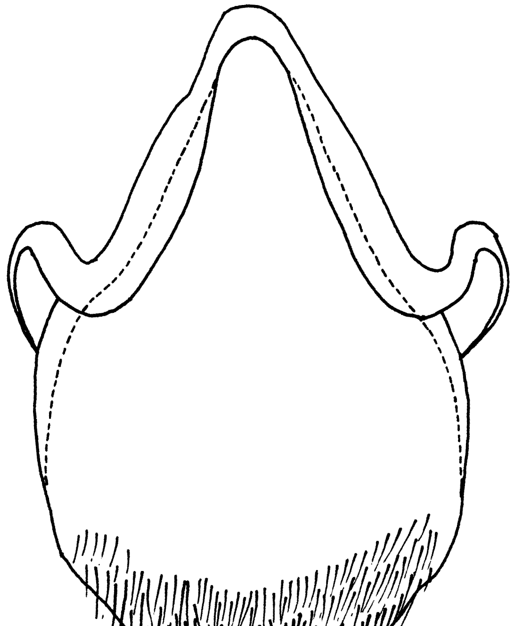
Fig. 79-85. *Cladotoma ovalis* Westwood. ♂: 79, 79a, left maxilla (general dorsal, seta of galea); 80, aedeagus (ventral); 81, labium; 82, 9th sternite; 83, 9th and 10th tergites; 84, right mandible (ventral); 85 membranous wing. Scale: Fig. 79, 81, 84; 80, 82, 83 = 0.5 mm; 85 = 1 mm.

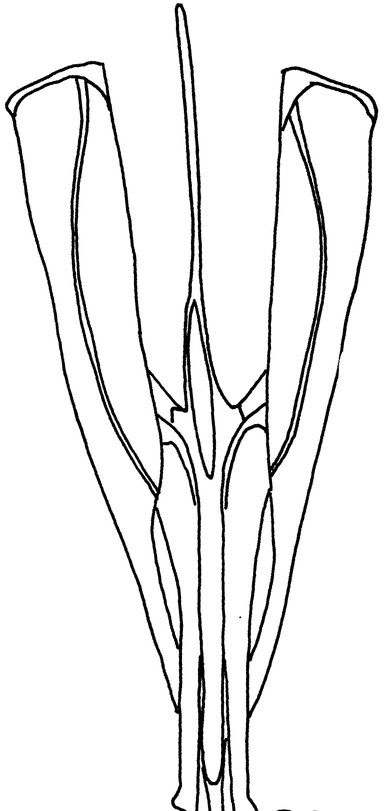


86



87





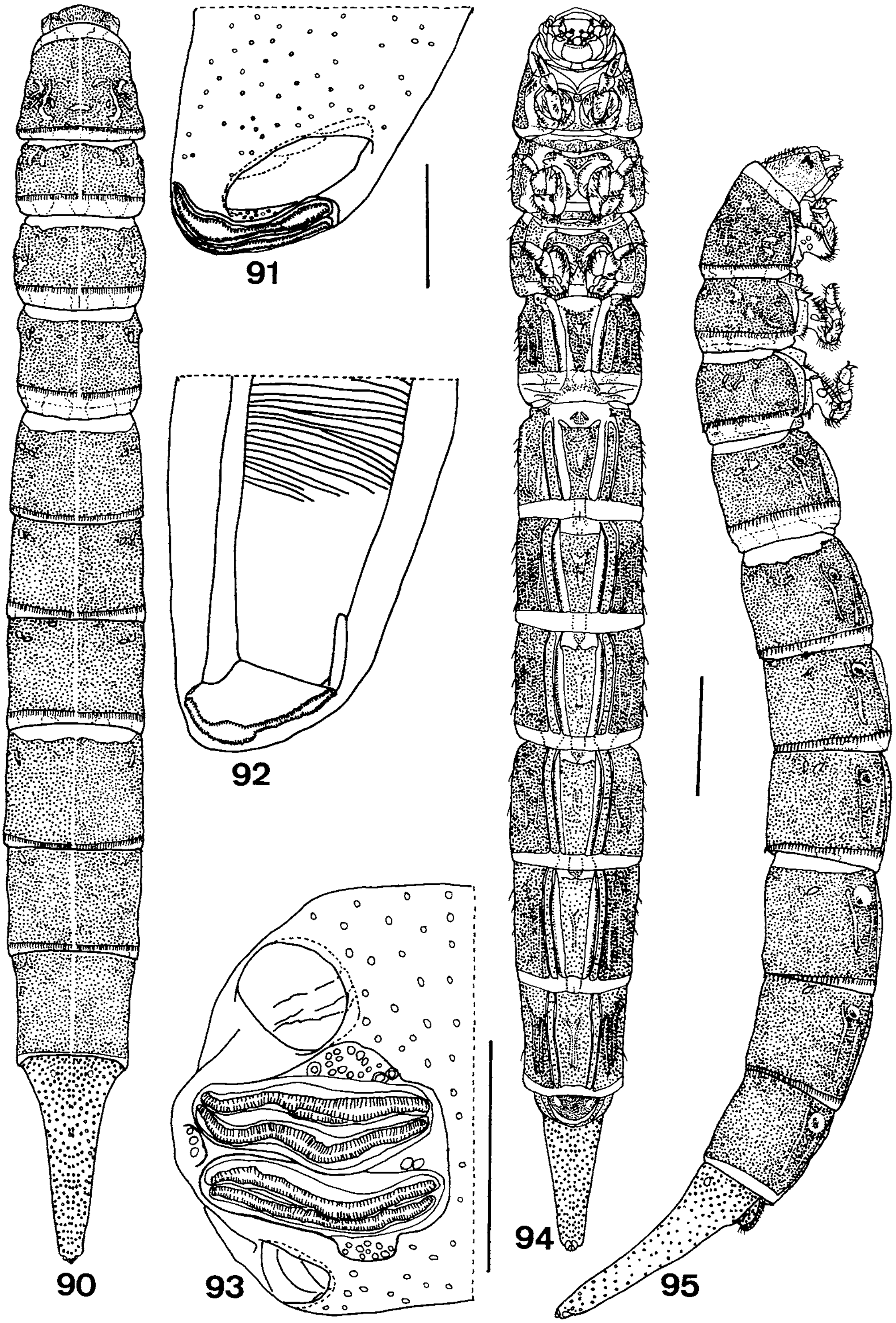


Fig. 90-95. *Paralichas pectinata* (Kiesenwetter). Mature larva: 90, 94, 95, general (dorsal, ventral, lateral); 91-93, 8th spiracle (lateral external, lateral internal, caudal). Scale: Fig. 90, 94, 95 = 3 mm; 91, 92; 93 = 0.2 mm.

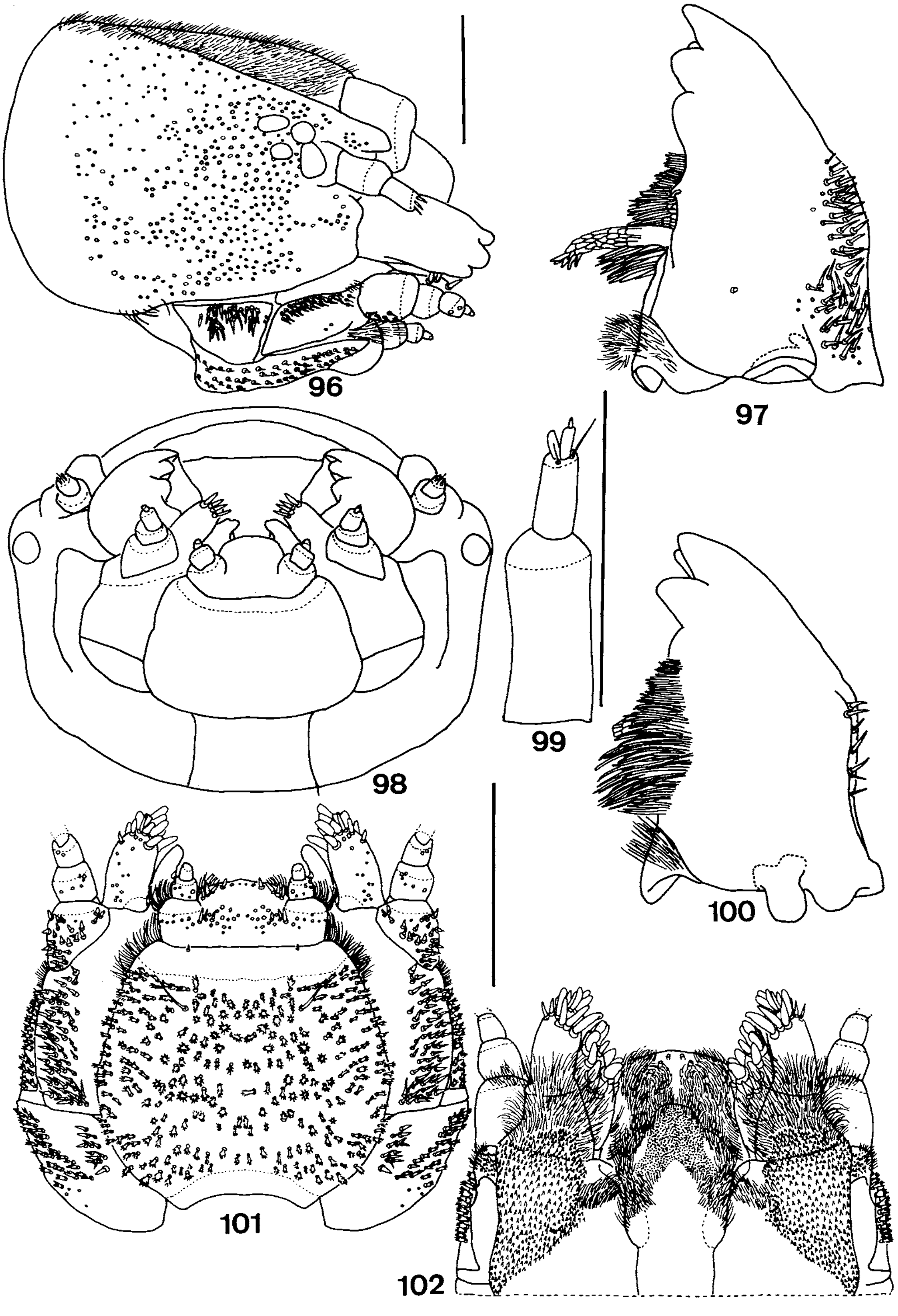


Fig. 96-102. *Paralichas pectinata* (Kiesenwetter). Mature larva: 96, 98, head, general (lateral, fronto-ventral (setae omitted)); 97, 100, mandibles (right dorsal, left ventral); 99, antenna; 101, maxillae (ventral) and labium; 102, maxillae (dorsal) and hypopharynx. Scale: Fig. 96, 98; 97, 99, 100; 101, 102 = 0.5 mm.

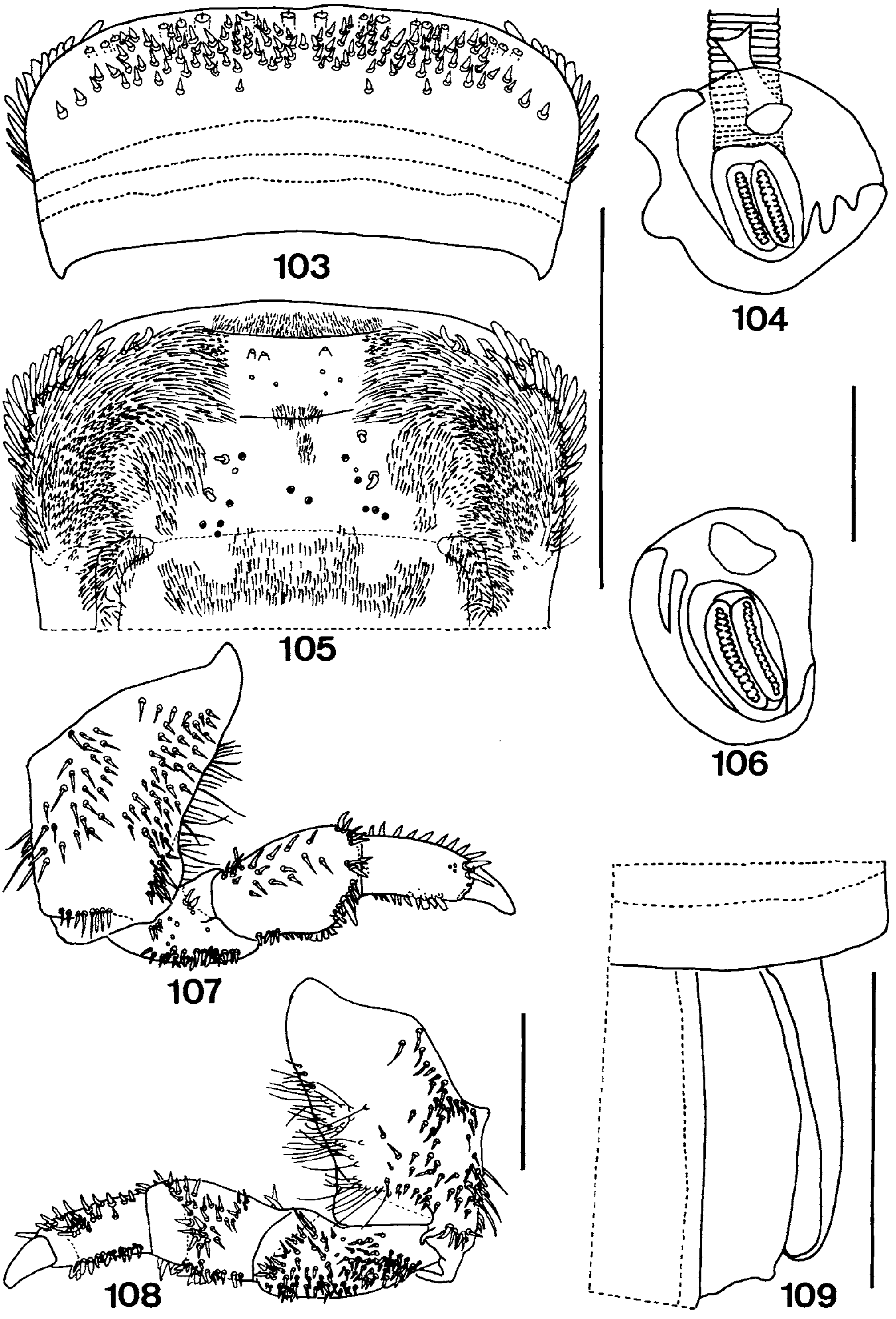


Fig. 103-109. *Paralichas pectinata* (Kiesenwetter). Mature larva: 103, labrum; 104, 106, spiracles (abdominal, thoracic); 105, epipharynx; 107, 108, anterior leg (external, internal); 109, 9th and 10th segments (lateral). Scale: Fig. 103, 105; 107, 108 = 0.5 mm; 104, 106 = 0.1 mm; 109 = 1 mm.

