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A review of the classification of the Melyridae and related families (Coleoptera, Cleroidea)

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Abstract: The family Melyridae sensu Crowson, 1955 is divided into six families. The former subfamilies Prionocerinae, Dasytinae, Melyrinae, and Malachiinae are given family rank. Two other families are described as new to science: Mauroniscidae (type genus *Mauroniscus* Bourgeois, 1911) and Attalomimidae (type genus *Attalomimus* Wittmer, 1976). A so-called "Melyrid lineage", where all seven families are placed (together with the family Acanthocnemidae), is defined. Both larval and adult characters are taken into consideration and some homologous features between them are found. Each family is defined by major transformations in at least three structures in both larvae and adults. The family Dasytidae is divided into six subfamilies: (1) Rhadalinae, (2) Gietellinae, (3) Danaceinae (n.stat.), (4) Chaetomalachiinae (n.stat.), (5) Listrinae (n.stat.), (6) Dasytinae (n.stat.). Important structures are figured, and cladistic analyses of all major taxa are provided.

Key words: Coleoptera Cleroidea – higher classification – new families – adult and larval morphology

I. INTRODUCTION

The superfamily Cleroidea, defined by CROWSON (1955), belongs in the family series Cucujiformia and has clear relationships with the Lymexyloidea, Cucujoidea, and Tenebrionoidea. CROWSON (1955) united several of the families of older authors and created a new broad concept of the family Melyridae, corresponding in part to the views of certain earlier entomologists. CROWSON (1964, 1970) subsequently reviewed the superfamily again and classified it into several families, reaching the same conclusions over its higher classification. These conclusions have been followed unquestioningly by some authors, e.g. FIORI (1962, 1972), but not by others.

Crowson's concept of the family Melyridae was based mostly on larval characters, with no attempted synthesis between larval and adult classifications. Larval structures, such as the endocarina or epicranial suture, were considered to be of decisive importance, whereas significant adult structures such as the male tegmen were almost completely ignored.

The inappropriateness of this procedure had already been suggested by, for example, the uncertain position of the family Phycosecidae: the larvae and the adults could each be classified into different families. The

adult morphology (prominent antennal club (Fig. 12), transverse mediostipes (Fig. 16), closed front coxal cavities (Fig. 18), inverted tegmen with tegminal struts isolated from phallobasic apodeme) indicates a relationship with the Trogositidae, whereas the larval morphology (Y-shaped epicranial suture, absent endocarina, elongate stipes, etc.) suggests a Melyrid lineage as defined here.

Classifications based on larvae and adults are often very different, as the aims of existence and mode of life are completely different in these two life-stages and very few structures may be homologous in the course of ontogenesis. Larvae of large numbers of species would be required in order to confirm certain suggested correlations.

In the present paper, an attempt is made to harmonise adult and larval characters, and several characters have been found that are apparently homologous between larvae and adults.

II. METHODS

The dissection techniques are the same as those used in another paper of mine dealing with the major classification of the Malachiidae (MAJER, in press). The cladistic principles of HENNIG (1950, 1965, 1966) are followed and upgraded by the principle of transformation series, adopted from KOLIBÁČ, (1992). All the keys aim to facilitate the identification of the higher taxa as rapidly as possible: they are based on external characters alone, and do not reflect the true relationships among the higher taxa.

Special morphological terms have been adopted from the key works dealing with this subject (e.g. EKIS, 1977, KOLIBÁČ, 1987, 1989a,b).

To ensure that the higher classification is well balanced, the following principle has been consistently followed in the present paper. Different modes of transformation (i.e. transformation series) of the same structure have been sought in each family in the following groups of characters:

(1) larval mouthparts
(2) adult mouthparts
(3) larval alimentary canal
(4) adult alimentary canal
(5) wings
(6) male copulatory organs

If major differences were found in at least three of these groups, then the taxon has been considered of family rank.

Abbreviations used

ADULT MORPHOLOGY

hab	habitus
int	integument
pub	surface pubescence
cum	cuticular modifications in general
egl	extrusible (defence) glands

Head

cuc	cuticular modifications on cranium
cra	cranium
crd	cranium dorsal
crl	cranium lateral
crv	cranium ventral
tem	temples
eye	eye
ocs	ocular suture
ocn	ocular notch
frs	frons
eps	epistomal suture
cly	clypeus
ces	cervical sclerites
ofo	occipital foramen
gul	gula
gup	gular process
gus	gular sutures
tnt	tentorium
tcb	tentorial cross-bar
ant	antenna in general
cua	cuticular modifications on antenna
sca	scapus
ped	pedicel
fla	flagellum (antennal segments 3 onwards)
aas	apical antennal segment
acl	antennal club
lar	labrumame articulating membrane
eph	epipharynx
top	tormal process
mep	median tormal process
ltp	lateral tormal process
man	mandible
mad	mandible dorsal
mal	mandible lateral
mav	mandible ventral
mco	mandibular condyle
mop	molar part
cue	cutting edge
prt	prostheca
pen	penicillus
mde	median dens
ade	anterior dens
pde	posterior dens
max	maxilla
cup	cuticular modifications on maxillary palpi
car	cardo
ocp	outer cardinal process
inp	inner cardinal process
bst	basistipes
mst	mediostipes
lac	lacinia
mla	mediolacinia
bga	basigalea
dga	distigalea
paf	palpifer
mpa	maxillary palp
tmp	terminal segment of maxillary palp
lai	labium in general
lad	labium dorsal
lav	labium ventral
hyp	hypopharynx
hys	hypopharyngeal sclerites
msu	suspensory sclerites on mentum
msc	mental sclerites
mec	mental crescent
men	mentum
prm	prementum
prn	premental notch
hyb	hypopharyngeal bar
lig	ligula
lpa	labial palpus
tsl	terminal segment of labial palpus

Thorax

prx	prothorax
pro	pronotum
prc	pronotal collar
pxd	prothorax dorsal
pxv	prothorax ventral
fcc	front coxal cavities
aff	anterior foraminal flange
pff	posterior foraminal flange
hme	hypomeron
eme	"epimeron" (hypomeral process) [name homonymous with the true hypomeron]
sps	sternopleural suture
prs	prosternum
pip	prosternal intercoxal process
pre	proendosternite
crs	cryptosternum
pra	prosternal apophysis
msx	mesothorax
mmt	meso- and metathorax ventral
msd	mesoscutellum dorsal
msl	mesoscutellum lateral
scu	scutum
scl	scutellum
mes	mesosternum
msp	mesothoracic intercoxal process
mcc	middle coxal cavities
msn	mesepisternum
msm	mesepimeron
mtx	metathorax
mto	metanotum
mts	metasternum
mtp	metathoracic intercoxal process
mtn	metepisternum
mpm	metepimeron
mwp	metapleural wing process
dil	discriminal line
acs	antecoxal suture
vco	ventral condyle
met	metendosternite
mel	metendosternite lateral
sta	stalk
mke	median keel
lan	lamina
fua	furcal arms
ten	tendon
ely	elytron
eld	elytron dorsal
elp	elytral puncturation
els	elytral swelling (humerus)
elv	elytron ventral
epp	epipleuron
win	wing
Rc	radial cell
RM	radiomedial vein
Rs	vein in radial sector
M	medial vein
M1	medial vein 1
ave	anal veins
1A	anal vein 1
2A	anal vein 2
3A	anal vein 3
4A	anal vein 4
Ac	anal cell
axl	axillary lobe

Legs

cul	cuticular modifications on legs
cut	cuticular modifications on tibia
cox	coxa
tre	trochanter
tri	trochantin
fem	femur
tib	tibia
tar	tarsomeres 1-4
pul	pulvilli
bta	basitarsus
pta	praetarsus
clw	claws
cla	claw, appendages
emp	empodium
fle	front leg
fco	front coxa
fta	front tarsomeres
fba	front basitarsus
com	front tarsal comb (tarsomere 2)
pcl	protarsal claw
mle	middle leg
hle	hind leg
hco	hind coxa
hti	hind tibia
hta	hind tarsus
hcl	hind tarsal claw

Abdomen

sas	abdominal sternum II
fvs	abdominal sternum III (1st visible)
icp	intercoxal process on 1st visible sternite

Male terminalia

mpy	male pygidium
stm	abdominal sterna II-VII in male
mss	male sternum VII
mse	male sternum VIII
mms	median projection of sternum VIII
spf	spicular fork
isp	interspicular plate
aeg	aedeagus (tegmen and phallus)
aed	aedeagus dorsal
ael	aedeagus lateral
teg	tegmen
ted	tegmen dorsal
tel	tegmen lateral
tev	tegmen ventral
pap	phallobasic apodeme
tgs	tegminal struts
bri	basal ring (in Malachiinae)
phb	phallobase
llo	lateral lobes
pam	paramere
pha	phallus
phd	phallus dorsal
phl	phallus lateral
phv	phallus ventral
phs	phallic struts
ins	internal sac
spn	spinules
ost	ostium (phallotreme)
dle	dorsal lever

Female terminalia

fpy	female pygidium
fss	female sternum VII
fse	female sternum VIII
spv	spiculum ventrale

ADULT ANATOMY

Alimentary canal

phy	pharynx
eso	oesophagus
prv	proventriculus
ven	ventriculus
pyl	pylorus
pvl	lobe of pyloric valve
ile	ileum
mlt	Malpighian tubules
map	posterior attachment of Malpighian tubules
col	colon
rev	rectal valve
rec	rectum

Male reproductive organs

vde	vas deferens
tes	testes
mag	median accessory gland
lag	lateral accessory glands
ejd	ejaculatory duct

Female reproductive organs

vag	vagina
ute	uterus
agl	accessory gland
ovi	oviduct
spt	spermatheca
spd	spermathecal duct
spc	spermathecal capsule
spg	spermathecal gland
sgd	spermathecal gland duct
sct	sclerites of seminal canal
asg	accessory spermathecal gland
boc	bursa copulatrix
sec	seminal canal

LARVAL MORPHOLOGY

lgd	larva, general view, dorsal
lgv	larva, general view, lateral

Head

lcd	cranium of larva, dorsal
csu	cranial suture in larvae
eca	endocarina in larvae
ocl	ocelli in larvae
atl	antenna in larvae
pua	penultimate antennomere in larvae
tal	terminal antennomer in larvae
aap	antennal appendix in larvae
lal	larval labrum
tpl	tormal processes in larvae

lmv	larval mandible ventral
prl	prostheca mandibulae in larvae
lma	lacinia mobilis in larval mandible
mol	mola in larval mandible
pdl	posterior dens in larval mandible
cel	cutting edge in larval mandible
mdl	median dens in larval mandible
adl	anterior dens in larval mandible
lmx	labiomaxillary complex in larvae
stp	stipes in larvae
maa	mala in larvae
pes	pedunculate seta in larvae
cal	cardo in larvae
pml	prementum in larvae
mna	mental area in larvae
lil	ligula in larvae

Thorax and abdomen

lat	larval terga
stg	stigma in larvae
ing	integumental glands in larvae
dog	dorsal glands in larvae
txl	thoracic sclerites in larvae
fll	front leg in larva
and	abdominal segment 9 in larvae dorsal
anl	abdominal segment 9 in larvae lateral
ugo	urogomphi in larvae

LARVAL ANATOMY

mll	Malpighian tubules in larvae

CLADISTIC CRITERIA

a	apomorphy
p	plesiomorphy
A	autapomorphy
t	tendency or trend (partial apotypy: apomorphous state of a structure is not present in all species examined and/or the state is not well manifested). Following the cladistic principle, if a character state of a structure within a major subgroup is not found in all the species, this is classified as "t". Such expressions as e.g. "usually present", "nearly always distinct", etc, convey no information.
TS	transformation series (ways in which a structure is modified)

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IV. TAXONOMY OF THE SUPERFAMILY CLEROIDEA

A re-definition of this superfamily and of its position among related superfamilies is not the aim of this paper. The Cleroidea may be divided

into three or four independent lineages based on different transformation series of the mouthparts in larvae and adults and of the copulatory organs in adults. These lineages may be named as (1) Peltid lineage (but the former family Peltidae has recently been classified in the Trogositidae), (2) Clerid lineage, and (3) Melyrid lineage. The latter can be divided into (3) Acanthocnemid and (4) Melyrid s.str. lineages. In the present paper, a Melyrid s.lat. lineage is defined and referred to simply as the "Melyrid lineage".

CROWSON (1964) suggested that there was a close affinity between the families Phycosecidae and Dasytidae, but the former probably belongs in the Peltid lineage, as mentioned above.

Melyrid lineage

Definition (Fig. 197):

Plesiomorphies. Larva: epicranial suture mostly Y-shaped, mandibular lacinia mobilis present. Adult: tentorial cross-bar simple when present (Figs 26, 76); gular process absent (Fig. 164); maxilla without spinulose lacinia (Fig. 16); front coxal cavities broadly open; tarsi without pulvili (Figs 35,177).

Apomorphies. Larva: endocarina absent; mandibles with median dens situated above anterior one, mola absent (Figs 68, 78), prostheca long, spine-shaped (Figs 68, 88); labiomaxillary complex with elongate stipes (character state possibly homologous with that in adults) which is longer than cardo (Figs 69, 89, 127), pedunculate seta present; terga with annuliform stigma (Figs 120, 121). Adult: mandibles without well-defined molar part (e.g. Fig. 71); maxilla with well-defined lacinia which is not divided in laterolacinia and mediolacinia (Figs 94, 16), mediostipes elongate (Fig. 79); mesepisternum triangular in outline (Fig. 32); tibia never with stout spines along outer edges; aedeagus uninverted.

Remarks. A divided tegmen and complete interspicular plate in the spicular fork, as well the prominent median dens in the mandibles and rows of punctures on the elytra, may justify treating the family Acanthocnemidae as a separate lineage.

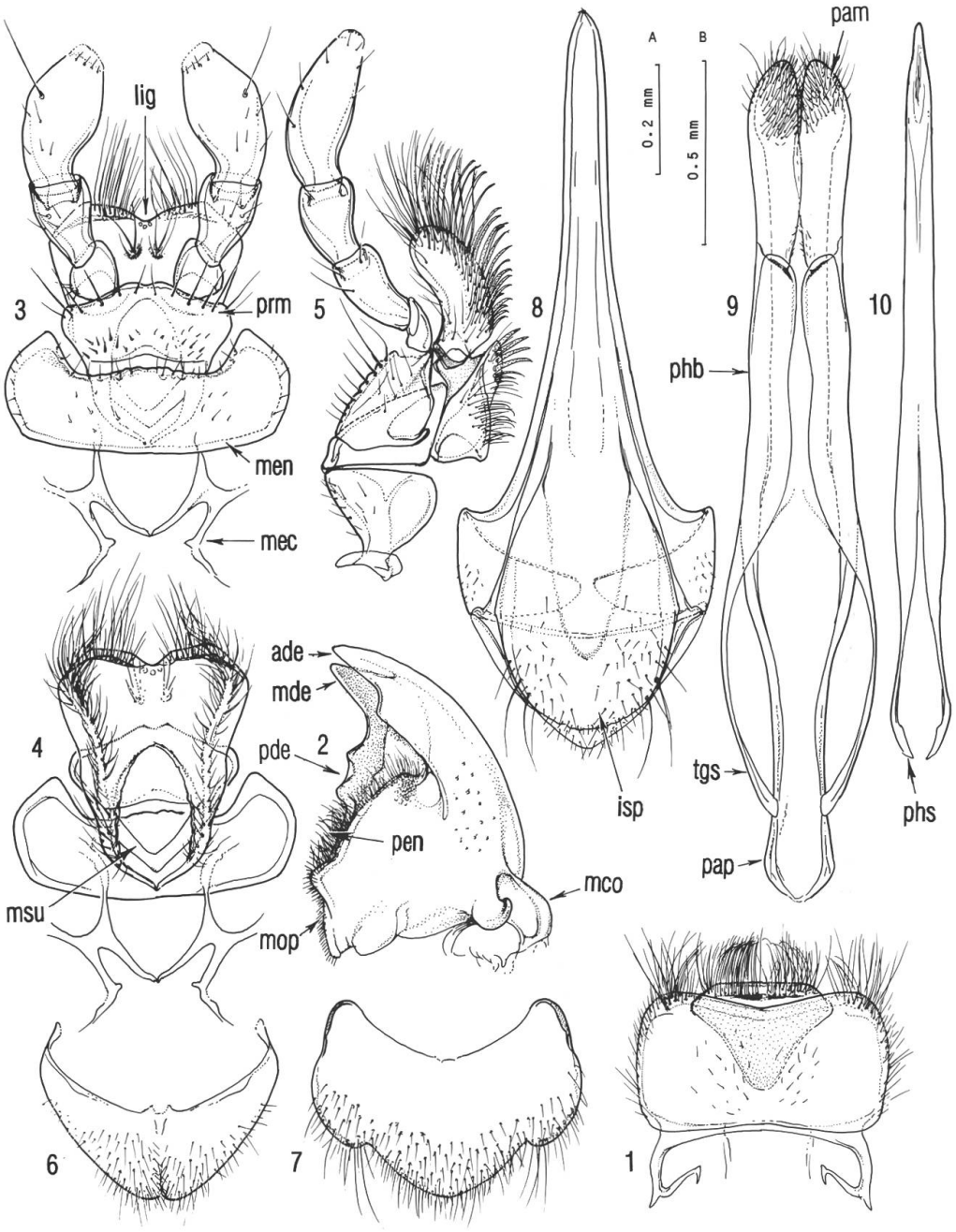
As a matter of fact, this definition of the Melyrid lineage based on larval characters agrees with Crowson's concept of the family Melyridae.

Check list of the families

Acanthocnemidae Crowson, 1964 (I)
Attalomimidae **n. fam.** (VII)
Dasytidae Laporte de Castelnau, 1840 (IV)
Malachiidae Erichson, 1840 (VI)
Mauroniscidae **n. fam.** (II)
Melyridae Leach, 1815 (V)
Prionoceridae Lacordaire, 1857 (III)

Key to the families of the Melyrid lineage (adults)

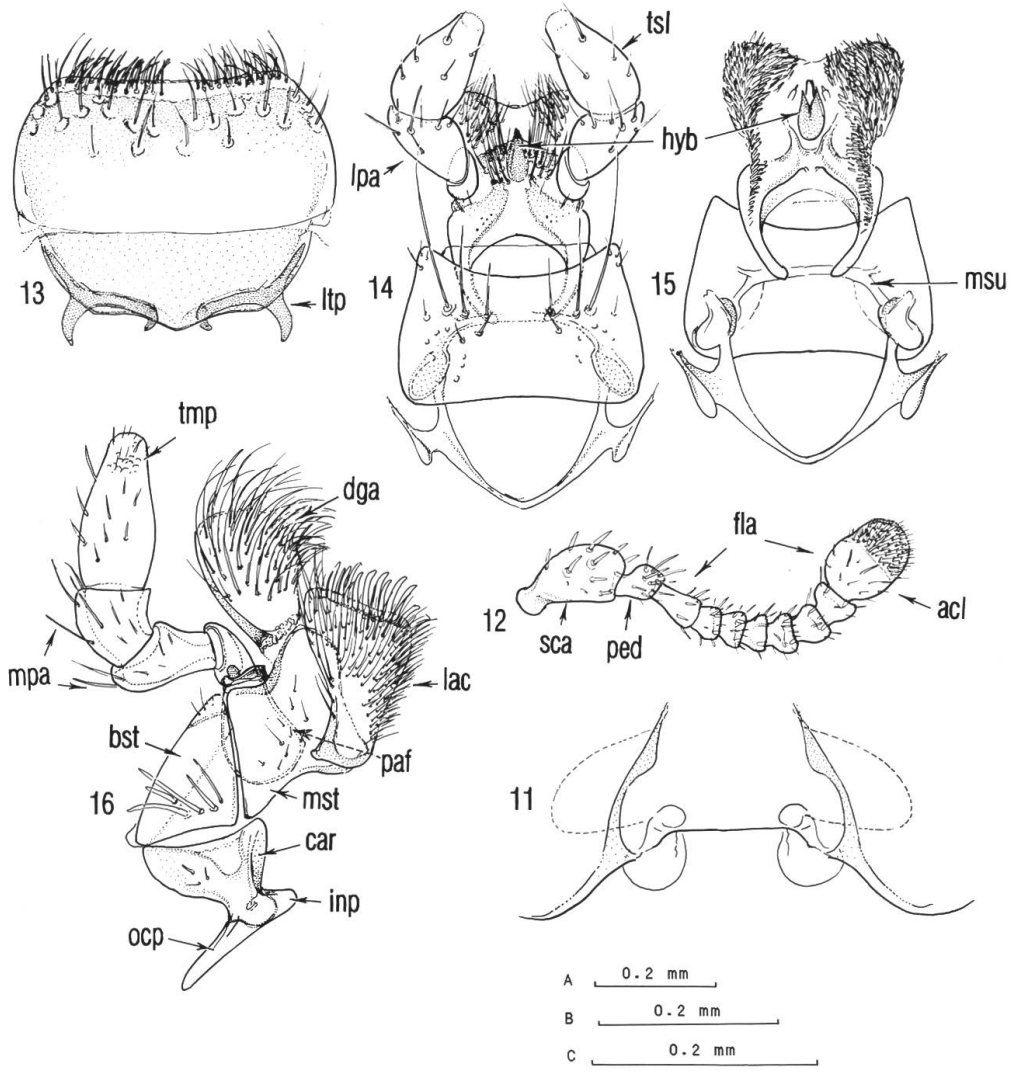
1. Tarsi 4-segmented on all legs and in both sexes (Figs 176, 177). Antennal segments swollen on middle and here with a fringe of long hairs (Fig.166). **VII. Attalomimidae** n.fam.
– Tarsi sometimes 4-segmented on male front legs (Fig.35), middle and hind legs almost always 5-segmented. Antennae not as above 2
2. Anterior tarsomere 3 pectinate in male. Apical antennal segment at least slightly emarginate on inner side or strongly constricted. **III. Prionoceridae**
– Anterior tarsomere 3 unarmed in males. Apical antennal segment often slightly constricted but never asymmetrically emarginate on inner side 3
3. Antennal flagellum composed of conical segments, club mostly well-defined (Figs 23, 46). Claws long and slender, never appendiculate (Figs 35, 36, 55) 4
– Antennal flagellum composed of segments that are more produced inwards than outwards, club sometimes weakly indicated 5
4. Elytra with rows of punctures. Large and flattened species. **I. Acanthocnemidae**
– Elytra with very fine irregular puncturation. Small, strongly convex species. **II. Mauroniscidae** n.fam.
5. Basitarsus on all legs distinctly shorter than tarsomere 2 (Fig. 149). **V. Melyridae**
– Basitarsus sometimes shorter than tarsomere on hind legs, almost as long as tarsomere 2 on front and middle legs. 6
6. Extrusible glands present, even though sometimes hardly visible. Body mostly malacodermiform and sternites capable of



Figs 1-10:1-5, *Tenebroides mauritanicus* (L.), ♀; 6-10, *Ostoma ferruginea* (L.), ♂: 1,labrum. 2, mandible ventral. 3, labium dorsal. 4, labium ventral. 5, maxilla. 6, male pygidium. 7, male sternite VIII. 8, spicular fork. 9, tegmen ventral. 10, phallus dorsal. (Scales: A- 1,3,4,5; B- 2,6,7,8,10).

contraction. Elytra often truncate at apex and not completely covering abdomen. Body very often with modifications related to the male pheromone glands. Male front tarsi often pectinate or 4-segmented. **VI. Malachiidae**

– Extrusible glands absent. Body more heavily sclerotised (although sometimes rather malacodermiform), sternites rarely very weakly capable of contraction. Elytra very rarely truncate at apex, nearly always completely covering abdomen. Body very rarely with modified legs and/or antenna. Male front tarsi without a comb, very rarely 4-segmented. **IV. Dasytidae**



Figs 11-16: *Phycosecis littoralis* Pascoe, ♀: 11, tentorium. 12, antenna. 13, labrum. 14, labium dorsal, 15, labium ventral. 16, maxilla. (Scales: A- 12; B- 11: C-13- 16).

