

---

CSIRO PUBLISHING

---

# Invertebrate Taxonomy

Volume 14, 2000

© CSIRO 2000



An international journal of southern hemisphere biodiversity and systematics

**[www.publish.csiro.au/journals/it](http://www.publish.csiro.au/journals/it)**

All enquiries and manuscripts should be directed to

*Invertebrate Taxonomy*

**CSIRO PUBLISHING**

PO Box 1139 (150 Oxford St)

Collingwood

Vic. 3066

Australia

Telephone: 61 3 9662 7629

Facsimile: 61 3 9662 7611

Email: [camilla.myers@publish.csiro.au](mailto:camilla.myers@publish.csiro.au)



Published by **CSIRO PUBLISHING**  
for CSIRO and  
the Australian Academy of Science



## Larval head morphology of *Phycosecis litoralis* (Pascoe) (Coleoptera : Phycosecidae) with phylogenetic implications

Rolf G. Beutel<sup>A</sup> and Darren A. Pollock<sup>B</sup>

<sup>A</sup>Institut für Spezielle Zoologie und Evolutionsbiologie, Friedrich-Schiller Universität,  
07743 Jena, Germany. Email: rolf.beutel@rz.uni-jena.de

<sup>B</sup>Texas Agricultural Experiment Station, The Texas A & M University System,  
2301 Experiment Station Road, Bushland, TX 79012, USA.  
Email: beetledude@hotmail.com

**Abstract.** The larval head of a *Phycosecis* species is described and illustrated. Characters are compared to those found in larvae of other groups of Cucujiformia. Monophyly of all cleroid families examined is supported by several apomorphic features at least partly correlated with predacious habits: antennae directed anteriorly, absence of the mandibular mola, presence of a pedunculate seta on the mala, presence of a median endocarina, origin of antennal muscles exclusively from the head capsule, and presence of a weakly pigmented, parallel-sided gular plate. A possible apomorphy of Cleroidea excluding Phloiophilidae is the parallel-sided, prognathous head. A sister-group relationship between Phycosecidae and Melyridae is supported by the presence of a plumose lacinia mobilis and secondary loss of the median endocarina. A monophylum comprising Cleridae + Chaetosomatidae is characterised by a strongly elongated, sclerotised larval gula, the strongly protracted position of the ventral mouthparts, and a cardo as long as or longer than the stipes. Monophyly of Trogossitidae is only weakly supported. Several apomorphies indicate a sister-group relationship between Cleroidea and Nitidulidae. These two taxa are characterised by a fully developed maxillolabial complex, an elongated prepharyngeal tube, and tergal sclerotisation restricted to the prothorax and tergite IX. A tentorial bridge completely separated from the remaining tentorium, and a maxillolabial complex with partly restricted motility of the maxilla are shared derived features of larvae of Cleroidea, Nitidulidae, Coccinellidae and Endomychidae. An unusual attachment of a part of the tentoriostipital muscle to the floor of the prepharyngeal tube is found in all cleroid and cucujoid larvae examined. Cleroidea are a well-defined monophyletic group and may form a monophylum together with a paraphyletic assemblage of Cucujoidea. A close relationship between Cleroidea and Lymexylidae is refuted.

### Introduction

*Phycosecis* was described by Pascoe (1875) based on four species from Australia and New Zealand. The genus was placed originally in Tenebrionidae (*Phaleriides* Latreille), notwithstanding the 5-segmented hind tarsi. Champion (1894) recognised the clavicorn affinities of *Phycosecis* and referred the genus to either Trogossitidae or Cucujidae. Lea (1899, 1921) included *Phycosecis* in Trogossitidae. Crowson (1952) erected a separate family Phycosecidae for *Phycosecis* and *Alfieriella* Wittmer, the latter now considered to belong in Cryptophagidae (Lawrence and Newton 1995; Leschen 1996). He also described the larva of *Phycosecis limbata* (Fabricius) based on a specimen collected on the remains of a dead bird (Crowson 1964). Phycosecidae were initially placed in Cucujoidea, section Clavicornia, near Helotidae and Cryptophagidae by Crowson (1952). The same author later redefined Cleroidea and transferred *Phycosecis* from Cucujoidea to this superfamily (Crowson 1964). This position was retained by Lawrence and Newton (1995), who placed Phycosecidae between Acanthocnemidae and Prionoceridae.

The geographical distribution of *Phycosecis* encompasses marine beach habitats in Australia, New Zealand, New Caledonia and New Hebrides (Lawrence and Newton 1995). The known species are scavengers on dead animals, in both larval and adult stages (Lawrence 1991). Crowson (1964) found insect fragments in the larval gut contents. However, larvae of *P. litoralis* (Pascoe) have been found clustered beneath pieces of dead fish and were probably feeding on these (Lawrence and Britton 1994). Rearing phycosecids exclusively on fish, lettuce and bran was also reported by these authors.

Crowson (1964) provided a detailed history of cleroid systematics, including that of the constituent families. In addition to the three large families Trogossitidae, Melyridae and Cleridae, which were first united in a single taxon (Cleroidea) by Böving and Craighead (1931), Crowson (1964) added Phloiophilidae, Chaetosomatidae and Phycosecidae. Lawrence and Newton (1995) included the following eight families in Cleroidea: Phloiophilidae, Trogossitidae, Chaetosomatidae, Cleridae, Acanthocnemidae, Phycosecidae, Prionoceridae

and Melyridae. Crowson (1960) indicated that the relationships among the cucujiform superfamilies Cleroidea, Lymexyloidea and Cucujoidea were unclear, but suggested an early trichotomy within the Cucujiformia, analogous to the basic split among the four recognised suborders of Coleoptera. The Cleroidea represented the predacious component (analogous to Adephegata), the Lymexyloidea the wood-boring component (Archostemata), and the Cucujoidea the originally fungivorous component (Myxophaga and Polyphaga). Within Cleroidea, Crowson (1960) postulated a basal bifurcation Melyridae–Phycosecidae and Trogossitidae–Phloiophilidae. Lawrence and Newton (1982) placed Cleroidea in close proximity to Lymexyloidea. They identified two groups of derived Cleroidea, based on both adult and larval characters: Chaetosomatidae–Cleridae and Melyridae–Acanthocnemidae–Phycosecidae. Relationships among the more primitive groups of Cleroidea, and within some of these among the more primitive families (e.g. Trogossitidae), were considered to be unclear (Lawrence and Newton 1982).

The main goal of this study is to improve the knowledge of the head morphology of the little known phycosecid larvae. A preliminary hypothesis of relationship among Cleroidea and other cucujiform taxa is presented.

## Materials and methods

### Taxa examined

**Cleroidea:** Phycosecidae: \**Phycosecis litoralis* (Pascoe); Trogossitidae: *Calitys* sp.; Cleridae: \**Lemidia* sp.; Melyridae: \**Collops* sp., *Prionocerus* sp.; Phloiophilidae: *Phloiophilus edwardsi* Stephens. **Eucinetoidae:**

Eucinetidae: \**Eucinetus* sp. **Derodontoidea:** Nosodendridae: \**Nosodendron fasciculare* (Olivier); Derodontidae: \**Derodontus esotericus* Lawrence, *D. maculatus* (Melsheimer). **Lymexyloidea:** Lymexylidae: \**Elateroides dermestoides* (Linnaeus). **Cucujoidea:** Endomychidae: \**Mycetina cruciata* (Schaller); Sphindidae: \**Sphindus americanus* LeConte; Protocucujidae: \**Ericmodes* sp.; Cucujidae (incl. Silvanidae): *Pediacus* sp., \**Oryzaeophilus* sp., \**Silvanus* sp., *Uleiota* sp.; Coccinellidae: \**Coccinella* sp.; Nitidulidae: \**Glischrochilus* sp. **Tenebrionoidea:** Pyrochroidae: \**Pyrochroa* sp.; Colydiidae: Tenebrionidae: \**Bitoma crenata* (Fabricius); Melandryidae: \**Orchesia* sp. **Chrysomeloidea:** Chrysomelidae: \**Altica* sp.