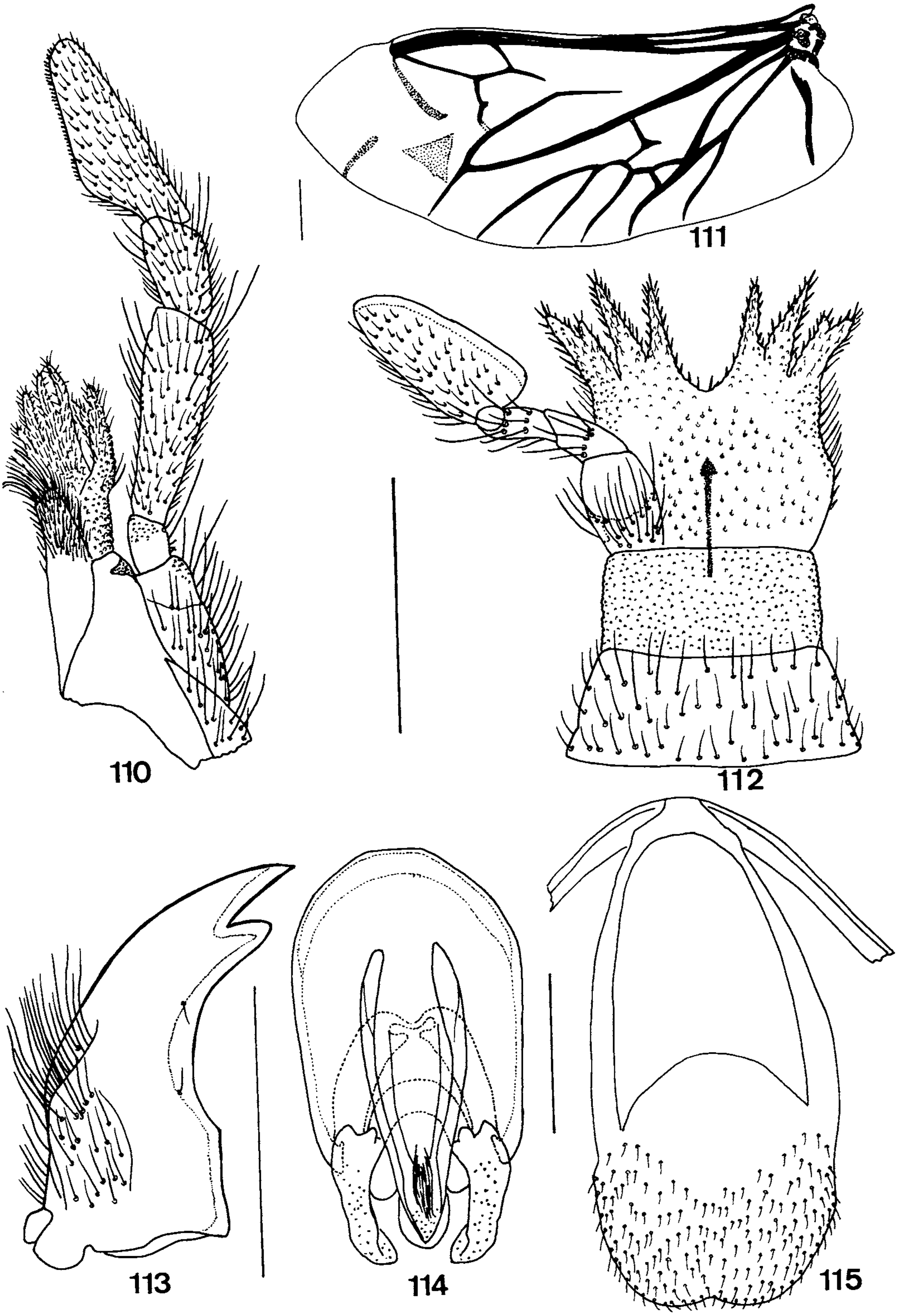


Fig. 110-115. *Paralichas pectinata* (Kiesenwetter). ♂: 110, left maxilla (ventral, cardo omitted); 111, membranous wing; 112, labium (left palp omitted); 113, right mandible (ventral); 114, aedeagus; 115, 9th sternite. Scale: Fig. 110, 112; 113; 114, 115 = 0.5 mm; 111 = 1 mm.

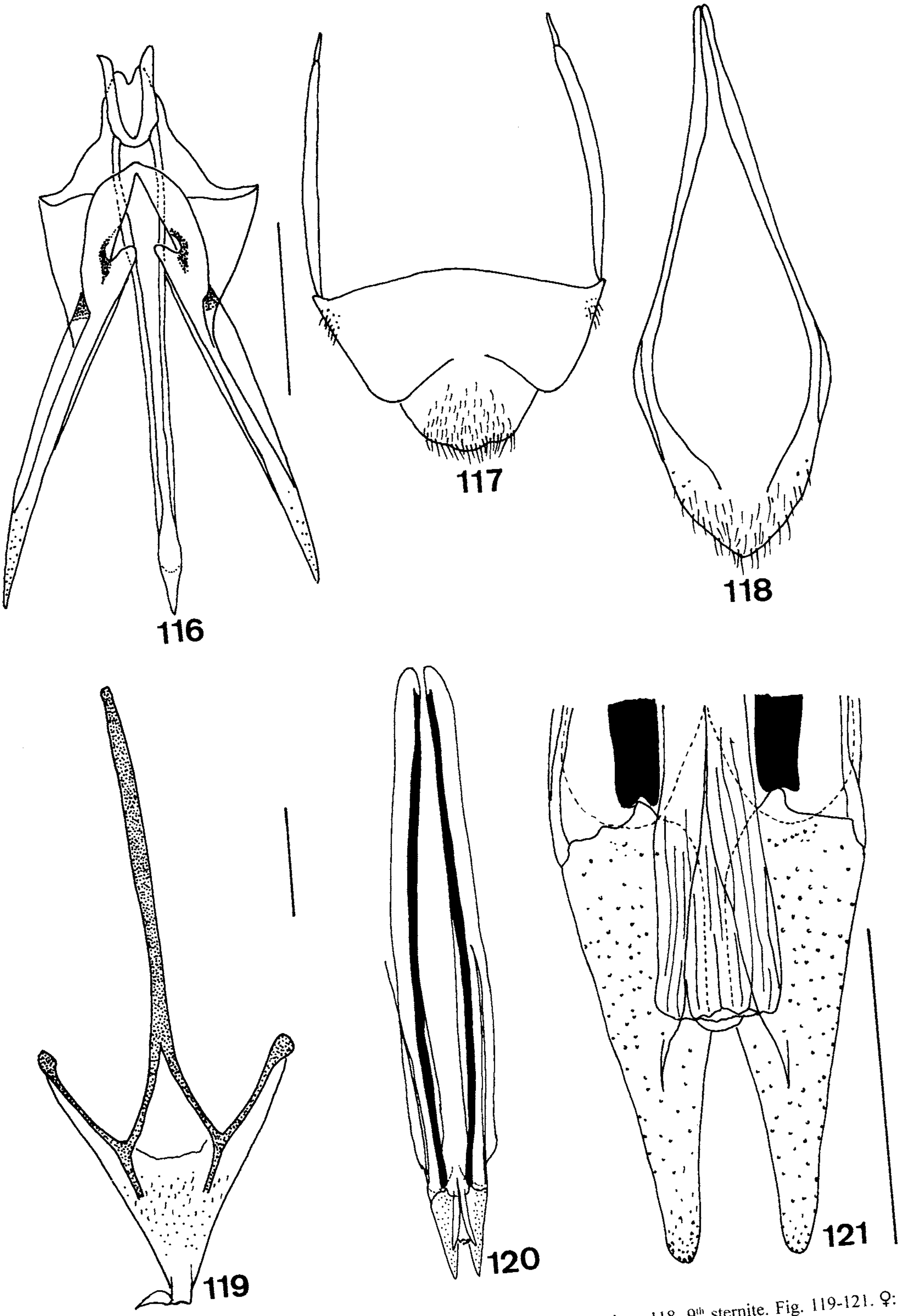


Fig. 116-118. *Ptilodactyla* sp. ♂: 116, aedeagus (ventral); 117, 9th and 10th tergites; 118, 9th sternite. Fig. 119-121. ♀: 119, 8th sternite; 120, ovipositor; 121, coxites. Scale: Fig. 116-118; 119, 120; 121 = 0.5 mm.

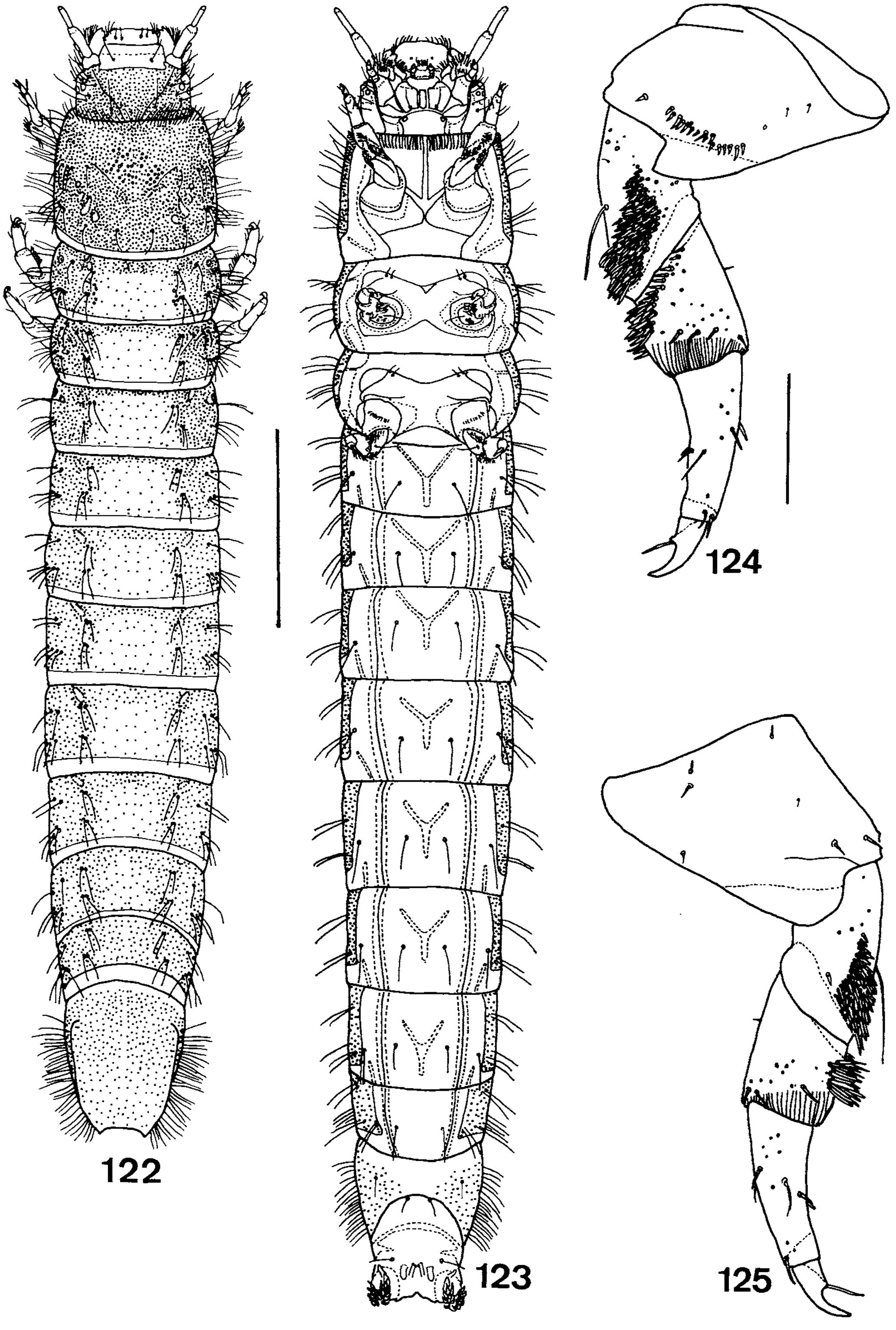


Fig. 122-125. *Anchytarsus palpalis* (Champion). Mature larva: 122, 123, general (dorsal, ventral); 124, 125, posterior leg (internal, external). Scale: Fig. 122, 123 = 3 mm; 124, 125 = 0.5 mm.