Table for Cladograms of the Melyrid lineage (Figs 197, 198)

Structure		Plesiomorphous state	Apomorphous state	
1A		defined (e.g. Fig. 34)	absent (e.g. MAJER, 1987b: Figs 404–406, 413, etc.)	A1
2A		defined (e.g. Fig. 34)	absent (Figs 156, 178)	A2
Ac		present (e.g. MAJER, 1987b: Figs 371, 372, 373, etc.)	absent (e.g. Fig. 34)	A1
M	01	defined (e.g. MAJER, 1987b: Figs 371–380, 386–398)	connected with RM (e.g. MAJER, 1987b: Figs 399–420)	A1
M	02	very long (MAJER, 1987b: Figs 371–373)	abbreviated (MAJER, 1987b: Figs 375–433)	A1
M1	01	well-defined (Fig. 156 or MAJER, 1987b: Figs 374–387)	reduced to absent (e.g. MAJER, 1987b: Figs 388–433)	A2
M1	02	indicated (e.g. MAJER, 1987b: Figs 422–433)	absent (Fig. 34, or MAJER, 1987b: Figs 388–421)	A1
Rc		well-developed (e.g. Fig. 34)	sclerotised into a target (Fig. 156, 178)	TS
Rs		defined (e.g. MAJER, 1987b: Figs 371–373, 388–403, 420)	absent (e.g. MAJER, 1987b: Figs 374–387, 404–416, etc)	TS
aas		entire or slightly constricted (e.g. Fig. 96)	emarginate on inner side or strongly constricted (MAJER, 1987b: Fig. 240)	A2
acl		indistinct (Fig. 96)	distinct (Figs 12, 23, 46)	A2
acs		horizontal (Figs 19, 32, 99, 153)	oblique (e.g. MAJER, 1987b: 310, 360)	A1
aeg		inverted (e.g. Fig. 9, or CROWSON, 1964: Fig. 65)	uninverted (e.g. Figs 42, 62, 109, etc)	A2
ant		11-segmented	less than 11-segmented (e.g. Fig. 23)	A1
asg		absent (e.g. Fig. 195)	present (MAJER, 1990 c: Figs 16–19)	A1
axl		defined (e.g. Fig. 34)	indistinct (e.g. Fig. 178)	A1
bri		absent (e.g. Figs 9, 109)	present (Figs 184, 185)	TS
bst		well-marked (e.g. Figs 5, 16, 79, etc)	concealed with mst (Figs 49, 72, 75)	A2
bta		more than half length of tar 2 (e.g. Figs 35, 55)	half length of tar 2 (Fig. 149)	A1
cel		uneven (Figs 68, 69)	straight (Figs 125, 138)	A1
cla	01	absent (e.g. Fig. 35)	present (e.g. Fig. 103)	A1
cla	02	well-developed (Fig. 103)	reduced (e.g. Fig. 105)	A1
cla	03	membranous (Fig. 103)	sclerotised (e.g. MAJER 1987b: Fig. 99)	A1

Structure		Plesiomorphous state	Apomorphous state	
com		absent (e.g. Fig. 35)	present (e.g. MAJER, 1987b: Figs 254, 331)	A2
crs		defined (e.g. Figs 31, 52)	not defined (e.g. Fig. 171)	A2
csu		V-shaped (e.g. KOLIBÁČ, 1989b: Fig. 1)	Y-shaped (e.g. Fig. 122)	A2
cua		absent (e.g. Fig. 46)	present (e.g. MAJER, 1987b: 329, 332)	A2
cue		entire (e.g. Fig. 93)	finely denticulate (e.g. Figs 48, 71, 111)	A2
cul		absent (e.g. Fig. 149)	present (e.g. MAJER, 1987b : Fig. 160)	A2
cum		absent	present	A2
dga		divided in two (Fig. 72)	undivided (e.g. Fig. 94)	A2
dog	01	absent	present (Fig. 120)	A2
dog	02	not eversible	eversible	A2
eca		present	absent	A1
egl	01	absent	present	A2
egl	02	situated on aas and ltp	situated on prx and mtx	A2
eld		with indicated costae (e.g. MAJER, 1987b: Fig. 28)	situated on prx and mtx	A2
eld		with indicated costae (e.g. MAJER, 1987b: Fig. 28)	costae not indicated	A2
elp		arranged in striae	irregular	A1
eme		distinct (e.g. Fig. 31)	reduced (Fig. 171)	A2
eph		distinct (e.g. Figs 1–3, 13)	indistinct (e.g. Fig. 1)	A1
epp		complete (e.g. Figs 33, 155)	incomplete (e.g. MAJER, 1987b: Figs 97, 312)	A1
fba	01	at most about as long as tar 2 (e.g. Figs 35, 103)	much longer than tar 2 (Figs 176, 177)	A2
fba	02	unarmed in males (e.g. Fig. 103)	combed in males (MAJER, 1987b: Fig. 254)	A2
fla	01	segments symmetrical, subconical (Figs 12, 23, 46)	segments asymmetrical, produced inwards (Figs 96, 166)	A1
fla	02	segments normally pubescent (e.g. Fig. 23)	segments with fringes of long hairs (Fig. 166)	A2
fro		of saccular type (boc not defined, see MAJER, 1990c: Figs 16–18)	of tubular type (boc defined; e.g. Fig. 195)	A1
fta		3 unarmed in males (e.g. Fig. 55)	pectinate in males (MAJER, 1987b: Fig. 254)	A2
hab		uniformly dark, not metallic	multicoloured and/or metallic	A1
hco		transverse (Figs 19, 32, 99, etc)	projecting (e.g. MAJER, 1987b: Figs 310, 360)	A1

Structure		Plesiomorphous state	Apomorphous state	
hme		well-defined (e.g. Fig. 31)	strongly reduced (MAJER 1987b: Fig. 358)	A2
hyb		present (e.g. MAJER, 1986: Figs 16–18, 20, etc)	absent (e.g. MAJER, 1986: Figs 19, 30)	A1
icp		well-defined (Fig. 106)	reduced to absent (Fig. 158)	A2
ing		absent	present	A2
int		heavily sclerotised	weakly sclerotised	A1
isp	01	present (Figs 8, 41, 61, 83)	absent (Figs 108, 160, 182)	TS
isp	02	complete (Figs 8, 41)	reduced (Figs 61, 83)	TS
lac	01	completely fused with mst (Fig. 5)	well-defined (Figs 16, 29, etc)	A2
lac	02	well-defined (Figs 5, 16, 29)	fused with bga and dga (Fig. 49)	A2
lac	03	ciliate, attached to mst through base (Figs 5, 94, etc)	not ciliate, attached to mst through side only (Fig. 169)	A1
lac	04	not spinulose	spinulose (e.g. Fig. 5)	A1
lac	05	not divided (e.g. Figs 16, 94, etc)	divided into mla and lla (e.g. KOLIBÁČ, 1989a: 61)	A1
lan		present (e.g. Fig. 38)	absent (e.g. Fig. 154)	A1
lar		of transverse outline (e.g. Fig. 1)	triangular (Fig. 47)	A1
lat		without sclerotised plates (e.g. Fig. 120)	with sclerotised plates (e.g. CONSTANTIN, 1989: Fig. 29)	A1
lig	01	apex emarginate (e.g. Fig. 3)	apex arched (e.g. Fig. 110)	A1
lig	02	without suspensory sclerites (e.g. Fig. 117)	with suspensory sclerites (e.g. Fig. 4)	A1
lma		present (Figs 114, 125)	absent (e.g. CROWSON, 1964: Fig. 2)	A2
lmv		without deep impression (Figs 88, 114)	with deep impression (Fig. 68)	A1
ltp	01	neither projecting nor meeting proximally (e.g. Fig. 145)	far projecting and meeting proximally (e.g. MAJER, 1986: Fig. 1)	TS
ltp	02	compact (e.g. Fig. 1)	divided into two (Fig. 47)	TS
ltp	03	not projecting and upcurved posteriorly (Fig. 92)	with a long upcurved projection posteriorly (e.g. Fig. 77)	TS
mad		with membranous tendons (e.g. Figs 2, 17, 78, etc)	tendons heavily sclerotised (Figs 71, 74)	A2
mag		well-defined (MAJER, 1990c: Figs 8–13, 15)	hard to locate (MAJER, 1990: Fig. 14)	A2
man	01	not emarginate above pde (e.g. Figs 2, 17, 48, etc)	emarginate above pde and provided with a membranule (Fig.168)	A2
med		nor reduced (Figs 2, 17, 28, 78, etc)	reduced to absent (Figs 48, 71, 74, etc)	A1
mdl		below adl (e.g. Fig. 2)	above adl (e.g. Fig. 78)	A2

Structure		Plesiomorphous state	Apomorphous state	
mec		present (e.g. Figs 3, 14, 30, 80, etc)	no sclerites on mentum (e.g. MAJER, 1986: Figs 18–21)	A2
men		irregularly pubescent (Figs 14, 30, 50, etc)	only with two long setae (Fig. 170)	A2
mke		absent (e.g. Fig. 82)	present (e.g. Fig. 134)	A1
mll	01	all simple	one dual	A2
mll	02	without pyloric lobes at bases	with pyloric lobes as in adults	A2
mlt	01	6 in number, all of the same length (MAJER, 1990c: Fig. 7)	4 or 5 in number, one abbreviated (MAJER, 1990c: Fig. 7)	A2
mlt	02	of the same length	one abbreviated (MAJER, 1990c: Fig. 7)	A2
mlt	03	evenly attached around prv (MAJER, 1990c: Figs 1, 4–7)	grouped as 4+2 (Majer, 1990c: Fig. 2)	A1
mms		present (e.g. Fig. 40)	absent (e.g. Fig. 183)	A1
mna		well-defined (Figs 89, 127)	fused with cal and stp (Fig. 69)	A2
mol		present (e.g. CROWSON, 1964: Fig. 24)	absent (e.g. Fig. 68)	A1
mop		distinct (e.g. Figs 2, 17)	not defined (e.g. Fig. 71, 74)	A1
msc		present instead of mec (Fig. 148)	no sclerites on mentum (e.g. Fig. 170)	A2
msn		quadrate to oblong (e.g. KOLIBÁČ, 1989a: Figs 67, 76, etc)	triangular in outline (e.g. Figs 32, 99, etc)	A1
msp		well-developed (e.g. Fig. 32)	reduced (e.g. Fig. 173)	A1
mst		not elongate (e.g. Fig. 16)	elongate (e.g. Fig. 79)	A1
msu		present (e.g. Fig. 4)	absent (e.g. Fig. 30)	A1
mtp		present (e.g. Fig. 32)	absent (e.g. Fig. 173)	A1
ocl	01	1 in number	more than 1	A1
ocl	02	2 in number	4 or 5 in number	A1
ocl	03	4 in number	5 in number	A1
paf		of normal size (e.g. Fig. 5)	strongly reduced (Fig. 169)	A1
pam		well-defined (e.g. Fig. 62)	represented at most as by terminal lobes (Fig. 109)	TS
pap		long and narrow (Figs 9, 42, 82)	short, broad, fused with tgs (Figs 62, 109)	TS
pde		prominent, cue emarginate below (Figs 2, 17, 28)	absent (e.g. Figs 71, 78)	A1
pdl		at the most slightly projecting (Fig. 88)	strongly projecting (Figs 125, 138)	A2
pen	01	present (e.g. Figs 2, 17, 111)	absent (e.g. Figs 142, 146)	A1
pen	02	short, ciliate (e.g. Figs 2, 17, 74)	elongate, membranous (e.g. Figs 78, 11, 112)	A2

Structure		Plesiomorphous state	Apomorphous state	
pen	03	not sclerotised (e.g. Fig. 2)	sclerotised proximally (Fig. 71)	A2
pes		absent	present	A1
pha	01	without defined base (e.g. Figs 10, 110)	with swollen base (e.g. MAJER, 1987b: Figs 127, 147, 156, etc.)	A2
pha	02	with complete tube (e.g. Figs 10, 191, etc)	ins uncovered (e.g. MAJER, 1988a: Figs 95–111)	A2
pha	03	apex entire (e.g. Figs 10, 43, 110)	apex divided (Figs 191–194)	A2
phb		envelopes greater part of pha (e.g. Figs 9, 42, 62)	reduced and covering pha distally only (e.g. Figs 84, 109)	A1
phl		almost straight (Figs 10, 43)	more or less arcuate (Fig. 110)	A2
phs	01	present (Fig. 10, etc)	absent (e.g. Figs 110, 162)	TS
phs	02	long (Figs 10, 43, 63, etc)	very short (e.g. MAJER 1987b: Fig. 228)	TS
pip		narrow (Figs 18, 31, 91, etc)	broad diverging (Fig. 171)	A2
pml	01	complete, high (Fig. 69)	reduced, low, sometimes divided into two (Figs 89, 127)	A2
pml	02	with several setae (Fig. 69)	with two main setae (Figs 89, 127)	A1
prc		not defined (e.g. Fig. 31)	defined (e.g. EKIS, 1977: Fig. 14)	A2
prm		fully developed (Figs 3, 14, 80)	strongly reduced (Fig. 50)	A1
prn		present (Figs 30, 80, etc)	absent (Figs 3, 14)	A1
prs	01	closely placed on hypomera (Figs 31, 171)	placed freely through a fork (e.g. MAJER, 1987b: Figs 302, 325)	A2
prs	02	simple at sides (Figs 18, 81, etc)	with pits at sides (Fig. 31)	A2
prl		short, broad (CROWSON, 1964: Fig. 2)	long, spine-shaped (Figs 68, 88, 114)	A1
prv		not narrowed (MAJER, 1990c: Figs 1–6)	constricted and elongate-narrow at base (MAJER, 1990c: Fig. 7)	A2
pub	01	uniform	forming ornamentation	A1
pub	02	distinct	indistinct	A1
pul		absent (Figs 35, 177)	defined (KOLIBÁČ, 1989a: Figs 29, 35)	A2
pvl		absent (MAJER, 1990c: Figs 4–7)	present (MAJER, 1990c: Figs 1–3)	A1
spc		membranous (MAJER, 1990c: Figs 22–47)	sclerotised (MAJER, in press: Fig. 314)	A1
spf		with diverging base (e.g. Fig. 108)	with broad compact base (e.g. Figs 182, 188)	TS
sps		distinct (e.g. Figs 31, 81)	indistinct (e.g. Fig. 151)	A1
stg		bicameral (CROWSON, 1964: Fig. 25)	annuliform (Figs 120, 121)	A1

Structure		Plesiomorphous state	Apomorphous state	
stp		transverse, shorter than cal (KOLIBÁČ, 1989b: Fig. 13)	elongate, longer than cal (Figs 69, 89, 127)	A2
tal		with long collateral setae (CONSTANTIN, 1989: Fig. 30)	with very reduced collateral setae (Figs 66, 86, 126)	A2
tar	01	5-segmented in both sexes	4-segmented in both sexes (Figs 176, 177)	A1
tar	02	5-segmented in males	4-segmented in males (Fig. 35)	
tbc	01	present (Figs 26, 76, etc)	absent (Figs 11, 45, 70 etc)	A1
tbc	02	simple (Figs 26, 76, etc)	modified (e.g. KOLIBÁČ, 1989a: Figs 130, 147, etc)	A2
ted		walls well-developed (Figs 9, 62, 190)	walls strongly reduced (Fig. 161, etc)	TS
teg		distally divided (Figs 9, 42)	entire (Figs 62, 84, 109, etc)	A1
tel		high (Figs 9, 62, etc)	flat (Figs 84, 109, 161)	TS
ten		defined (Figs 38, 100, 154, etc)	not defined (Fig. 54)	A1
tes		medium-sized (MAJER, 1990c: Figs 8–13)	very large, triangular in outline (MAJER, 1990c: Fig. 14)	A1
tgs		isolated (Figs 9, 42)	fused with pap (Figs 62, 109, etc)	TS
tib		outer edges with stout spines	outer edges at most with scattered spinules	A2
tmp		not attenuated (Figs 5, 16, etc)	strongly attenuated (Fig. 169)	A2
tpl	01	isolated (Figs 87, 113)	connected by transverse bar (Fig. 67)	A2
tpl	02	simple (Fig. 124)	with round targets (Figs 87, 113)	A1
txl		not markedly longer than abdominal ones	markedly longer than abdominal ones	A1

A1 Autapotypy within Melyrid lineage
A2 Autapotypy within Cleroidea
TS Transformation series

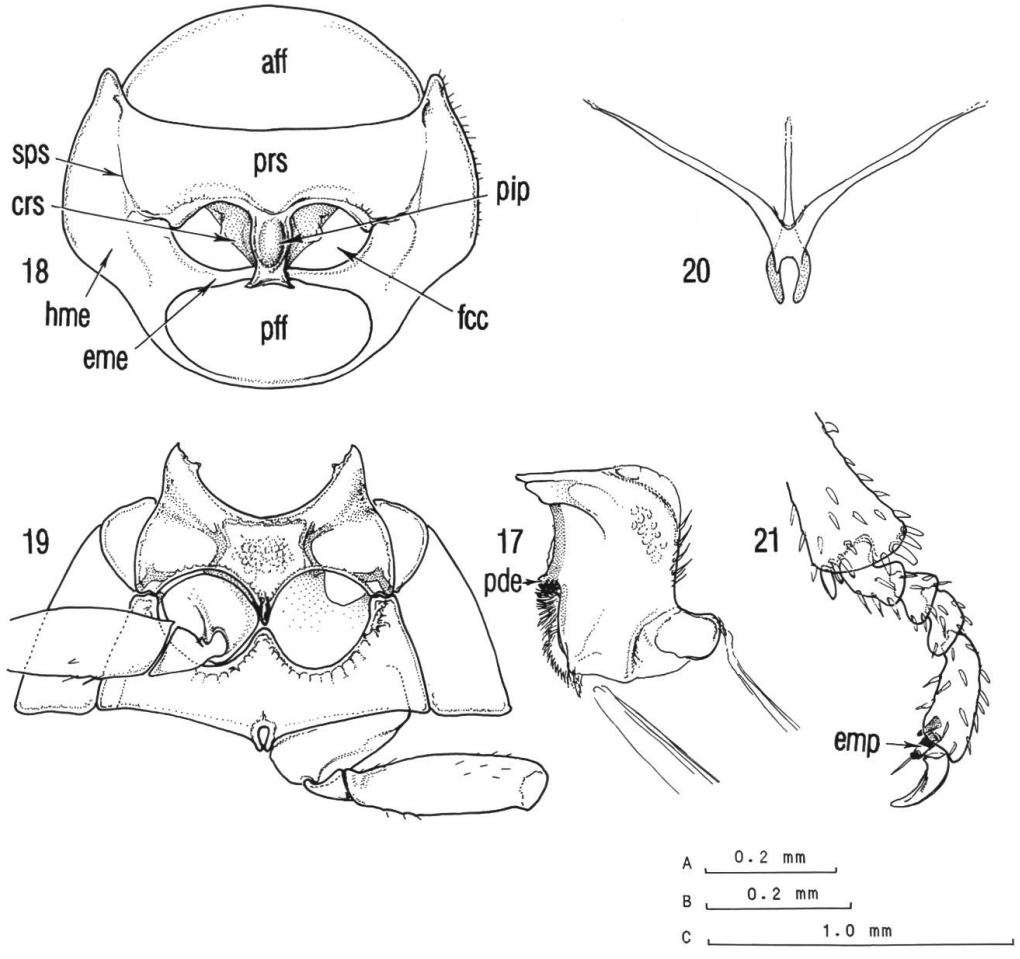
I. ACANTHOCNEMIDAE
(Figs 22–40)

Acanthocneminae [in Melyridae] CROWSON, 1964: 317. Acanthocnemidae: CROWSON, 1970: 3, 16.
Type genus: *Acanthocnemus* Perris, 1866

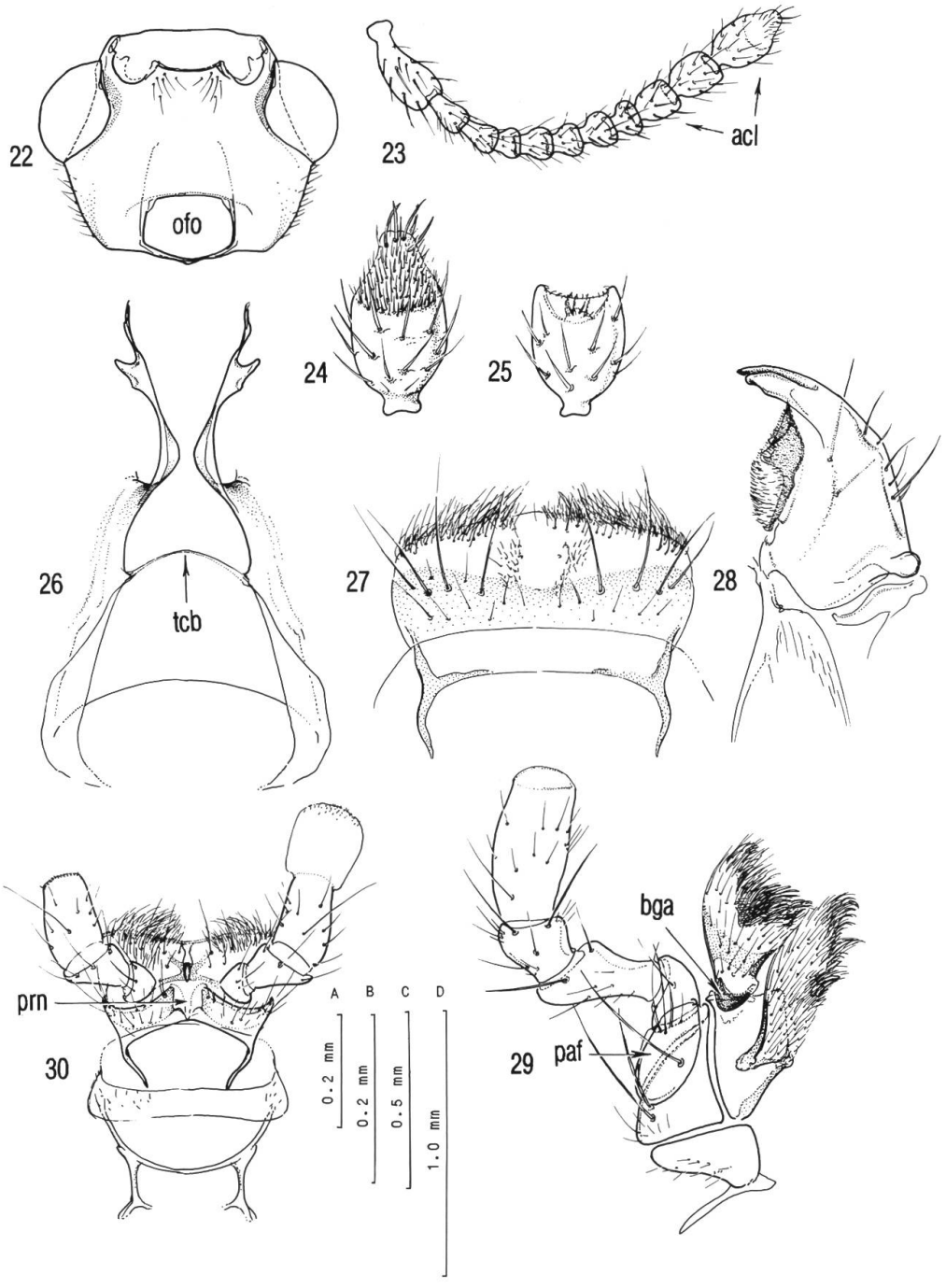
Differential diagnosis (Fig. 198):

Larva: unknown; the putative *Acanthocnemus*-larva described by CROWSON (1970) belongs to the Trogositidae subfamily Larinotinae (Crowson, pers. comm.).

Adult: extrusible glands absent but some gland openings present on sides of prosternum, cuticular modifications associated with pheromone

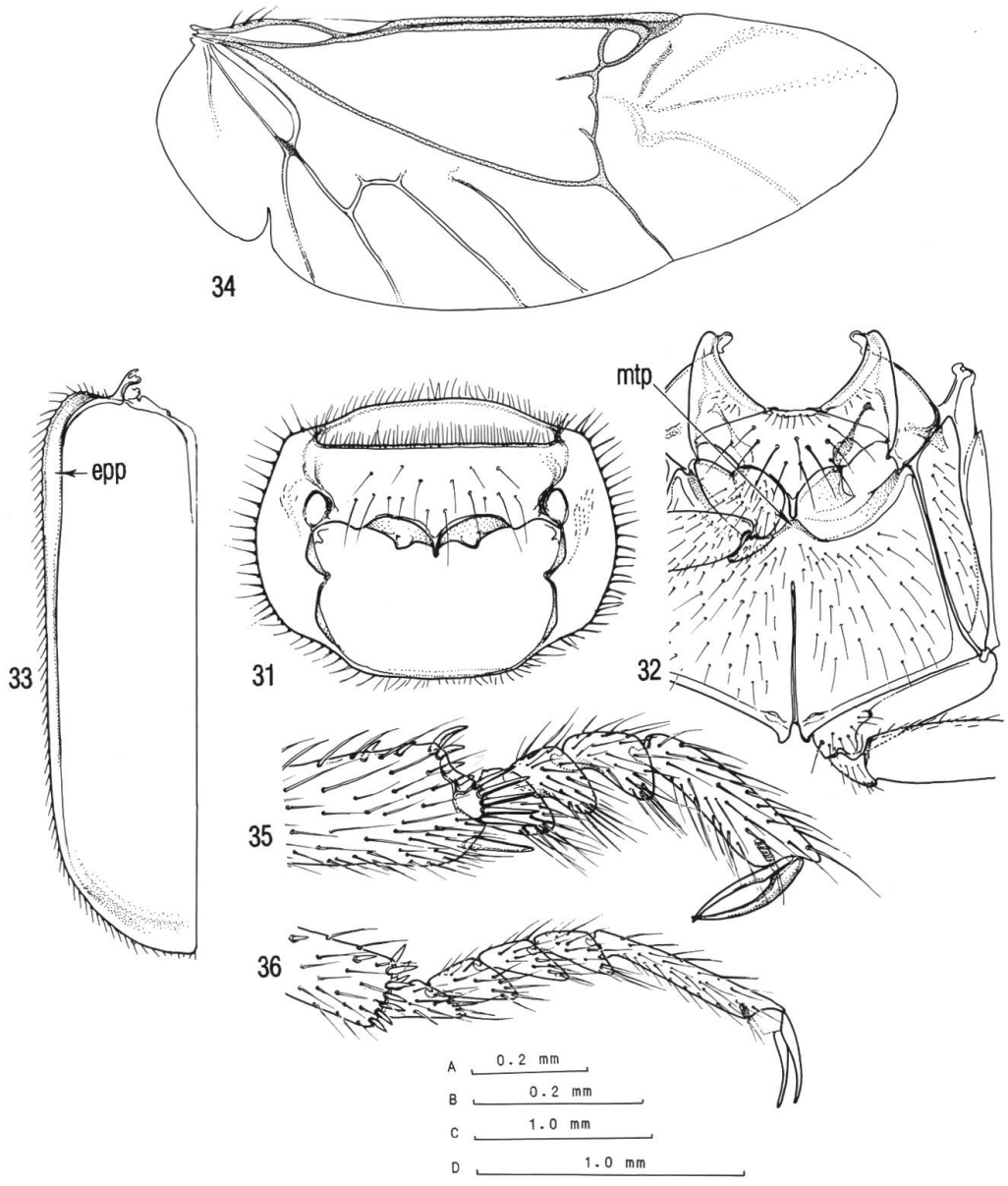


Figs 17-21: *Phycosecis littoralis* Pascoe, ♀: 17, mandible ventral. 18, prothorax ventral. 19, meso- and metathorax ventral. 20, metendosternite. 21, front tarsus. (Scales: A- 20; B- 17,21; C- 18,19)



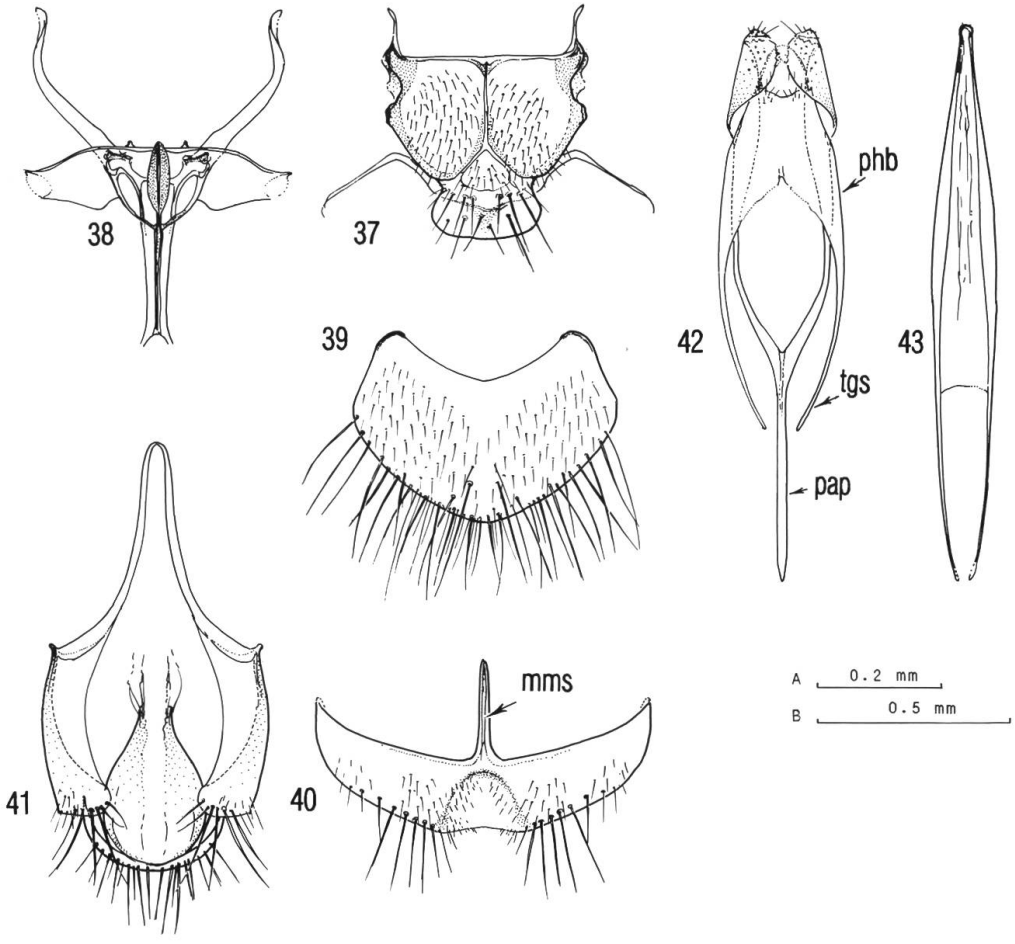
Figs 22-30: *Acanthocnemus nigricans* (Hope), ♂: 22, cranium ventral. 23, antenna. 24, 25, apical antennal segment [24 extruded, 25 retracted]. 26, tentorium. 27, labrum. 28, mandible ventral. 29, maxilla. 30, labium dorsal. (Scales: A- 28; B- 24- 27,29,30; C- 23,D- 22).

glands situated on apical segments of antennae and of labial palps, tentorial cross-bar very fine; antennal club distinct; tormal processes simple (shaped as in Attalomimidae), mandibles with prominent posterior dens, basistipes and mediostipes defined, palpifer normal, lacinia normal, mental crescent present; sternopleural suture on prothorax reduced, lamina on metendosternite present, elytral surface with rows of punctures, anal wing sector of the common Cleroidea type, vein M1 not defined, Rc nor-



Figs 31-36: *Acanthocnemus nigricans* (Hope), ♂: 31, prothorax ventral. 32, meso- and metathorax ventral. 33, elytron ventral. 34, wing. 35, front tarsus. 36, hind tarsus. (Scales: A-36; B- 35,C- 33,34; D- 31,32).

mal, tarsomeres normal, male fore tarsi with 4 tarsomeres, claws simple and slender, sides of antecoxal suture weakly oblique, hind coxae transverse; intercoxal process on first visible sternite distinct, median process on male sternum VIII present, spicular fork of the Rhadaline type but with complete and divided interspicular plate, tegmen with forked phallobasic apodeme, separated tegminal struts and divided apex (in most Dasytidae-Rhadalinae, phallobasic apodeme also present but reduced and isolated, and apex of tegmen also divided in some *Pelecophora*-species, so that the Rhadaline tegmen cannot belong to the same transformation-series as Acanthocnemidae), phallus not arcuate, phallic struts very long; female copulatory organs of the saccular-type of Heberdey; proventriculus unknown, pyloric valve unknown, probably 6 Malpighian tubules.