There are no known larvae of Acanthocnemidae, and thus this family was not taken into consideration. The larva tentatively assigned to Acanthocnemidae by Crowson (1970) probably belongs to Melyridae (Lawrence personal communication; Beutel personal observation).

The description presented below is based on larvae of *Phycosecis litoralis* (Pascoe) (Fig. 1), which were reared from eggs laid by adults collected at the mouth of the Thomas River, 23 km NW by W Mt Arid, Western Australia, 5–6 November 1977, J. F. Lawrence, coll. These larvae were also compared with the illustrations of *P. limbata* larvae described by Crowson (1964). Specimens are in the Australian National Insect Collection (ANIC) (Lawrence personal communication).

Larvae of *Phycosecis* were fixed and preserved in 70% ethanol. Specimens of all species indicated above by an asterisk (\*) were imbedded in Historesin, cut at 3 µm and stained with methylene-blue and acid fuchsin. Drawings were made using an ocular grid or a camera lucida (cross sections). For scanning electron micrographs (SEMs) specimens were cleaned by ultrasonication, critical point dried and coated with gold.

von Kéler's (1963) muscle nomenclature is used in the text, and the corresponding numbers are used in the illustrations.

### Phylogenetic analysis

The characters used for analysis are listed below under 'Phylogenetically relevant characters'. The data matrix is shown in the Table 1. Characters were analysed using PAUP (version 3.1; Swofford, 1991).

Table 1. Data matrix used for phylogenetic analysis

Characters	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
Taxa																				
<i>Ochthebius</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Eucinetus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Derodontus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
<i>Elateroides</i>	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	1
<i>Phloiophilus</i>	0	1	1	1	0	0	?	1	0	2	0	0	1	1	?	?	?	?	?	1
<i>Phycosecis</i>	1	0	1	1	1	1	1	1	1	2	0	0	1	1	1	1	1	2	1	1
<i>Chaetosoma</i>	1	1	5	1	0	0	?	1	2	2	1	1	1	1	?	?	?	?	?	1
<i>Calitys</i>	1	1	4	1	0	0	1	1	0	2	0	0	1	1	1	1	1	2	1	1
<i>Temnoscheila</i>	1	1	4	1	0	0	1	1	0	2	0	0	1	0	1	1	1	2	1	1
<i>Lemidia</i>	1	1	5	1	0	0	1	1	0	2	1	1	1	1	1	1	1	2	1	1
<i>Platynoptera</i>	1	1	5	1	0	0	?	1	0	2	1	1	1	1	?	?	?	?	?	?
<i>Collops</i>	1	0	3	1	0	0	1	1	1	2	0	0	1	1	1	1	1	2	2	1
<i>Sphindus</i>	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	1	0	0	1
<i>Ericmodes</i>	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	1	1	0	1
<i>Coccinella</i>	0	0	0	0	0	0	0	0	0	1	0	0	1	0	1	1	1	1	0	1
<i>Glischrochilus</i>	0	0	2	0	0	0	0	2	0	2	0	0	1	0	1	1	1	2	2	1
<i>Mycetina</i>	0	0	0	0	0	0	0	0	0	1	0	0	1	0	1	1	1	1	0	1
<i>Cucujus</i>	0	0	6	0	0	0	0	0	0	0	0	0	1	0	1	0	1	1	0	1
<i>Silvanus</i>	0	0	6	0	0	0	0	0	0	0	0	0	1	0	1	0	1	1	0	1
<i>Pyrochroa</i>	0	0	6	0	0	0	0	0	0	0	0	0	1	0	0	2	1	1	0	1
<i>Bitoma</i>	0	0	6	0	0	0	0	0	0	0	0	0	1	0	0	2	1	1	0	1
<i>Altica</i>	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	1	0	0	1

The outgroup comprises *Ochthebius* (Hydraenidae), *Derodontus* (Derodontidae), *Elateroides* (Lymexylidae), *Altica* (Chrysomelidae) and several cucujoid and tenebrionoid taxa. All characters were weighted equally and not ordered. All question marks in the matrix refer to missing data.

Most parsimonious trees were generated using branch and bound search. The outgroup taxa were treated as all other groups in the analysis (simultaneous analysis; Nixon and Carpenter, 1993). Analysis of character evolution was conducted in MacClade (version 3; Maddison and Maddison, 1992).

## Results

### Description of the head

**External features (Figs 1–4, 10).** Head distinctly declined, about as broad as long, moderately flattened; almost parallel-sided, very slightly rounded laterally; most sclerotised parts testaceous, parts of clypeal area darkened; distribution of setae as in Figs 2–4 and Fig. 10. Six stemmata present, arranged as in Fig. 4. Labrum free (Figs 2, 4), connected with clypeal margin by a broad membrane; fairly broad and moderately long, but scarcely visible from above due to angle of head capsule to longitudinal body axis. Anterior tentorial grooves visible as dark spots close to antennal base. Clypeofrontal suture absent. Clypeofrons V-shaped and fairly elongate. Frontal suture distinct, almost straight. Coronal suture present, moderately long. Dorsomedian endocarina absent. Ventral side of head distinctly shorter than dorsal side, with distinct lateral longitudinal ridges or hypostomal rods converging towards hind margin of head (Fig. 3). Groove for insertion of maxillolabial complex deep, U-shaped. Gula nearly parallel-sided, moderately broad and long, less strongly pigmented than other parts of head capsule (Fig. 3).

**Internal skeletal structures (Figs 5, 7).** Tentorium strongly modified. Tentorial bridge well developed, straight, arising close to foramen occipitale (Figs 3, 7). Posterior arms originating immediately behind maxillolabial complex, completely detached from bridge. Dorsal and anterior arms strongly reduced, no connection between anterior tentorial grooves and posterior tentorium.

**Labrum (Figs 2, 4, 5, 10).** Fairly broad and moderately long, connected with clypeus by a broad membrane (Figs 4, 5). Horizontal in relation to longitudinal axis of head. Distribution of setae as in Fig. 2 and Fig. 10.

**Musculature (Fig. 5):** M 7 (*M. labroepipharyngalis*): absent; M 9 (*M. frontoepipharyngalis*): absent.

**Antenna (Figs 2, 4, 10).** Inserted on prominent, semimembranous, antennomere-like elevation; very short, 3-segmented, directed anteriorad. Antennomere I distinctly wider than long, antennomere II extremely short, with large, rounded, hyaline appendage. Distal antennomere moderately long, with three apical setae.

**Musculature (Figs 8, 9):** Mm 1, 2, 4 (*M. tentorioscapalis anterior, posterior, medialis*), O: dorsal wall of head capsule, lateral to origin of posterior component of *M. frontopharyngalis*, I: anteriorly and posteriorly on the base of antennomere I.

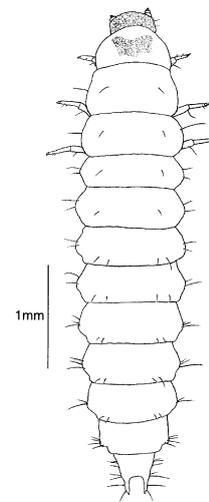
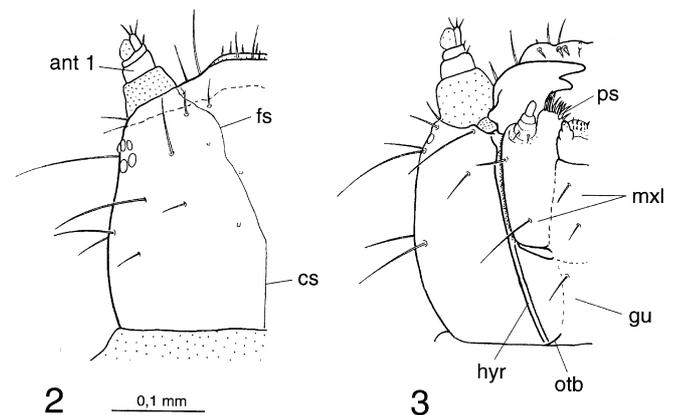


Fig. 1. *Phycosecis litoralis*, habitus, dorsal view.