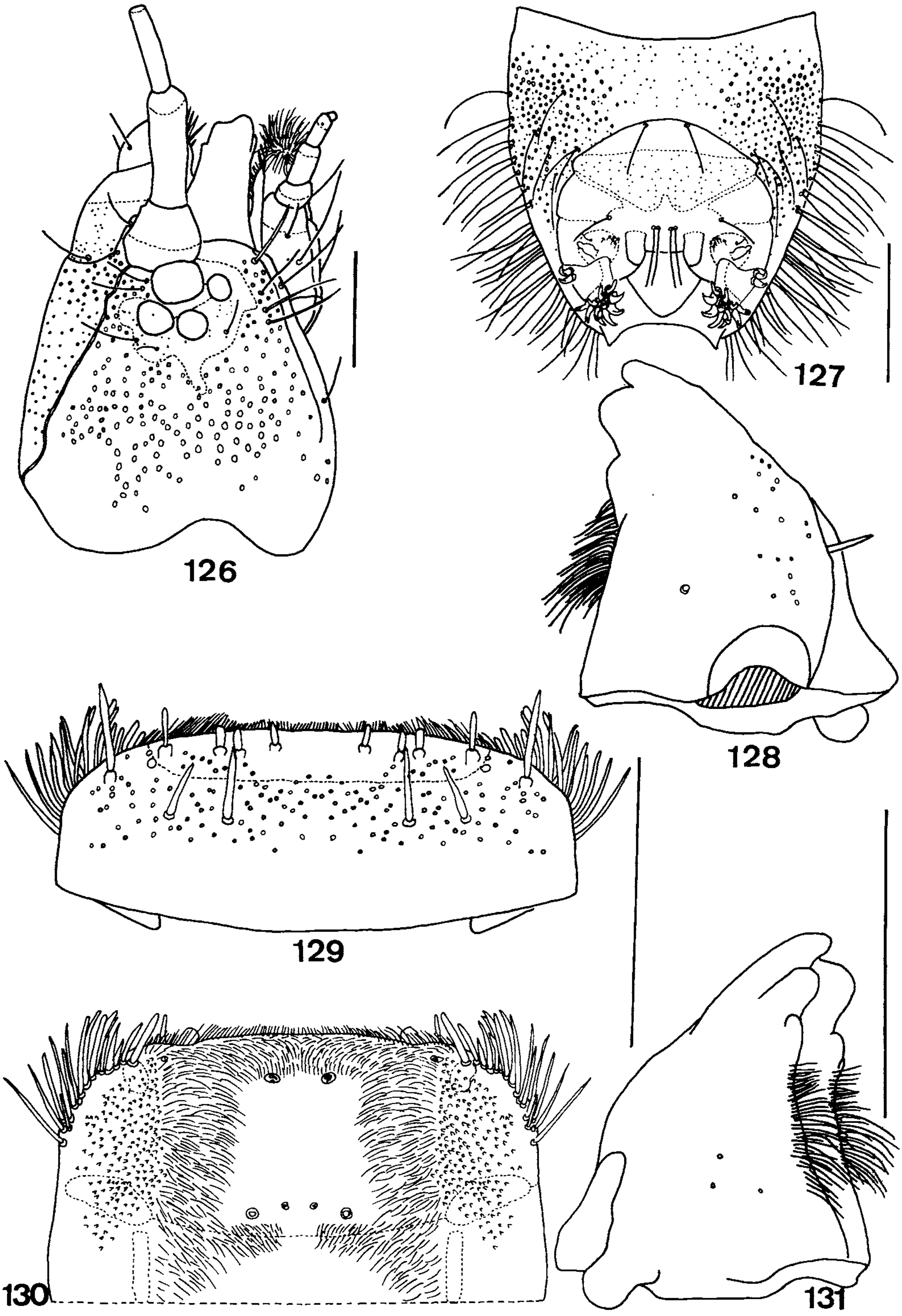


Fig. 126-131. *Anchytarsus palpalis* (Champion). Mature larva: 126, head, general (lateral); 127, 9th and 10th segments (ventral); 128, 131, right mandible (dorsal, ventral); 129, labrum; 130, epipharynx. Scale: Fig. 126; 128, 131; 129, 130 = 0.5 mm; 127 = 1 mm.

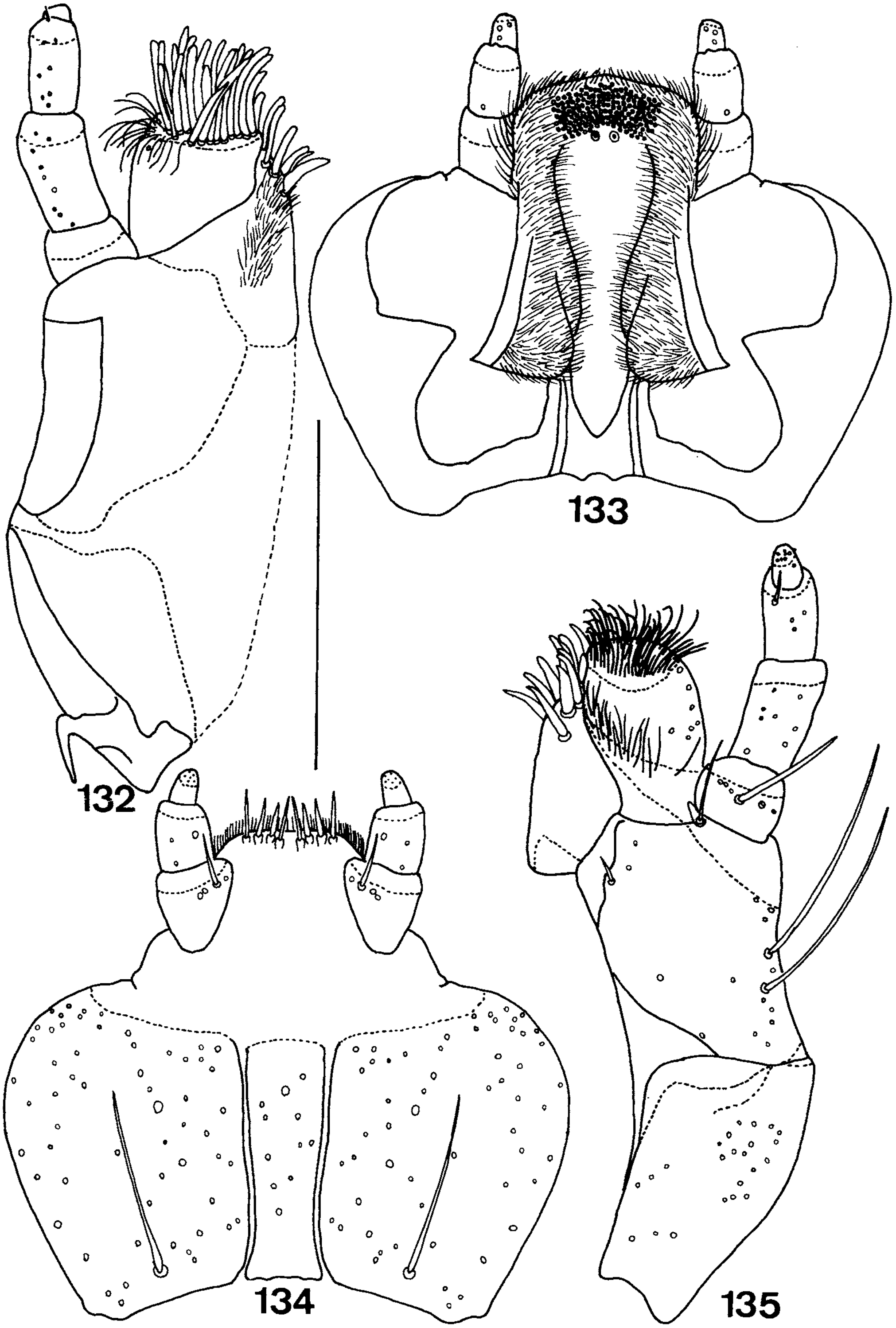


Fig. 132-135. *Anchytarsus palpalis* (Champion). Mature larva: 132, 135, left maxilla (dorsal, ventral); 133, hypopharynx; 134, labium. Scale = 0.5 mm.

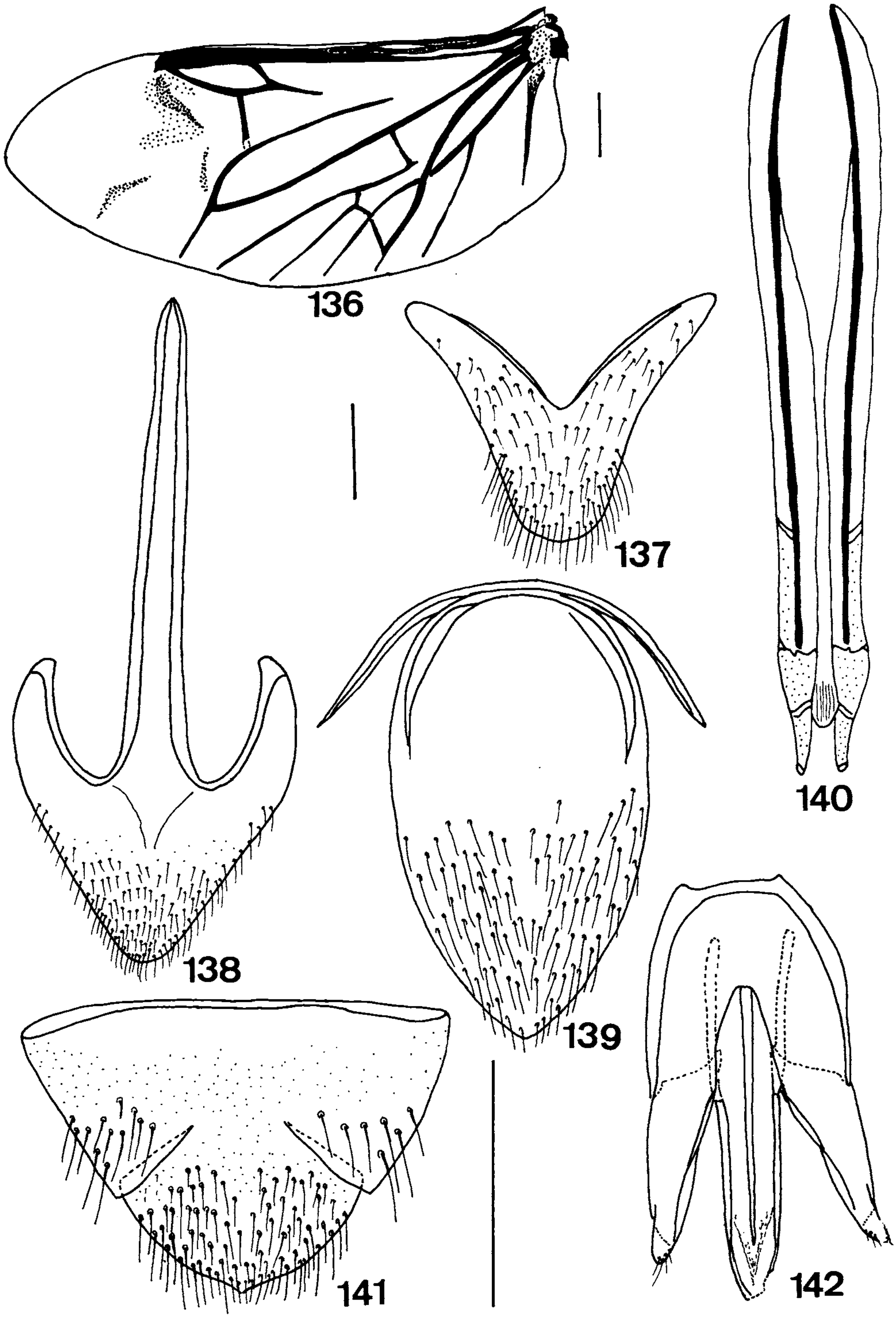


Fig. 136-139, 140. *Anchytarsus palpalis* (Champion). ♀: 136, membranous wing; 137, 8th tergite; 138, 8th sternite; 140, ovipositor. Fig. 139, 141, 142. *A. bicolor* (Melsheimer). ♂: 139, 9th sternite; 141, 9th and 10th tergite; 142, aedeagus (ventral). Scale: Fig. 136 = 1 mm; 137, 138, 140; 139, 141, 142 = 0.5 mm.

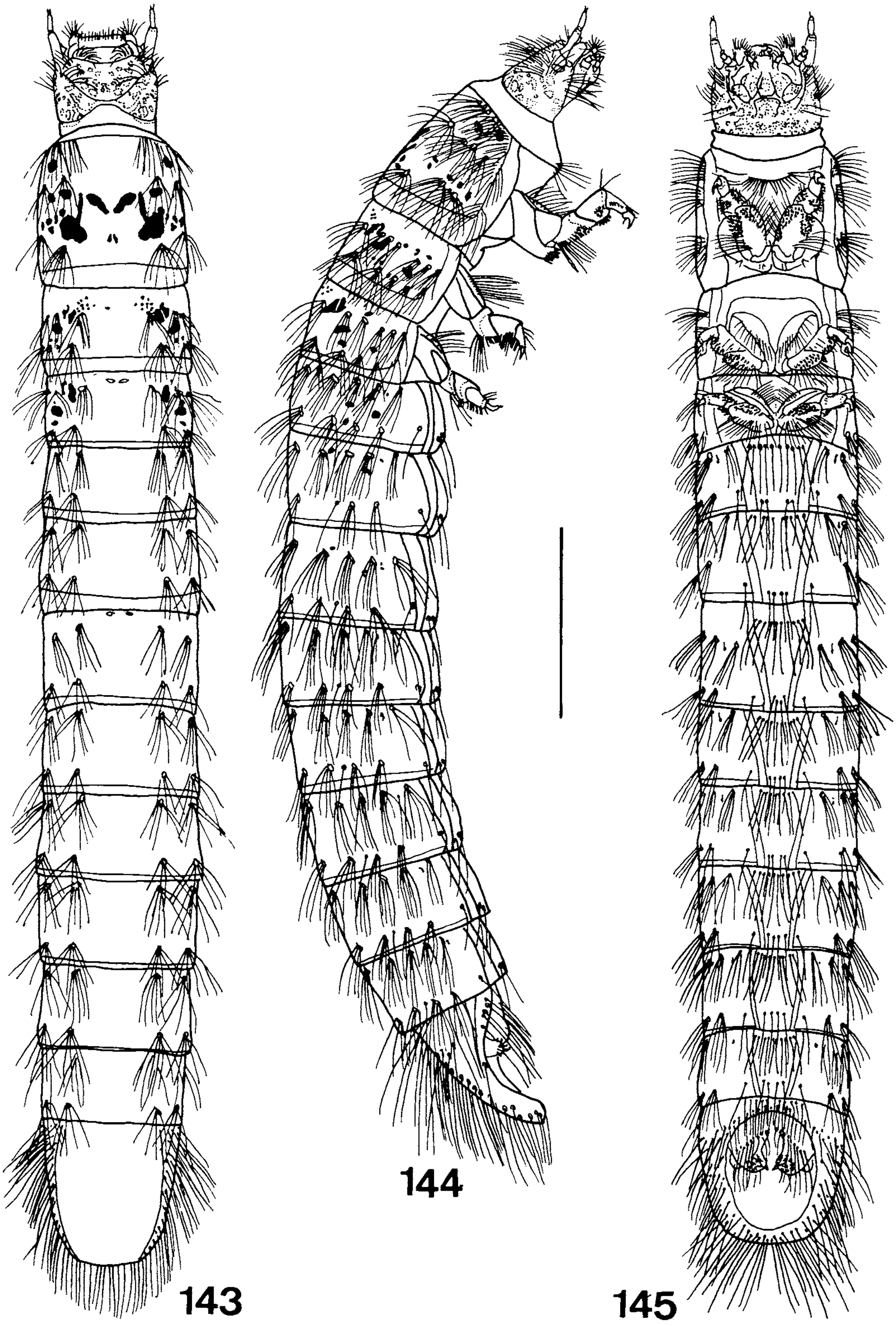


Fig. 143-145. *Epilichas flabellatus* (Kiesenwetter). Mature larva: general (dorsal, lateral, ventral). Scale = 3 mm.