Figs 37-43: *Acanthocnemus nigricans* (Hope), ♂: 37, mesoscutellum dorsal. 38, metendosternite. 39, pygidium. 40, sternite VIII. 41, spicular fork. 42, tegmen dorsal. 43, phallus dorsal. (Scales: A- 41-43,B- 37,38,40).

Transformation series:
(1) larval mouthparts: unknown
(2) adult mouthparts: plesiomorphous combination of maxilla and mandible.
(3) larval alimentary canal: unknown
(4) adult alimentary canal: unknown
(5) wings: symplesiomorphous with some primitive Dasytidae, e.g. *Amecocerus* Solier.
(6) male copulatory organs: (aut)plesiomorphous.

Plesiomorphy: Male terminalia.

Apomorphy: Presence of glands on head and pits on prosternum.

Supplementary description. The single species is strongly flattened and resembles both Trogositidae and Dasytidae, deep-brown and shining, with strong long bristles.

Remarks. It is very likely that this taxon represents an independent lineage as its tegmen is divided, the spicular fork has complete and divided sternum IX (interspicular plate), and the phallus has long struts, as in many other primitive Cleroidea. The mandibles with posterior dens are hard to classify within the Melyrid lineage, whereas the other head parts such as the tentorium, labrum, and all thoracic parts (e.g. the wing venation, which is almost identical with that in some taxa related to *Amecocerus* [Dasytidae]) make this taxon monophyletic with Dasytidae. In particular, the weakly oblique sides of the antecoxal suture imply Malacoderm affinities, and all these features may be correlated with the unusually situated extrusible glands.

This family includes the recent genus *Acanthocnemus* and the Coenozoic *Acanthocnemoides* Zherichin for which the subfamily Acanthocnemidinae was erected (ZHERICHIN & SUKACHEVA, 1973). This may indicate that the distribution was wider and the taxa of this group more numerous during the Coenozoic.

Distribution: Palaeotropical and Australian (here probably autochthonous).

Mauroniscidae & Prionoceridae family group

Definition (Fig. 197):

Head without tentorial cross-bar (convergent with the Melyridae and part of the Malachiidae).

Plesiomorphy. Adult: tegmen with distinctly defined parameres as in e.g. *Opilo* Germar (Cleridae).

Apomorphies. Adult: labrum with complex tormal processes that can easily be divided into median and lateral ones, mandibles with strongly denticulate cutting edge, maxilla with fused basistipes and mediostipes. Remarks. Although species of the two families have a totally dissimilar appearance, the structure of the mouth parts and of the tegmen seems correlated in the same way and suggests that the two families are monophyletic.

II. MAURONISCIDAE n.fam.

(Figs 44–64)

Type genus: *Mauroniscus* Bourgeois, 1911

Differential diagnosis (Fig. 198):

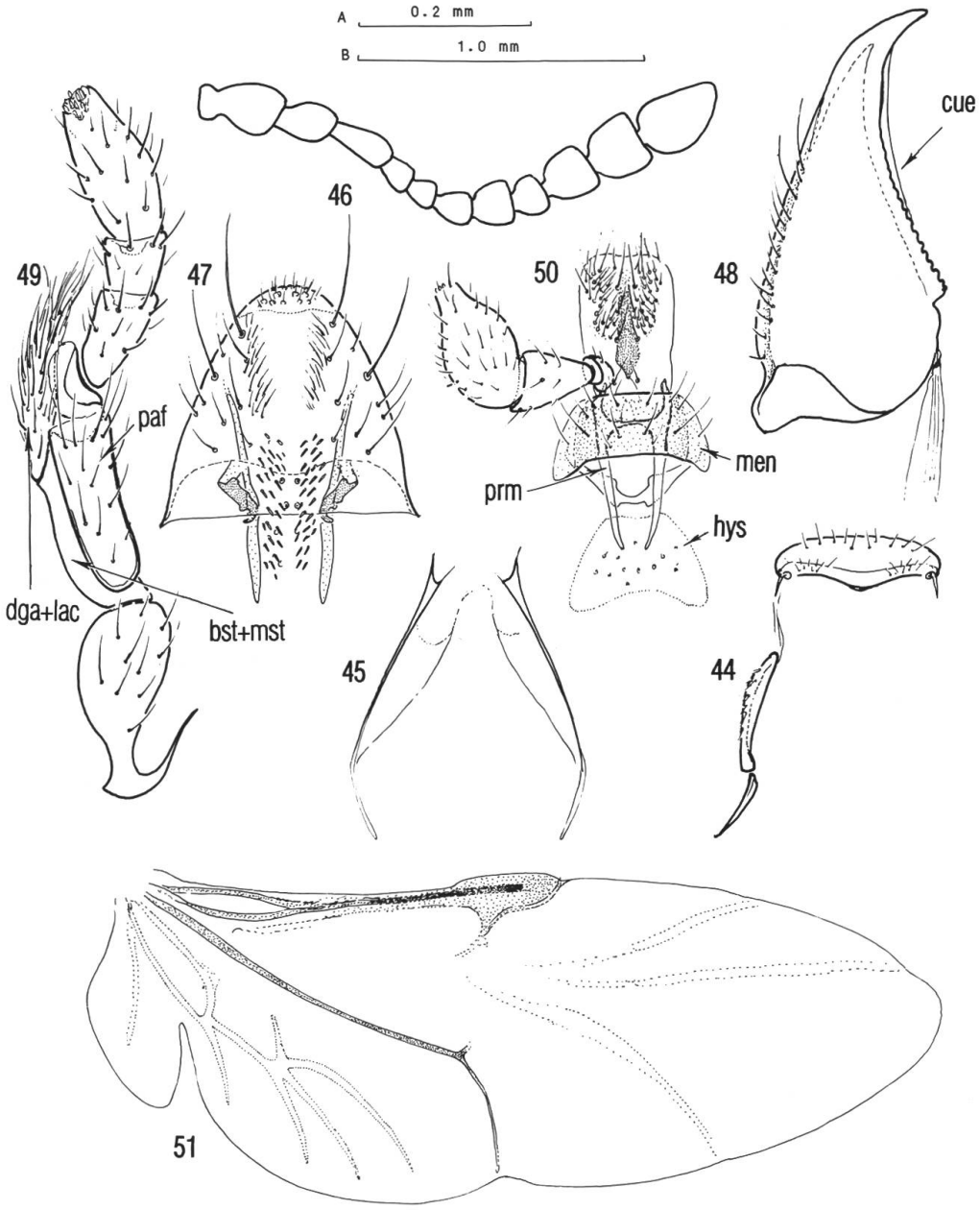
Larva: unknown.

Adult: extrusible glands absent, cuticular modifications associated with pheromone glands sometimes present on sternum VIII; tentorial cross-bar absent (tentorium extremely reduced), antennal club mostly distinct, tormal processes complex, mandibles without posterior dens, median one reduced, cutting edge strongly crenulate, basistipes and mediostipes fused, palpifer strongly enlarged, lacinia fused with distigalea, mental crescent present; sternopleural suture on prothorax indistinct, lamina on metendosternite present, elytral surface with irregular punctures, veins 1A-3A in anal wing sector with a common base ("autplesiomorphy" within the Melyrid lineage), vein M1 not defined, Rc more or less reduced, tarsomeres normal, claws simple and rather slender (almost as in Acanthocnemidae), sides of antecoxal suture almost straight, hind coxae transverse; intercoxal process on first visible sternite distinct; median process on male sternum VIII present, spicular fork rather of Dasytine type with complete interspicular plate, tegminal struts fused with phallobasic apodeme, phallobase fused with well-defined parameres, phallus not arcuate, phallic struts very long (as in Acanthocnemidae); female copulatory organs of the saccular type of Heberdey; proventriculus, pyloric valve and Malpighian tubules unknown, the latter probably six in number.

Transformation series:

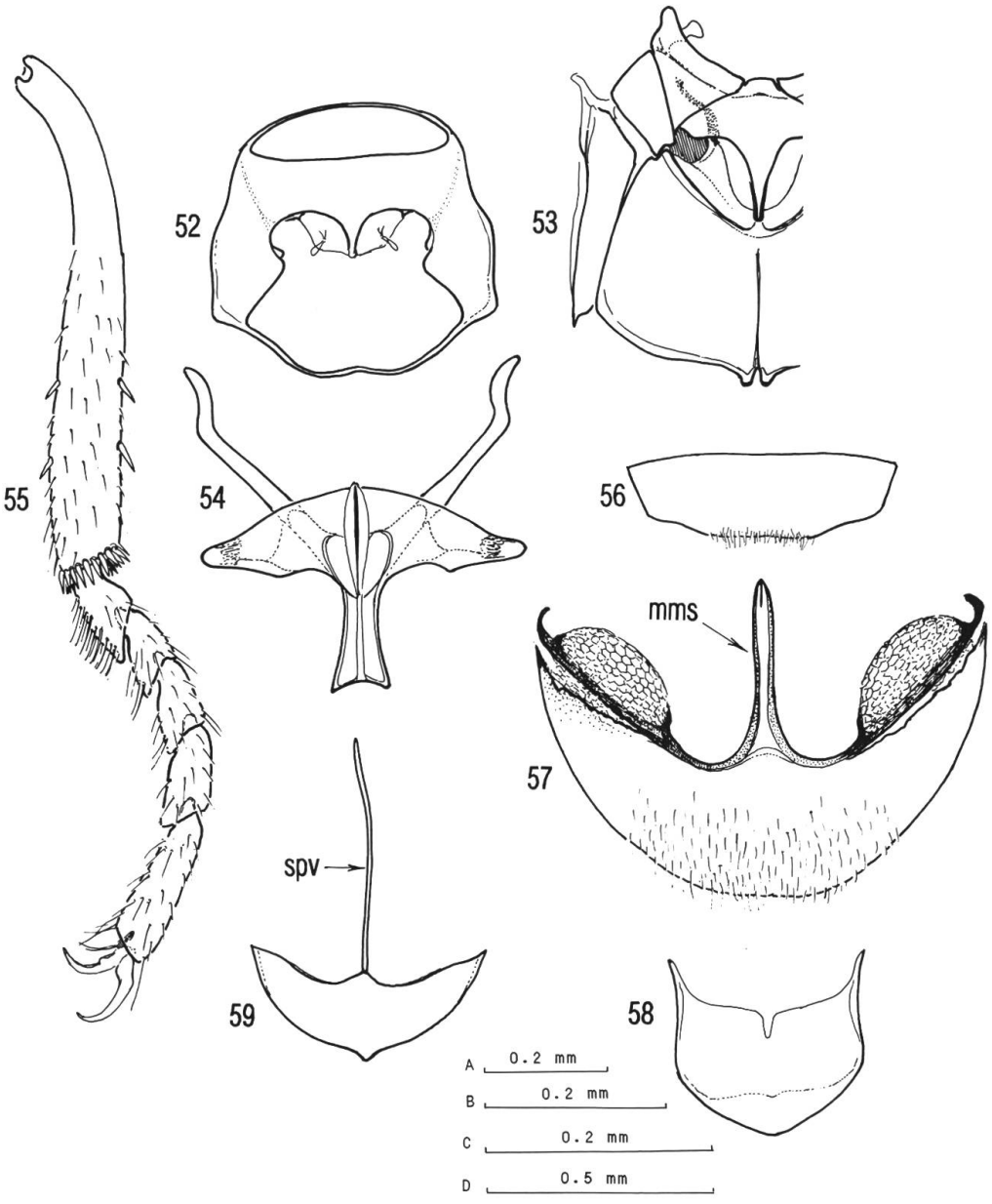
(1) larval mouthparts: unknown

(2) adult mouthparts: distigalea, lacinia and palpifer autapomorphous within the Cleroidea.



Figs 44-51: *Mauroniscus maculatus* Pic, ♂: 44, cervical sclerites. 45, tentorium. 46, antenna. 47, labrum. 48, mandible ventral. 49, maxilla. 50, labium dorsal. 51, wing. (Scales: A-44-50; B- 51). In Fig. 46 all setae omitted.

(3) larval alimentary canal: unknown
(4) adult alimentary canal: unknown
(5) wings: anal sector plesiomorphous within the Melyrid lineage.
(6) male copulatory organs: autapomorphous structure of tegmen and phallus.

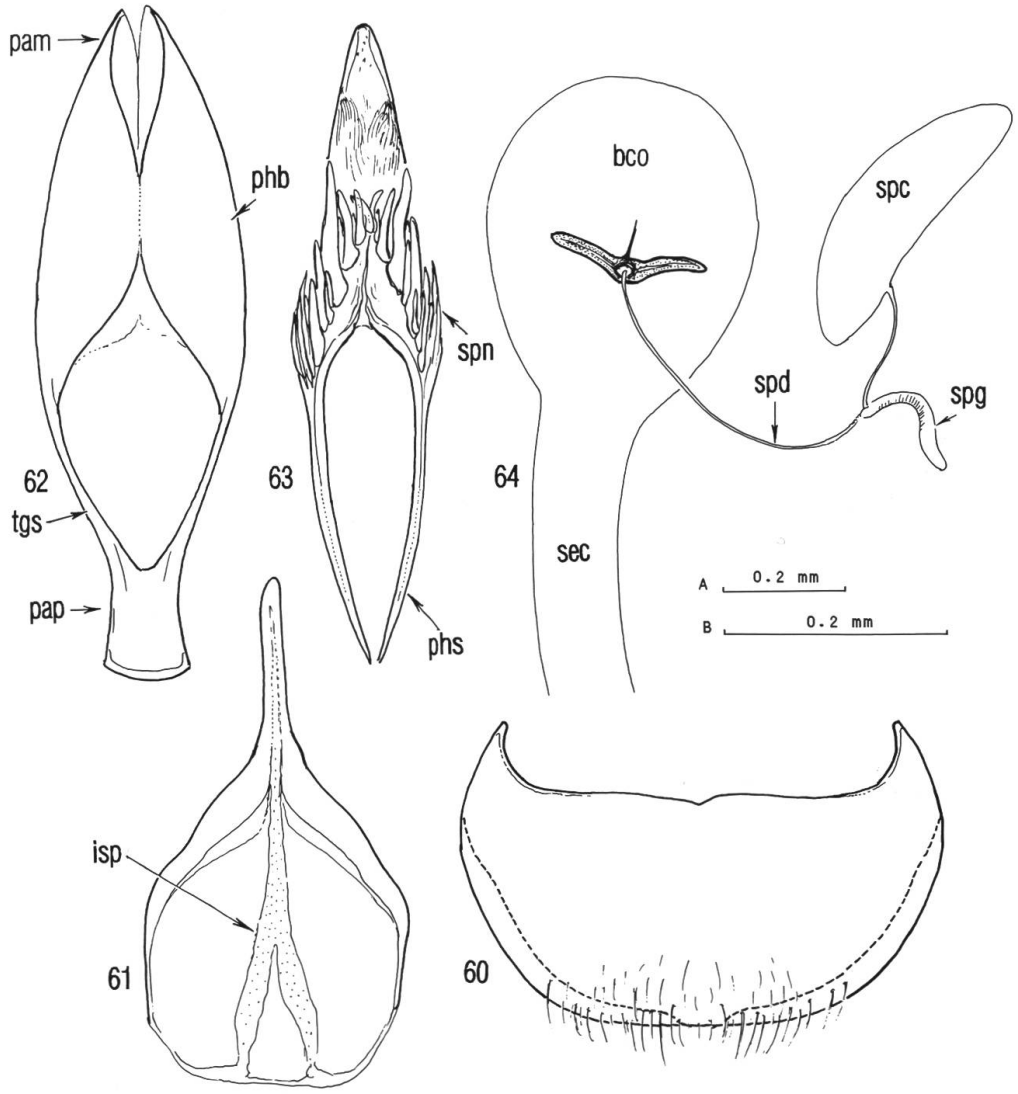


Figs 52-59: *Mauroniscus maculatus* Pic (52-57, ♂; 58-59, ♀): 52, prothorax ventral. 53, meso- and metathorax ventral. 54, metendosternite. 55, hind leg. 56, sternite VII. 57, sternite VIII. 58, pygidium. 59, sternite VIII. (Scales: A- 58,59; B- 54; C- 55,57; D- 52,53,56). [In Figs 58, 59 all setae omitted].

Plesiomorphies: Mouthparts, and elytral puncturation.

Apomorphies: Tentorium, distigalea and lacinia.

Supplementary description: Very small species, mostly about 3 mm in size, often variegated, strongly convex, head mostly rostrate. They often resemble small species of the Korynetinae (Cleridae), but differ at the first sight from the Melyridae s.lat. by the usually well-defined antennal club.



Figs 61-64: *Mauroniscus maculatus* Pic (60-63, ♂; 64, ♀): 60, sternite VIII. 61, spicular fork. 62, tegmen dorsal. 63, phallus dorsal. 64, female reproductive organs. (Scales: A- 64; B- 60- 63).

Remarks. This small taxon also includes the genus *Mecomycter* Horn which is very closely allied to *Mauroniscus* and may be synonymised with the latter, in which case only the family name would remain. I have not yet had any male of *Mecomycter* at my disposal. A third, undescribed, genus will include several species described by Pic in the genera *Listrus* or *Amecocerus*.

The Mauroniscidae are the distinct sister group of the Prionoceridae, and the latter is much more strongly derived. I have not seen such reduced maxillae as are found in the Mauroniscidae. The Mauroniscidae and Prionoceridae appear to be of Gondwanan origin. The genus *Mauroniscus* s.lat. spread into the Nearctic region after the Americas were rejoined, whereas the Prionoceridae live only in the Old World. No *Mauroniscus*-larvae are known, but I would not exclude the possibility that the presence of the endocarina and/or V-shaped epicranial suture is correlated with the clubbed antenna and long phallic struts of the adults.

Distribution. Nearctic and Neotropical regions.

III. PRIONOCERIDAE

(Figs 65–75)

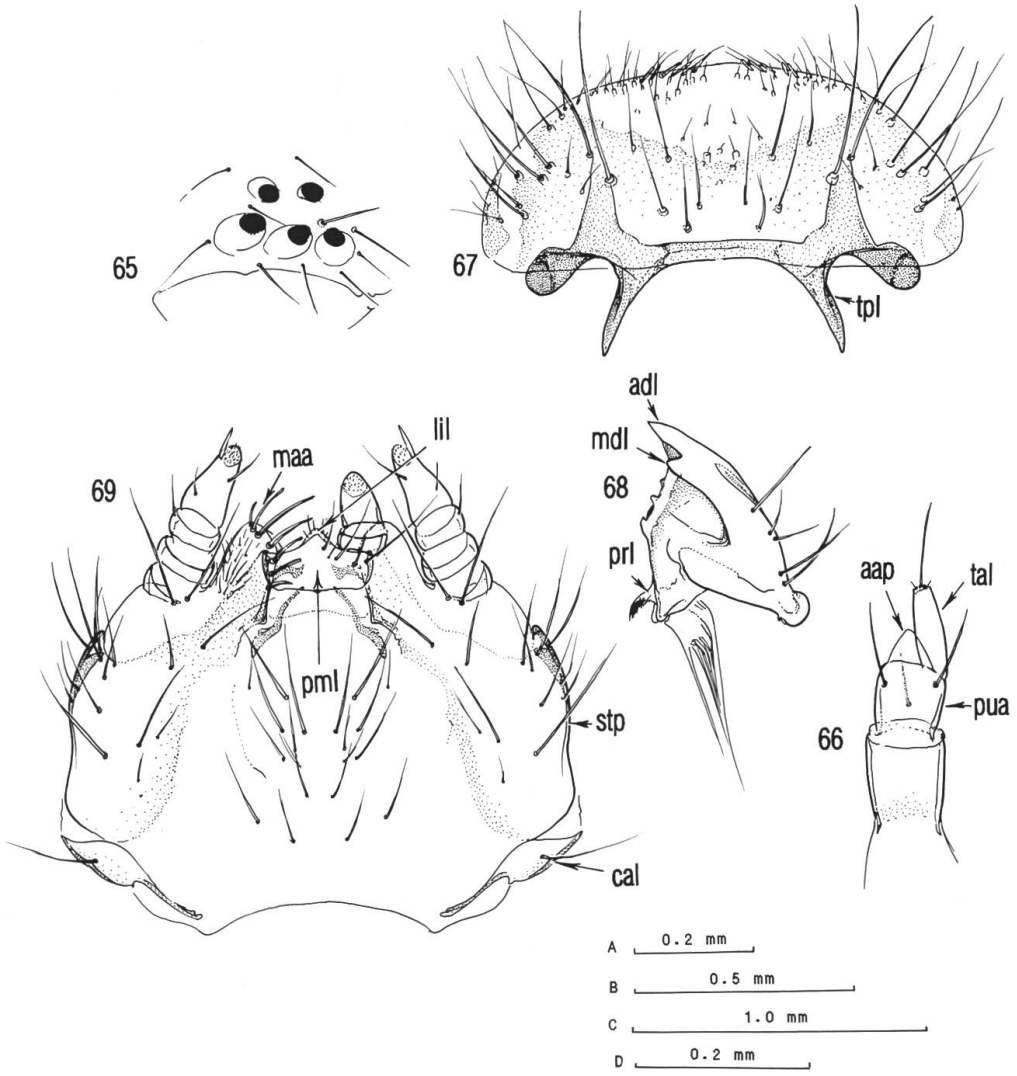
Prionocerides LACORDAIRE, 1857: 410. Prionocerini [in Zygiidae]: JACOBSON, 1911: 688. Prionoceridae: PIC, 1926: 4. Prionocerinae [in Melyridae]: CROWSON, 1955: 84.
Type genus: *Prionocerus* Perty, 1831.

Differential diagnosis (Fig. 198):

Larva: 5 ocelli, tormal processes complex (as in adults), mandibles excavated ventrally (as in adults), with denticulate cutting edge, posterior dens indistinct, prementum complete, high, with numerous setae, ligula with numerous setae; six pyloric valves and six Malpighian tubules (as in adults!).

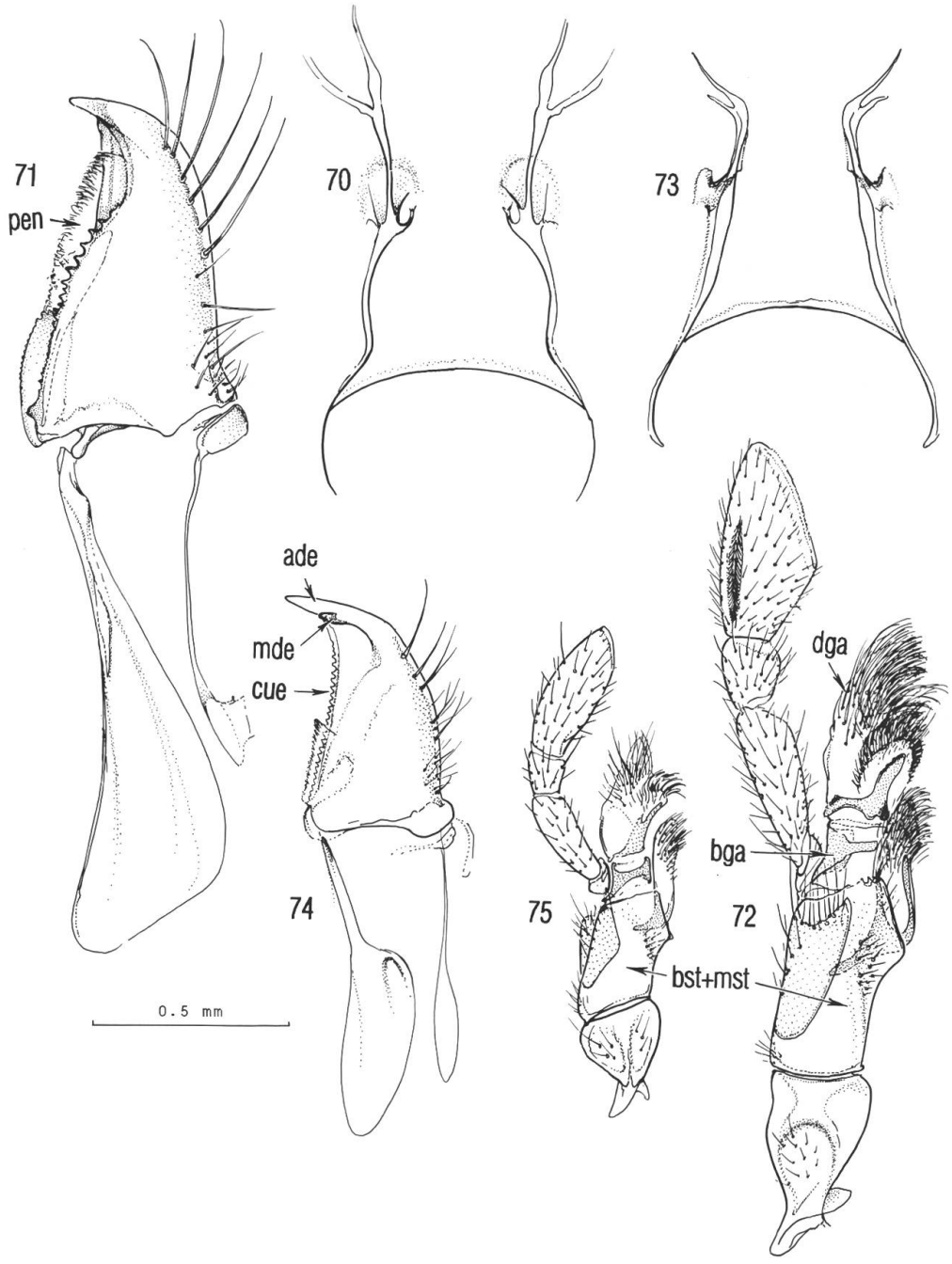
Adult: extrusible glands absent, cuticular modifications associated with pheromone glands absent, tentorial cross-bar absent, antennal club not indicated, terminal segment emarginate or constricted, tormal processes complex (as in some Cleridae), mandibles without posterior dens, median one reduced, cutting edge strongly crenulate, basistipes and mediostipes fused, palpifer weakly enlarged, lacinia normal, distigalea differentiated into two parts, terminal maxillar segment densely pubescent,

mental crescent present; sternopleural suture on prothorax very distinct (as prosternum tends to sit freely on hypomera as in some Malachiidae), lamina on metendosternite strongly reduced to absent, elytral surface with dense pupillate texture without normal setae, anal wing sector with veins of the common ancestral type, vein M1 not defined, Rc distinct, front tarsomeres 2–3(–4) pectinate in males, claws simple to appendiculate, not very slender, sides of antecoxal suture moderately oblique, hind coxae rather projecting; intercoxal process on visible sternite 1 distinct; median process on male sternum VIII present, spicular fork of Dasytine type without interspicular plate, tegmen with tegminal



Figs 65-69: *Idgia* sp., mature larva: 65, ocelli. 66, antenna. 67, labrum. 68, mandible ventral. 69, labiomaxillar complex. (Scales: A- 66; B- 65,69; C- 68; D- 67).

struts fused with phallobasic apodeme, phallobase fused with well-defined parameres, phallus at most weakly bent, phallic struts absent; female copulatory organs of the saccular type of Heberdey; proventriculus small, six pyloric valves, 6 Malpighian tubules.