Figs 2–3. Head of *P. litoralis*: 1, dorsal view; 2, ventral view. Abbreviations: ant 1, antennomere 1; cs, coronal suture; fs, frontal suture; gu, gula; hyr, hypostomal rods; mxl, maxillolabial complex; otb, origin of tentorial bridge; ps, pedunculate seta.

**Mandible (Figs 3, 4, 10).** Moderately long, with 2 strong apical teeth. Mola and retinaculum absent, with plumose basal appendage.

**Musculature (Figs 5, 7–9):** M 11 (*M. craniomandibularis internus*): strongest muscle of head capsule, O: extensive parts of the dorsal, dorsolateral, lateral and ventrolateral areas of the head capsule, I: adductor tendon; M 12 (*M. craniomandibularis externus*): composed of two moderately strong bundles, nearly parallel to longitudinal axis of head, O: laterally and ventrolaterally from the head capsule, I: abductor tendon.

**Maxilla (Figs 3, 10).** Maxilla and labium forming a closely connected maxillolabial complex inserted in a deep U-shaped fossa on the ventral side of the head capsule.

Articulatory membrane completely absent. Cardo very short and transverse, undivided. Stipes approximately parallel-sided and fairly long. Separate galea absent. Rounded, flat mala densely set with a row of strong spines and with a pedunculate seta (Figs 3, 10). Palp 3-segmented, inserted on a distinct palpomere with two ventral setae. Palpomeres I–II short, palpomere III distinctly longer.

Maxillary musculature (Figs 5, 8, 9): M 15 (M. craniocardinalis), O: ventrolaterally from the posterior margin of the head capsule, I: posterolateral margin of cardo by means of a short tendon; M 17 (M. tentoriocardinalis), O: posterior tentorial arm, I: ventral surface of cardo; M 18 (M. tentoriostipitalis): divided into two components, M 18a, O: posterior tentorial arm, I: ventral surface of stipes; M 18b, O: ventral sclerotised surface of posterior hypopharynx, I: ventral surface of stipes, anterior to M 18 a; M 19 (M. cranio-lacinalis): composed of two fairly thin bundles, O: ventrolaterally from the hind margin of the head capsule, on either side of M. craniocardinalis, I: dorsal base of mala; M 22, 23 (M. stipitopalpalis externus and internus), O: mesally and laterally from the ventral surface of the stipes, I: anteriorly and posteriorly on the base of the maxillary palp.

**Labium** (Figs 3, 5, 10). Closely connected with maxillae. Submentum not clearly defined, represented by an unpigmented area posteriorly of mentum, both parts not clearly separated. Mentum fairly elongated, parallel-sided. Prementum moderately sized, without distinct palpigers and ligula. Ligular area membranous, covered with short spines. Palp short, 2-segmented.

Musculature (Figs 5, 7–9): M 28 (M. submentopraementalis): atypical insertion, O: medially from gula, at the level of the tentorial bridge, I: ventromesally on mentum; M 29 (M. tentoriopraementalis inferior), O: mesally on the base of the tentorial bridge (Fig. 7), I: ventrolaterally on premental base; M 30 (M. tentoriopraementalis superior), O: tentorial bridge, together with M 29, I: dorsolaterally on premental base; M 34 (M. praementopalpalis ext.): absent.

Transverse muscle: absent.

**Epipharynx** (Figs 5, 9). Anterior epipharynx semimembranous, slightly convex in cross section, without distinct grooves and setose areas. Posterior part of epipharynx fused with dorsal wall of posterior hypopharynx, thus forming a fairly long, closed prepharyngeal tube. Prepharynx U-shaped in cross section, with very distinct lateral folds (Fig. 9).

Musculature (Fig. 5): M 43 (M. clypeopalatalis): composed of three subcomponents; M 43a, two bundles, O: anteromedian frontoclypeal region, I: medially and paramedially on anterior epipharynx; M 43b: two bundles, O: posterior to M 43a, I: laterally on the roof of the anterior prepharyngeal tube and on the lateral fold of the prepharynx; M 43c: one bundle, O: posterior to M 43b, I: laterally on the roof of the posterior prepharynx. Subcomponents of M 43 separated by strong transverse muscle bands.

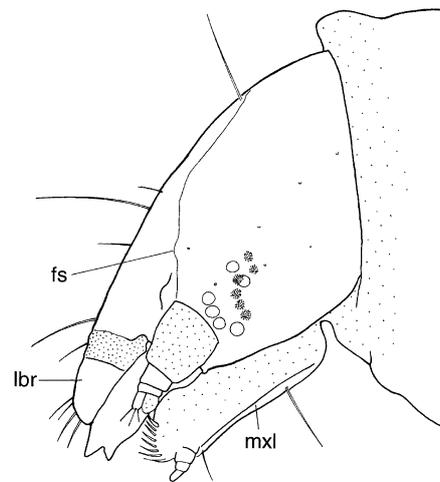


Fig. 4. Head of *P. litoralis*, lateral view. Abbreviations: fs, frontal suture; lbr, labrum; mxl, maxillolabial complex.

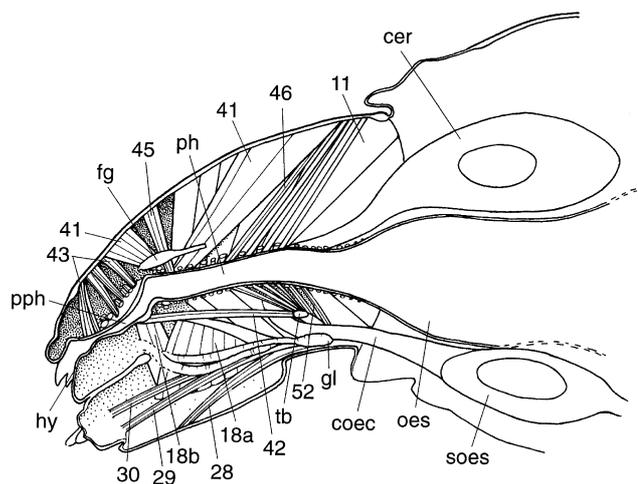


Fig. 5. Head of *P. litoralis*, sagittal section. Abbreviations: cer, cerebrum; coec, circumoesophageal connective; fg, frontal ganglion; gl, gland; hy, hypopharynx; oes, oesophagus; ph, pharynx; pph, prepharynx; soes, suboesophageal ganglion; tb, tentorial bridge; 11, M. craniomandibularis internus; 18a, tentorial part of M. tentoriostipitalis; 18b, hypopharyngeal part of M. tentoriostipitalis; 28, M. submentopraementalis; 29, M. tentoriopraementalis inferior; 30, M. tentoriopraementalis superior; 41, M. frontohypopharyngalis; 42, M. tentoriohypopharyngalis; 43, M. clypeopalatalis; 45, M. frontobuccalis anterior; 46, M. frontobuccalis posterior; 52, M. tentoriopharyngalis.

The possibility that the median bundle of M 43a is derived from a V-shaped M. frontoepipharyngalis (M 9) cannot be fully excluded. Such a muscle is present in the cucujoid larvae examined. However, the presumed subcomponent of M 43 of the *Phycosecis* larva is vertical and inserted on the anteriormost frontoclypeal region, whereas M 9 usually originates from the posterior frons.