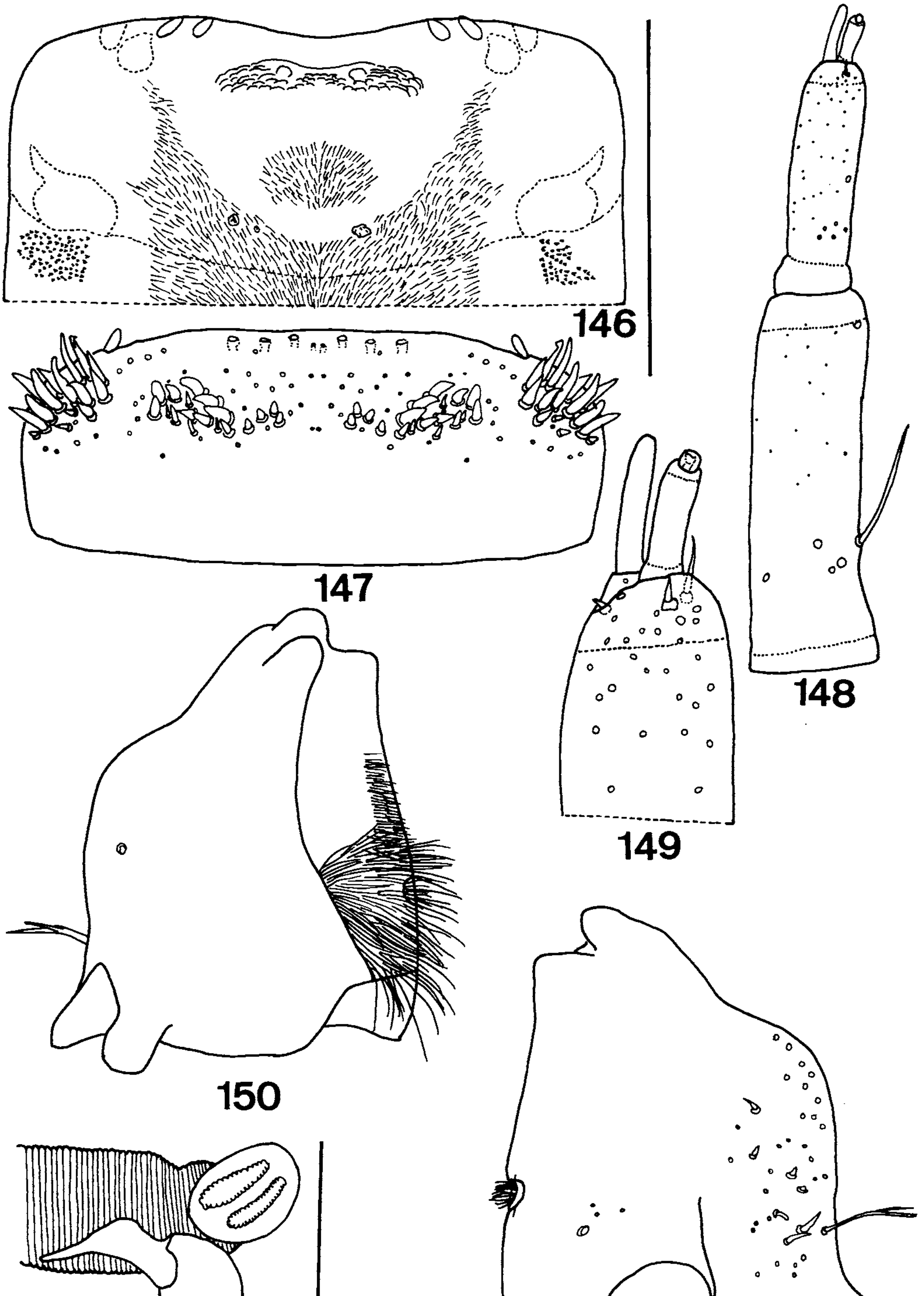


Fig. 146-152. *Epilichas flabellatus* (Kiesenwetter). Mature larva: 146, epipharynx; 147, labrum; 148, 149, antenna (general, apex); 150, 152, right mandible (ventral, dorsal); 151, thoracic spiracle. Scale: Fig. 146-148, 150, 152 = 0.5 mm; 149, 151 = 0.1 mm.

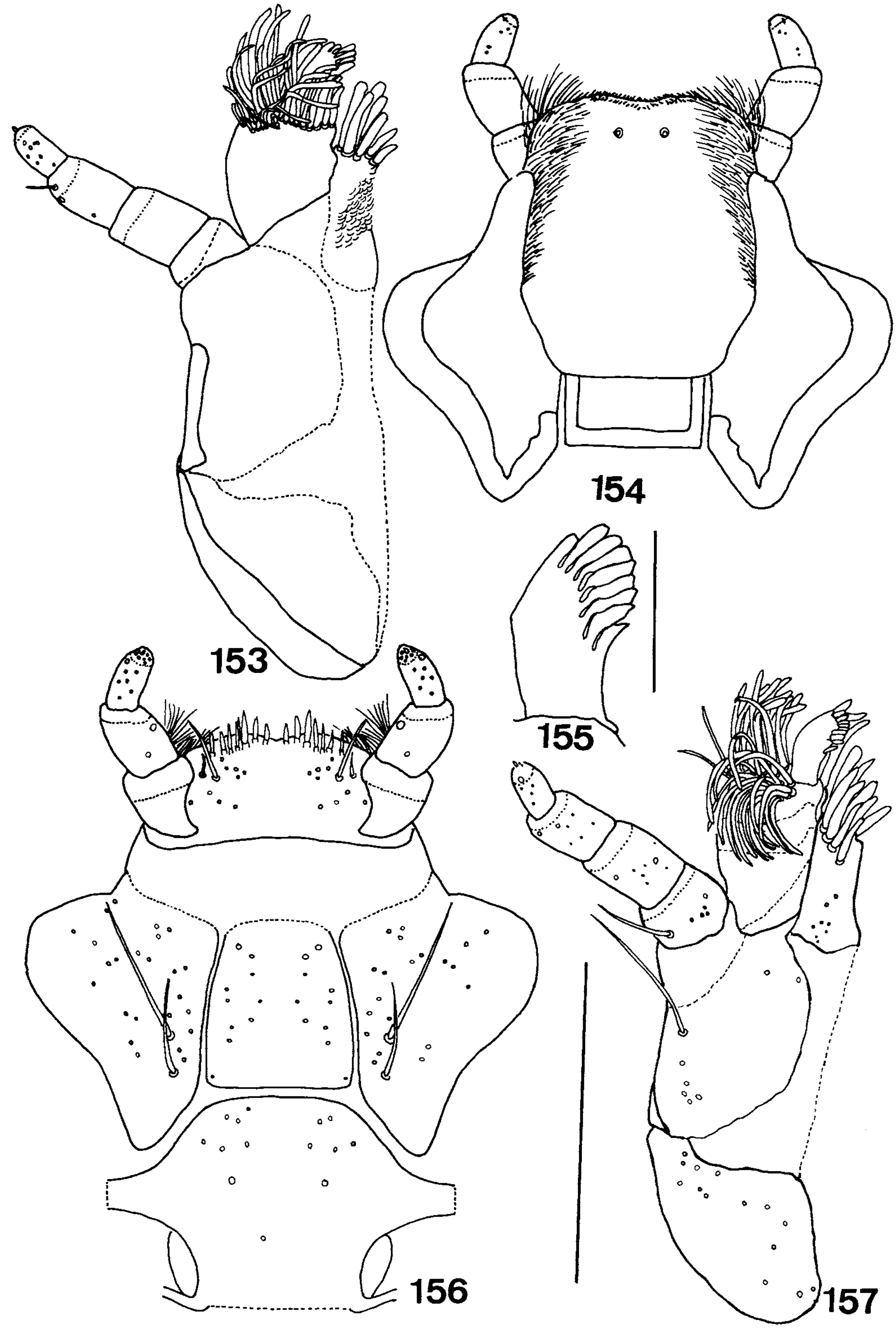


Fig. 153-157. *Epilichas flabellatus* (Kiesenwetter). Mature larva: 153, 155, 157, maxillae (left dorsal, apical segment of galea, right ventral); 154, hypopharynx; 156, labium. Scale: Fig. 153, 154, 156, 157 = 0.5 mm; 155 = 0.1 mm.

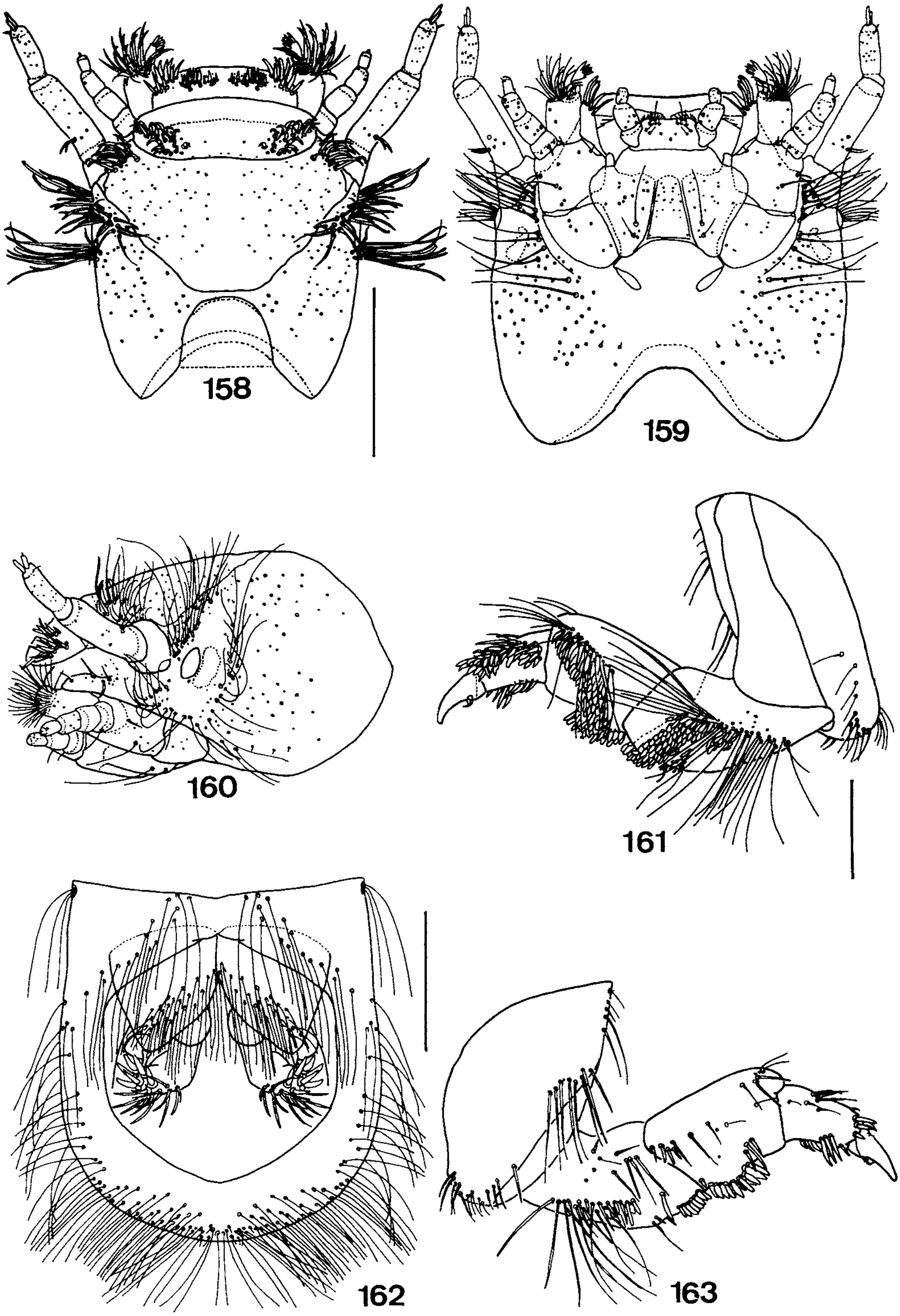


Fig. 158-163. 158-160. *Epilichas flabellatus* (Kiesenwetter) Young larva: head, general (dorsal, ventral, lateral). 161-163. Mature larva: 161, 163, anterior leg (internal, external); 162, 9th and 10th segments (ventral). Scale: Fig. 158-160; 161, 163 = 0.5 mm; 162 = 1 mm.

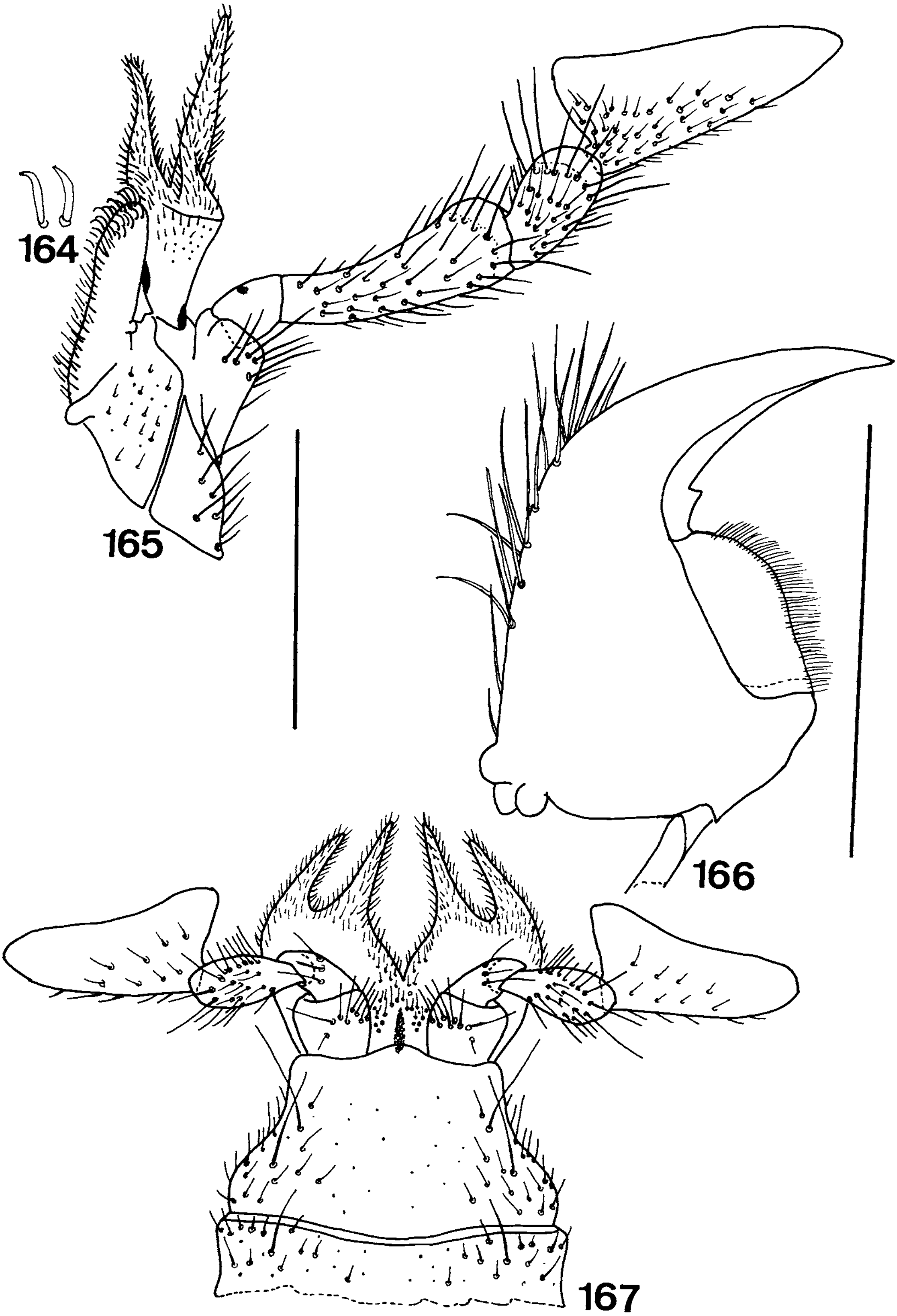


Fig. 164-167. *Epilichas flabellatus* (Kiesenwetter). ♂: 164, 165, left maxilla (spatulate setae of lacinia, ventral (cardo omitted)); 166, right mandible (ventral); 167, labium. Scale: Fig 165, 167; 166 = 0.5 mm; 164, schematic, without scale.