Figs 71-75: 70-72, *Prionocerus caeruleipennis* Perty, ♂; 73-75, Lobonyx aeneus (F.), ♂: 70,73, tentorium. 71,74, mandible ventral. 72,75, maxilla.

Transformation series:

(1) larval mouthparts: plesiomorphous mandibles, tormal processes, prementum, and ligula.
(2) adult mouthparts: autapomorphous distigalea, lacinia, and palpifer.
(3) larval alimentary canal: autapomorphous pyloric valves homologous to those in adults.
(4) adult alimentary canal: autapomorphous pyloric valves.
(5) wings: plesiomorphous length of M.
(6) male copulatory organs: autapomorphous combination of well-defined parameres and apomorphous phallic struts.

Plesiomorphies: Tormal processes, mental crescent, surface of terminal segment of maxillary palps, wing vein M.

Apomorphies: Terminal antennal segment, more than 1 male tarsomere pectinate (at most, one is pectinate in some Malachiidae), surface densely pupillate without normal pubescence, apomorphous shape of tentorium, distigalea and lacinia.

Supplementary description. Strongly resembling some Oedemeridae (chiefly in the rostrate cranium) or Cantharidae. They are typically malacodermiform, weakly sclerotised, with long and slender extremities, lacking normal hairs but having a pupillate texture with very reduced setae; elytral border mostly crenelated.

Remarks. The labrum, labium, and tegmen in the Prionoceridae are parallel to those in some Cleridae, whereas the maxillae and wing venation are convergent with those in the Cantharidae (cf. BRANCUCCI, 1980). In the Prionoceridae the prementum and ligula are significantly polysetose whereas they are bisetose in all the remaining families of the Melyrid lineage as also in some Cleridae, e.g *Perilypus* (see EKIS, 1977) or *Tillus* (see FIORI, 1962) and the Trogositidae (e.g. CROWSON,1964: Fig. 49); a polysetose mentum does not seem to occur very often in the Cleridae and Trogositidae. The tarsal comb and some thoracic structures resemble those of the Malachiidae and are probably of a parallel nature because of the weak sclerotisation in both groups. The very strongly sclerotised mandibular tendons run throughout the cranium, which is a phenomenon without analogy.

The larval characters again support the independence of this family: the structure of the prementum, the mental region, and the presence of sclerotised plates on the larval terga appear to be unique within the whole superfamily. The homologies between the larvae and adults are

very significant: the pyloric valve, the tormal processes and the impressions on the ventral side of mandibles.

The family appears to replace the Dasytidae in the Oriental Region.

Distribution. In nearly all subtropical and tropical zones of the Old World, except South Africa, Madagascar, and Australian region (here rarely introduced).

Dasytidae & Attalomimidae family group

Definition (Fig. 197):

Plesiomorphies. Adult: Tendency to preserve tentorial cross-bar. Apomorphies. Larva: Prementum and ligula bisetose. Adult: labrum with tormal processes that can hardly be divided into median and lateral ones, mandibles at most with weakly denticulate cutting edge, maxilla with well-defined basistipes and mediostipes; tegmen without defined parameres (except in some Dasytidae-Rhadalinae), these indicated at most as an emargination of the tegminal apex.

Remarks. This is a complex of more or less related families, but the Attalomimidae have direct common ancestors with the Acanthocnemidae (see Fig. 197). It would be impossible to divide this family group into two families only.

Dasytidae & Melyridae family group

Definition (Fig. 197):

Larva: Prementum thin, divided into sclerotised and membranous parts, setae situated on the latter part (homologous with that of the adults below). Apical antennomere with only one long seta. Thoracic sclerites not much longer than abdominal ones. Six Malpighian tubules of approximately the same length (homologous with those of adults).

Adults: Prementum not produced distally, more or less broadly incised. Spicular fork of the Rhadaline type or guttate. Tegmen without basal ring and extensive dorsal wall. Extrusible glands absent. Six Malpighian tubules of approximately the same length, proventriculus small.

Plesiomorphies. Adult: prementum not produced, intercoxal process on 1st visible sternum more or less distinct, apex of tegmen ciliate.

Apomorphies. Larva: Prementum reduced (thin). Adult: tegmen without distinctly defined basal ring and/or extensive dorsal wall.

Remarks. This family-group is much less derived than the Malachiidae & Attalomimidae.

IV. DASYTIDAE
(Figs 76–119)

Dasytides LAPORTE, 1840: 280. Dasytites: BLANCHARD, 1845: 84. Dasytines: MOTSCHULSKY, 1845: 35. Dasytina [in Malacodermata Melyridae]: KIESENWETTER, 1863: 621, 624. Floricoles MULSANT & REY, 1868: 1 [olim]. Dasytiens: MULSANT & REY, 1868: 27, 28. Dasytini [in Melyridae Melyrinae]: CASEY, 1895: 457. Dasytesii: ACLOQUE, 1896: 307. Dasytinae: EVERTS, 1903: 189. Dasytinae [in Cantharidae]: KUHNT, 1913: 460. Dasytidae: PIC, 1917: 1-4. Dasytinae [in Dasytidae]: PIC, 1937: 3. Dasytini [in Melyridae Melyrinae] BLAISDELL, 1938: 3. Dasytinae [in Melyridae]: CROWSON, 1955: 84. Dasytina [in Melyridae]: MAJER, 1987: 798, 805.

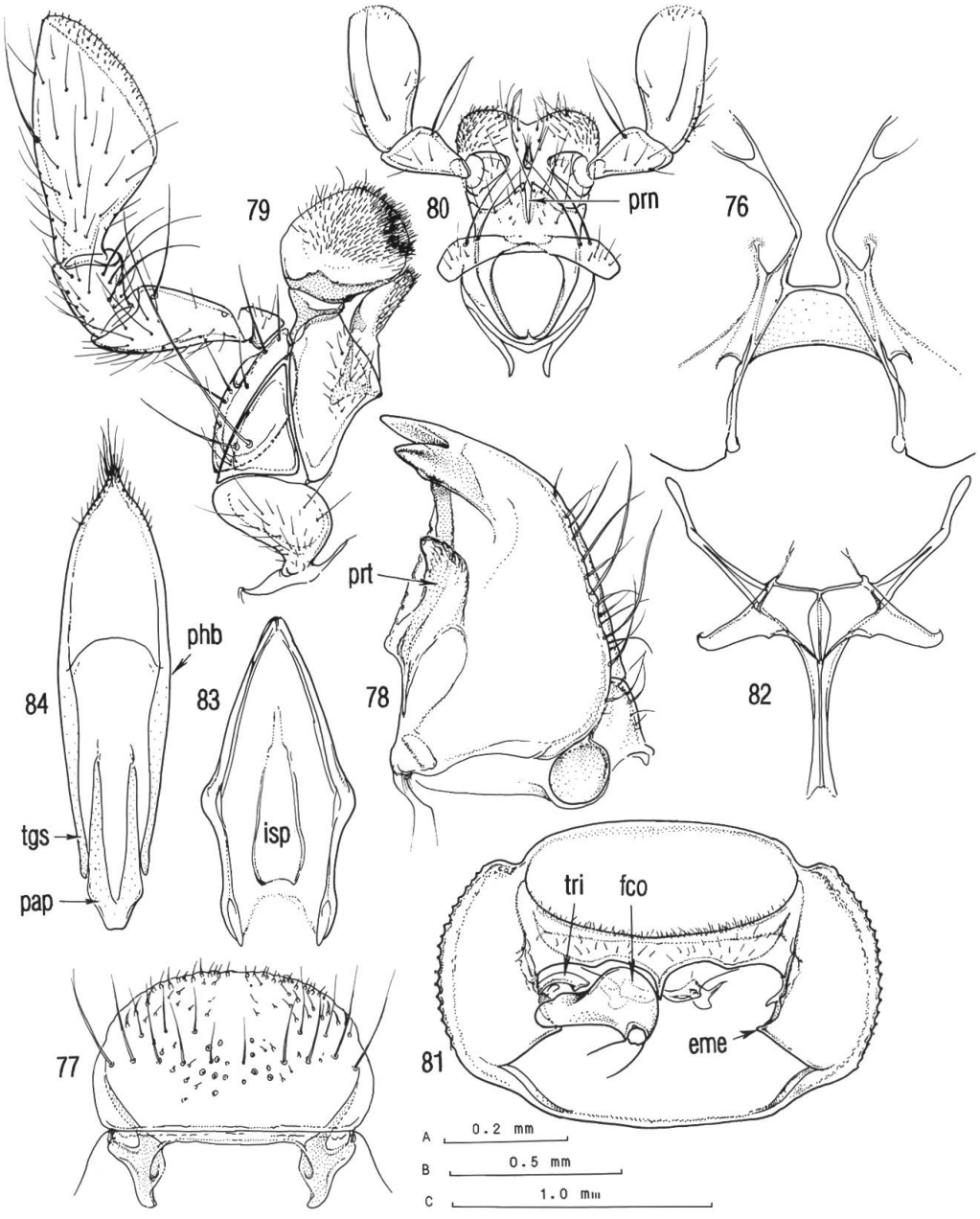
Type genus: *Dasytes* Paykull, 1798.

Differential diagnosis (Fig. 198):

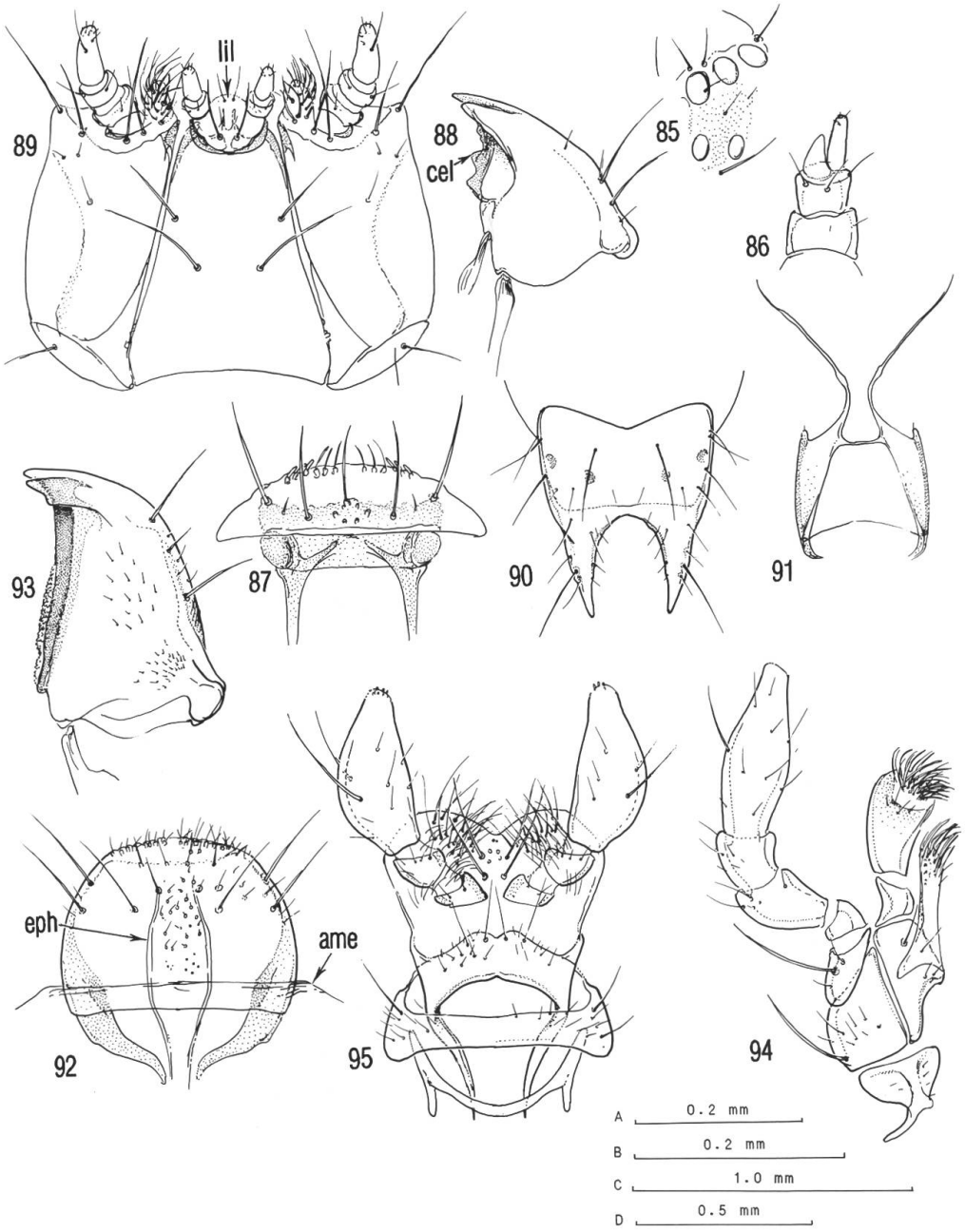
Larva: 2 or 5 ocelli, tormal processes and mandibles simple, with more or less denticulate cutting edge, posterior dens distinct, prementum complete, thin, with two main setae, ligula also bisetose; distinct pyloric valves absent, 6 Malpighian tubules.

Adult: extrusible glands absent, cuticular modifications associated with pheromone glands rarely present on antennae and/or legs, tentorial cross-bar present (but sometimes very fine), antennal club rarely indicated, tormal processes simple (not distinctly divided into lateral and median ones), mandibles without posterior dens, median one distinct, cutting edge glabrous (exceptionally with large dentes in Danacea); basistipes, mediostipes, palpifer, lacinia, and distigalea normal, mental crescent present (its presence equivalent to a compact larval prementum); sternopleural suture on prothorax distinct, lamina on metendosternite present or absent, elytral surface with irregular punctures, anal wing sector with veins of usual primitive type but sometimes strongly reduced, vein M1 not defined, Rc rarely reduced, front tarsomeres simple, very rarely 4 on all legs (probably only in males of the Rhadaline genus *Anthriboclerus* Schenkling), claws simple to appendiculate, shorter and broader, sides of antecoxal suture rather horizontal, hind coxae almost transverse; intercoxal process on 1st visible sternite rarely reduced; median process on male sternum VIII either present or absent, spicular fork of the Dasytine type without interspicular plate, tegmen with teg-

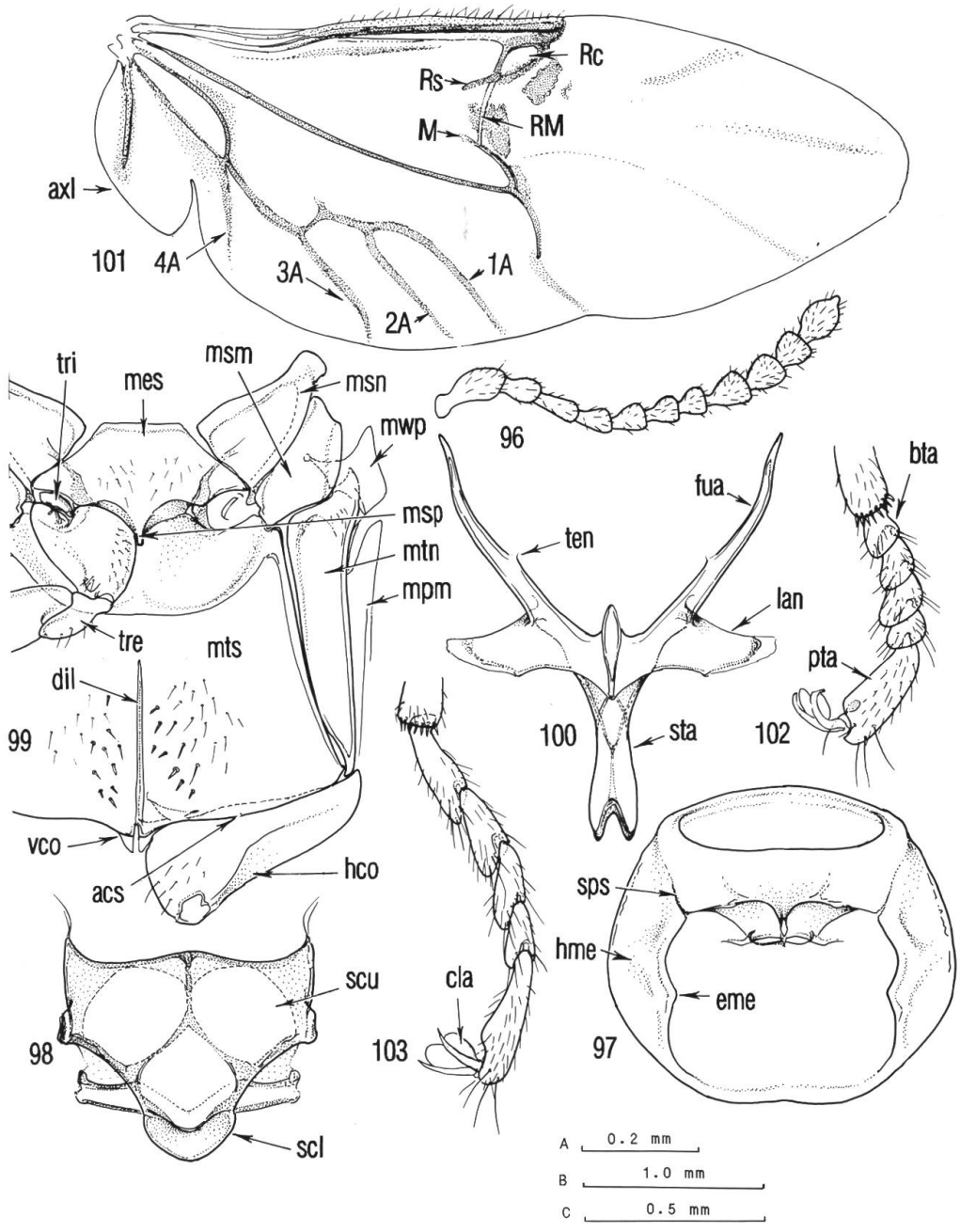
minal struts completely fused with phallobasic apodeme (except some in Rhadalinae), phallobase fused with parameres, the latter fused distally and forming so-called tegmen "en cavalier" of JEANNEL (1944); in some Rhadalinae, tegmen resembling that of the Acanthocnemidae but Rhadalinae phallobasic apodeme is reduced, isolated, and tegminal struts



Figs 77-83: *Rhadalus testaceus* LeConte, ♂: 77, labrum. 78, mandible ventral. 79, maxilla. 80, labium dorsal. 81, prothorax ventral. 82, metendosternite. 83, spicular fork. 84, tegmen dorsal. (Scales: A- 77- 80; B- 76; C- 81- 84).



Figs 85-95: *Haplamaurus suturalis* Kirsch (85-90, mature larva; 91-95, adult, ♂): 85, ocelli. 86, antenna. 87, labrum. 88, mandible ventral. 89, labiomaxillar complex. 90, abdominal segment 9 dorsal. 91, tentorium. 92, labrum. 93, mandible ventral. 94, maxilla. 95, labium dorsal. (Scales: A- 88,93,94; B- 85-87,89,92,95; C- 90; D- 91).

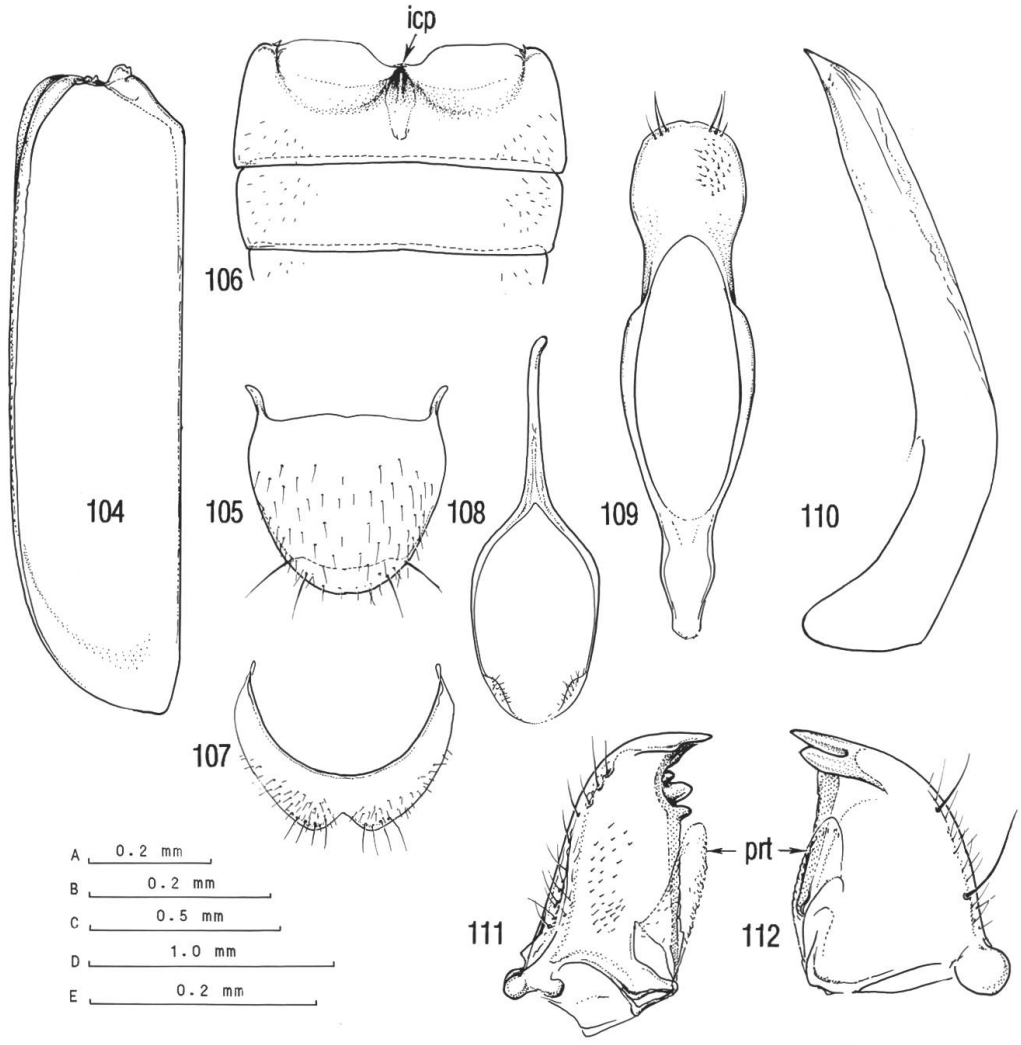


Figs 99-103: *Haplamaurus suturalis* Kirsch, ♂: 96, ant. 97, prothorax ventral. 98, mesoscutellum dorsal. 99, meso- and metathorax ventral. 100, metendosternite. 101, wing. 102, front tarsus. 103, hind tarsus. (Scales: A- 98,100; B- 101; C- 96,97,99,102,103).

are closely attached to the latter, tegmen rarely divided distally in several *Pelecophora*-species; phallus weakly to strongly arcuate and then with a large distinct base; female copulatory organs nearly always of the tubular type of Heberdey; proventriculus small, no distinct pyloric valves, 6 Malpighian tubules.

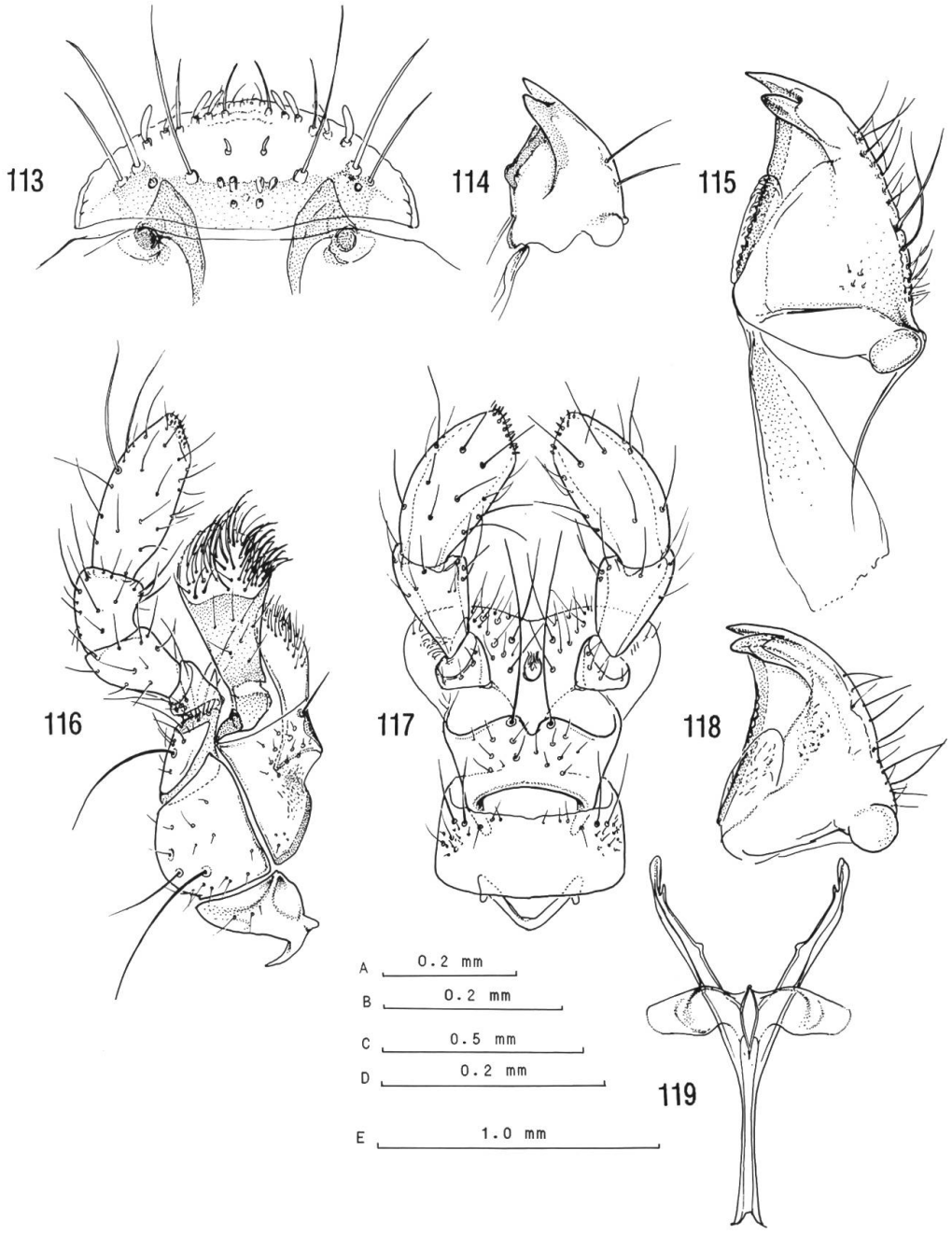
Transformation series:

(1) larval mouthparts: plesiomorphous state of prementum, stipes, and cutting edge of mandible.