**Hypopharynx** (Fig. 5). Anterior hypopharynx semimembranous, distinctly separated from dorsal premental surface by a deep fold. Strong internal transverse bar separating anterior hypopharynx from posterior part, which is sclerotised and laterally fused with posterior epipharynx (see above).

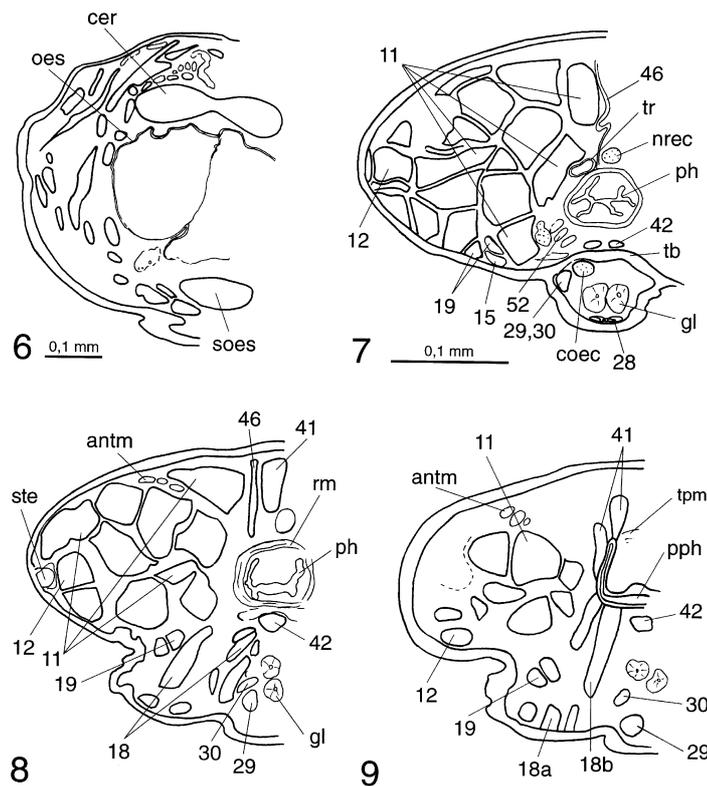
Musculature (Figs 5, 8, 9): M 41 (*M. frontohypopharyngalis*): strong muscle, composed of two parts, M 41a: O: anterior frons, anteriorly of *M. frontobuccalis anterior*, I: laterally on posterior margin of prepharynx; M 41b, O: posteromedian part of frons, I: together with M 41a on dorsolateral fold of prepharynx, immediately anterior to *M. frontobuccalis anterior*; M 42 (*M. tentoriohypopharyngalis*): composed of two parts, M 42 m, O: tentorial bridge, I: posteromedially on hypopharynx, M 42 l, O: distal part of posterior tentorial arm, I: laterally on posterior margin of hypopharynx, posterior of M 18b.

**Pharynx** (Figs 5, 7, 8). Moderately broad, but with strongly narrowed lumen, with narrow dorsolateral, dorsal and ventrolateral folds.

Musculature (Figs 5, 7): M 45 (*M. frontobuccalis anterior*), O: frons; I: dorsolaterally on pharynx, immediately poster of frontal connective; M 46 (*M. frontobuccalis posterior*): composed of several thin bundles, O: mesally of M 41b, I: successively on dorsolateral folds of pharynx; M 51 (*M. verticopharyngalis*): absent; M 52 (*M. tentoriopharyngalis*): strong muscle, composed of two rows of bundles, O: ventrolaterally, from posterior part of head capsule, I: ventrolaterally and laterally on posterior pharynx.

A well-developed ring musculature is present over the whole length of the pharynx.

**Cerebrum and suboesophageal ganglion** (Figs 5, 6). Cerebrum and suboesophageal ganglion elongate, slightly



**Figs 6–9.** Head of *P. litoralis*, cross sections: 6, oesophageal region; 7, posterior pharyngeal region; 8, anterior pharyngeal region; 9, prepharyngeal region. Abbreviations: antm, antennal muscles; cer, cerebrum; coec, circumoesophageal connective; gl, gland; nrec, nervus recurrens; oes, oesophagus; ph, pharynx; pph, prepharynx; rm, ring muscle; soes, suboesophageal ganglion; ste, stemma; tb, tentorial bridge; tpm, transverse prepharyngeal muscle; tr, trachea; 11, *M. craniomandibularis internus*; 12, *M. craniomandibularis externus*; 15, *M. craniocardinalis externus*; 18a, tentorial part of *M. tentoriostipitalis*; 18b, hypopharyngeal part of *M. tentoriostipitalis*; 19, *M. craniolacinalis*; 28, *M. submentopraementalis*; 29, *M. tentoriopraementalis inferior*; 30, *M. tentoriopraementalis superior*; 41, *M. frontohypopharyngalis*; 42, *M. tentoriohypopharyngalis*; 46, *M. frontobuccalis posterior*; 52, *M. tentoriopharyngalis*.

tapering cranially, both completely removed from head capsule to prothorax. Circumoesophageal connective unusually elongated due to posterior position of brain, strongly bent anterior to tentorial bridge.

*Glands* (Figs 5, 7, 8). Tube-like glands, presumably producing salivary secretions, originate in posterior gular region.

*Gut* (Figs 5, 6). Oesophagus unusually wide. Strongly extending posteriad to cerebrum and suboesophageal ganglion, thus forming a very voluminous crop.

#### *Phylogenetically relevant characters*

1. *Head shape*: (0) distinctly rounded laterally; (1) parallel-sided

A nearly parallel-sided head is characteristic for most cleroid larvae (Phycosecidae, Trogossitidae part., Chaetosomatidae, Cleridae, Melyridae; Figs 1, 2). The head is distinctly rounded laterally in larvae of *Phloiophilus* (Crowson 1964; Lawrence 1991) and larvae of most other cucujiform families (e.g. Lymexylidae, Sphindidae, Protocucujidae, Cucujidae, Cavognathidae, Nitidulidae, Colydiidae, Pyrochroidae, Chrysomelidae).

2. *Median endocarina*: (0) absent; (1) present

A median endocarina is presumably an apomorphic character state found in the wood-boring larvae of Lymexylidae (Costa *et al.* 1988; Beutel personal observation), in larvae of Phloiophilidae (Crowson 1964), *Calitys*, *Temnoscheila* (Trogossitidae) and most larvae of Cleridae (including *Lemidia*; Lawrence 1991; Beutel personal observation). This feature has certainly evolved several times independently within Coleoptera. An endocarina is also present in the xylobiontic larvae of Cerambycidae, Archostemata and others (e.g. *Porculus*, Ciidae; Costa *et al.* 1988).

3. *Gula*: (0) absent or very short, semimembranous and inserted between posterior tentorial grooves; (1) present, parallel-sided, less strongly pigmented than other parts of head; (2) quadrangular and clearly defined but very small, inserted between epicranial halves; (3) parallel-sided, moderately elongated, without lateral gular sutures; (4) parallel-sided, moderately elongated, lateral gular sutures present; (5) parallel-sided, strongly elongated; (6) short and transverse, diverging posteriorly, inserted between gular ridges

A moderately long, nearly parallel-sided gula is present posteriorly to the origin of the posterior tentorial arms in larvae of *Phycosecis* (Fig. 3) and *Phloiophilus* (Beutel personal observation). It is less strongly pigmented than the other parts of the head capsule. A sclerotised gula without distinct lateral gular sutures is characteristic of larvae of Melyridae (e.g. *Collops*, *Prionocerus*). A clearly delimited, parallel-sided gula is present in larvae of Trogossitidae (moderately elongated in larvae of *Lophocateres* and

*Promanus*; Crowson 1964; Lawrence 1991). It is strongly elongated in larvae of Cleridae and Chaetosomatidae (Crowson 1964; Lawrence 1991). A transverse, posteriorly diverging gula inserted between distinct internal gular ridges is present in larvae of some cucujoid and tenebrionoid families with distinctly prognathous mouthparts (Cucujidae, Pyrochroidae, Colydiidae). The gula is unsclerotised and very short or completely absent in most cucujoid larvae (e.g. *Ericmodes*, *Sphindus*, *Mycetina*) and in larvae of many other groups with a subprognathous or hypognathous orientation of mouthparts (e.g. Agrytidae, Eucinetidae, Lymexylidae, Chrysomelidae).