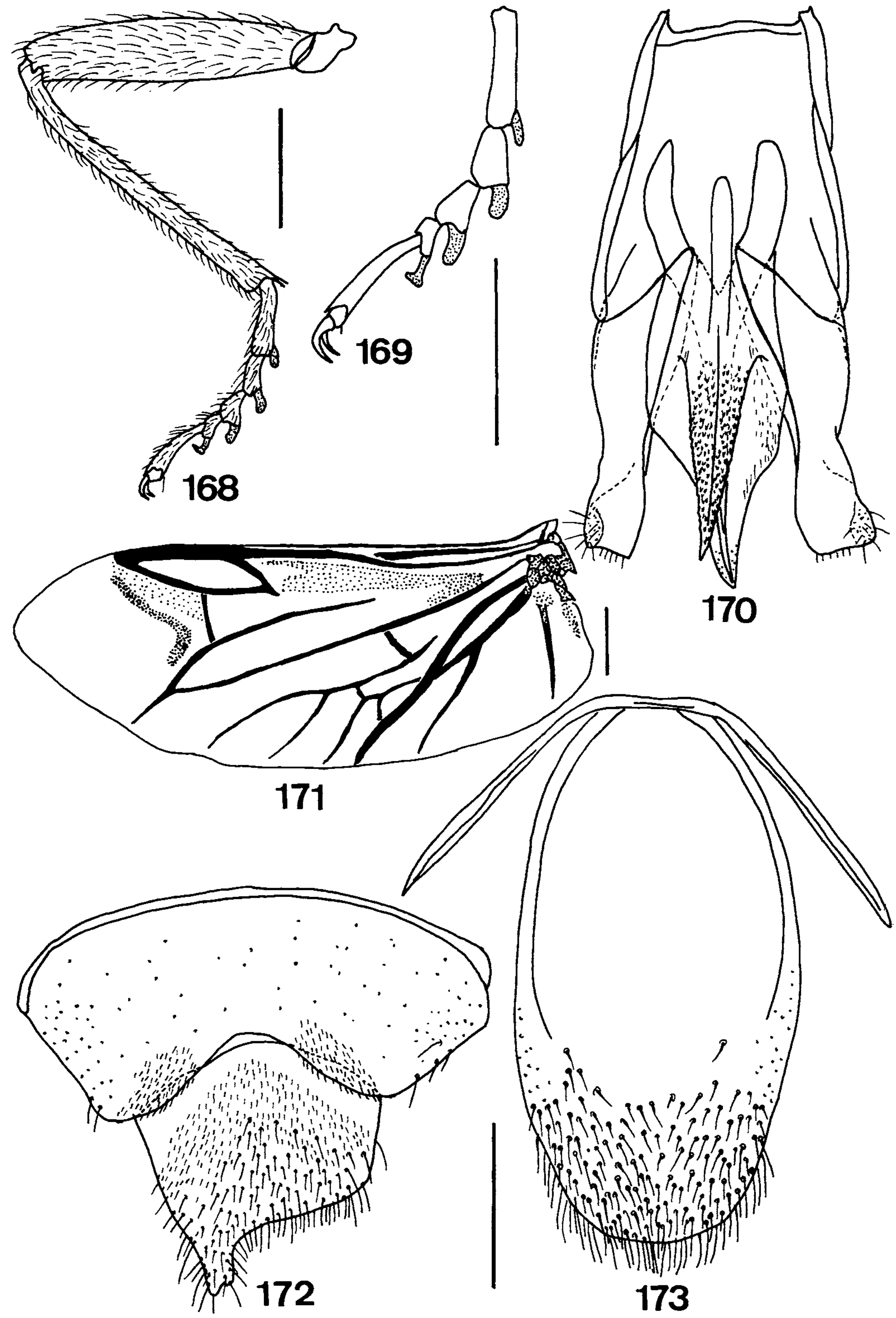


Fig. 168-173. *Epilichas flabellatus* (Kiesenwetter). ♂: 168, 169, right hind leg (general, tarsus); 170, aedeagus (ventral); 171, membranous wing; 172, 9th and 10th tergites; 173, 9th sternite. Scale: Fig. 168; 169; 171 = 1 mm; 170, 172, 173 = 0.5 mm.

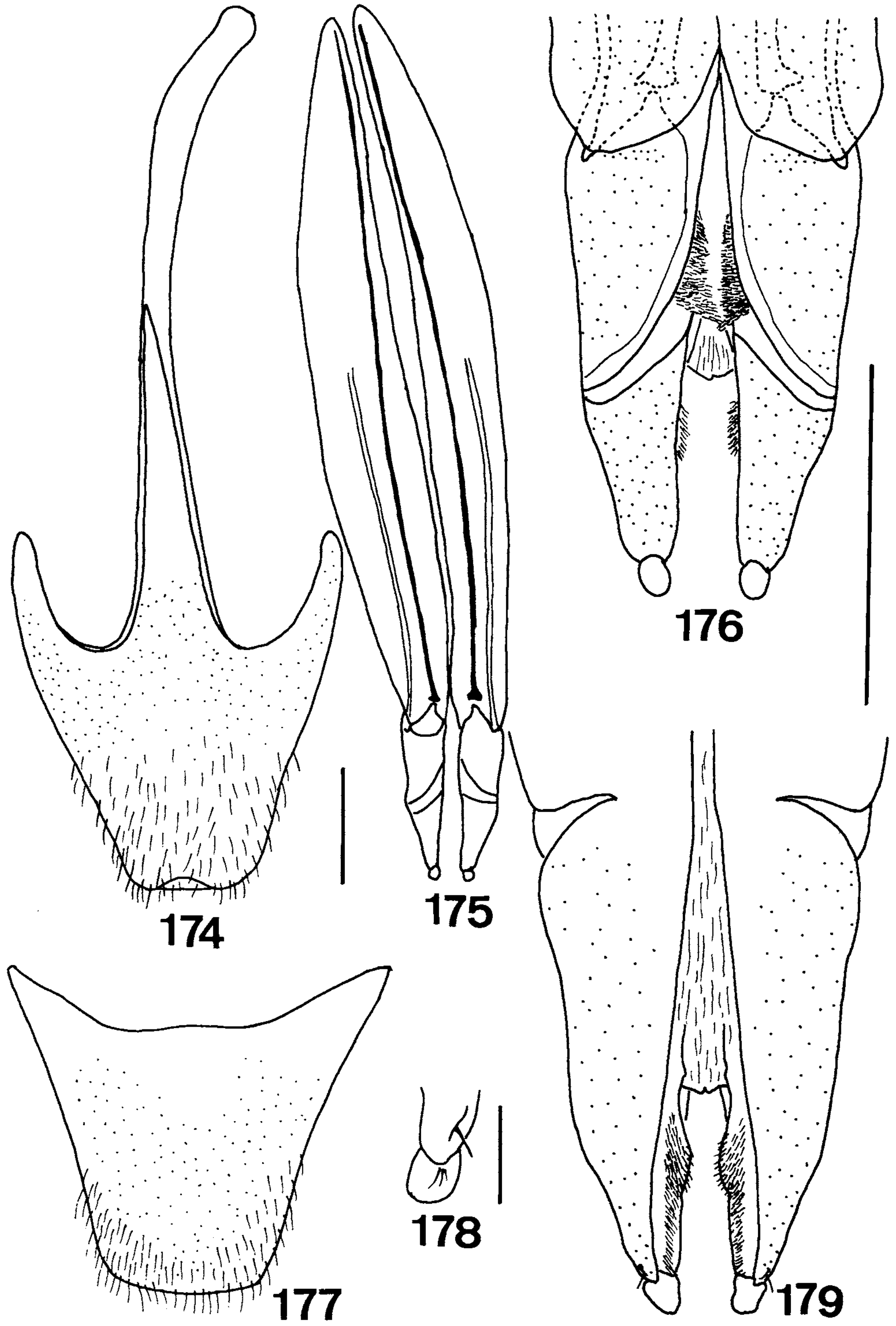


Fig. 174-179. *Epilichas flabellatus* (Kiesenwetter). ♀: 174, 8th tergite; 175, ovipositor (dorsal); 176, 179, coxites (dorsal, ventral); 177, 8th sternite; 178, style. Scale: Fig. 174, 175, 177; 176, 179 = 0.5 mm; 178 = 0.1 mm.