Figs 104-112: 104-110, *Haplamaurus suturalis* Kirsch, ♂. 111, *Danacea pallipes* Panz., ♀. 112, *Amauronia subaenea* Westwood, ♂. 104, elytron ventral. 105, pygidium. 106, first two visible abdominal sterna. 107, sternite VIII. 108, spicular fork. 109, tegmen dorsal. 110, phallus lateral. 111,112, mandible ventral. (Scales: A- 108-110; B- 111; C- 105,107; D- 104,106; E- 112).

(2) adult mouthparts: plesiomorphous state of mandibles and mental sclerites.
(3) larval alimentary canal: plesiomorphous.
(4) adult alimentary canal: plesiomorphous.



Figs 113-119: 113- 117, 119, *Psilothrix viricaerulea* (Geoffr.) (113, 114, mature larva; 115- 117,119, adult, ♂). 118, *Dasytes niger* (L.), ♂. 113, labrum. 114,115,118, mandible ventral. 116, maxilla. 117, labium dorsal. 119, metendosternite. (Scales: A- 114,115; B- 118; C- 116; D- 113,117; E- 119).

(5) wings: plesiomorphous shape of Rc, M1, and M.
(6) male copulatory organs: autapomorphous.
Plesiomorphies: Mouthparts and wings.
Apomorphies: Tegmen, alimentary canal in both larvae and adults.
Supplementary description. Very strongly diversified in size, body-shape, and colour. Externally sometimes resembling Melyridae, at others resembling Malachiidae-Carphurinae, but never as soft-bodied as most Malachiidae.

Remarks. Dasytidae are most closely allied to their sister group, the Melyridae, with which they cannot form a common family because the latter has a different transformation series in the mouthparts (viz. the prementum, in both larvae and imagines), wing- venation, terminalia, and alimentary canal.

The most significant differences between the Dasytidae and Melyridae are the entire vs divided larval prementum and the presence vs absence of the adult mental sclerites. A parallel tendency with the Malachiidae is the presence of cuticular modifications associated with the male pheromone glands (the so-called "excitators") in several Dasytinae species. If the number of larval ocelli was the sole character for defining subfamily rank in the Dasytidae, it would destabilise the entire systematic conception. Two ocelli occur in the Gietellinae and Rhadalinae but also in the Dasytine genus *Dolichosoma* Stephens (see EMDEN, 1932), which is very closely allied to *Psilothrix* Redtenbacher with 5 ocelli. The number of larval ocelli thus seems rather irrelevant when the Cleroidea are viewed as whole.

Distribution: Almost worldwide, but not in the greater part of the Oriental region (especially the Indomalayan and Oceanian subregions), where they are replaced by the Prionoceridae.

Checklist of subfamilies:

Chaetomalachiinae Majer, 1987 **n.stat.** (4)
Danaceinae Thomson, 1859 (3)
Dasytinae Jacobson, 1911 **n.stat.** (6)
Gietellinae Constantin & Menier, 1987 (2)
Listrinae Majer, 1990 **n.stat.** (5)
Rhadalinae LeConte, 1861 (1)

Explanation of the cladogram of the Dasytidae (Fig. 199)

Structure		Plesiomorphous state	Apomorphous state	
1A		present (MAJER, 1987b: Figs 388–394, 398–403)	absent (MAJER, 1987b: Figs 395–397, 404–413)	TS
2A		present (MAJER, 1987b: Figs 388, 397, etc)	strongly reduced (MAJER, 1990b: Figs 41, 44)	TS
3A		with transverse vein between 2A (MAJER, 1987b: Figs 388–394, 402–406, etc)	without transverse vein (MAJER, 1987b: Figs 396, 407–419)	TS
Ac		present (MAJER, 1987b: Figs 388–395)	absent (MAJER, 1987b: Figs 396–421)	TS
RM		terminating alone (MAJER, 1987b: Figs 388–403)	completely fused with M (MAJER, 1987b: Figs 404–419)	TS
Rc		well-defined (MAJER, 1987b: Figs 393–403)	reduced (MAJER, 1987b: Figs 388–392, 404–419)	TS
Rs		well-defined (MAJER, 1987b: Figs 390–403)	fused with RM (MAJER, 1987b: Figs 404–415)	TS
acl		indicated (Fig. 96)	not at all indicated (Fig. 166)	A1
cla		membranous (Figs 102, 103)	sclerotised (MAJER, 1987b: Fig. 99)	A2
clw		appendiculate (Figs 102; MAJER, 1987b: Fig. 99)	not appendiculate (MAJER, 1989b: Figs 15–17)	A1
cue		glabrous (Figs 93, 112)	denticulate (Fig. 111)	A1
cul		absent	present (MAJER, 1987b: Fig. 160)	A1
dga		simple (Figs 79, 94)	with sensillae fused into a spine (MAJER, 1989b: Fig. 295)	A2
dle		absent (Fig. 110)	present (MAJER, 1987b: Figs 204, 213, 216 etc)	A3
epp		well-defined as far as apex (Fig. 104)	strongly reduced (MAJER, 1987b: Fig. 97)	A1
fla		at most serrate	pectinate	A1
fta		5 in males	4 in males	A1
fvs		free (Fig. 106)	firmly fused with IV (MAJER, 1987b: Fig. 188)	A3
hyb		present (Fig. 80)	absent (Fig. 95)	A1
isp		present (Fig. 83)	absent (Fig. 108)	A1
lan		present (Figs 82, 100)	absent	A1
ltp	01	not of the Rhadaline type (Fig. 92); MAJER, 1986: Figs 11–14)	of the Rhadaline type (Fig. 77; MAJER, 1986: Figs 7–8)	TS
ltp	02	not of Danaceine type	of several Danaceine types (Fig. 92; MAJER, 1986: Figs 10, 12)	TS

Structure		Plesiomorphous state	Apomorphous state	
ltp	03	not of the Chaetomalachiine type	of the Chaetomalachiine type (MAJER, 1989c: Figs 5, 34, 49, 62, 96, 110)	TS
ltp	04	not of the Listrine type	of the Listrine type (MAJER, 1990b: Figs 3, 60)	TS
ltp	05	not of the Dasytine type	of the Dasytine type (MAJER, 1986: Fig. 14)	TS
mde		well-developed (Figs 78, 93, 112)	reduced (Fig. 111)	A1
mes	01	compact (Fig. 99)	divided into two (MAJER, 1987b: Figs 114, 188)	A1
mes	02	divided into two	divided into three (MAJER, 1987b: Fig. 233)	A1
mms	01	present (MAJER, 1987b: Figs 125, 194, etc)	absent (Fig. 107)	A1
mms	02	well-developed (MAJER, 1987b: Figs 125, 194)	strongly reduced (MAJER 1990b: Figs 36, 51; 1989c: Fig. 44)	A1
mms	03	isolated (MAJER, 1990b: Fig. 36); 1989c: Fig. 44)	fused with mes	A1
mop		with a sclerite (CONSTANTIN & Menier, 1987: Figs 22, 23)	not defined at all	A2
mse	01	entire (Fig. 107 etc)	divided in two (MAJER, 1989b: Figs 124, 165)	A1
mse	02	simple (Fig. 107 etc)	strongly modified (MAJER, 1989b: Figs 165, etc)	A1
msn	01	compact (Fig. 99)	divided into two (MAJER, 1987b: Figs 114, 188)	A1
msn	02	divided into two	divided into three (MAJER, 1987b: Fig. 223)	A1
pam		defined (MAJER, 1987b: Figs 205, 214)	fused as in typical tegmen (Fig. 109)	TS
pap	01	isolated (Fig. 84)	fused with tgs (Fig. 109)	TS
pap	02	indicated as constricted base of (Fig. 109)	not indicated at all (MAJER, 1987b: Figs 100, 165, 167–168, etc)	TS
pha	01	scarcely arched, base not defined (Fig. 110)	strongly arched, base swollen (MAJER, 1987b: Figs 147, 156, etc)	A3
pha	02	with normal phallic tube	phallic tube absent, spines exposed (MAJER, 1988a: Figs 95–111)	TS
phl		emarginate dorsally at base (MAJER, 1990b: Figs 42, 53, etc)	evenly convex on dorsal side	TS
phs		distinguishable (Fig. 84)	completely absent (Fig. 109)	A1

Structure		Plesiomorphous state	Apomorphous state	
prm		simple	with dorsal sclerite (CONSTANTIN & MENIER, 1987: Fig. 5)	A2
spf		*Aplocnemus*-like in outline (Fig. 83)	guttate in outline (Fig. 108)	A1
tar	01	4 sometimes slightly shorter than 3 (Fig. 103)	4 always distinctly shorter and more slender than 3 (MAJER, 1989b: Figs 15–17)	TS
tar	02	4 well-defined	4 deeply sunk in emargination of 3 (CONSTANTIN & MENIER, 1987: Figs 12–13)	TS
ted		extensively covering pha (MAJER, 1987b: Fig. 231)	only briefly covering pha (MAJER, 1987b: Fig. 6)	TS
teg	01	apex ciliate (Fig. 109)	apex bare, often strongly reduced (MAJER, 1990b: Fig. 71, 1987a: Fig. 22; 1989c: Fig. 78)	TS
teg	02	not *Gietella*-like	*Gietella*-like (CONSTANTIN & MENIER, 1987: Fig. 18)	TS
ten		up on fua (Figs 100, 119)	very close to one another (Fig. 82)	A1
tsl		not broadened (Fig. 116)	broadened (Fig. 79)	A1

A1 Autapotypy within Dasytidae
A2 Autapotypy within Melyrid lineage
A3 Autapotypy within Cleroidea
TS Transformation series

Key to subfamilies

1. Tarsomere 4 not reaching apical margin of tarsomere 3. **2. Gietellinae**
– Tarsomere 4 reaching beyond apical margin of tarsomere 3 . . 2
2. Tarsomeres 2–3 broadened, 4 distinctly more slender and shorter than 3. Claws simple. **4. Chaetomalachiinae**
– Tarsomeres 2–3 not broadened, if so then only very weakly so, 4 at most slightly shorter than 3. Claws often appendiculate 3
3. Visible abdominal sterna 1 and 2 almost always firmly fused. Antenna often strongly serrate to pectinate, or segments 6(7)–11 much broader than 1-5. Pronotum sometimes explanate at sides and/or elytra adorned with excavations and/or ornamentations. Eyes sometimes pubescent. **1. Rhadalinae**

– Visible abdominal sterna 1 and 2 freely articulated. Antenna at most moderately serrate, at least segments 4–5 about as broad as 6–11. Pronotum never explanate at sides, elytra simple. Eyes never pubescent 4

4. Tarsomeres equal in length, mostly transverse. Claws always with free membranous appendages only. Sides of pronotum and elytra with a distinct fringe. Body predominantly cylindrical, pubescence mostly adpressed **5. Listrinae**

– Tarsomeres seldom transverse, tarsomere 4 often slightly shorter than 3. Claws with free appendages, or with these modified in various ways, or entirely absent. Sides of pronotum and elytra without a distinct fringe. Body not very often cylindrical, pubescence variable 5

5 Tarsomere 4 mostly as long as 3. Claws often with membranous appendages. Pubescence often adpressed and/or scale-like, head often subrostrate. **3. Danaceinae**

– Tarsomere 4 always slightly shorter than 3. Claws never with simple membranous appendages. Pubescence always normal, moderately long. Head not subrostrate. **6. Dasytinae**

In the classification of the individual subfamilies given below, I am omitting larval characters as no larvae of the Chaetomalachiinae or Listrinae are known. The number of ocelli is of no importance, as mentioned above, but some attention should be paid to details of the mouthparts, urogomphi, and perhaps the structure of the dorsal surface.

Individual subfamilies are based upon the different transformation series of the following structures in the adults. If at least three of eight series are found to be different, the taxon is considered to merit subfamily rank.

Transformation series:
(1) mandibles
(2) tormal processes
(3) wing
(4) shape of tarsomeres
(5) claws
(6) male sternum VIII
(7) tegmen
(8) phallus

1. Subfamily Rhadalinae
(Figs 76–83)

Rhadalini LeConte, 1861: 191, 194. Haplocnemates Mulsant & Rey, 1868: 181. Rhadalinae [in Melyridae]: Casey, 1895: 457. Rhadalidae: Pic, 1926a: 3. Rhadalinae [in Melyridae]: Blaisdell, 1938: 3. Haplocneminae Crowson, 1964: 318. Aplocneminae: Majer, 1983: 385. Aplocnemina [in Melyridae Dasytinae]: Majer, 1987: 800. Rhadalinae [in Melyridae]: Peacock, 1987: 129, 131.
Type genus: *Rhadalus* LeConte, 1852.

Differential diagnosis (Fig. 199):

Definition of the subfamily: Antenna mostly serrate to pectinate, rarely forming a loose club, tormal processes uniform and typical of the subfamily (e.g. Fig. 77), mandibles normal, terminal segment of maxillary palps elongate to securiform, Rc almost distinct, extensive and semicircular in outline, M isolated, M1 indistinct, anal veins complete or reduced to 2, anal cell mostly present, tarsomeres equal or tarsomere 4 slightly smaller, claws with membranous appendages → sclerotised ones → with minute basal teeth, sterna 1 and 2 mostly firmly fused (freely articulated in the genus *Dasyrhadus* Fall), male sternum VIII with more or less reduced median projection which is fused with body of sternum, spicular fork of the Rhadaline type, often with reduced interspicular plate, tegmen of the Rhadaline type – a very primitive stage has isolated tegminal struts and phallobasic apodeme. A divided apex of the tegmen in some Mascarene Rhadalinae represents the most primitive tegmen within the Dasytidae → Attalomimidae family group, if the division is not secondary. On the other hand, the most derived Rhadaline tegmen is almost cylindrical with nearly complete dorsal wall. Phallus at most weakly bent, mostly with dorsal lever (absent in *Indiodasytes* Pic and *Dasyrhadus*), base never differentiated.

Transformation series:

(1) mandibles: parallel with those in other subfamilies.
(2) tormal processes: autapomorphous.
(3) wing: autapomorphous.
(4) shape of tarsomeres: parallel with e.g. that of the Danaceinae or Listrinae.
(5) claws: parallel with e.g. those of some Danaceinae.
(6) male sternum VIII: probably parallel with that of the Dasytinae.
(7) tegmen: plesiomorphous.
(8) phallus: autapomorphous.

Plesiomorphy: tegmen.

Apomorphies: tormal processes, approximated tendons in metendosternite, tendencies towards this condition in the first two ventrites and dorsal lever of phallus.

Supplementary description. See the key to subfamilies.

Remarks. A rather heterogeneous subfamily, like the Danaceinae, but characterised by the stable arrangement of Rs, RM, and M in the wings, which is correlated with the position of the tendons on metendosternite which are approximated. In addition, ventrites 1 and 2 are mostly firmly fused, which is an important trend. The dorsal lever may be absent *(Indiodasytes)*, or may be indicated in some Danaceinae.

The subfamily was reviewed by PEACOCK (1986), but this work gives no morphological analysis and the tegmen and spicular fork, in particular, which are the most significant structures, were hardly mentioned. Some of the tribes defined by me (MAJER, 1987b, 1990a) need re-definition because many Mascarene and most of the New World taxa were not known to me at that time.

Distribution. Worldwide, except for most of the Nearctic and all of the Australian regions.

2. Subfamily Gietellinae

Gietellinae [in Melyridae] CONSTANTIN & MENIER, 1987: 53, 62.
Type genus: *Gietella* Constantin & Menier, 1987.

Differential diagnosis (Fig. 199):

Definition of the subfamily: Antenna weakly clubbed, tormal processes dual, typical of the subfamily, mandibles with molar sclerite, terminal segment of maxillary palps subovate, prementum with a special dorsal sclerite; wings absent, tarsi with extremely small tarsomere 4, claws simple, sterna 1 and 2 freely movable, male sternum VIII without median projection, spicular fork rather of the Rhadaline type, without interspicular plate, tegmen of a special *Gietella* type with defined tegminal struts but without phallobasic apodeme and with apical lateral lobes, phallus slender and arcuate as it is in some Danaceinae.

Transformation series:

(1) mandibles: autapomorphous.
(2) tormal processes: autapomorphous.
(3) wing: absent.

(4) shape of tarsomeres: autapomorphous.
(5) claws: parallel with e.g. those of the Chaetomalachiinae.
(6) male sternum VIII: parallel with e.g. that of some Danaceinae.
(7) tegmen: autapomorphous.
(8) phallus: parallel with that of some Danaceinae.

Plesiomorphies: antenna and phallus.

Apomorphies: tormal processes, mandibles, prementum, tarsi, and tegmen.

Supplementary description: Small, apterous, rather weakly sclerotised species, body outline converging with that of *Ifnidius* Escalera (Malachiidae) which inhabits similar biotopes.

Remarks. This easily recognised monotypic group is monophyletic with both the Rhadalinae and the primitive Danaceinae. The molar sclerite in the mandibles and the shape of the tarsi are outstanding autapomorphies. The reduction of tarsomere 4 accompanied by the reduction of the claw appendages is a single genetic mechanism and has an analogy in the Malachiidae-Lemphinae or Dasytidae-Chaetomalchiinae.

Distribution. Canary Islands.

3. Subfamily Danaceinae n.stat.

(Figs 85–112)

Danacaeini THOMSON, 1859: 65. Danaceini [in Melyridae Dasytina]: KIESENWETTER, 1863: 626. Danacéens: MULSANT & REY, 1868: 27, 266. Danaceina [in Zygiidae Zygiini]: JACOBSON, 1911: 688. Danaceini: PIC, 1927: 81. Danacaeini: PIC, 1937: 5. Danaceina [in Melyridae Dasytinae]: MAJER, 1987: 798, 802.

Type genus: *Danacea* Laporte de Castelnau, 1836.

Differental diagnosis (Fig. 199):

Definition of the subfamily: Antenna never pectinate, often forming a loose club, tormal processes representing several transformation series, some of them convergent with those in the Dasytidae-Dasytinae, others with those in the Melyridae, mandibles normal, terminal segment of maxillary palps subovate to subsecuriform; Rc distinct, extensive and lenticular in outline, M connected with RM, 4 anal veins; tarsomeres equal in size or tarsomere 4 slightly reduced, claws simple or variably appendiculate, sterna 1 and 2 freely articulated, male sternum VIII with or without median projection, spicular fork of the Rhadaline or Dasy-

tine type, without interspicular plate, tegmen constricted at middle and/or at apex or its base narrow and conical, phallus weakly to strongly arcuate, with or without distinct base, rarely with dorsal lever indicated.

Transformation series:
(1) mandibles: parallel with e.g. those of the Dasytinae.
(2) tormal processes: parallel with those of some Dasytinae, Chaetomalachiinae or the Melyridae.
(3) wing: autapomorphous.
(4) shape of tarsomeres: parallel with e.g. that of the Rhadalinae.
(5) claws: parallel with e.g. those of the Rhadalinae.
(6) male sternum VIII: parallel with that of the Chaetomalachiinae.
(7) tegmen: plesiomorphous.
(8) phallus: plesiomorphous.
Plesiomorphies: tegmen and phallus.
Apomorphy: wings.
Supplementary description: See key to subfamilies.

Remarks. This is the most heterogeneous taxon within the Dasytidae and could be divided into further subfamilies. Since the subfamilies of the Dasytidae are defined chiefly upon the transformation series of the wings, all Danaceinae species share a common series in this structure. Furthermore, the larval characters of *Haplamaurus* and *Danacea* are very similar. The closely related tribes Danaceini and Amauronioidini of the Danaceinae represent a derived section of the transformation series of the terminalia, which makes the Danaceinae monophyletic with the Chaetomalachiinae. Another unique type of terminalia occurs in *Bilyella* Majer and some related genera. The latter is an unnamed subgroup, including amongst others the American *Hoppingiana* Blaisdell and most of the North American *"Dasytes"*.

The Danaceinae are in need of a tribal classification. Among the most primitive Danaceinae taxa, one can find quite primitive stages of the tegmen, and even the indications of a dorsal lever which illustrates their common ancestry with the Rhadalinae.

Distribution: Worldwide.

4. Subfamily Chaetomalachiinae n.stat.

Chaetomalachiini MAJER, 1987b: 799, 804.
Type genus: *Chaetomalachius* Kraatz, 1882.

Differential dagnosis (Fig. 199):

Definition of the subfamily: Antenna never pectinate, often forming a loose club, tormal processes representing a rather heterogeneous transformation series, as in the Dasytidae-Dasytinae but with a recognisable direction to the modifications, mandibles normal, terminal segment of maxillary palps subovate; Rc small, round in outline, M connected with RM and Rs, 3 anal veins 2A and 3A connected by transverse vein; tarsomere 4 distinctly smaller than adjacent tarsomeres, claws simple, sterna 1 and 2 freely movable; male sternum VIII with or without isolated median projection, spicular fork of the Dasytine type, without interspicular plate, tegmen more or less constricted, base extensive, apex without indications of lateral lobes, sometimes reduced, phallus strongly arcuate with distinct base.

Transformation series:
(1) mandibles: parallel with e.g. those in the Dasytinae.
(2) tormal processes: autapomorphous.
(3) wing: autapomorphous.
(4) shape of tarsomeres: autapomorphous.
(5) claws: autapomorphous.
6) male sternum VIII: parallel with e.g. that in the Listrinae.
(7) tegmen: autapomorphous.
(8) phallus: autapomorphous.
Plesiomorphy: antenna.
Apomorphies: labrum, wings, tarsi, tegmen, and phallus.

Supplementary description: Species externally resembling either the Listrinae or the Dasytinae.

This rather small group of restricted distribution is very easily recognised by the autapomorphous legs and wings. There seems to be only a single transformation series of the tormal processes and tegmen, and the latter suggests that the group is related particularly to the Danaceinae via the tribes Danaceini and Amauronoidini.

Distribution: Palaearctic only, with several species extending into Central Africa.

5. Subfamily Listrinae n. stat.

Listrini MAJER, 1990b: 371.
Type genus: *Listrus* Motschulsky, 1860.

Differential diagnosis (Fig. 199):

Definition of the subfamily: Antenna never pectinate, often forming a loose club, tormal processes representing a unique transformation series, mandibles normal, terminal segment of maxillary palps subovate, Rc moderately sized, round in outline, M connected with RM and Rs, 3 anal veins, 2A missing or reduced and isolated, tarsomeres equal, claws with free appendages, sterna 1 and 2 freely articulating, male sternum VIII with isolated and reduced median projection (sometimes absent), spicular fork of the Dasytine type, without interspicular plate, tegmen not constricted, base extensive, apex mostly reduced and without setae and indications of lateral lobes, phallus strongly arcuate with distinct base.

Transformation series:

(1) mandibles: parallel with e.g. those of the Dasytinae.
(2) tormal processes: autapomorphous.
(3) wing: autapomorphous.
(4) shape of tarsomeres: parallel with e.g. that of some Rhadalinae or Danaceinae.
(5) claws: parallel with e.g. that of some Rhadalinae or Danaceinae.
(6) male sternum VIII: autapomorphous.
(7) tegmen: autapomorphous.
(8) phallus: autapomorphous.

Plesiomorphy: tarsi.

Apomorphies: labrum, wings, and terminalia.

Supplementary description: Most of the species have a distinctive lateral fringe of stouter hairs at sides of pronotum and elytra and a special structure of the basal corners of pygidium (see MAJER, 1990b).

Remarks. On account of its internal morphology the subfamily is very closely related to the Dasytinae but has the clear habitus of the Chaetomalachiinae, with legs that resemble those of primitive Danaceinae. Its distribution is archaic, analogous to that of the Rhadalinae; both are probably of Gondwanan origin.

Distribution. Abundant in the Nearctic region, less so in the Neotropics; only a very few in southern Africa; completely absent from

the Australian region, Western Palaearctic, and Central Africa, and only a very scattered occurrence in Central Asia and south of the Himalayas: from here they extend deeply towards the Indian and Indochinese subregions, where other Dasytidae do not occur.

6. Subfamily Dasytinae n. stat.
(Figs 113–119)

Dasytaires [in Dasytiens] MULSANT & REY, 1868: 28, 53. Dasytina [in Zygiidae]: JACOBSON, 1911: 688. Dasytini & Henicopini [in Dasytinae]: PIC, 1937: 20. Dasytina [in Melyridae Dasytinae]: MAJER, 1987: 798, 805.
Type genus: *Dasytes* Paykull, 1798.

Differential diagnosis (Fig. 199):

Definition of the subfamily: Antenna neither pectinate nor with indications of a club but serrate to moniliform, tormal processes representing a unique transformation series, mandibles normal, terminal segment of maxillary palps subovate to subsecuriform; Rc small, rather ovate, M connected with RM and Rs, 3 to 4 anal veins present but no transverse one, 2A and 3A isolated; tarsomere 4 slightly smaller than 3, claws with semi-membranous or sclerotised appendages which may be absent in females, sterna 1 and 2 freely articulating, male sternum VIII with long a median projection with base fused with the body of sternum, spicular fork of the Dasytine type without interspicular plate, tegmen flat, not constricted, base extensive, broad, apex with indications of lateral lobes and numerous setae, phallus strongly arcuate with distinct base.

Transformation series:

(1) mandibles: parallel with e.g. those in Chaetomalachiinae.
(2) tormal processes: autapomorphous.
(3) wing: autapomorphous.
(4) shape of tarsomeres: autapomorphous.
(5) claws: autapomorphous.
(6) male sternum VIII: autapomorphous.
(7) tegmen: autapomorphous.
(8) phallus: autapomorphous.

Plesiomorphy: antenna.

Apomorphies: labrum, wings, tarsomeres, male sternum VIII, and tegmen.

Supplementary description: See the key to subfamilies.