4. *Orientation of antenna*: (0) parallel to longitudinal body axis; (1) angled at least 30° to longitudinal body axis

Antennae directed anteriorly with an orientation parallel to the body axis and a transverse basal line of antennomere I are characteristic of larvae of Phycosecidae (Fig. 2) and the other cleroid families (Lawrence 1991). A similar condition is found in larvae of *Porculus* (Costa *et al.* 1988) and especially in other groups with predacious habits and a more or less parallel-sided head capsule (e.g. Carabidae (in part); Histeridae; Elateridae, Cantharoidea; Beutel 1993, 1995, 1999). Anterolaterad-directed antennae are present in the larvae of the cucujoid families examined (Sphindidae, Nitidulidae, Cucujidae etc.; Lawrence 1991; Beutel personal observation) and larvae of most other groups of Coleoptera (e.g. Eucinetidae, Derodontidae, Pyrochroidae, Pythidae).

5. *Antennomeres I and II*: (0) not distinctly wider than long; (1) distinctly wider than long

Strongly shortened antennae with unusually wide and short antennomeres I and II are characteristic of larvae of *Phycosecis* (Fig. 2). Distinctly shortened antennae are also present in some trogossitid and clerid larvae such as *Calitys* and *Necrobia* (Foster and Lawrence 1991; Beutel personal observation). However, in these larvae the basal antennomere is invaginated and not distinctly wider than long. Shortened antennae are a derived feature that has evolved in many lineages, especially in larvae with burrowing or wood-boring habits (e.g. Lymexylidae, Heteroceridae, Callirhipidae; Beutel 1995).

6. *Antennal sensorial appendage*: (0) absent or slender; (1) present, enlarged

An enlarged sensorial appendage of antennomere II (Fig. 2) is a possible autapomorphy of Phycosecidae.

7. *Origin of antennal muscles*: (0) tentorium; (1) head capsule

The antennal muscles originate exclusively from the dorsal wall of the head capsule, without any attachment to the tentorium, in all larvae of Cleroidea examined (Fig. 8). This is a result of the reduced condition of the endoskeleton. The antennal muscles are at least partly attached to the flattened dorsal tentorial arms in the larvae of Cucujoidea and Tenebrionoidea examined. They originate exclusively from

the anterior or dorsal arm in larvae of most other groups of Coleoptera (e.g. Aephaga, Hydraenidae, Agyrtidae, Staphylinidae, Eucinetidae, Nosodendridae, Derodontidae; Beutel 1993, 1996; Beutel and Molenda 1997).

8. *Mandibular mola*: (0) well developed at least on one mandible; (1) absent; (2) spine-like, with posteriad directed hooks

A mola is absent in the larvae of Cleroidea examined, whereas it is well developed in most larvae of Cucujoidea (e.g. Sphindidae, Protocucujidae, Cucujidae, Endomychidae) and Tenebrionoidea (e.g. Colydiidae, Mycetophagidae, Archaeocrypticidae; Lawrence 1991: fig. 34.637). A very atypical spine-like mola with posteriad directed hooks is present in larvae of *Glischrochilus*. Loss of the mandibular mola is correlated in most cases with predacious habits (e.g. Aephaga, Staphylininae, Histeroidea, Hydrophiloidea, Elateriformia (in part); Beutel 1993, 1995, 1999; Beutel and Molenda 1997).

9. *Basal mandibular appendage (lacinia mobilis)*: (0) plumose; (1) absent; (2) represented by two slender spines and a seta

The plumose appendage of the mandibular base of larvae of *Phycosecis* is similar to the basal appendage (lacinia mobilis; Foster and Lawrence 1991) of larvae of Melyridae. Two slender spines and a seta are present in larvae of Chaetosomatidae (Lawrence 1991).

10. *Maxilla and labium*: (0) separate; (1) lateral motility of the maxilla partly restricted; (2) ventral mouthparts forming maxillolabial complex

A characteristic maxillolabial complex is found in larvae of Cleroidea (Figs 3, 10) and *Glischrochilus*. A similar condition has probably evolved independently in *Porculus* (Ciidae; Costa *et al.* 1988) and Elateriformia (excluding Byrrhidae, Buprestidae, Eulichadidae, Ptilodactylidae; Beutel 1995). A full lateral motility is retained in larvae of Tenebrionoidea and larvae of most cucujoid families (e.g. Protocucujidae, Sphindidae). It is partly restricted in *Mycetina* (Endomychidae) and Coccinellidae. However, this is still clearly different from a true maxillolabial complex as found in cleroid and nitidulid larvae.

11. *Position of ventral mouthparts*: (0) retracted; (1) protracted

A strongly protracted position of the ventral mouthparts is characteristic of larvae of Cleridae (Costa *et al.* 1988; Lawrence 1991; Beutel personal observation) and *Chaetosoma* (Crowson 1964: fig. 49).

12. *Cardo*: (0) shorter than stipes; (1) longer than stipes

A cardo distinctly shorter than the stipes is present in larvae of *Phycosecis* and most other groups of Coleoptera (Figs 3, 10). It is as long as or longer than the stipes in larvae

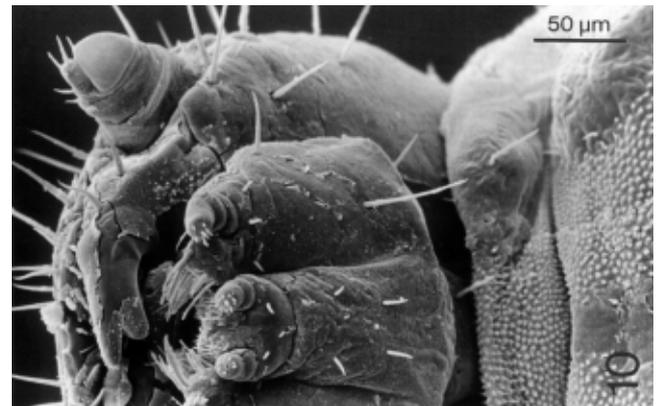


Fig. 10. *P. litoralis*, ventral view of head (SEM).

of Cleridae (Costa *et al.* 1988; Lawrence 1991; Beutel personal observation) and *Chaetosoma* (Crowson 1964: fig. 49).

13. *Maxillary apex*: (0) galea and lacinia separate; (1) mala

Galeae and laciniae are completely fused in larvae of *Elateroides*, *Melittomma* (Costa *et al.* 1988; Lymexylidae), Phycosecidae and other families of Cucujiformia (Costa *et al.* 1988; Lawrence 1991). An apically divided mala is present in some larvae of Lymexylidae (Wheeler 1991). The formation of a single mala has taken place several times independently in different lineages of Coleoptera (e.g. Myxophaga, Staphyliinoidea (in part); Beutel and Molenda 1997; Beutel *et al.* 1999).

14. *Pedunculate malar setae*: (0) absent; (1) present

A characteristic pedunculate seta is present on the mala of most larvae of Cleroidea (Fig. 3) but absent on larvae of Trogossitidae (in part, e.g. *Temnoscheila*).