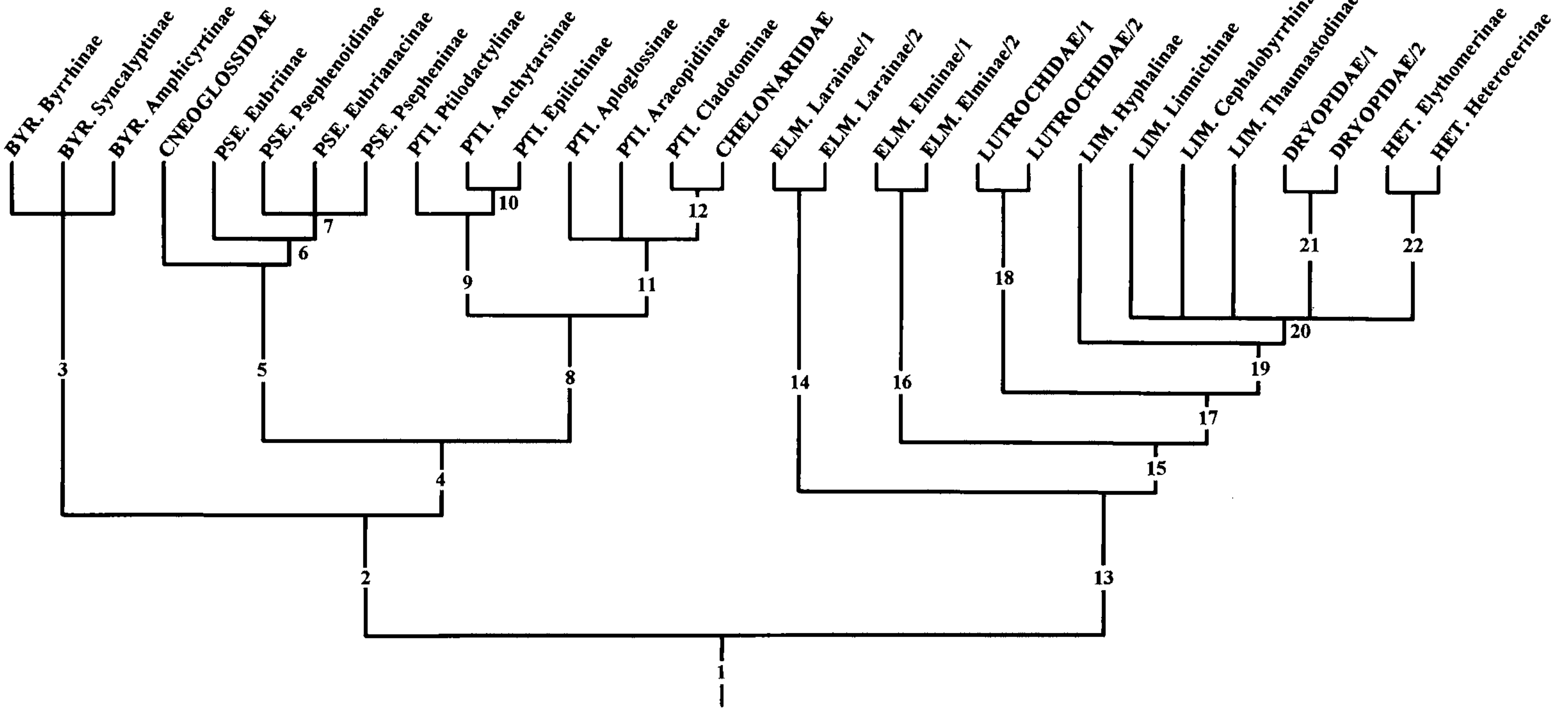


Fig. 180. Phylogenetic hypothesis of Byrrhoidea (*sensu* Lawrence & Newton, 1995), Eulichadidae and Callirhipidae excluded, based on characters of adult and immatures. Strict consensus cladogram (CI = 43; RI = 73) of 24 most parsimonious tree (L = 186). Numbers correspond to characters transforming in each branch or terminal (* = convergence, R = reversal). BYR. = Byrrhidae; PSE. = Psephenidae; PTI. = Ptilodactylidae; ELM. = Elmidae; LIM. = Limnichidae; HET. = Heteroceridae. BRANCH 1: 16.1, 29.2, 58.1; BRANCH 2: 1.1*, 14.1, 27.1*, 28.1*, 44.1*, 58.2; BRANCH 3: 8.1*, 11.1*, 13.1*, 41.1*; BYR. Amphicyrtinae: 6.2*, 23.1*; BRANCH 4: 24.1, 32.1*, 37.1*, 54.1; BRANCH 5: 2.1*, 3.2*, 4.1*, 15.1*, 30.1, 54.2*; CNEOGLOSSIDAE: 5.1*, 8.1*, 11.1*, 25.1*, 31.1, 42.1*, 47.1*, 71.1*; BRANCH 6: 41.1*, 43.1*, 44R, 48.1, 58R, 69.1; PSE. Eubriinae: 9.1*, 10.1*, 49.1*, 60.1*, 65.1*, 72.1*; BRANCH 7: 1R, 3.1*, 6.1*, 61.1; PSE. Psephenoidinae: 14R, 61.2, 65.1*; PSE. Eubrianacinae: 3.2*, 8.1*, 11.1*, 15.2, 24R, 48.2*, 64.1*; PSE. Psepheninae: 6.2*, 27R, 48.3*, 64.1*, 67.1*; BRANCH 8: 7.1*, 9.1*, 21.1, 38.1, 42.1*; BRANCH 9: 54.2*, 72.1*; PTI. Ptilodactylinae: 12.1*, 19.1, 22.1*, 25.1*, 37R, 38.2*, 39.1*, 46.1*, 68.1; BRANCH 10: 47.1*, 55.1, 71.1*; PTI. Anchytarsinae: 21R, 28R; PTI. Epilichinae: 3.1*, 4.1*, 6.2*, 22.1*; BRANCH 11: 6.1*, 15.1*, 28R, 49.1*, 60.1*, 70.1; PTI. Aploglossinae: 23.1*, 38R; PTI. Araeopidiinae: 3.1*, 9R, 21R, 27R, 36.1, 67.1; BRANCH 12: 4.1*, 6.2*, 7R, 11.1*, 15R, 23.1*, 38.2*, 39.1*, 40.1*; PTI. Cladotominae: 22.1*, 24R, 48.4, 62.1, 67.3; CHELONARIIDAE: 2.1*, 3.2*, 5.1*, 13.1*, 18.1, 25.1*, 28.1*, 34.1, 51.1*, 52.1*, 53.2*, 54R; BRANCH 13: 11.1*, 13.1*, 35.1, 43.1*, 51.1*, 60.1*, 65.1*, 66.1; BRANCH 14: 6.1*, 27.1*, 46.1*; BRANCH 15: 10.1*, 28.1*, 44.1*; BRANCH 16: 12.1*, 32.1*, 48.1*; BRANCH 17: 38.2*, 39.1*, 40.1*; BRANCH 18: 6.2*, 28R, 48.2*, 52.1*, 53.2*, 70.3; LUTROCHIDAE/2: 3.1*; BRANCH 19: 26.1, 49.1*, 60R; BRANCH 20: 37.1*, 65R, 72.1*; LIM. Limnichinae: 53.1; LIM. Thaumastodinae: 37R; BRANCH 21: 52.1*, 60.1*, 67.1*, 70.2; DRYOPIDAE/1: 28R; DRYOPIDAE/2: 1.1*; BRANCH 22: 3.1*, 7.1*, 8.1*, 15.1*, 17.1, 20.1, 40R, 41.1*, 66R, 72R.

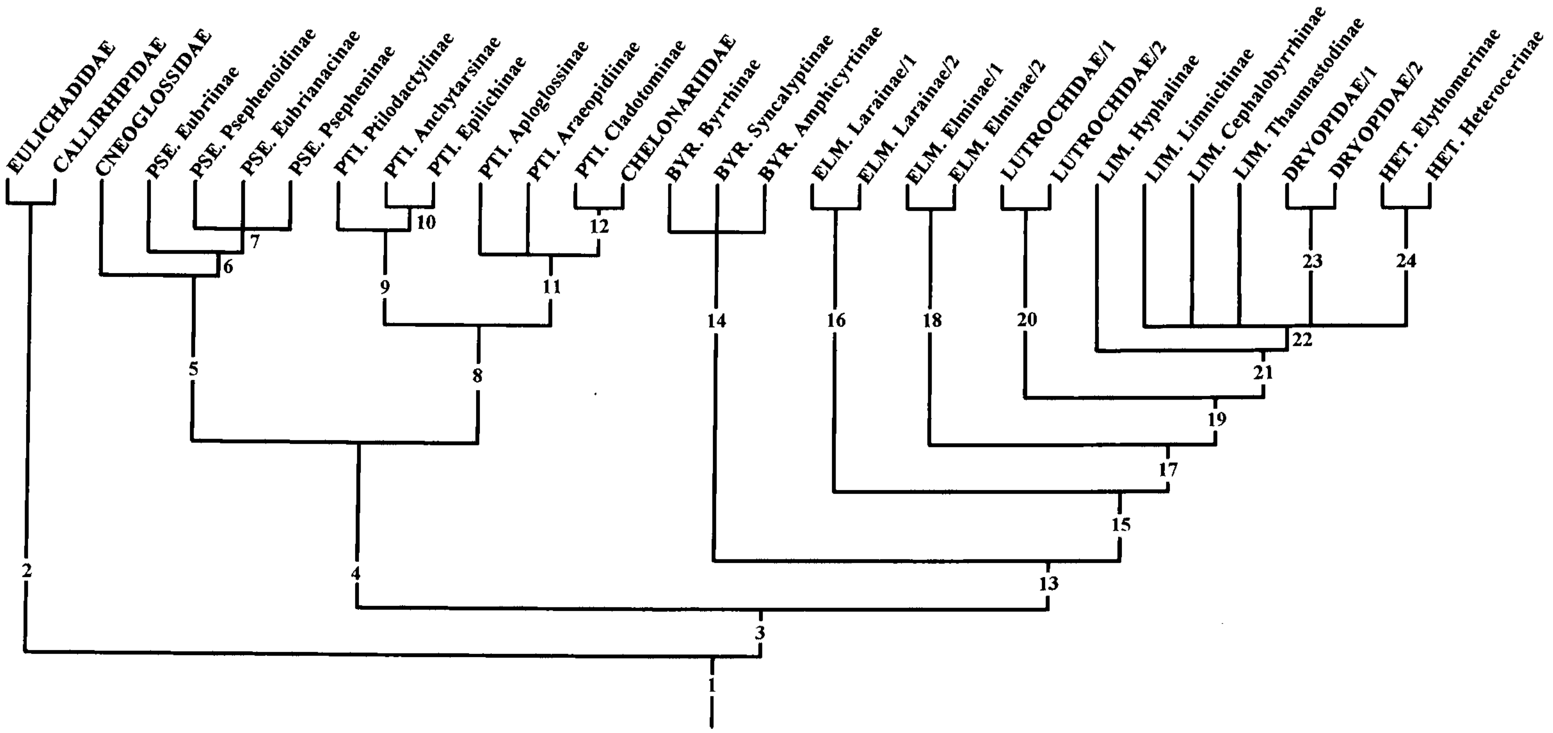


Fig. 181. Phylogenetic hypothesis of Byrrhoidea (*sensu* Lawrence & Newton, 1995), based on 72 characters of adult and immatures. Strict consensus cladogram (CI = 41, RI = 71) of 24 most parsimonious tree (L = 213). BRANCH 1: 14.1, 29.1, 44,1, 58.2; BRANCH 2: 3.1*, 36.1*, 37.1*, 38.1*, 39.1*, 42.1*; EULICHADIDAE: 9.1*, 32.1*, 33.1, 46.1*, 63.1, 64.1*; CALLIRHIPIDAE: 4.1*, 7.1*, 8.1*, 38.2*, 40.1*, 45.1, 49.1*, 50.1, 53.1*, 56.1, 57.1, 59.1, 70.1; BRANCH 3: 16.1, 27.1, 28.1*, 29.2; BRANCH 4: 1.1*, 24.1, 31.1*, 37.1*, 42.1*, 54.1; BRANCH 5: 2.1*, 3.2*, 4.1*, 15.1*, 30.1, 54.1*; CNEOGLOSSIDAE: 5.1*, 8.1*, 11.1*, 25.1*, 31.1, 47.1*, 71.1*; BRANCH 6: 41.1*, 42R, 43.1*, 44R, 48.1, 58R, 69.1; PSE. Eubriinae: 9.1*, 10.1*, 49.1*, 60.1*, 65.1*, 72.1*; BRANCH 7: 1R, 3.1*, 6.1*, 61.1; PSE. Psephenoidinae: 14R, 61.2, 65.1*; PSE. Eubrianacinae: 3.2*, 8.1*, 11.1*, 15.2, 24R, 48.2*, 64.1*; PSE. Psepheninae: 6.2*, 27R, 48.3*, 64.1*, 67.1*; BRANCH 8: 7.1*, 9.1*, 21.1, 38.1*; BRANCH 9: 54.2*, 72.1*; PTI. Ptilodactylinae: 12.1*, 19.1, 22.1*, 25.1*, 37R, 38.2*, 39.1*, 46.1*, 68.1; BRANCH 10: 47.1*, 55.1, 71.1*; PTI. Anchytarsinae: 21R, 28R; PTI. Epilichinae: 3.1*, 4.1*, 6.2*, 22.1*; BRANCH 11: 6.1*, 15.1*, 28R, 49.1*, 60.1*, 70.1; PTI. Aploglossinae: 23.1*, 38R; PTI. Araeopidiinae: 3.1*, 9R, 21R, 27R, 36.1*, 67.2; BRANCH 12: 4.1*, 6.2*, 7R, 11.1*, 14R, 22.1*, 38.2*, 39.1*, 40.1*; PTI. Cladotominae: 22.1*, 24R, 48.4, 62.1, 67.3; CHELONARIIDAE: 2.1*, 3.2*, 5.1*, 13.1*, 18.1, 25.1*, 28.1*, 34.1, 51.1*, 52.1*, 53.2*, 54R; BRANCH 13: 11.1*, 13.1*; BRANCH 14: 1.1*, 8.1*, 41.1*; BYR. Amphicyrtinae: 6.2*, 23.1*; BRANCH 15: 14R, 35.1, 43.1*, 51.1*, 58.1R, 60.1*, 65.1*, 66.1; BRANCH 16: 6.1*, 28R, 44R, 46.1*; BRANCH 17: 10.1*, 27R; BRANCH 18: 12.1*, 32.1*, 48.3*; BRANCH 19: 38.2*, 39.1*, 40.1*; BRANCH 20: 6.2*, 28R, 48.2*, 52.1*, 53.2*, 70.3; LUTROCHIDAE/2: 3.1*; BRANCH 21: 26.1, 49.1*; 60R; BRANCH 22: 37.1*, 65R, 72.1*; LIM. Limnichinae: 53.1*; LIM. Thaumastodinae: 37R; BRANCH 23: 52.1*, 60.1*, 67.1*, 70.2; DRYOPIDAE/1: 28R; DRYOPIDAE/2: 1.1*; BRANCH 24: 3.1*, 7.1*, 8.1*, 15.1*, 17.1, 20.1, 40R, 41.1*, 66R, 72R.

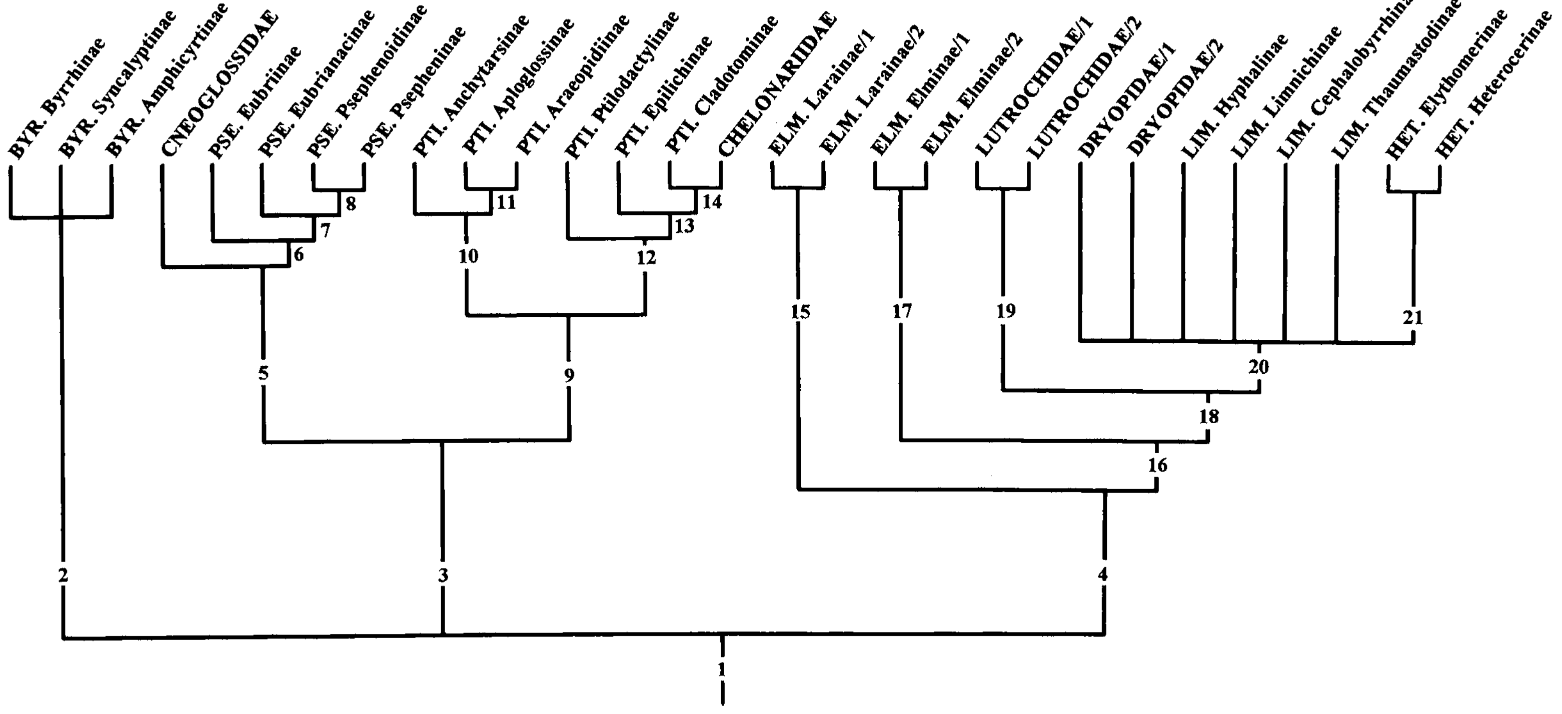


Fig. 182. Phylogenetic hypothesis of Byrrhoidea (*sensu* Lawrence & Newton, 1995), Eulichadidae and Callirhipidae excluded. Only characters of adult considered. Strict consensus cladogram (CI = 57, RI = 79) of 357 most parsimonious tree (L = 114). BRANCH 1: 16.1, 27.1, 28.1, 29.1; BRANCH 2: 1.1*, 8.1*, 11.1*, 13.1*, 14.1*, 41.1*; BYR. Amphicyrtinae: 6.2*, 23.1*; BRANCH 3: 1.1*, 14.1*, 24.1, 32.1*, 37.1*; BRANCH 4: 11.1*, 13.1*, 35.1, 43.1*; BRANCH 5: 2.1*, 3.2*, 4.1*, 15.1*, 30.1; CNEOGLOSSIDAE: 5.1*, 8.1*, 11.1*, 25.1*, 31.1, 42.1*; BRANCH 6: 41.1*, 43.1*; PSE. Eubriinae: 9.1*, 10.1*; BRANCH 7: 1R, 6.1*; PSE. Eubrianacinae: 8.1*, 11.1*, 15.2, 24R; BRANCH 8: 3.1*; PSE. Psephenoidinae: 14R; PSE. Psepheninae: 6.2*; 27R; BRANCH 9: 7.1*, 9.1*, 38.1, 42.1*; BRANCH 10: 28R; BRANCH 11: 6.1*; 15.1*; PTI. Aploglossinae: 21.1*; 23.1*, 38R; PTI. Araeopidiinae: 3.1*, 9R, 27R, 36.1; BRANCH 12: 21.1*, 22.1; PTI. Ptilodactylinae: 12.1*, 19.1, 25.1*, 37R, 38.2*, 39.1*; BRANCH 13: 4.1*, 6.2*; PTI. Epilichinae: 3.1*; BRANCH 14: 7R, 11.1*, 23.1*, 38.2*, 39.1*, 40.1*; PTI. Cladotominae: 24R, 28R; CHELONARIIDAE: 2.1*, 3.2*, 5.1*, 13.1*, 18.1, 22R, 25.1*, 34.1; BRANCH 15: 6.1*, 28R; BRANCH 16: 10.1*, 27R; BRANCH 17: 12.1*, 32.1*; BRANCH 18: 38.2*, 39.1*, 40.1*; BRANCH 19: 6.2*, 28R; LUTROCHIDAE/2: 3.1*; BRANCH 20: 26.1, 37.1*; DRYOPIDAE/1: 28R; DRYOPIDAE/2: 1.1*; LIM. Thaumastodinae: 37R; BRANCH 21: 3.1*, 7.1*, 8.1*, 15.1*, 17.1, 20.1, 40R, 41.1*.