Remarks: A rather small, not easily recognised group, with rather unicolourous, weakly sclerotised, mostly malacodermiform taxa. This is apparently the most recent subfamily, with the most difficult internal classification as the genera and species are very closely allied to each other. It is the only subfamily in which cuticular modifications parallel to those in the Malachiidae occur very rarely. This group is most closely related to the Chaetomalachiinae because of the slight reduction of tarsomere 4. On the other hand, Dasytine terminalia suggest monophyly with the Listrinae.

Distribution: What is probably the most ancestral Dasytine genus, *Psilothrix* Redtenbacher, is the only taxon with species that extend into the Nearctic and Afrotropical (excepting South Africa) regions. The subfamily is otherwise distributed in the Palaearctic, except for the Himalayas, but several species are found in the Indochinese subregion (Taiwan).

V. MELYRIDAE
(Figs 120–162)

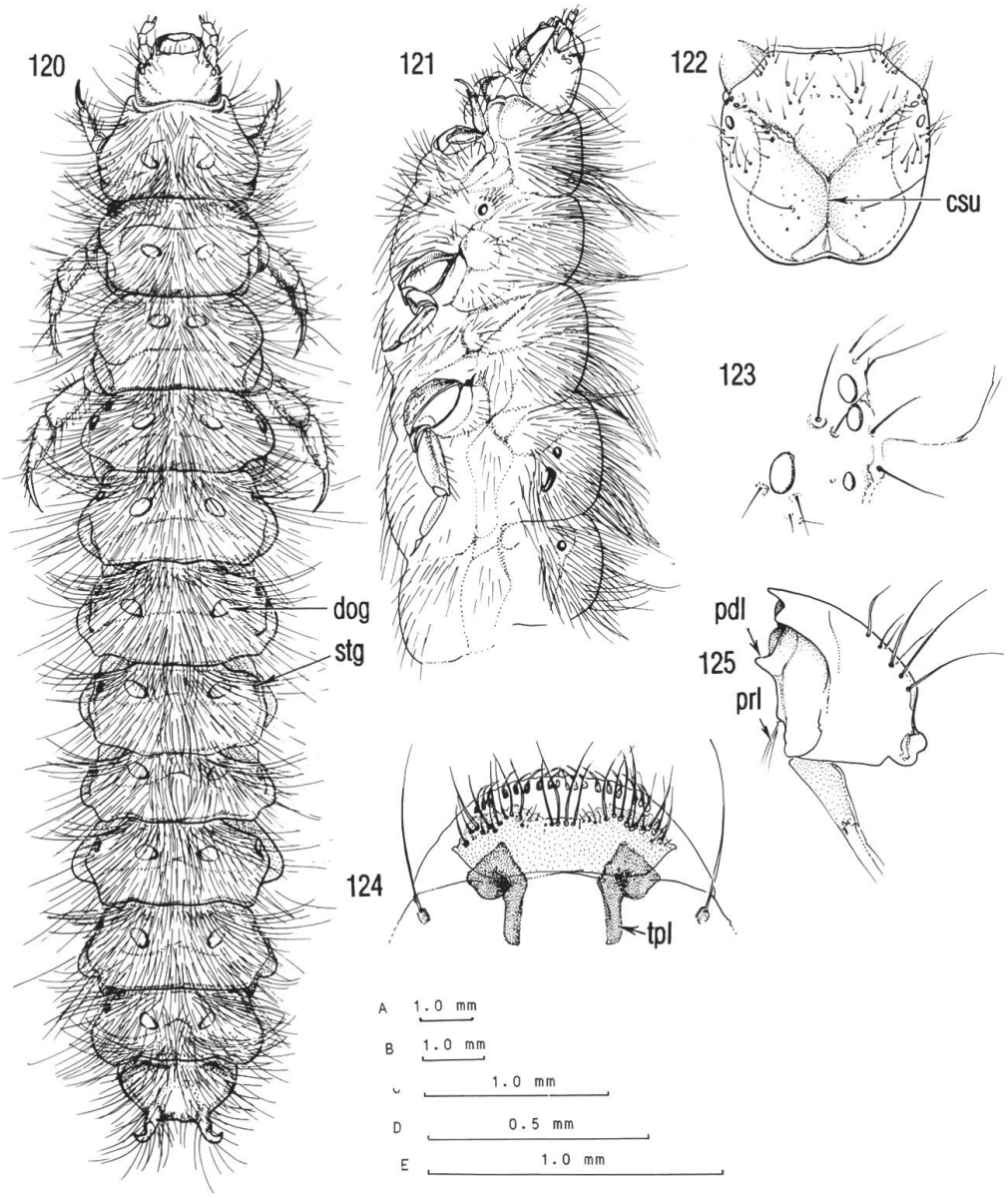
Melyridae LEACH, 1815 [olim: Dasytidae, Malachiidae]. Melyrides LACORDAIRE, 1815: 380 [olim: Dasytidae, Melyridae, Prionoceridae]. Melyrini [in Melyridae Dasytina] KIESENWETTER, 1863: 664. Mélyriens: MULSANT & REY, 1868: 27, 256. Melyrini [in Melyridae Melyrinae]: CASEY, 1895: 457. Melyridae [olim: Dasytidae, Melyridae, Malachiinae] GANGLBAUER, 1903: 78. Zygiina [in Zygiidae Zygiini]: JACOBSON, 1911: 688. Melyrinae [in Cantharidae]: KUHNT, 1913: 464. Melyridae [olim: Dasytidae, Melyridae, Malachiidae]: ORCHYMONT, 1920: 3. Melyridae [olim: Dasytidae, Melyridae]: BERNET KEMPERS, 1922: 1. Melyridae: WINKLER, 1925: 562. Melyrinae [in Dasytidae]: PIC, 1929: 3. Melyrini [in Melyridae Melyrinae]: BLAISDELL, 1938: 3. Melyrinae [in Melyridae]: CROWSON, 1955: 84. Melyridae [olim: Dasytidae, Melyridae, Prionoceridae]: CROWSON, 1970: 3. Melyridae [olim: Dasytidae, Melyridae]: LOHSE, 1979: 69. Melyrina [in Melyridae]: MAJER, 1987: 788.

Type genus: *Melyris* Fabricius, 1775.

Differential diagnosis (Fig. 199):

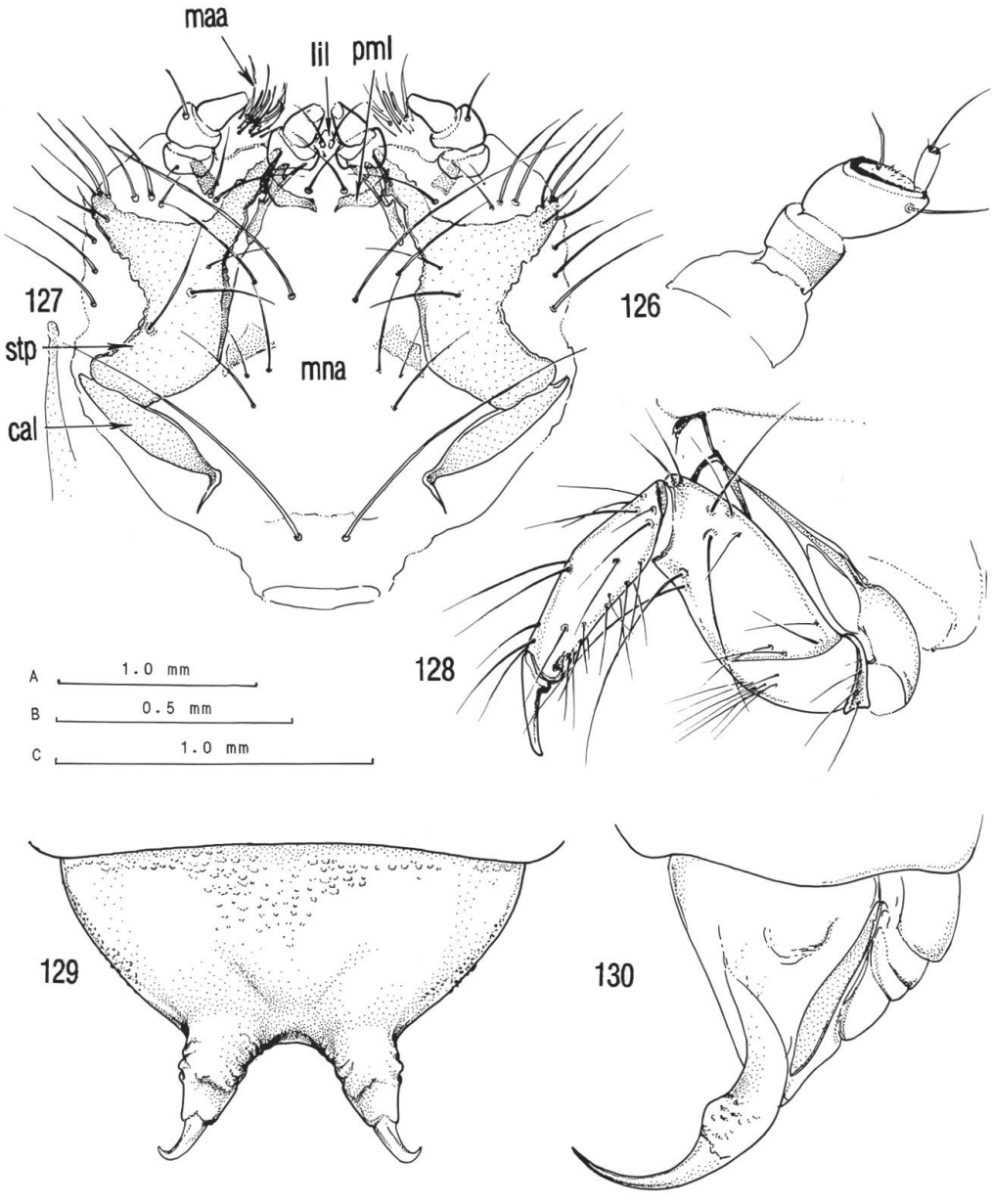
Larva: 4 ocelli, tormal processes simple, mandibles simple, with almost glabrous cutting edge, posterior dens distinct, prementum thin, divided into two (related to absent mental crescent in adults) and bisetose, also ligula with two setae; supposedly without numerous pyloric valves as in adults, and with 6 Malpighian tubules. Adult: extrusible glands absent, cuticular modifications associated with pheromone glands absent, tentorial cross-bar absent, never with indications of an-

tennal club, tormal processes very simple, mandibles without posterior dens, median dens mostly strongly reduced, cutting edge finely denticulate; basistipes, mediostipes, palpifer, lacinia, and distigalea normal; mental crescent absent (exceptionally with tiny isolated sclerites present at sides of mentum); sternopleural suture on prothorax not distinct, lamina on metendosternite absent, elytral surface with common irregular



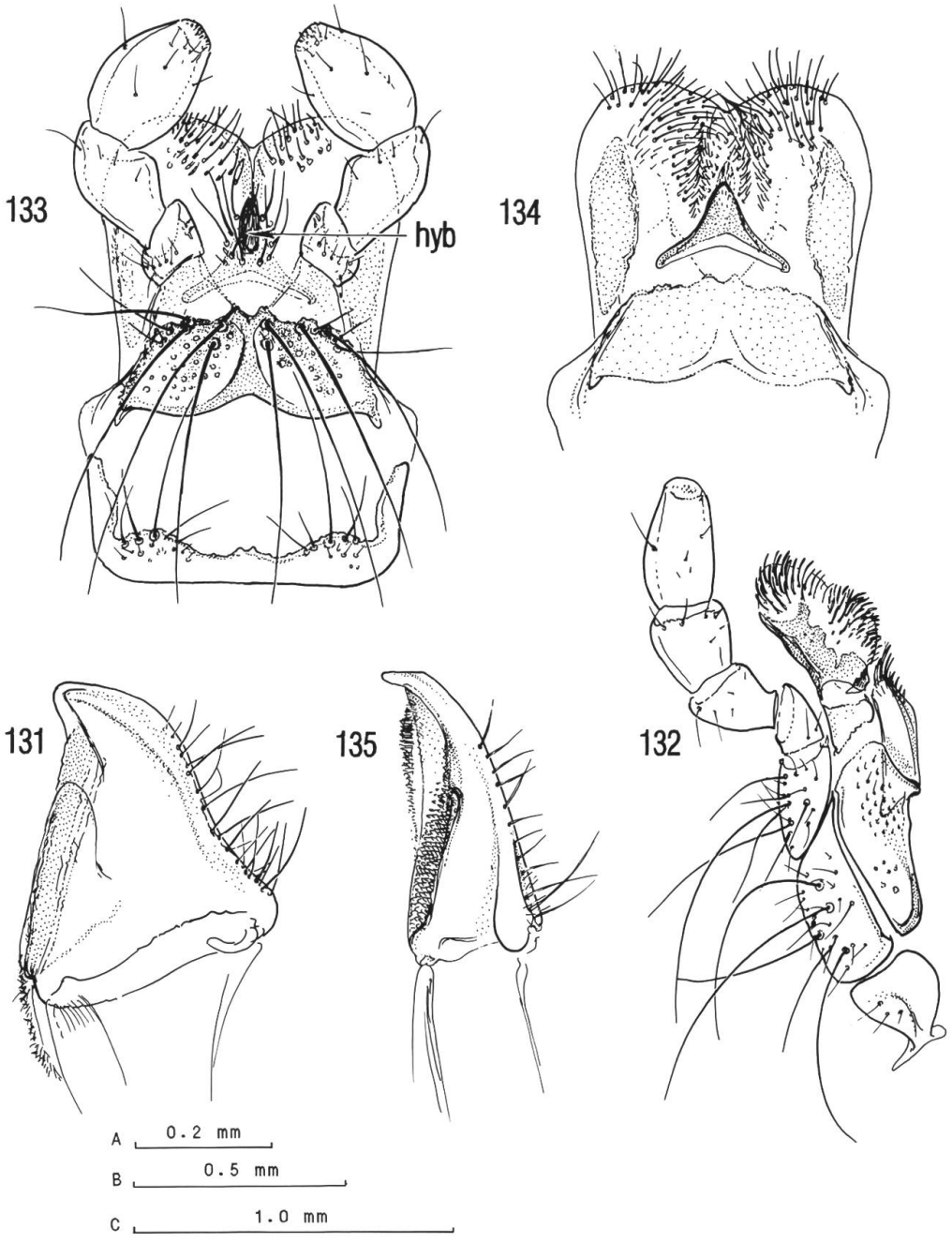
Figs 120-125: *Astylus aulicus* Pic, mature larva: 120, general view, dorsal; 121, anterior part of body, lateral; 122, cranium ventral. 123, ocelli. 124, labrum. 125, mandible ventral. (Scales: A- 120, B- 121; C- 122; D- 123; E- 124,125).

punctures but often costate, anal wing sector with 1(!),2,3, or 4 veins of common arrangement, vein M1 strongly defined, Rc strongly reduced, front tarsomeres simple (a tendency to be pectinate is shown in the presence of stout setae to short spinules, which is evidence for a relationship with the Malachiidae), all basitarsi distinctly shorter than tarsomere 2, claws rather shorter and broader, simple to appendiculate, sides



Figs 126-130: *Astylus aulicus* Pic, mature larva: 126, antenna. 127, labiomaxillar complex. 128, front leg, lateral. 129, abdominal segment 9 dorsal. 130, abdominal segment 9 lateral. (Scales: A- 129,130; B- 126,127; C- 128). In Figs 129,130 all setae omitted.

of antecoxal suture rather horizontal, hind coxae scarcely projecting; intercoxal process on 1st visible sternite rarely reduced; median process on male sternum VIII absent, spicular fork of the Dasytine type without interspicular plate, tegmen with tegminal struts completely fused with

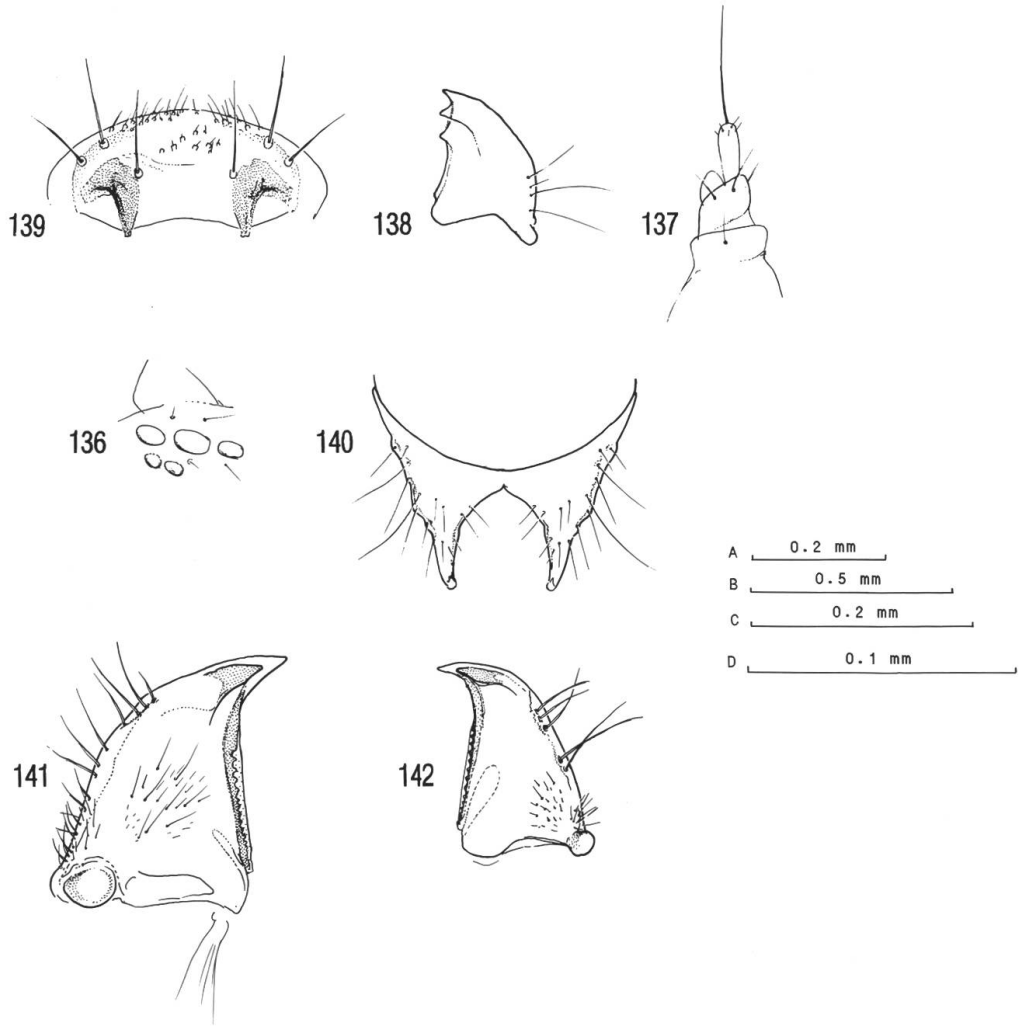


Figs 133-135: 131-134, *Astylus aulicus* Pic, ♂. 132, maxilla. 135, *Astylus sexmaculatus* Perty, ♂. 133, labium dorsal. 134, labium ventral. 131, 135, mandible ventral.(Scales: A- 133,134; B- 131,132; C- 135).

phallobasic apodeme, phallobase always fused with parameres and forming the tegmen "en cavalier" of Jeannel, but generally tegmen more cylindrical than in Dasytidae, phallus at most weakly arcuate, mostly without distinct base; female copulatory organs of the tubular type of Heberdey; proventriculus small, pyloric valves not numerous, 6 Malpighian tubules.

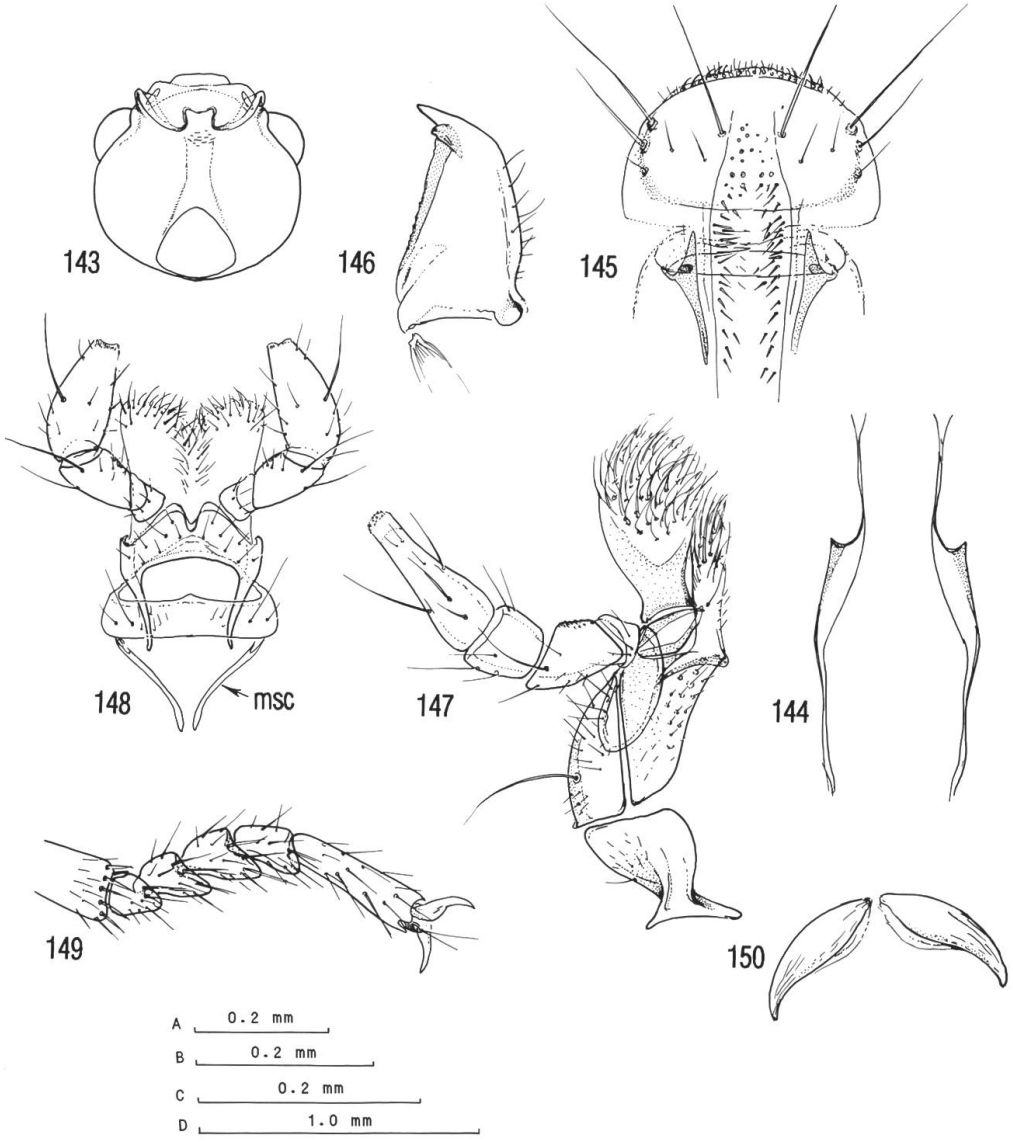
Transformation series:

(1) larval mouthparts: autapomorphous prementum divided into two and almost glabrous cutting edge of mandibles, with stipes heavily sclerotised.



Figs 136-142: 139-141, *Melyris scutellaris* Muls., (139-140, larva of the 1st instar; 141, adult, ♀). 142, *Cerallus rubidus* (Gyll.), ♂. 136, ocelli. 137, antenna. 138, mandible ventral. 139, labrum. 140, abdominal segment 9 dorsal. 141, 142, mandible ventral. (Scales: A- 142; B- 141; C- 136,138,140; D- 137, 139).

(2) adult mouthparts: autapomorphous mental sclerites absent, mandibles with reduced median dens.
(3) larval alimentary canal: as in the Dasytidae, but probably mostly with two pyloric valves.
(4) adult alimentary canal: parallel to that in the Dasytidae, but probably mostly with two pyloric valves.



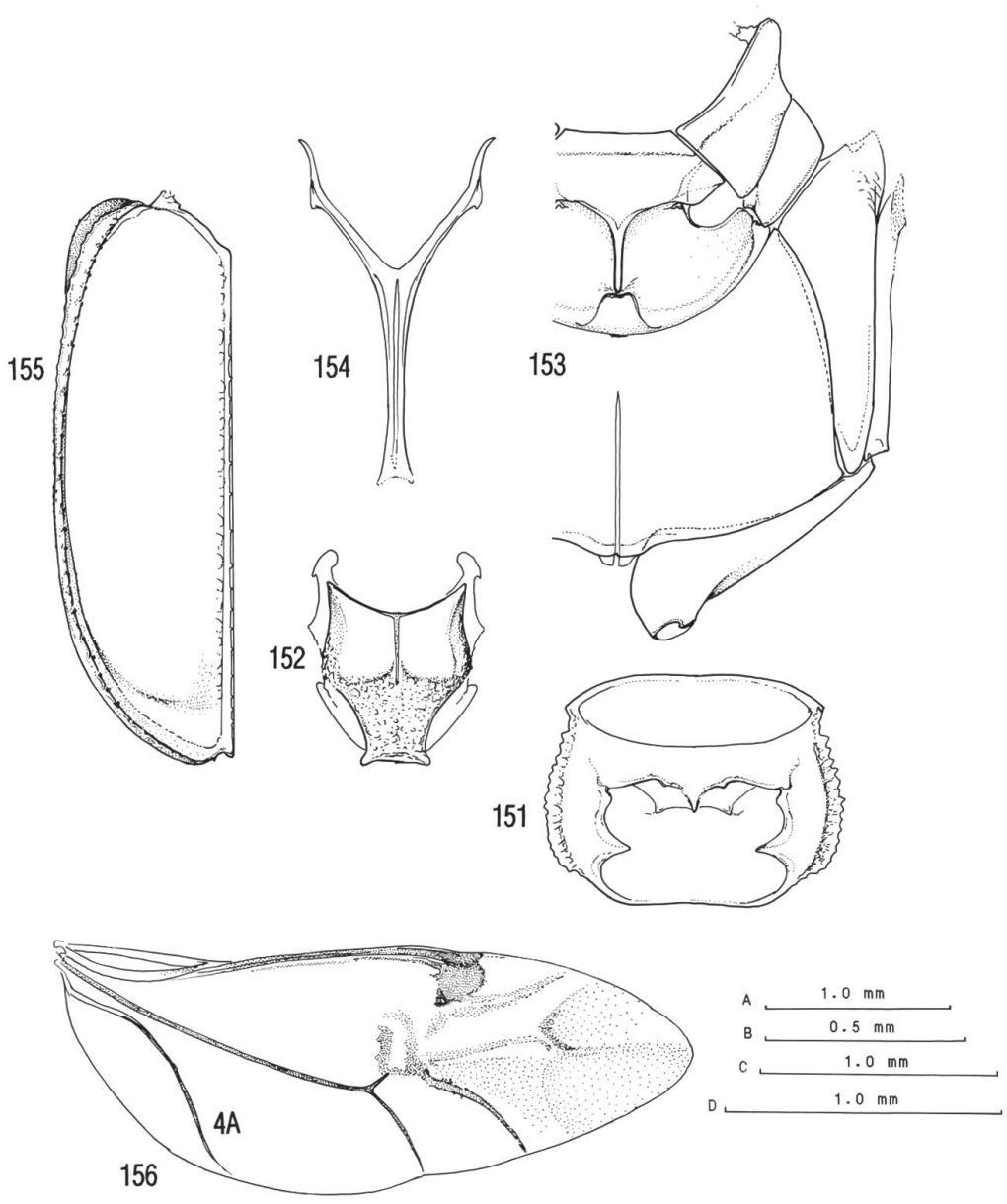
Figs 143-150: *Melyrodes basalis* (LeConte), ♂: 143, cranium ventral. 144, tentorium. 145, labrum. 146, mandible ventral. 147, maxilla. 148, labium dorsal. 149, front tarsus. 150, protarsal claws. (Scales: A- 144,146; B- 149; C- 145,147,148,150; D- 143).