15. *Origin of maxillary muscles*: (0) on posterior tentorial arm; (1) on posterior tentorial arm and ventral wall of hypopharynx

The origin of a more or less strongly developed part of M. tentoriostipitalis (M 18b) on the ventral side of the hypopharynx is an unusual condition so far only described in Lampyridae (Beutel 1995). It is also found in larvae of *Phycosecis* (Fig. 9), *Lemidia*, *Calitys* and *Collops* (Cleroidea), and also in all larvae of Cucujoidea examined. The presumed plesiomorphic condition occurs in larvae of Tenebrionoidea, Chrysomelidae and other groups of Coleoptera (Beutel 1993, 1995, 1996, 1999; Beutel and Molenda 1997). The attachment of M 18b to the hypopharynx allows a double function: levation of the maxillolabial complex and dilation of the prepharynx. This extrinsic maxillary muscle is an antagonist of M. clypeopalatalis (M 43).

16. *Tentorial bridge and posterior tentorial arm:* (0) connected, bridge in posterior position; (1) posterior arm and bridge separate; (2) bridge connected with posterior arm, shifted anteriorly

A tentorium with a posterior arm clearly separate from the tentorial bridge is found in larvae of Cleroidea (Fig. 5), Nitidulidae, Endomychidae and Coccinellidae. A similar tentorium has evolved independently within the series Elateriformia (Beutel 1995), probably in correlation with the formation of a maxillolabial complex. A tentorial bridge connected with the posterior arm but distinctly shifted anteriorly occurs in the tenebrionoid larvae examined.

17. *Anterior tentorial arm:* (0) well developed, connected with posterior tentorium; (1) strongly reduced, disconnected from posterior tentorium

The anterior tentorial arms are extremely thin and disconnected from the posterior tentorium or absent in the larvae of Cucujiformia examined. They are well developed in larvae of most other groups of Coleoptera (e.g. Adephaga, Myxopaga, Hydraenidae, Eucinetidae, Derodontidae; Beutel 1993, 1999; Beutel *et al.* 1999; Beutel and Molenda 1997).

18. *Prepharyngeal tube:* (0) absent; (1) present short; (2) present, elongated

A closed, elongated prepharyngeal tube with attachment of several bundles of *M. clypeopalatalis* (M 43) is present in larvae of *Phycosecis* (Figs 5, 9), *Lemidia*, *Calitys*, *Temnoscheila*, *Collops* and also *Glischrochilus*. It is also present but distinctly shorter in larvae of *Mycetina*, *Coccinella*, *Ericmodes* and *Silvanus*. Elongated prepharyngeal tubes seem to be correlated with liquid feeding and predacious habits. They are also found in larvae of Adephaga (in part, Beutel 1993), Helophoridae, Hydrophilidae, Histeridae (Beutel 1999), Elateroidea and Cantharoidea (Beutel 1995). An open cibarium (i.e. prepharyngeal tube absent) is found in most non-predacious groups of Coleoptera (e.g. Myxophaga (in part), Staphylinoidea (in part), Eucinetidae, Derodontidae, Sphindidae, Chrysomelidae; Beutel and Molenda 1997; Beutel *et al.* 1999).

19. *Position of cerebrum:* (0) within head capsule; (1) completely shifted into thorax; (2) partly shifted into prothorax, cerebrum strongly asymmetric

The cerebrum is completely shifted into the thorax in the larvae of *Phycosecis*, *Lemidia* and Trogossitidae examined (Figs 5, 6). This results in a strong elongation of the circumoesophageal connective. A posterior shift of the cerebrum is the result of miniaturisation in some taxa (e.g. Hydroscaphidae, Microsporidae; Beutel and Haas 1998). However, this is not the case in Cleroidea, in which the cerebrum is also completely dislocated in large larvae such as *Calitys*. This derived condition is apparently correlated with a strongly extended attachment area of the internal craniomandibular

muscle (M 11) and the absence of postcerebral pharyngeal dilators. It also occurs in other taxa with prognathous and predacious larvae, such as Helophoridae, Hydrophilidae, Histeridae, Elateridae and Cantharoidea (Beutel 1995, 1999). The cerebrum is strongly asymmetric and located in the posterior head region and the anterior prothorax in larvae of *Collops* and *Glischrochilus*. A similar condition is not described for other groups of Coleoptera.

20. *Tube-like glands:* (0) absent; (1) present

Tube-like glands, structurally resembling Malpighian tubules (Figs 5, 7–8), originate in the thorax or posterior head region in all cucujiform larvae examined. They are absent from larvae of other groups of Coleoptera (Beutel 1993, 1995, 1996; Beutel and Molenda 1997; Beutel *et al.* 1999).

#### Phylogenetic analysis

The branch and bound search yielded 28 trees of length 39, consistency index (CI) 0.816 and retention index (RI) 0.923. Tree 28 is shown in Fig. 11 and the 50% majority rule consensus tree in Fig. 12. Tree 28 was chosen as preferred tree as the trogossitid genera are sister-groups and *Phycosecis* the sister-group of *Collops*. A close relationship between Phycosecidae and Melyridae (and Acanthocnemidae) has already been suggested by Foster and Lawrence (1991).

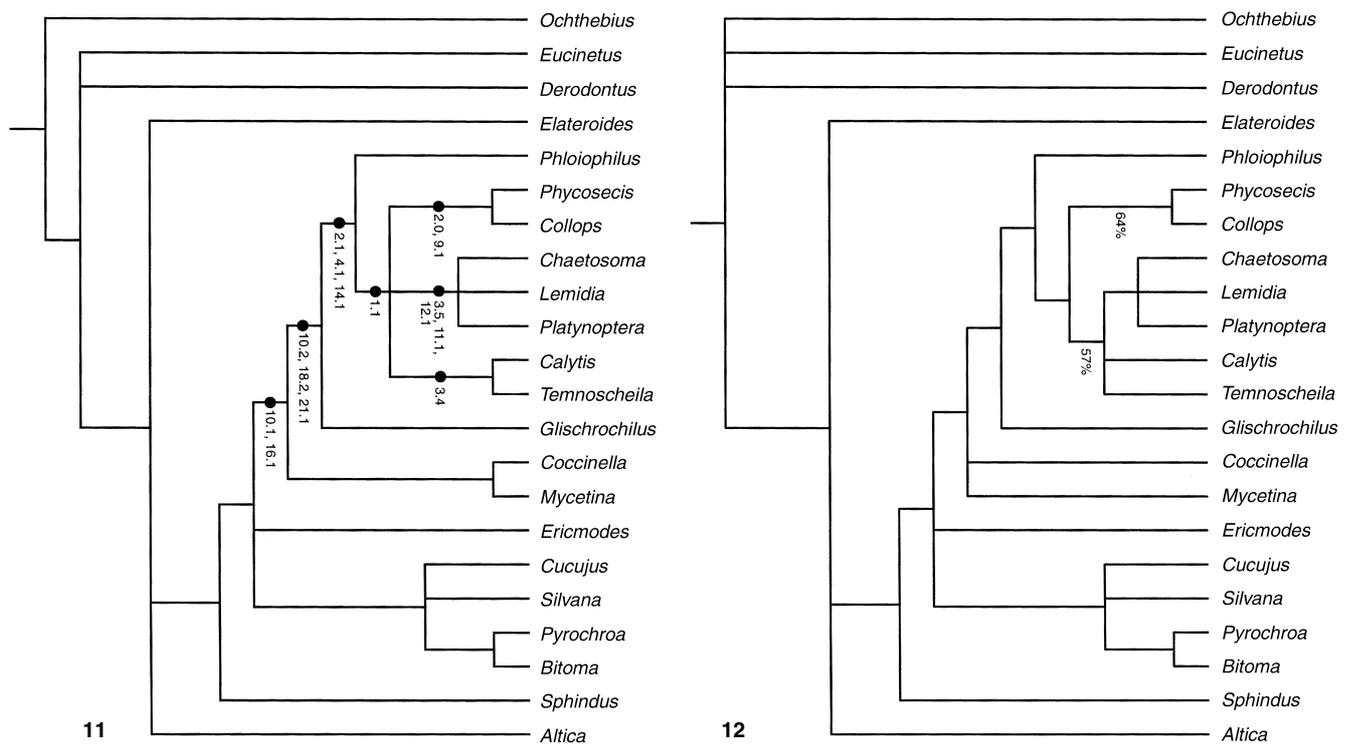
#### Discussion

The cladistic analysis is based on a limited set of 20 characters of the larval head and 22 taxa. The results should therefore be considered as preliminary.