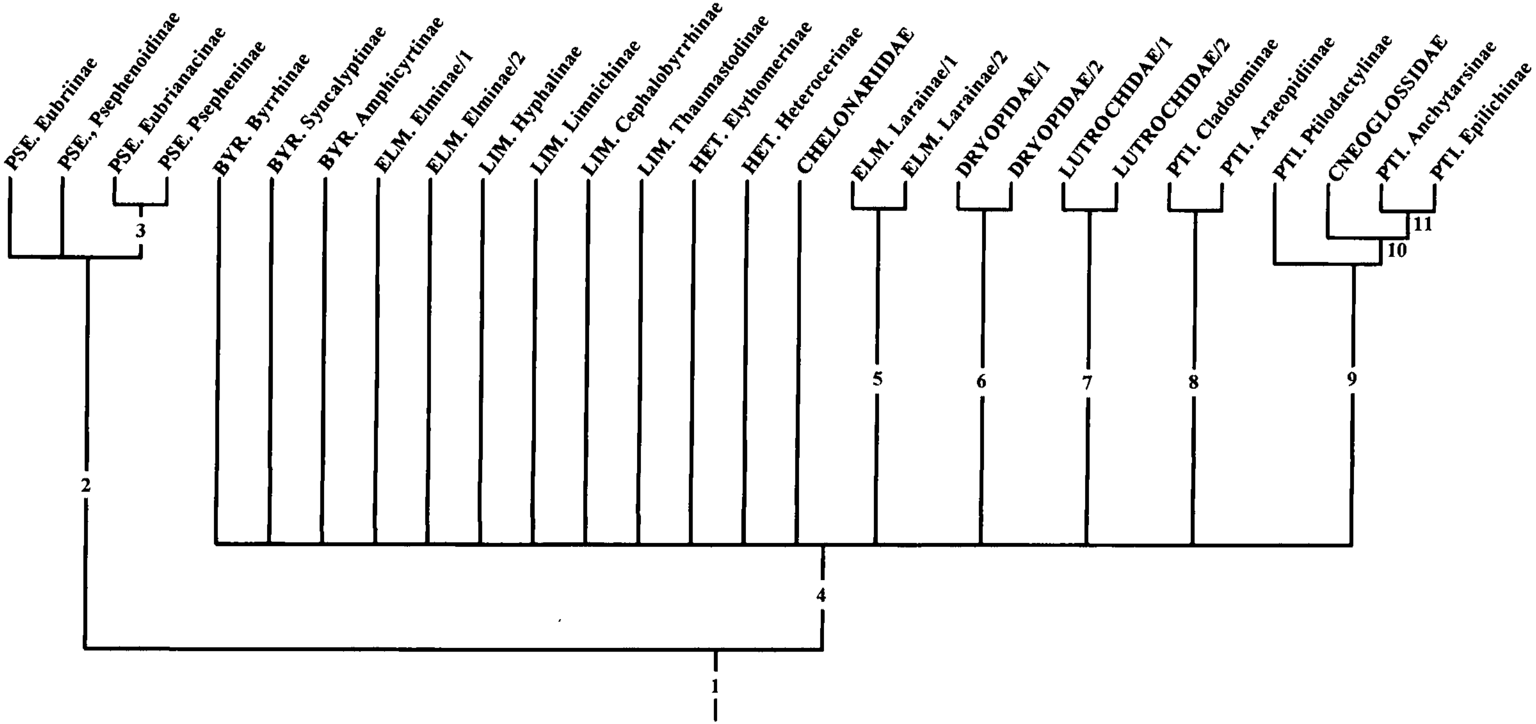


Fig. 183. Phylogenetic hypothesis of Byrrhoidea (*sensu* Lawrence & Newton, 1995), Eulichadidae and Callirhipidae excluded. Only characters of immatures considered. Strict consensus cladogram (CI = 57, RI = 79) of 3157 most parcimonious tree (L = 59). BRANCH 2: 48.1, 54.2*, 69.1; PSE. Eubriinae: 49.1*, 60.1*, 65.1*, 72.1*; PSE. Psephenoidinae: 61.2, 65.1*; BRANCH 3: 61.1, 64.1; PSE. Eubrianacinae: 48.2*; PSE. Psepheninae: 48.3*, 67.1*; BRANCH 4: 44.1, 51.1, 58.1; BYR. Byrrhinae, BYR. Syncalyptinae, BYR. Amphicyrtinae: 51R, 58.2*; ELM. Elminae/1, ELM. Elminae/2: 48.3*, 60.1*, 65.1*, 66.1*; LIM. Hyphalinae: 49.1*, 65.1*, 66.1*; LIM. Limnichinae: 49.1*, 53.1, 66.1*, 72.1*; LIM. Cephalobyrrinae, LIM. Thaumastodinae: 49.1*, 66.1*; HET. Elythomerinae, HET. Heterocerinae: 49.1*; CHELONARIIDAE: 49.1*, 52.1*, 53.2*, 60.1*, 70.1*; BRANCH 5: 44R, 46.1*, 60.1*, 65.1*, 66.1*; BRANCH 6: 49.1*, 52.1*, 60.1*, 66.1*, 67.1*, 70.2, 72.1*; BRANCH 7: 48.2*, 52.1*, 53.2*, 60.1*, 65.1*, 66.1*, 70.3; BRANCH 8: 49.1*, 51R, 54.1, 60.1*, 67.2, 70.1*; PTI. Cladotominae: 48.4, 62.1, 67.3; BRANCH 9: 51R, 54.2*, 57.2*; PTI. Ptilodactylinae: 46.1*, 68.1, 72.1*; BRANCH 10: 47.1, 71.1; BRANCH 11: 55.1, 72.1*.

Curiously, our first aproach to identify the cneoglossid larvae brought to laboratory, was a tentative placement in the Anchytarsinae, due to the overall similarity. Only after rearing the immatures, and subsequent study of adults, the correct identification was possible.

Although we present many taxonomical suggestions, we are not implementing nomenclatural decisions. There is still much incongruence in the phylogenetic conclusions presented by different authors (e. g., Beutel, 1995; Lawrence, 1988; Lawrence *et al*., 1995). Further studies are needed before presenting a new classification.

ACKNOWLEDGMENTS

We wish to thank the following institutions and individuals for allowing us to study the specimens under their care: Dr. J. F. Lawrence (ANIC), Miss C. M. F. von Hayek (BMNH), Dr. N. Berti (MNHN), Dr. M. Brancucci (NHMB), Dr. N. Hayashi (NHCK), Dr. H. P. Brown (OMNO), and Dr. S. I. Frommer (UCRC). Special thanks to John F. Lawrence for advise, comments concerning the phylogeny and classification of the Elateriformia, and encouragement during this study. Thanks must be given to Tiago Courrol Ramos (MZSP) for allowing the use of unpublished information on Treegardner computer software, also employed in the cladistic analysis. We thank also Dr. Mario de Pinna (DZSP) for comments and suggestions; and Dr. Sônia A. Casari (MZSP) for reading the manuscript. Research funds were provided by the Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) and Fundação de Amparo à Pesquisa do Estado de São Paulo (FAPESP).

REFERENCES

Published papers

Arnett, Jr., R. H. 1968. *The beetles of the United States (a manual for identification)*. Ann Arbor, The American Entomological Institute, xii + 1112 p.

Arnett, Jr., R. H.; G. A. Samuelson & G. M. Nishida. 1993. *The insect and spider collections of the world*. Gainesville, Sandhill Crane Press, Inc., vi + 310 p.

Bertrand, H. P. I. 1935. Voyage de Chappuis dans l'Afrique occidentale Française. Larves de Coléoptères aquatiques. *Revue fr. Ent*. 2:132-140.

Bertrand, H. P. I. 1939. Les larves et nymphes des dryopides paléarctiques. *Annls Sci. nat. Zool. Biol. anim*. (11) *2*:299-412.

Bertrand, H. P. I. 1956. Les larves des Anchytarsini (Col. Dascillidae). *Bull. Mus. natn. Hist. nat., Paris* (2) *28*(3):275-281.

Bertrand, H. P. I. 1966. Les premiers états des Ptilodactylidae (Col.) aquatiques. *Bull. Mus. natn. Hist. nat., Paris* (2) *38*(2):143-150.

Bertrand, H. P. I. 1972. *Larves et nymphes des coléoptères aquatiques du globe*. Paris, Imprimerie F. Paillart, 804 p.

Beutel, R. G. 1995. Phylogenetic analysis of Elateriformia (Coleoptera: Polyphaga) based on larval characters. *J. Zool. Syst. Evol. Res*. *33*(4):145-171.

Blackwelder, R. E. 1944. Checklist of the coleopterous insects of Mexico, Central America, The West Indies, and South America. *Bull. U. S. natn Mus*. *185*(2):189-341.

Blanchard, C. E. 1845. *Histoire naturelle des insectes, leurs moeurs, leurs métamorphoses et leur classification*. Paris, Librairie F. Savy, v. 2, 524 p., pls. 11-20.

Blatchley, W. S. 1910. The Coleoptera or beetles of Indiana. *Bull. Indiana Dep. Geol. Nat. Res*. *1*:1-1386.

Böving, A. G. & F. C. Craighead. 1930-1931. An illustrated synopsis of the principal larval forms of the order Coleoptera. *Entomologica am*. (n. s.) *11*(1/4):1-351.

Brown, H. P. 1972. *Aquatic dryopoid beetles (Coleoptera) of the United States*. Washington, United States Environmental Protection Agency, Biota of Freshwater Ecosystems Identification Manual 6, ix + 82 p.

Brown, H. P. 1975. A distributional checklist of North American genera of aquatic dryopoid and dascilloid beetles (Elmidae, Dryopidae, Limnichidae, Chelonariidae, Heteroceridae, Psephenidae, Ptilodactylidae, Cyphonidae, Georyssidae). *Coleopts Bull*. *29*(3):149-160.

Brown, H. P. 1981. A distributional survey of the world genera of aquatic dryopid beetles (Coleoptera: Dryopidae, Elmidae, and Psephenidae *sens. lat*.). *Pan-Pacif. Ent*. *57*(1):133-148.

Champion, G. C. 1897. Fam. Dascillidae, p. 586-662, pls. 26-27. *In Biologia Centrali-Americana. Insecta, Coleoptera, Serricornia*. London, Taylor & Francis, v. 3, pt. 1, xvi + 690 p., 27 tabs.

Chenu, J. C. 1870. *Encyclopedie d'Histoire Naturelle*. Paris, v. 3, p. 16.

Cockerell, T. D. A. 1906. Preoccupied generic names in Coleoptera. *Ent. News* *17*:240-244.

Costa, C.; S. A. Vanin & S. A. Casari-Chen. 1988. *Larvas de Coleoptera do Brasil*. São Paulo, Museu de Zoologia, Universidade de São Paulo, vi + 282 p., 165 est.

Costa Lima, A. M. da. 1953. *Insetos do Brasil. Coleópteros. 2ª parte*. Rio de Janeiro, Escola Nacional de Agronomia, v. 8, 323 p.

Crowson, R. A. 1938. The metendosternite in Coleoptera: a comparative study. *Trans. R. ent. Soc. Lond*. *87*(17):397-415, 13 pls.

Crowson, R. A. 1944. Further studies on the metendosternite in Coleoptera. *Trans. R. ent. Soc. Lond*. *94*(2):273-310, 10 pls.

Crowson, R. A. 1955. *The natural classification of the families of Coleoptera*. London, Nathaniel Lloyd & Co, Ltd., 187 p.

Crowson, R. A. 1960. The phylogeny of Coleoptera. *A. Rev. Ent*. *5*:111-134.

Crowson, R. A. 1971. Observations on the superfamily

Dascilloidea (Coleoptera: Polyphaga). with the inclusion of Karumiidae and Rhipiceridae. *Zool. J. Lin. Soc., Lon.* *50*(1):11-19.

Crowson, R. A. 1972. A review of classification of Cantharoidea (Coleoptera), with the definition of two new families, Cneoglossidae and Omethidae. *Revta Univ. Madr.* *21*(82):35-77.

Crowson, R. A. 1973. On a new superfamily Artematopoidea of polyphagan beetles, with the definition of two new fossil genera from the Baltic Amber. *J. nat. Hist., Lond.* *7*(2):225-238.

Crowson, R. A. 1978. Problems of phylogenetic relationships in Dryopoidea. *Entomologica germ.* *4*(3/4):250-257.

Crowson, R. A. 1981. *The biology of Coleoptera.* London, Academic Press Inc. (London) Ltd., xii + 802 p.