(5) wings: autapomorphous combination of strongly reduced Ac and prominent M1.

(6) male copulatory organs: rather plesiomorphous – more cylindrical, even if similar to those in Dasytidae.

Plesiomorphy: male copulatory organs.

Apomorphies: mouthparts, and wings.



Figs 151-156: *Melyrodes basalis* (LeConte), ♂: 151, prothorax ventral. 152, mesoscutellum dorsal. 153, meso- and metathorax ventral. 154, metendosternite. 155, elytron ventral. 156, wing. (Scales: A- 156, B- 152- 154; C- 155; D- 151).

Supplementary description: Mostly larger species, metallic, shining, although often small and dark as well. At first sight, many species have costate and almost bare elytra, or, on the contrary, elytra are evenly convex and extraordinarily long pubescent and/or variegated. Antennal flagellum strongly serrate to pectinate, mostly with transverse segments.

Remarks. The group is a connecting link between the Dasytidae and Malachiidae, but its divided larval prementum, absent adult mental crescent, autapomorphous wing (the striking M1) and abbreviated basitarsi (such tarsi also occur in many Cleridae) justify its separation as a distinct family. In addition to the characters just mentioned, the tentorial cross-bar is absent and Rc is modified, which are characters parallel with those in most of the Malachiidae. The transformation series of the terminalia is similar to that in the Dasytidae but I consider the tegmen to belong to a different transformation series as it is cylindrical, without broadened base; if it is flat, then the apex is divided (tribe Cerallini).

Although some attempts have been made to clarify the internal classification of the Melyridae (MAJER, 19897b), there is at least one large undescribed subgroup including the genus *Melyrodes* Gorham (Figs 143–160) and others, which will have a profound effect on the major subdivisions of this family.

Distribution: Worldwide, in tropical to temperate zones, except for the Oriental and Australian regions.

Malachiidae & Attalomimidae family group

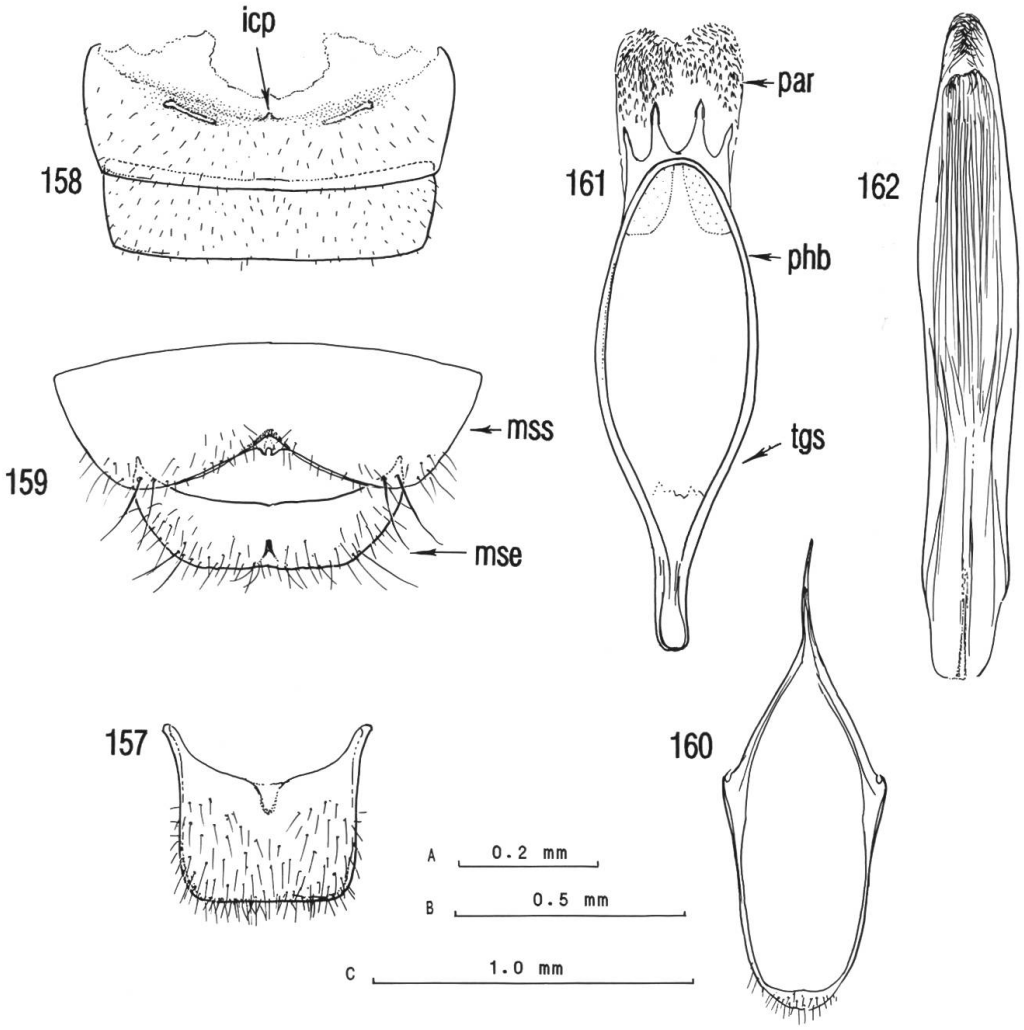
Definition (Fig. 198):

Larva [characters very probably applicable to both families]: Body mostly strongly flattened dorsoventrally, prementum compact, broad, bisetose, not divided into two parts (homologous in shape to that of adults). Apical antennomere with 4 long setae. Thoracic sclerites distinctly longer than abdominal ones. Four, five, or six Malpighian tubules, one of them strongly abbreviated and paired (homologous to that in adults).

Adults: Prementum strongly produced mediodistally, not or narrowly incised. Spicular fork roof-shaped to ovate to plate-shaped. Tegmen with basal ring and/or extensive dorsal wall, apex very rarely emarginate and/or ciliate. Extrusible glands present. Four, five or six Malpighian tubules, one of them shortened but entire (not dual as in larvae), proventriculus very extensive.

Plesiomorphies: Larva: Prementum not reduced. Adult: tegmen with distinctly defined basal ring and/or dorsal wall.

Apomorphies: Adult: Prementum strongly produced. Intercoxal process on 1st visible sternum always strongly reduced, often replaced by an emargination. Apex of tegmen mostly bare. Extrusible glands present.



Figs 157-162: *Melyrodes basalis* (LeConte), ♂: 157, pygidium. 158, first two visible abdominal sterna. 159, sternites VII and VIII. 160, spicular fork. 161, tegmen dorsal. 162, phallus dorsal. (Scales: A- 160- 162); B- 157,159; C- 158).

VI. MALACHIIDAE

Malachien ERICHSON, 1840: 44. Malachiina [in Melyridae]: KIESENWETTER, 1863: 572. Vésiculifères (Malachiens) MULSANT & REY, 1867: 1. Malachiidae PEYRON, 1877: 7. Malachiini [in Zygiidae]: JACOBSON, 1911: 688. Malachiini [in Cantharidae]: REITTER, 1911: 111. Malachiini [in Cantharidae Cantharinae] KUHNT, 1913: 456. Malachiidae [in Trichodermata]: BERNET KEMPERS, 1922: 1. Malachiinae [in Melyridae]: BLAISDELL, 1938: 3.
Type genus: *Malachius* Fabricius, 1775.

Differential diagnosis (Fig. 198):

Larva: 4 ocelli, tormal processes simple, mandibles simple, with almost glabrous cutting edge, posterior dens distinct, prementum compact, extensive, with two main setae, ligula also bisetose; no pyloric valves, 4, 5, or 6 Malpighian tubules, one of them strongly abbreviated and dual. Adult: extrusible glands present, cuticular modifications associated with pheromone glands very often occurring on various structures, tentorial cross-bar present or absent, antenna sometimes weakly clubbed, tormal processes simple, Malachiid-like (completely different from those in the Attalomimidae), mandibles without posterior dens, median dens distinct, cutting edge glabrous; basistipes, mediostipes, palpifer, lacinia and distigalea normal, mental crescent absent, prementum strongly produced mediodistally (corresponding to the extensive bisetose prementum in larvae); sternopleural suture on prothorax mostly distinct, and prosternum often separated from hypomera and situated through forks on them, lamina on metendosternite absent, elytral surface with irregular punctures, anal wing sector with veins of common arrangement, vein M1 indicated, Rc reduced, front tarsomeres in males often 4 in number or 5 and then tarsomere 1 or 2 pectinate, claws simple to appendiculate, long or broader, sides of antecoxal suture strongly oblique, hind coxae strongly projecting; intercoxal process on 1st visible sternite strongly reduced, mostly replaced by an emargination; median process on male sternum VIII absent, spicular fork roof-shaped, ovate, to plate-shaped, without interspicular plate, tegmen with tegminal struts fused with phallobasic apodeme, phallobase always fused with parameres, base of tegmen with basal ring (sometimes reduced) and/or dorsal wall of tegmen extensive, apex of tegmen very rarely emarginate and/or ciliate; phallus at most weakly arcuate, never with a large distinct base; female copulatory organs of the tubular type of Heberdey; proventriculus very large, no distinct pyloric valves, 4, 5, or 6 Malpighian tubules, one of them strongly abbreviated, testes enlarged.

Transformation series:

(1) larval mouthparts: plesiomorphous, stipes heavily sclerotised (character state parallel to that in the Melyridae).
(2) adult mouthparts: apomorphous combination of absent mental sclerites and prementum strongly produced mediodistally.
(3) larval alimentary canal: autapomorphous.
(4) adult alimentary canal: autapomorphous.
(5) wings: autapomorphous (combination of reduced Rc and indicated M1).
(6) male copulatory organs: autapomorphous tegmen with basal ring and/or extensive dorsal wall, exceptionally emarginate and/or ciliate.

Plesiomorphies: larval antenna, prementum in both larvae and adults.

Apomorphies: absence of adult mental crescent, tegmen, alimentary canal in both stages, strongly enlarged proventriculus and testes in adults. Supplementary description: Most of the species are typically malacodermiform, soft-bodied, resembling the family Cantharidae, but some of them (e.g. *Amalthocus* Fairmaire) greatly resemble the Melyridae or the Cleridae-Krynetinae. Metallic and/or variegated (aposematic) colours are very common, and most species possess cuticular modifications or modified front tarsomeres in males.

Remarks. The group is very heterogeneous, but all taxa share common transformation series in the wings and terminalia. In addition, autapomorphies are found in the proventriculus, Malpighian tubules, testes, male terminalia, extrusible glands, etc. The abbreviated Malpighian tubule in the larva is developed as a very thin, paired structure (KOLIBÁČ, pers. comm.), and is highly significant. The alimentary tract appears to be stable during ontogenesis (cf. the Prionoceridae). The ciliate terminal antennal segment in larvae may be plesiomorphous. The internal classification of the family Malachiidae is being discussed in a separate paper (MAJER, in press).

Distribution. Worldwide; tropical to temperate zones, preferring hot desert and semi-desert biotopes.

VII. ATTALOMIMIDAE n.fam.

(Figs 163–196)

Type genus: *Attalomimus* Wittmer, 1976.

Differential diagnosis (Fig. 198):

Larva: unknown; most likely with the general appearance of the Malachiidae but probably with different mandibles, maxilla, and antennae.

Adult: extrusible glands present, cuticular modifications associated with pheromone glands absent, tentorial cross-bar robust, antennal club not indicated (antenna autapomorphously transformed), tormal processes simple, *Dasytes*-like, mandibles with posterior dens, median dens distinct, a lamella present between the two teeth, cutting edge glabrous, basistipes strongly transverse, mediostipes normal, palpifer and lacinia strongly reduced, the latter scale-like, attached to side of mediostipes, distigalea almost fused with basigalea, mental crescent absent, prementum very strongly produced (would probably correspond to an extensive prementum in the unknown larva); sternopleural suture on prothorax distinct, lamina on metendosternite absent, elytral surface with irregular punctures, anal wing sector with veins uniquely arched, vein M1 indicated, Rc reduced, all tarsomeres in both sexes 4 in number, claws very weakly appendiculate, fine, sides of antecoxal suture strongly oblique, hind coxae strongly projecting; intercoxal process on first visible sternite replaced by an emargination; median process on male sternum VIII absent, spicular fork plate-shaped with a tendency to envelop phallus, without interspicular plate, tegmen with tegminal struts completely fused with phallobasic apodeme, phallobase fused with parameres, apex not emarginate, bare, base of tegmen complete, with basal ring and complete dorsal wall of tegmen, phallus weakly arcuate with divided base and apex; female copulatory organs of the tubular type of Heberdey; alimentary canal very probably as in the Malachiidae, i. e. with 6 Malpighian tubules (deduced from primitive Malachiidae- Lemphinae).

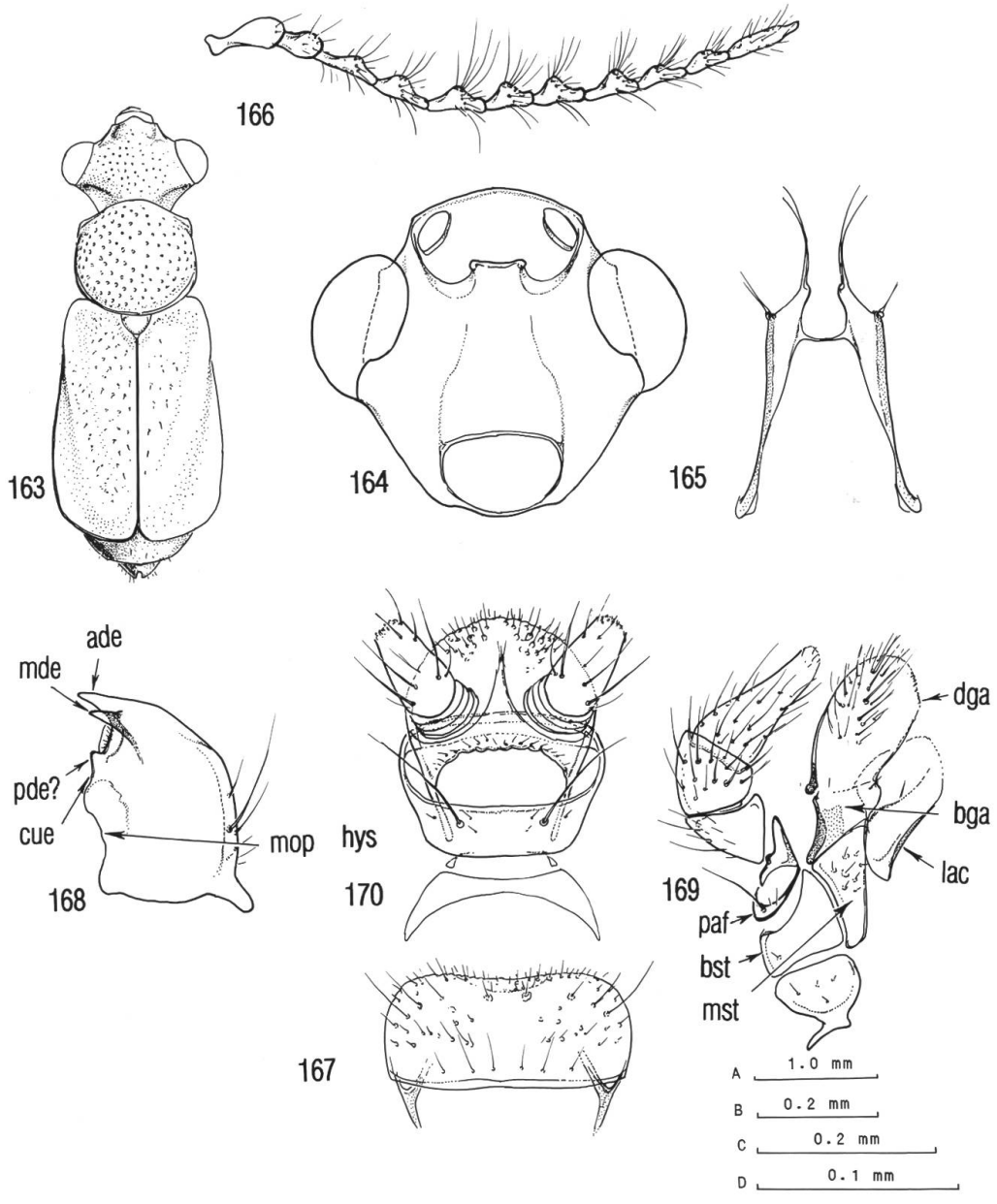
Transformation series:

(1) larval mouthparts: unknown.
(2) adult mouthparts: unique combination of plesiomorphous mandibles and autapomorphous maxilla.
(3) larval alimentary canal: unknown.
(4) adult alimentary canal: unknown, probably synapomorphous.

(5) wings: autapomorphous anal veins.
(6) male copulatory organs: autapomorphous spicular fork, tegmen, but especially phallus.

Plesiomorphies: Mandibles, and tentorial cross-bar.

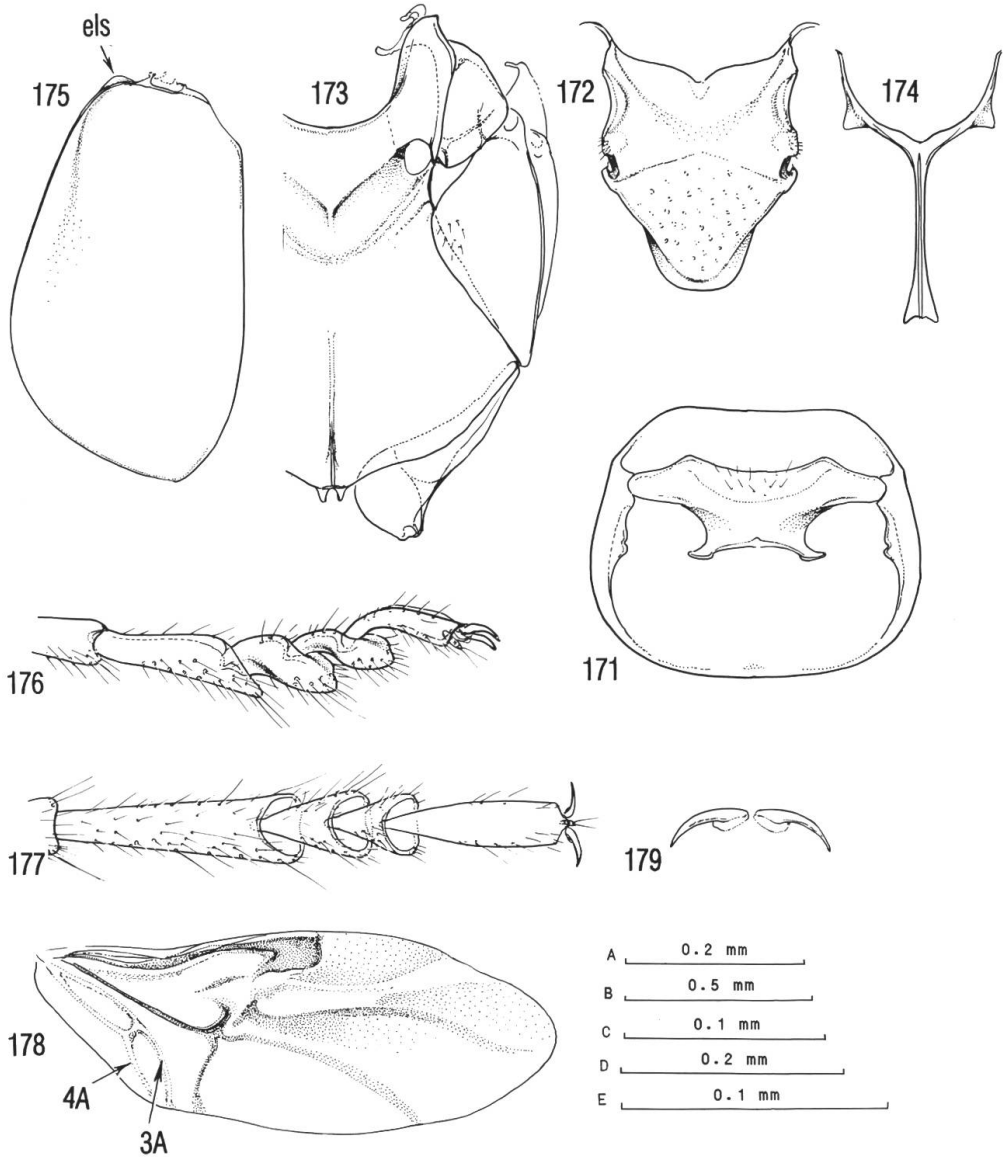
Apomorphies: Antenna, maxilla, wing anal sector, tarsomeres, tegmen and phallus. Supplementary description. Very small, strongly me-



Figs 163- 170: *Attalomimus viridis* Wittmer, ♂: 163, habitus. 164, cranium ventral. 165, tentorial cross-bar. 166, antenna. 167, labrum. 168, mandible ventral. 169, maxilla. 170, labium dorsal.(Scales: A- 163; B- 166; C- 164,165; D-167-170).

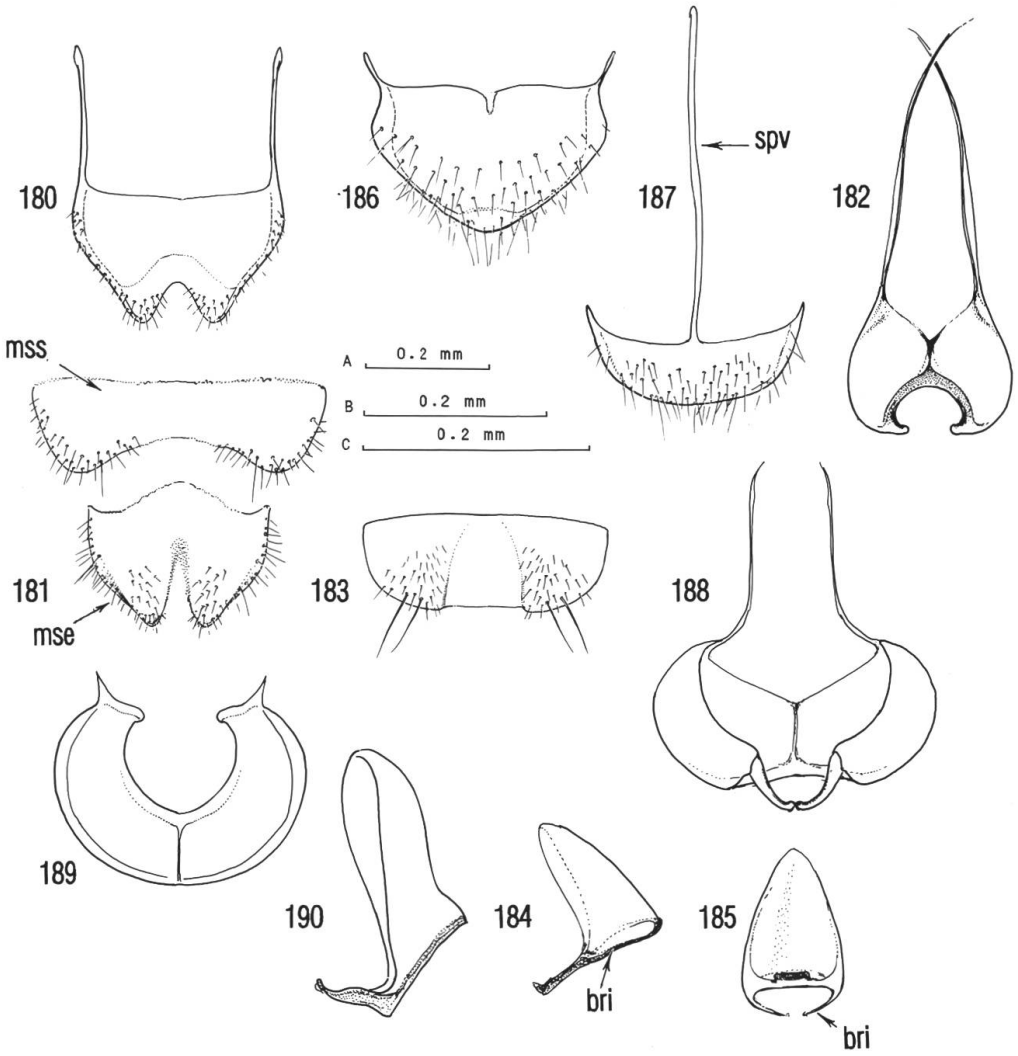
tallic, shining, almost bare species, resembling typical Malachiidae in body appearance.

Remarks. Although the family closely resembles the Malachiidae in the extrusible glands and weak sclerotisation, it is very distant from all the preceding families. Because of its symplesiomorphous mandibles and tormal processes it is monophyletic with the Acanthocnemidae. The remaining mouthparts are autapomorphic, derived from the basic evo-



Figs 171- 179: *Attalomimus viridis* Wittmer, ♂: 171, prothorax ventral. 172, mesoscutellum dorsal. 173, meso- and metathorax ventral. 174, metendosternite. 175, elytron ventral. 176, front tarsus. 177, hind tarsus. 178, wing. 179, protarsal claws. (Scales: A- 171,173,174; B- 175; C- 176,177; D- 172; E- 178,179).

lutionary plan of the Cleroidea, as is the Mauroniscidae & Prionoceridae family group. It is very improbable that the presence of a posterior dens in the mandible would be a convergent character with the Acanthocnemidae. The anal wing sector is hard to classify; the terminalia have strong analogies with those of the Malachiidae, but the phallus has a complex apex, divided base, etc. The 4-segmented tarsi on all legs in both sexes have no analogy within the Melyrid lineage. So far as their



Figs 180-190: 180-182, 184-187, *Attalomimus viridis* Wittmer (180- 182, 184, 185 ♂; 186,187, ♀). 183, 188- 190, *Attalomimus cephalotes* Wittmer,♂. 180, pygidium. 181, sternite VII, sternite VIII. 182, 188, 189, spicular fork (182 dorsal, 188 ventral, 189 frontal). 183, sternite VIII. 184, 190, tegmen lateral. 185, tegmen ventral. (Scales: A- 186,187; B- 180-185; C- 189-190).

relationship with the Malachiidae is concerned, the Attalomimidae seem to have common ancestors with the Malachiidae-Lemphinae; the latter group are primitive Malachiidae in which tarsomere 4 is greatly reduced.

If a different mandible and/or maxilla is found in the larva, this will support the family status of the Attalomimidae.

Distribution: Central America.