The monophyly of the cleroid families examined seems to be well supported by several apomorphic features: presence of a median endocarina (2.1, unambiguous apomorphy, CI: 0.333), antennae directed anteriorly (4.1, unambiguous apomorphy, CI: 1.000), presence of a pedunculate seta on the mala (14.1, unambiguous apomorphy, CI: 0.500), origin of antennal muscles exclusively on the head capsule (7.1, accelerated transformation, CI: 1.000), presence of a weakly pigmented, parallel-sided gular plate (3.1, delayed transformation, CI: 1.000), and loss of the mandibular mola (8.1, delayed transformation, CI: 0.667).

The monophyly of Cleroidea excluding Phloiophilidae (e.g. tree 28; Fig. 11) is supported by the parallel-sided head (1.1, unambiguous apomorphy, CI: 1.000). Further possible apomorphies are the origin of the antennal muscles from the head capsule (7.1, accelerated transformation, CI: 1.000) and a cerebrum completely shifted into the prothorax (19.1, delayed transformation, CI: 0.667). However, these characters and the placement of Phloiophilidae remain uncertain as long as most internal features of the larvae of this family are unknown.

A sister-group relationship between Phycosecidae and Melyridae is supported in all trees (Fig. 12). Shared apomorphies are the plumose lacinia mobilis (9.1, unambiguous



**Figs 11–12.** Cladograms showing proposed interrelationships of cleroid families: *11*, tree 28 of 28 minimum length trees with 39 steps, unambiguous apomorphies mapped on tree; *12*, 50% majority-rule consensus tree.

apomorphy, *CI*: 1.000) and secondary loss of the median endocarina (2.0, unambiguous apomorphy, *CI*: 0.333). This implies that the asymmetrical condition of the cerebrum has evolved independently in *Collops* (Melyridae) and *Glischrochilus* (Nitidulidae).

A close relationship between Cleridae and Chaetosomatidae, as already suggested by Lawrence (1991), is also supported by all trees. These groups are characterised by a strongly elongated, sclerotised larval gula (3.5, unambiguous apomorphy, *CI*: 1.000), a strongly protracted position of the ventral mouthparts (11.1, unambiguous apomorphy, *CI*: 1.000), and a cardo as long as or longer than the stipes (12.1, unambiguous apomorphy, *CI*: 1.000).

The trogossitid genera under consideration group together in the preferred tree (tree 28). However, this is supported only by one doubtful apomorphy, the presence of a parallel-sided, moderately long and sclerotised gula (3.4, unambiguous apomorphy, *CI*: 1.000). It is highly plausible that the elongate gula as found in larvae of Chaetosomatidae and Cleridae is derived from a shorter trogossitid-like gula.

Larvae of Cleroidea and Nitidulidae (*Glischrochilus*) share two unambiguous apomorphies: a fully developed maxillolabial complex with completely restricted motility of the maxillae (10.2, *CI*: 1.000) and an elongated prepharyngeal tube (18.2, *CI*: 0.667).

A tentorial bridge completely separated from the remaining tentorium (16.1, unambiguous apomorphy, *CI*: 1.000) is

a possible synapomorphy of Cleroidea, Nitidulidae and the cucujoid families Coccinellidae and Endomychidae. A partly restricted motility of the maxillolabial complex is probably a derived groundplan character state of this lineage (10.1, accelerated transformation, *CI*: 1.000). A strong anterior component of the tentoriostipital muscle is attached to the floor of the prepharyngeal tube in larvae of these cleroid and cucujoid families, resulting in an improved prepharyngeal pumping apparatus. At least a small bundle of *M. tentoriostipitalis* has the same unusual attachment in all other cucujoid larvae examined so far (Sphindidae, Protocucujidae, Cucujidae), while this condition is not found in tenebrionoid or chrysomelid larvae. In the present analysis, the exclusive origin of the muscle from the tentorium in the larvae of *Bitoma* and *Pyrochroa* is interpreted as a reversal (15.0, *CI*: 0.500). However, this appears unlikely, as this presumed plesiomorphic origin is also found in larvae of *Orchesia* (Melandryidae) and *Tenebrio* (Tenebrionidae) (not included in the analysis).

Another phylogenetically relevant feature is the presence of elongated glands structurally resembling Malpighian tubules in all cucujiform larvae examined. This may be considered as a potential autapomorphy of Cucujiformia. The glands are simple tubes in the cleroid, cucujoid and tenebrionoid larvae examined, but distinctly extended and modified proximally in larvae of *Altica* and an undescribed lepturine cerambycid larva. This specialised condition is probably

derived from the presumed groundplan character state of Cucujiformia.

Our results support the monophyly of Cleroidea as defined by Lawrence (1991) and Lawrence and Newton (1995). The proposed interrelationships within the group are in agreement with those proposed by Lawrence and Newton (1982), except for the affinities of Lymexylidae.

It appears plausible that Cleroidea form a large monophylum together with some or all families of the non-monophyletic Cucujoidea. The last common ancestor of this lineage was largely characterised by plesiomorphic features of the immature stages (e.g. Protocucujidae, Sphindidae) and probably mycetophagous. Cleroidea have evolved as a distinctive clade with primarily predacious larval habits. Several derived features described above are characteristic for carnivorous beetle larvae (Beutel 1995, 1999): distinctly prognathous and more or less parallel-sided head, antennae directed anteriad, loss of mandibular mola, elongated prepharyngeal tube, and a strong extension of the cranial attachment area of the mandible adductor (M11) resulting in a posterior shift of the cerebrum. These features have probably evolved earlier in other lineages with predacious larvae, such as Adephegata, the staphylinine lineage of Staphylinidae, Hydrophiloidea (in part), Histeroidea and Cantharoidea. It is interesting that a fused labrum, which is characteristic of immatures of all these taxa, is not found in cleroid larvae. Carrion feeding is probably a secondary specialisation within Cleroidea, having evolved in Phycosecidae and some Melyridae. This may have resulted in the distinctly declined position of the head of *Phycosecis*, which should not be mistaken as a subprognathous condition. Larvae of other Cleroidea such as *Protopeltis* (Trogossitidae) and *Necrobia* (Cleridae) have obviously abandoned predacious habits (Lawrence 1991). Whether fungus feeding in larvae of Phloiophilidae is a primitive feature retained from cucujoid ancestors or a secondary condition is open to question. This may be revealed by a detailed study of these larvae.

### Acknowledgments

We are greatly indebted to Dr J. F. Lawrence (CSIRO) for the gift and loan of valuable specimens and for valuable comments on the manuscript, and to Dr R. A. B. Leschen (New Zealand Arthropod Collection) for the donation of valuable larval material. Comments made by Dr E. Arndt and by an anonymous reviewer are also gratefully acknowledged. The scanning electron micrograph was made with support of Dr W. Fischer (Institut für Allgemeine Botanik, FSU Jena). We also wish to thank Dr R. E. Roughley. Study of selected specimens was made possible by Natural Sciences and Engineering Research Council of Canada, operating grant No. A0428 held by R. E. R. (Dept. of Entomology, University of Manitoba). The study was also supported by the Deutsche Forschungsgemeinschaft (R. G. Beutel, grant No. BE 1789/1-2).