Crowson, R. A. 1995. Some interesting evolutionary parallels in Coleoptera, p. 63-85. *In* J. Pakaluk & S. A. Slipinski (eds.). *Biology, phylogeny, and classification of Coleoptera: papers celebrating the 80th birthday of Roy A. Crowson.* Warszawa, Muzeum i Instytut Zoologii PAN, v. 1, i-xii + 1-558 p.

Delève, J. 1972. Ptilodactylidae des Iles Philippines et de l'Archipel Bismark (Insecta, Coleoptera, Dryopoidea). *Steenstrupia* *2*(18):263-294.

Downie, N. M. & R. H. Arnett, Jr. 1996. Family 42. Ptilodactylidae. The toad-winged beetles. *In The beetles of Northeastern North America.* Gainesville, The Sandhill Crane Press, v. 1, xiv + 880 p.

Doyen, J. T. & G. Ulrich. 1978. Aquatic Coleoptera, ch. 16, p. 203-231. *In* R. W. Merritt & K. W. Cummins (eds.). *An introduction to the aquatic insects of North America.* Dubuque, Kendall/Hunt Publishing Company, xiii + 441 p.

Fairmaire, L. 1886. Descriptions de coléoptères de l'intérieur de la Chine. *Annls Soc. ent. Fr.* (6) *6*:303-356.

Farris, J. S. 1988. *Hennig86 version 1.5.* Ann Arbor, James S. Farris.

Forbes, W. T. M. 1926. The wing folding patterns of the Coleoptera. *Jl N. Y. ent. Soc.* *34*(2):91-139.

Forey, P. L.; C. J. Humphries; I. J. Kitching; R. W. Scotland; D. J. Siebert & D. M. Williams. 1992. *Cladistics. A practical course in systematics.* New York, Oxford University Press, x + 191 p.

Guérin-Méneville, F. E. 1843a. *Spécies et iconographie générique des animaux articulés ou représentation des genres avec leur description et celle de toutes les espèces de cette grande division du regne animal...* I, *Coléoptères.* Paris, auteur, v. 2, p. 10-12.

Guérin-Méneville, F. E. 1843b. Note sur un groupe naturel ou une petite tribu de coléoptères de la famille des Malacodermes. *Revue zool.* *6*(7):193-194.

Guérin-Méneville, F. E. 1849. *Spécies et iconographie générique des animaux articulés ou représentation des genres avec leur description et celle de toutes les espèces de cette grande division du règne animal...* I, *Coléoptères.* Paris, auteur, v. 9, p. 1.

Guérin-Méneville, F. E. 1861. Monographie du nouveau genre *Dicranopselaphus* et description de quelques autres insectes coléoptères appartenant aussi à la famille des dascillides. *Revue mag. Zool. pure appl.* (2) *13*:531-547.

Hayashi, N. 1986. Larvae, p. 202-218, pls. 1-113. *In* K. Morimoto & N. Hayashi (eds.). *The Coleoptera of Japan in color.* Osaka, Hoikusha Publishing Co., Ltd., v. 1, vi + 323 p. (In Japanese).

Hennig, W. 1966. *Phylogenetic systematics.* Urbana, University of Illinois Press, vii + 263 p.

Hlavac, T. F. 1975. The prothorax of Coleoptera: (except Bostrichiformia-Cucujoidea). *Bull. Mus. comp. Zool. Harv.* *147*(4):37-183.

Horn, G. H. 1880. Synopsis of the Dascyllidae of the United States. *Trans. Am. ent. Soc.* *8*:76-115.

Horn, G. H. 1881. Notes on Elateridae, Cebrionidae, Rhipiceridae and Dascyllidae. *Trans. Am. ent. Soc.* *9*:76-90.

Illiger, J. C. W. 1807. Vorschlag zur Aufname in Fabricischen System fehlender Käfergattungen. *Mag. Insektenk.* *6*:318-349.

Kasap, H. & R. A. Crowson. 1975. A comparative anatomical study of the Elateriformia and Dascilloidea (Coleoptera). *Trans. R. ent. Soc. Lond.* *126*(4):441-495.

Kirsch, T. F. W. 1866. Beiträge zur Käferfauna von Bogotá. *Berl. ent. Z.* *10*(1/2):173-216.

Kirsch, T. F. W. 1874. Beiträge zur Kenntnis der Peruanischen Käferfauna auf Dr. Abendroth's Sammlungen basirt. *Berl. ent. Z.* *17*(3/4):338-418.

Lacordaire, J. T. 1857. *Histoire naturelle des insectes. Genera des coléoptères ou exposé méthodique et critique de tous le genres proposés jusqu'ici dans cet ordre d'insectes.* Paris, Librairie Encyclopédique de Roret, v. 4, 579 p.

Laporte, F. L. N. de C. de. 1836. Étude entomologiques, ou description d'insectes nouveaux et observations sur la synonymie. *Revue ent.* *4*:5-60.

Laporte, F. L. N. de C. de. 1840. Histoire naturelle des insectes coléoptères, v. 1. *In Histoire naturelle des animaux articulés annelides, crustacés, arachnides, myriapodes et insectes.* Paris, P. Duménil, v. 2, 324 p., 19 pls.

Latreille, P. A. 1829. Les crustacés, les arachnides et les insectes, tome iv-v. *In* C. Cuvier (ed.). *Le règne animal distribue d'après son organization, pour servir de base à l'histoire naturelle des animaux, et d'introduction à l'anatomie comparée.* Paris, Deterville, 2nd edition, xxviii + 584 p.

Lawrence, J. F. 1982. Coleoptera, p. 482-553. *In* S. P. Parker (ed.). *Synopsis and classification of living organisms.* New York, McGraw-Hill, Inc., v. 2, 1232 p., pls. 88-141.

Lawrence, J. F. 1987. Notes on the classification of some Australian Elateriformia. *J. Aust. ent. Soc.* *26*(4):360.

Lawrence, J. F. 1988. Rhinorhipidae, a new beetle family from Australia, with comments on the phylogeny of Elateriformia. *Invert. taxon.* *2*(1987):1-53.

Lawrence, J. F. 1991. Larval morphology, Ptilodactylidae (Dryopoidea), Cneoglossidae (Cantharoidea), p. 146-177, 391-394, 422. *In* J. F. Lawrence (coord.). Order Coleoptera, ch. 34, p. 144-658. *In* F. W. Stehr (ed.). *Immature insects.* Dubuque, Kendall/Hunt Publishing Company, v. 2, xvi + 975 p.

Lawrence, J. F. & E. B. Britton. 1991. Coleoptera (Beetles), ch. 35, p. 543-683. *In* CSIRO Division of Entomology (ed.). *The insects of Australia. A textbook for students and research workers.* Carlton, Melbourne University Press, 2nd edition, v. 2, i-vi + 543-1137 p.

Lawrence, J. F. & E. B. Britton. 1994. *Australian beetles.* Carlton, Melbourne University Press, x + 192 p., 16 pls.

Lawrence, J. F.; A. Hastings; M. Dallwitz & T. Paine. 1993.

Beetle larvae of the world. Canberra, CSIRO Division of Entomology, iv + 48 p., 1 compact disc.

Lawrence, J. F. & A. F. Newton, Jr. 1982. Evolution and classification of beetles. *A. Rev. Ecol. Syst. 13*:261-290.

Lawrence, J. F. & A. F. Newton, Jr. 1995. Families and subfamilies of Coleoptera (with selected genera, notes, references and data on family-group names), p. 779-1092. *In* J. Pakaluk & S. A. Slipinski (eds.). *Biology, phylogeny, and classification of Coleoptera: papers celebrating the 80th birthday of Roy A. Crowson.* Warszawa, Muzeum i Instytut Zoologii PAN, v. 2, i-vi + 559-1092 p.

Lawrence, J. F.; N. B. Nikitsky & A. G. Kirejtshuk. 1995. Phylogenetic position of Decliniidae (Coleoptera: Scirtoidea) and comments on the classification of Elateriformia (*sensu lato*), p. 375-410. *In* J. Pakaluk & S. A. Slipinski (eds.). *Biology, phylogeny, and classification of Coleoptera: papers celebrating the 80th birthday of Roy A. Crowson.* Warszawa, Muzeum i Instytut Zoologii PAN, v. 1, i-xii + 1-558 p.

Lawrence, J. F. & J. B. Stribling. 1992. A new genus of Ptilodactylidae (Coleoptera: Elateriformia) from North Queensland, with description of the presumed larva. *J. Aust. ent. Soc. 31*(1):19-27.

LeConte, J. L. 1853. Synopsis of the Atopidae, Rhipiceridae and Cyphonidae of the United States. *Proc. Acad. nat. Sci. Philad. 6*:350-357.

LeConte, J. L. 1861. Classification of the Coleoptera of North America. Prepared for the Smithsonian Institution. Part 1. *Smithson. Misc. Coll. 3*:i-xxv + 1-208.

LeConte, J. L. 1866. List of the Coleoptera of North America. Prepared for Smithsonian Institution. Part 1. *Smithson. Misc. Coll. 6*(140):78 p.

LeConte, J. L. 1874. Description of new Coleoptera chiefly from Pacific slope of North America. *Trans. Am. ent. Soc. 5*:43-72.

LeConte, J. L. & G. H. Horn. 1883. Classification of the Coleoptera of North America. *Smithson. Misc. Coll. 507*:xxxviii + 567 p.

Legros, C. 1947. Dascilloidea, p. 90-98. *In* E. Fleutiaux, C. Legros, P. Lepesme & R. Paulian (eds.). *Faune de l'empire Français VII. Coléoptères des Antilles*, v. 1. Paris, Office de la Recherche Scientifique Coloniale, 239 p.

Lewis, G. 1895. On the Dascillidae and Malacoderm Coleoptera of Japan. *Ann. Mag. nat. Hist* (6) *16*:98-122.

Maddison, W. P.; M. J. Donoghue & D. R. Maddison. 1984. Outgroup analysis and parsimony. *Syst. Zool. 33*(1):83-103.

Nakane, T. 1948. On the Japanese Dascillidae (Coleoptera). *Bull. Takarazuka Insectarium 45*:1-16.

Nakane, T. 1956. The beetles of Japan, 31. *Shin Konchu 9*(2):51-55.

Nelson, G. & N. I. Platnick. 1981. *Systematic and biogeography. Cladistic and vicariance.* New York, Columbia University Press, xi + 567 p.

Nixon, K. C. 1992. *Clados version 1.2.* Ithaca, Kevin C. Nixon.

Nixon, K. C. & J. M. Carpenter. 1993. On outgroups. *Cladistics 9*(4):413-426.

Nixon, K. C. & J. I. Davis. 1991. Polymorphic taxa, missing values and cladistic analysis. *Cladistics 7*:233-241.

Pic, M. 1914. Dascillidae, Helodidae, Eucinetidae, *pars* 58, p. 1-65. *In* W. Schenkling (ed.). *Coleopterorum catalogus.* Berlin, W. Junk, v. 10.

Pic, M. 1916. Descriptions abrégées diverses. *Mélang. exot. ent. 20*:1-20.

Pic, M. 1925. Rhipiceridae, *pars* 81, p. 1-13. *In* W. Schenkling (ed.). *Coleopterorum catalogus.* Berlin, W. Junk, v. 11.

Spangler, P. J. 1966. The Catherwood Foundation Peruvian-Amazon expedition. XIII - Aquatic Coleoptera (Dytiscidae; Noteridae; Gyrinidae; Hydrophilidae; Dascillidae; Helodidae; Psephenidae; Elmidae). *Monogr. Acad. nat. Sci. Philad. 14*:377-443.

Spangler, P. J. 1981. Coleoptera, p. 129-220. *In* S. H. Hulbert, G. Rodrígues & N. D. Santos (eds.). *Aquatic biota of tropical South America, part 1: Arthropoda.* San Diego, San Diego State University, xii + 323 p.

Spangler, P. J. 1982. Coleoptera, p. 328-397. *In* S. H. Hulbert & A. Villalobos-Figueroa (eds.). *Aquatic biota of Mexico, Central America and the West Indies.* San Diego, San Diego University State University.

Spangler, P. J. 1983. Imatures stages of *Tetraglossa palpalis* Champion (Coleoptera: Ptilodactylidae). *Ent. News 94*(5):161-175.

Stribling, J. B. 1986. Revision of *Anchytarsus* (Coleoptera: Dryopoidea) and a key to the New World genera of Ptilodactylidae. *Ann. ent. Soc. Am. 79*(10):219-234.

Watrous, L. E. & Q. D. Wheeler. 1981. The out-group comparison method for character analysis. *Syst. Zool. 30*(1):1-11.

Westwood, J. O. 1837. Description of some new species of exotic coleopterous insects from collection of Sir Patrick Walker. *Mag. Zool. Bot. 1*:251-257.

White, A. 1859. Note on the pupa-case of a coleopterous insect from northern China. *Ann. Mag. nat. Hist* (3) *3*:284-290.

White, D. S. 1980. Coleoptera (Dryopoidea), p. 94-99. *In* J. C. Morse; J. W. Chapin; D. D. Herlong & R. S. Harvey (eds.). 1980. Aquatic insects of upper Three Runs Creek, Savannah River plant, South Carolina. Pt. I: Orders other than Diptera. *J. Georgia ent. Soc. 15*:73-101.

White, D. S.; W. U. Brigham & J. T. Doyen. 1984. Aquatic Coleoptera, ch. 19, p. 361-437. *In* R. W. Merritt & K. W. Cummins (eds.). *An introduction to the aquatic insects of North America.* Dubuque, Kendall/Hunt Publishing Company, 2nd edition, xiii + 722 p.

Wiley, E. O. 1981. *Phylogenetics. The theory and pratice of phylogenetic systematics.* New York, John Wiley & Sons, xv + 439 p.

Wittmer, W. 1948. 7. Beitrag zur Kenntnis der neotropischen Malacodermata. *Revta Soc. ent. argent. 14*(4):215-222.

Yaetes, D. 1992. Why remove autapomorphies? *Cladistics 8*(4):387-389.

Unplublished theses

Johnson, P. J. 1987. *Larval taxonomy, biology, and biogeography of the genera of North American Byrrhidae (Insecta: Coleoptera).* M. Sc. Thesis, Graduate School, University of Idaho, Moscow, x + 268 p.

Stribling, J. B. 1986. *World generic revision of Ptilodactylidae (Coleoptera: Dryopoidea).* Ph. D. Thesis, Graduate School, The Ohio State University, Columbus, xv + 200 p.

CREDENCIAMENTO E APOIO FINANCEIRO DO PROGRAMA
DE APOIO AS PUBLICAÇÕES CIENTÍFICAS PERIÓDICAS DA USP
COMISSÃO DE CREDENCIAMENTO