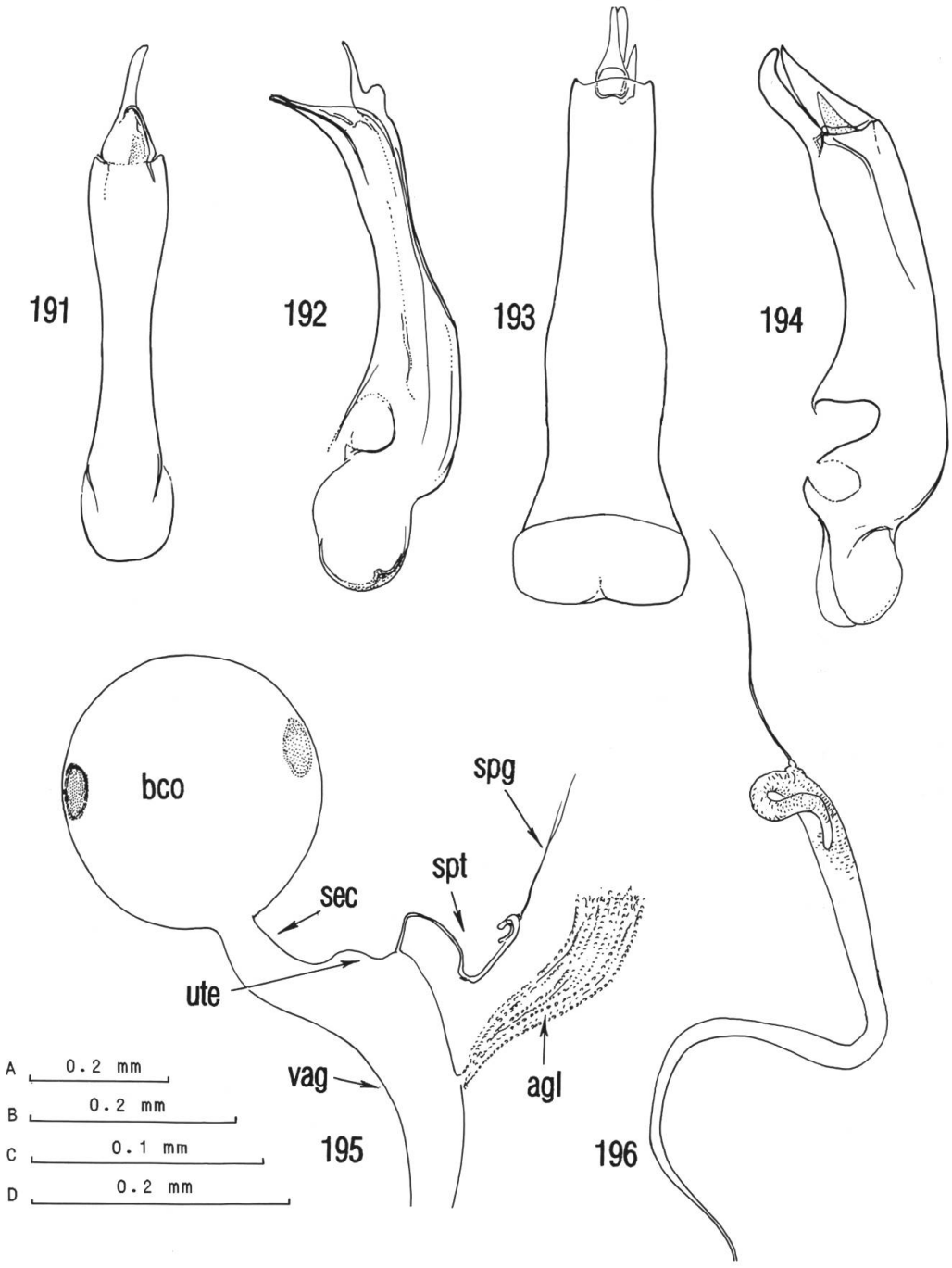
Conclusions

In an earlier contribution dealing with higher classification (MAJER, 1987b), I suggested that a further reclassification of the Melyridae sensu Crowson would be necessary.

In the present paper, the higher classification has been based mainly on the complex structure of the mouthparts and Malpighian tubules as they are structures that occur in both larvae and adults and are very likely homologous in the two stages, while the wings and male terminalia appear to be consistently correlated with the former characters. I have not considered the larval endocarina and epicranial suture (nor the variable number of larval ocelli) to be structures of sufficient weight for erecting individual families, as they are not represented by homologous or correlating structures in the adults.

On the other hand, the prementum in both larvae and adults seems to be a structure that remains homologous in the course of ontogenesis, and the four families in the Melyrid lineage in which both adults and larvae are known may be defined by this character alone:

1. Polysetose in larvae, not modified mediodistally in adults **Prionoceridae**
– Bisetose in larvae, modified mediodistally (emarginate and/or produced) in adults 2
2. Not reduced in larvae, strongly produced and often narrowly incised in adults **Malachiidae**
– Reduced (divided into sclerotised and membranous parts) in larvae, transverse and broadly incised in adults. 3
3. Entire in larvae, mental sclerites present in adults **Dasytidae**
– Divided into two in larvae, mental sclerites absent in adults **Melyridae**



Figs 191-196: 191, 192, 195, 196, *Attalomimus viridis* Wittmer (191, 192, ♂; 195, 196, ♀); 193, 194, *Attalomimus cephalotes* Wittmer, ♂: 191, 193, phallus dorsal. 192, 194, phallus lateral. 195, female reproductive organs. 196, spermatheca. (Scales: A- 195; B- 191,192; C- 196; D- 193,194).

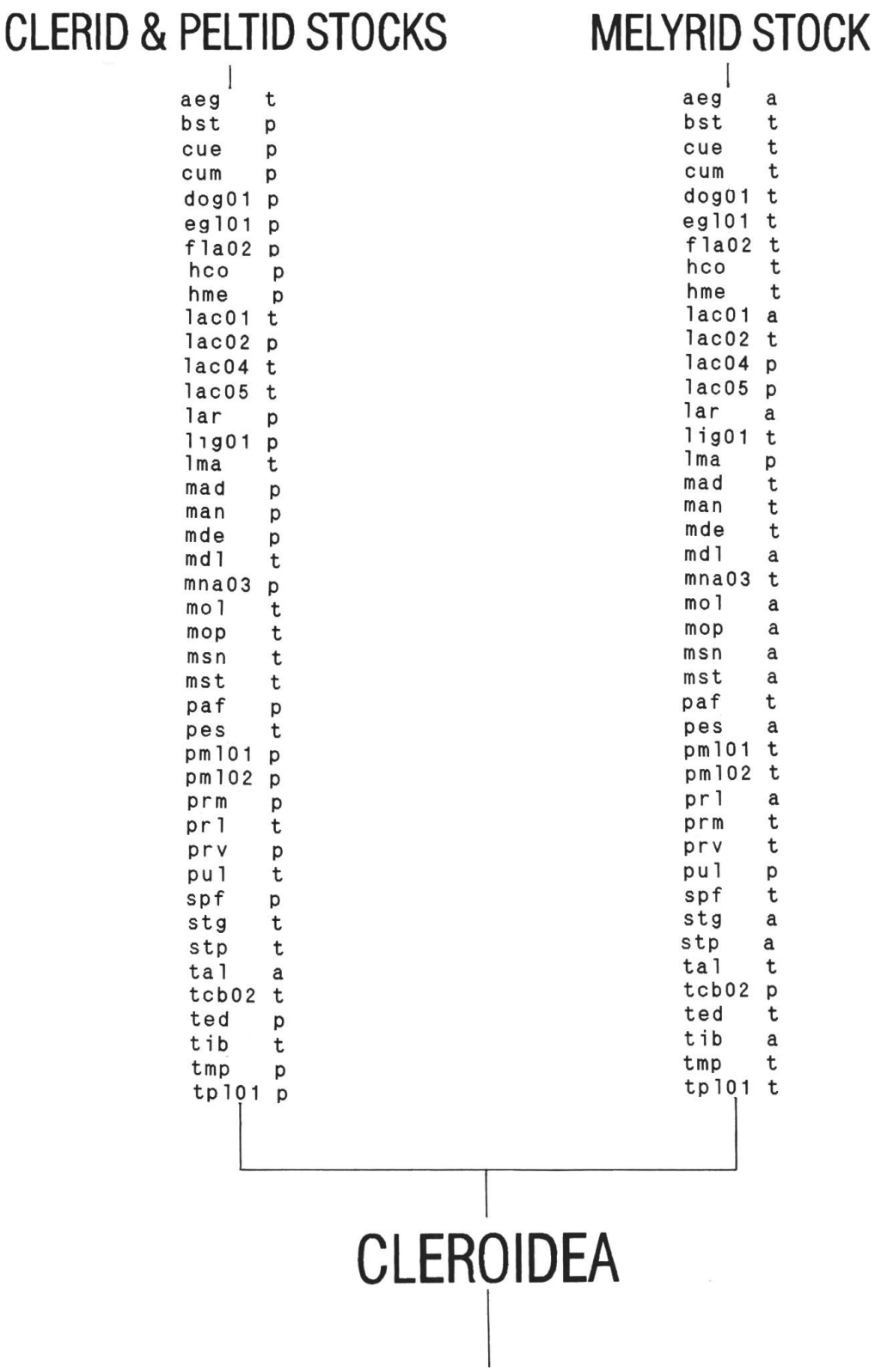


Fig. 197: Cladogram of the stocks (lineage).

Fig. 198: Cladogram of the Melyrid stock (lineage).

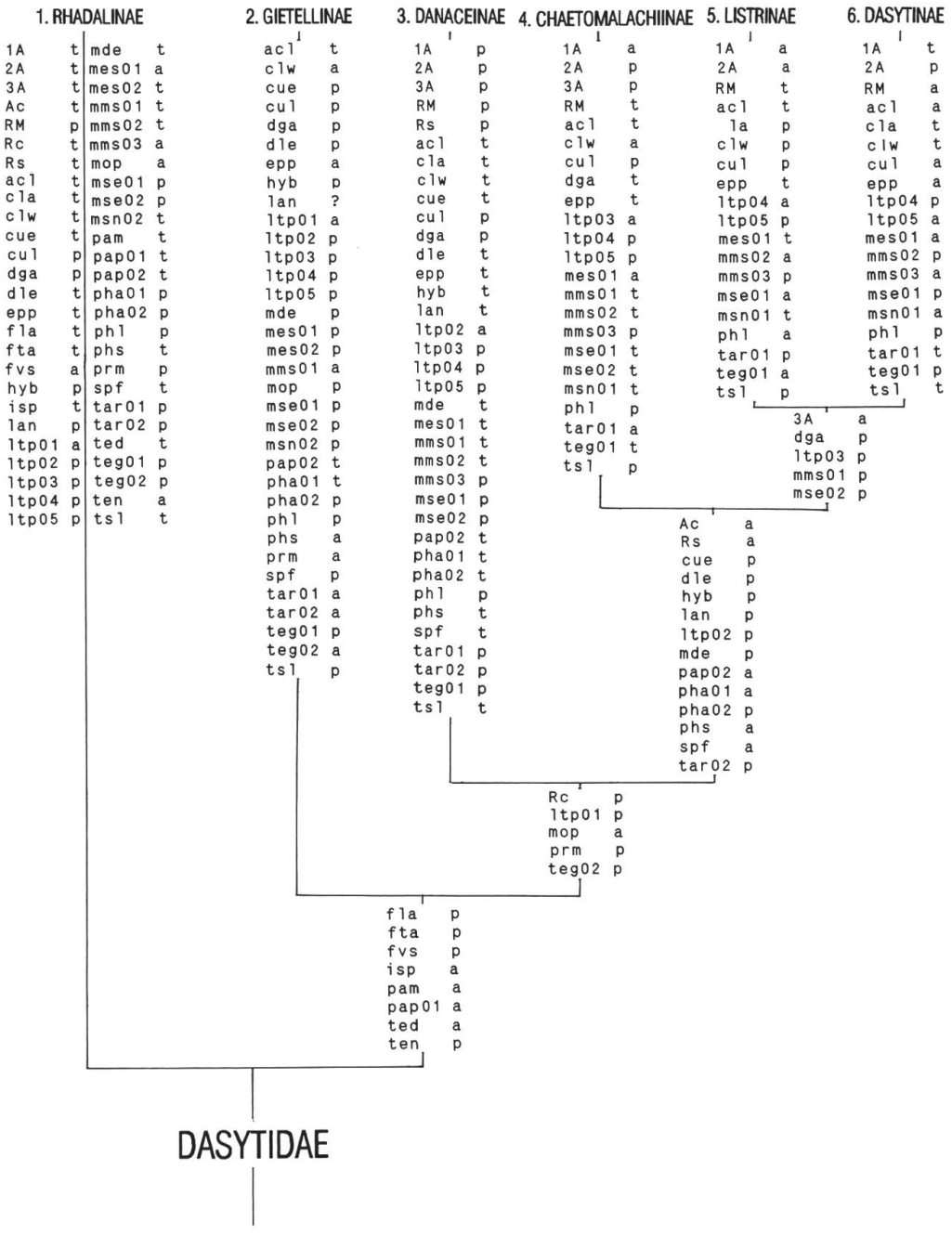


Fig. 199: Cladogram of the family Dasytidae.

Another homologous structure in both stages seems to be the stipes, which should be more or less elongate throughout the entire Melyrid lineage.

Certain special larval traits, such as the presence/absence of the endocarina (a particularly obscure structure) and the V/Y-shaped epicranial suture, do reflect relationships among groups of families and, among other things, define the Melyrid lineage of the present paper. If these characters were used on their own to define the family Melyridae (which is precisely how Crowson defined the family), then, following the principle of transformation series, the number of families in the Clerid and Peltid lineages would be 1 or 2.

There is a special phenomenon that I have called the "Malacoderm impulse" (MAJER, 1987b). This is a case of parallelism among unrelated groups. This parallelism is very strong and is sometimes difficult to distinguish from true phyletic relationships. The oblique sides of the antecoxal suture, the extrusible glands, and the reduced number of the front tarsomeres in *Acanthocnemus* and many Malachiidae are very good examples of this parallelism between the most distant groups. Further examples are the parallel loss of the tentorial cross-bar in the Melyridae, Prionoceridae and most of Malachiidae, accompanied by analogous transformations of the tarsomeres, and the excessive convergence between the Prionoceridae and Cantharidae in the structure of the maxilla, which can hardly be a common adaptation among predaceous adults. One explanation might be to date this phenomenon (which may be a good example of a great evolutionary grade) to the late Mesozoic, the time of the mass extinction of the Dinosauria.

V. References

ACLOQUE, A. (1896): *Faune de France, contennant la description des espèces indigènes en tableaux analytiques et illustrée de figures représentant les types caractéristiques des genres. 1. Coléoptères* 466 pp. J.-B. Baillière & Fils, Paris.

BERNET KEMPERS, K.J.W. (1922): *Nadere beschouwingen van het andersysteem der Coleoptera in verband met het systeem van Prof. Kolbe en anderen.* Tijdschr. Entomol. *65:* 1–38

BLAISDELL, F.E. (1938): *A generic synopsis and generic revision of the tribe Dasytini of North America, north of Panama (Coleoptera: Melyridae).* Trans. Amer. ent. Soc. *64:* 1–31.

BLANCHARD, M.C. (1845): *Histoire des Insectes, traitant de leurs moeurs et le leurs métamorphoses en général, et comprenant une nouvelle classification fondée sur leurs rapports naturels.* 2 Tom., 398 + 524 pp., Didot Paris.

BOURGEOIS, J. (1911): *Mission géodésique de l'Équateur. Collections recueillies par le Dr.P. Rivet. Coléoptères: Mélyrides.* Bull. Mus. Hist. nat. Paris 17(3): 208–214.

BÖVING, A.G. & CRAIGHEAD, F.C. (1931): *An Illustrated Synopsis of the principal larval forms of the order Coleoptera.* Ent. Amer. *11(1930–1931):* 1–352.

BRANCUCCI, M. (1980): *Morphologie comparée, évolution et systématique des Cantharidae (Insecta: Coleoptera).* Ent. Bas. *5*: 215–388.

CASEY, T.L. (1895): *Coleopterological Notices VI.* Ann. New York Acad. Sci. *8:* 435–838.

CONSTANTIN, R. (1989): *Descriptions des larves d' Enicopus pyrenaeus Fairmaire et de Danacea pallipes (Panzer). Contribution à l' étude de la biologie et de la systématique larvaire des Melyridae (Coleoptera).* Nouv. Revue Ent. (N. S.) *6(4):* 387–405.

CONSTANTIN, R. & MENIER, J.J. (1987): *Etude d'un remarquable Melyridae aptère des Iles Canaries: Gietella fortunata, n.gen., n.sp., type d'une sous- famille nouvelle Gietellinae (Coleoptera, Cleroidea).* Revue fr. Ent., (N.S.) *9(2):* 53–63.

CROWSON, R.A. (1955): *The natural classification of the families of Coleoptera.* 214 pp., E. W. Chasey Ltd.,Middlesex.

CROWSON, R.A. (1964): *A review of the classification of Cleroidea (Col.) with description of two new genera of Peltidae and of several new larval types.* Trans. R. Ent. Soc. London *116(12):* 175–327.

CROWSON, R.A. (1970): *Further observations on Cleroidea (Coleoptera).* Proc. Roy. Entom. Soc. London (B) *39:* 1–20.

EKIS, G. (1977): *Classification, Phylogeny, and Zoogeography of the Genus Perilypus (Coleoptera: Cleridae).* Smithsonian Contributions to Zoology *227:* 138 pp.

EMDEN, F. VAN (1932): *Die Larven der Callirhipini, ein mutmassliche Cerophytum-Larve und Familienbestimmungstabelle der Larven der Malacodermata- Sternoxia-Reihe (Coleoptera).* Bull. Soc. ent. Belg. *72:* 199–260.

ERICHSON, W.F. (1840): *Entomographien, Untersuchungen in dem Gebiete der Entomologie, mit besonderen Benutzung der Königl. Sammlung zu Berlin. 1(10)* + 180 pp.

EVERS, A.M.J.(1979): in FREUDE, HARDE, LOHSE: *Die Käfer Mitteleuropas. Vol. 6. 29. Familie: Malachiidae:* pp. 45–69, Goecke & Evers, Krefeld.

EVERTS, K.T. (1903): *Coleoptera Neerlandica.* II. pp.189–196., s'Gravenhage.

FABRICIUS, J.C. (1775): *Systema Entomologiae.* 30+832 pp. Lipsiae.

FIORI, G. (1963): *Alcuni appunti sulla sistematica dei Coleotteri Malachiidi e Dasytidi a livello delle famiglie e sulla loro etologia.* Centro di Entom. alpina e forestale 62: 265–288.

FIORI, G (1972): *Contributi alla conoscenza morphologica ed etologica dei Coleotteri. IX. Psilothrix viridicaeruleus (Geoffr.). (Melyridae Dasytidae).* Studi Sassaresi (III. Agr.) *19(1971):* 3–70.

GANGLBAUER, L. (1903): *Systematisch-Koleopterologische Studien.* Münch. Koleopt. Zeitschr. *1:* 271–319.

HENNIG, W. (1950): *Grundzuge einer Theorie der phylogenetischen Systematik.* Berlin.

HENNIG, W. (1965): *Phylogenetic Systematics.* Annual Rev. Entom. *10:* 97–116.

HENNIG, W. (1966): *Phylogenetic Systematics.* 263 pp., Univeristy of Illinois press, Urbana.

JACOBSON, G.G. (1911): *Zhuki Rossii i Zapadnoi Evropi 7:* 687–712. St. Petersburg.

JEANNEL, R. & PAULIAN, R. (1944): *Morphologie abdominale des Coléoptères et systematique de l' ordre.* Rev. franc. ent. *11(2)*: 65–110.

KIESENWETTER, H. von (1863): in ERICHSON et all.: *Naturgeschichte der Insekten Deutschlands.* IV. Band, erste Abt. p. 569–746. Nicolai, Berlin.

KOLIBÁČ, J. (1987): *Morphological comparison of type (or model) genera of the subfamilies of Cleridae (Coleoptera, Cleridae).* Mitt. Münch. Ent. Ges. 77: 103–135.

KOLIBÁČ, J. (1989)a: *Further observations on morphology of some Cleridae (Coleoptera) (I).* Acta Sc. Nat. Brno 23(1):1–50.

KOLIBÁČ, J. (1989)b: *Further observations on morphology of some Cleridae (Coleoptera) (II).* Acta Sc. Nat. Brno 23(2): 1–42.

KOLIBÁČ, J. (1992): *Revision of Thanerocleridae n. stat. (Coleoptera, Cleroidea).* Mitt. Schweiz. Ent. Ges. 65: 303- 340.

KRAATZ, G. (1882): *Zwei neue Melyriden – Gattungen aus Margelan.* Dtsch. Ent. Z. *26:* 96–98.

KUHNT, P.(1913): *Illustrierte Bestimmungs-Tabellen der Käfer Deutschlands.* 1138 pp, Stuttgart.

LACORDAIRE, J.T. (1857): *Histoire naturelle des Insectes. Genera des Coléoptères. 4. Buprestides – Cisides.* 554 pp., Roret, Paris.

LAPORTE DE CASTELNAU, F.L. (1836): in SILBERMANN, G.H.R: Revue Entomologique *4:* 280 pp., Strasbourg & Paris.

LAPORTE DE CASTELNAU, F.L. (1840): *Histoire naturelle des insectes. Coléoptères.* 1. CXXV + 324 pp. Paris.

LEACH, W.E. (1815): *Brewster's Edinburgh Encyclopaedia. Article.* Entomology *9(1): 57*–172. Edinburgh.

LECONTE, J.E.(1852): *Descriptions of new species of Coleoptera, from California.* Ann. Lyc. Nat. Hist. N. York *5:* 125–216.

LOHSE, G.A. (1979): in FREUDE, H., HARDE, K.W. & LOHSE, G.A.: *Die Käfer Mitteleuropas. Bd. 6. Dasytidae* p. 8, 69–83. Krefeld (Goecke & Evers).

MAJER, K. (1983): *A new genus and species of Dasytinae from Central Asia (Coleoptera, Melyridae).* Acta ent. bohemoslov. *80:* 385–389.

MAJER, K. (1986): *Comparative morphology of the labrum and labium of some Melyridae (Coleoptera).* Acta ent. bohemoslov. *83:* 137–151.

MAJER, K. (1987)a: *A revision of the genus Danacaeina Reitter, 1887.* Dtsch. ent. Z., N.F. *34(4–5):* 355–361.

MAJER, K. (1987)b: *Comparative morphology and proposed major taxonomy of the family Melyridae (Insecta, Coleoptera).* Pol. Pismo Entom. *56*: 719–859.

MAJER, K. (1988): *A revision of the genus Bilyella n.gen. (Coleoptera, Melyridae, Dasytinae).* Ent. Bas. *12:* 435–467.

MAJER, K. (1989)a: *A revision of he tribe Danacaeomimini (Coleoptera, Melyridae, Dasytinae).* Dtsch. ent. Z., N.F.36*(1–3)*:1–31.

MAJER, K. (1989)b: *A revision of the genus Chaetomalachius Kraatz (Coleoptera, Melyridae, Dasytinae).* Ent. Bas. *13:*303–355.

MAJER, K. (1989)c: *Generic classification of the tribe Chaetomalachiini (Coleoptera, Melyridae).* Pol. Pismo Entom. *58:* 745–774.

MAJER, K. (1990)a: *Results of the Czechoslovak-Iranian entomological expeditions to Iran, 1970, 1973 and 1977 together with results of collections made in Anatolia. Coleoptera, Melyridae: Part III (Rhadalinae).* Acta Ent. Mus. Nat. Pragae *43:* 183–202.

MAJER, K. (1990)b: *A new tribe Listrini trib. n., including two new genera (Coleoptera, Melyridae).* Acta Entomol. Bohemoslov. *87:* 368–384.

MAJER, K. (1990)c: *Anatomy of the alimentary canal and internal copulatory organs in Melyridae (Coleoptera)* Elytron *4* :83–99.

MAJER, K. (in press): *Subfamilial classification of the family Malachiidae (Coleoptera).* Ent. Bas.

MOTSCHULSKY, V. (1845): *Remarques sur la collection de Coléoptères Russes.* Bull. Soc. Imp. Nat. Moscou *18:* 3–127(37–38).

MOTSCHULSKY, V. (1860): *Coléoptères nouvelles de la Californie.* Bull. Moscou *32 (2)(1859):* 122–185; 357–410.

MULSANT, E. & REY, C. (1867): *Histoire naturelle des Coléoptères de France. Vésiculifères.* Ann. Soc. agric. Lyon *11(3):* 625–943, pls I–VII.(sep.7+308+7,7 pls., E. Savy, Paris).

MULSANT, E. & REY, C. (1868): *Histoire Naturelle des Coléoptères de France. 19. Floricoles.* Ann. Soc. Linn. Lyon (N.S.) *15:* 237–402.

PAYKULL, G. (1798): *Fauna Suecica: Insecta. (Col.).* 1.8+358 pp., Upsaliae (Edman).

PEACOCK, E.R. (1987): *A review of the Rhadalinae (=Aplocneminae) (Coleoptera: Melyridae).* Bull. Br. Mus. nat. Hist. (Ent.) *56(3):* 129–170.

PERRIS, J.P. (1866): *Descriptions de quelques insectes nouveaux (Coleoptera).* Ann. Soc. Ent. France *6(4):* 181–196.

PERTY, J.A.M.(1831): *Observationes nonnulae in Coleoptera Indiae orientalis.* Dissert. 44 pp., 1 pl. Monachii (Lindauer).

PEYRON, M.E. (1877): *Étude sur les Malachiides d'Europe et du Bassin Méditerranée.* Abeille *15:* 3–312.

PIC, M. (1917): *Contribution à l'étude des Dasytides.* Echange *33*: 1–4.

PIC, M. (1926): in JUNK & SCHENKLING: *Coleopterorum Catalogus. Pars 87. Phloeophilidae, Rhadalidae, Prionoceridae.* 11 pp., Berlin (W. Junk).

PIC, M. (1927): *Contribution à l'étude des Coléoptères Malacodermes. (1er article).* Ann. Soc. ent. France *96:* 77–83.

PIC, M. (1929): in JUNK & SCHENKLING: *Coleopterorum Catalogus. Pars 103: Dasytidae:* Melyrinae. 34 pp., Berlin (W. Junk).

PIC, M. (1937): in JUNK & SCHENKLING: *Coleopterorum Catalogus. Pars 155: Dasytidae Dasytinae.* 130 pp., s' Gravenhage.

REITTER, E. (1911): Fauna Germanica. *Die Käfer des Deutsches Reiches.* III. 436 pp., K. Lutz, Stuttgart.

THOMSON, C.G. (1859): *Synoptiskbearbetade Skandinaviens Coleoptera.* I. Lund.

WITTMER, W. (1976): *35. Beitrag zur Kenntnis der neotropischen Fauna. Coleoptera: Fam. Malachiidae.* Studia Ent. *19:* 421–449.

ZHERICHIN, V. V. & SUKACHEVA, I. D. (1973): *O melovych nasekomonosnych "jantarach" (retinitach) Severya Sibiri. In.: Doklady na dvadcat chetvertom ezhegodnom chtenii pamyati* N. A. Cholodkovskogo, 1–2 aprelya 1971. Voprosy paleontologii nasekomych. 3–48, 7 figs., 11 pls. Leningrad (Nauka).[in russian].

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