### References

- Beutel, R. G. (1993). Phylogenetic analysis of Adephegata (Coleoptera) based on characters of the larval head. *Systematic Entomology* **18**, 127–147.
- Beutel, R. G. (1995). Phylogenetic analysis of Elateriformia (Coleoptera: Polyphaga) based on larval characters. *Journal of Zoological Systematics and Evolutionary Research* **33**, 145–171.
- Beutel, R. G. (1996). Study of the larva of *Nosodendron fasciculare* (Olivier 1790) (Coleoptera: Nosodendridae) with implications to the phylogeny of Bostrichiformia. *Journal of Zoological Systematics and Evolutionary Research* **34**, 121–134.
- Beutel, R. G. (1999). Morphology and evolution of the larval head structures of Hydrophiloidea and Histeroidea (Coleoptera: Staphylinidae). *Tijdschrift voor Entomologie* **142**, 9–30.
- Beutel, R. G., and Haas, A. (1998). Larval head morphology of *Hydroscaapha natans* LeConte, 1874 (Coleoptera, Myxophaga, Hydroscaaphidae) with special reference to miniaturization. *Zoomorphology* **118**, 103–116.
- Beutel, R. G., and Molenda, R. (1997). Comparative morphological study of larvae of Staphylinidae (Coleoptera, Polyphaga) with phylogenetic implications. *Zoologischer Anzeiger* **236**, 37–67.
- Beutel, R. G., Maddison, D. R., and Haas, A. (1999). Phylogenetic analysis of Myxophaga (Coleoptera) using larval characters. *Systematic Entomology* **24**, 171–192.
- Böving, A. G., and Craighead, F. C. (1931). An illustrated synopsis of the principal larval forms of the order Coleoptera. *Entomologica Americana* **11**, 1–125.
- Champion, G. C. (1894). On the Tenebrionidae collected in Australia and Tasmania, by Mr. James J. Waler, R. N., F. L. S., during the voyage of H.M.S. "Penguin", with descriptions of new genera and species. *Transactions of the Entomological Society of London* **1894**, 351–408.
- Costa, C., Vanin, S. A., and Casari-Chen, S. A. (1988). 'Larvas de Coleoptera do Brasil.' (Universidade de Sao Paulo, Museo de Zoologia: Sao Paulo.)
- Crowson, R. A. (1952). The classification of the families of British Coleoptera [continued]. *Entomologist's Monthly Magazine* **88**, 64–72, 109–132.
- Crowson, R. A. (1960). The phylogeny of Coleoptera. *Annual Review of Entomology* **5**, 111–134.
- Crowson, R. A. (1964). A review of the classification of Cleroidea (Coleoptera), with descriptions of two new genera of Peltidae and of several new larval types. *Transactions of the Royal Entomological Society of London* **116** (12), 275–327.
- Crowson, R. A. (1970). Further observations on Cleroidea (Coleoptera). *Proceedings of the Royal Entomological Society of London (B)* **39**, 1–20.
- Foster, D. E., and Lawrence, J. F. (1991). Trogossitidae (Cleroidea) (=Trogossitidae; including Lophoceratidae, Ostomidae, Peltidae, Temnochilidae). In 'Immature Insects, Vol. 2'. (Ed. F. W. Stehr.) pp. 448–450. (Kendall/Hunt Publishing Company: Dubuque, Iowa.)
- Lawrence, J. F. (1991). Phloiophilidae (Cleroidea). Chaetosomatidae (Cleroidea), Cleridae (Cleroidea) (including Corynetidae, Korynetidae). Phycosecidae (Cleroidea). Anathocnemidae (Cleroidea). Melyridae (Cleroidea) (including Dasytidae, Malachiidae, Prionoceridae, Rhadalidae). Protocucujidae (Cucujoidea). Sphindidae (Cucujoidea). Nitidulidae (Cucujoidea) (including Brachypteridae, Cateretidae, Cybocephalidae, Smicripidae). Rhizophagidae (Cucujoidea) (including Monotomidae). Bogamiidae (Cucujoidea). Phloeostichidae (Cucujoidea). Helotidae (Cucujoidea). Cucujidae (Cucujoidea) (including Catogenidae, Laemophloeidae, Passandridae, Silvanidae). Propalticidae (Cucujoidea). Phalacridae (Cucujoidea). Hobartiidae (Cucujoidea). Cavognathidae (Cucujoidea). Cryptophagidae (Cucujoidea) (including Capotochrotidae, Hypocopridae).

- Lamingtoniidae (Cucujoidea). Languriidae (Cucujoidea) (including Cryptophilidae). Erotylidae (Cucujoidea) (including Dacniidae). Biphyllidae (Cucujoidea). Byturidae (Cucujoidea). Bothrideridae (Cucujoidea). Sphaerosomatidae (Cucujoidea). Cerylonidae (Cucujoidea) (= Cerylidae; including Agulagnathidae, Anommatidae, Dolosidae, Euxestidae, Murmiridae). Discolomidae (Cucujoidea) (= Notiophygidae). Endomychidae (Cucujoidea) (including Merophysiidae, Mycetaeidae). Lathridiidae (Cucujoidea). In 'Immature Insects, Vol. 2'. (Ed. F. W. Stehr.) pp. 446–448, 450–485, 497–498. (Kendall/Hunt Publishing Company: Dubuque, Iowa.)
- Lawrence, J. F., and Britton, E. B. (1994). 'Australian Beetles'. (Melbourne University Press: Melbourne.)
- Lawrence, J. F., and Newton, A. F. Jr. (1982). Evolution and classification of beetles. *Annual Review of Ecology and Systematics* **13**, 261–290.
- Lawrence, J. F., and Newton, A. F. Jr. (1995). Families and subfamilies of Coleoptera (with selected genera, notes, references and data on family-group names). In 'Biology, Phylogeny, and Classification of Coleoptera: Papers Celebrating the 80th Birthday of Roy A. Crowson'. (Eds J. Pakaluk and S. A. Slipinski.) pp. 779–1006. (Muzeum i Instytut Zoologii PAN: Warszawa.)
- Lea, A. M. (1899). Descriptions of new species of Australian Coleoptera. Part V. *Proceedings of the Linnean Society of New South Wales* **23**, 521–645.
- Lea, A. M. (1921). On Coleoptera. *Memoirs of the Queensland Museum* **7**, 182–240.
- Leschen, R. A. B. (1996). Phylogeny and revision of the genera of Cryptophagidae (Coleoptera: Cucujoidea). *University of Kansas Science Bulletin* **55** (15), 549–634.
- Maddison, W. P., and Maddison, D. R. (1992). 'MacClade, version 3: Analysis of phylogeny and character evolution'. (Sinauer: Sunderland, Massachusetts.)
- Nixon, K. C., and Carpenter, J. M. (1993). On outgroups. *Cladistics* **9**, 413–426.
- Pascoe, F. P. (1875). Descriptions of new genera and species of New Zealand Coleoptera. *Annual Magazine of Natural History* (4) **16**, 210–223.
- Swofford, D. L. (1991). PAUP: Phylogenetic analysis using parsimony, version 3.1. (Computer program distributed by the Illinois Natural History Survey: Champaign, Illinois.)
- von Kéler, S. (1963). 'Entomologisches Wörterbuch'. (Akademie Verlag: Berlin)
- Wheeler, Q. (1991). Lymexyloidea (Lymexyloidea). In 'Immature Insects, Vol. 2' (Ed. F. W. Stehr.) pp. 446–447. (Kendall/Hunt Publishing Company: Dubuque, Iowa.)

Manuscript received 31 May 2000; revised and accepted 20 July 2000.