Comparative morphology of sclerites used by Camptosomatan leaf beetles for formation of the extrachorion (Chrysomelidae: Cryptocephalinae, Lamprosomatinae)

SCHÖLLER, M.
2. Morphology and Anatomy

Comparative morphology of sclerites used by Camptosomatan leaf beetles for formation of the extrachorion (Chrysomelidae: Cryptocephalinae, Lamprosomatinae)

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Abstract. All Camptosomata, i.e. the chrysomelid subfamilies Lamprosomatinae and Cryptocephalinae with its three tribes Clytrini, Cryptocephalini and Chlamisini (formerly ranked as subfamilies), provide their eggs with a case. The anatomical structures for doing so are sclerites embedded in chitinous pads on the female rectum, the whole structure is called rectal apparatus or kotpresse. The kotpresse of 86 species representing all tribes and subtribes of Camptosomata were studied and illustrated, including all subgenera of Cryptocephalus. Based on the similarity of the pattern of rectal sclerites, several groups were recognised. The group Clytrini + Acolastus + Mylassa is characterised by two ventral and three dorsal sclerites, one being a central dorsal plate. Most species of Cryptocephalus studied and Melixanthus bear one ventral and two dorsal sclerites, as well as Coenobius + Isnus + Aprionota with additionally strongly developed branches of the dorsal sclerites. Madacryptus and Stylosomus bear two ventral and two dorsal sclerites. Another pattern can be found in the species-rich group Cadmus + Melatia + Aporocera + Chlamisini + Lamprosomatinae. A large ventral chitinpolster with or without two ventral sclerites is present, and a large dorsal chitinpolster with or without two dorsal sclerites. Unique patterns differing from the before mentioned were detected in Achaenops and Mecostethus, respectively. Sclerotised rectal plates were found for the first time in Lamprosomatinae.

Keywords. Clytrini, Chlamisini, oviposition, rectal apparatus, kotpresse

1. Introduction

A common feature of all Camptosomata, i.e. the chrysomelid subfamilies Lamprosomatinae and Cryptocephalinae with its three tribes Clytrini, Cryptocephalini
and Chlamisini (formerly ranked as subfamilies, see Seeno & Wilcox, 1982), is a peculiarity in their reproduction and development. The females cover their eggs with a case made by faeces and secretes. This case is subsequently worn as a protective case by the larvae and is enlarged as they grow. For this reason, the Camptosomata are called ‘case bearers’ (Erber 1988). Although all Camptosomata provide their eggs with a case, the anatomical structures for doing so are not the same in all species. Sclerites embedded in chitinous pads, the so-called chitinpolster, are present on the female rectum, the whole structure is called rectal apparatus or kotpresse. The rectum is differentiated into dorsal and ventral halves which differ in sclerotisation on the external surface, and it is bearing sensilla and rows of minute teeth on the inner surface (Erber 1968). Large muscles are attached to the sclerites which allow to change the shape of the rectal lumen. In consequence, the shape of the faecal plates covering the eggs is partly depending on the pattern and shape of these rectal sclerites. The rectal apparatus is developing during pupation. A detailed anatomical study of the rectal apparatus of *Clytra quadripunctata* and *Cryptocephalus trimaculatus* was provided by Erber (1968), as well as some additional information on other Central European species. De Monte (1957) suggested the existence of several kotpresse ‘types’, representing the four main taxa of Camptosomata. This hypothesis was based on the study of a few species only. Schmitt (1996), reviewing studies on the phylogeny of Chrysomelidae, pointed out the value of the presence or absence of a rectal apparatus for the higher classification of Chrysomelidae. Beside the Camptosomata group, a rectal apparatus can also be found in certain Eumolpinae (including Synetinae). If the kotpresse found in these groups is homologous, it is likely that they are a monophyletic taxon. However, more research is needed to decide this question (Schmitt 1996).

Even though the rectal apparatus is of interest both for studies on reproduction of Camptosomata as well as phylogenetic studies on Camptosomata and Chrysomelidae in general, its variability was never evaluated for the group as a whole. In this study, the kotpresse of 86 species representing all tribes and subtribes of Camptosomata is described and illustrated.

2. Materials and methods

Dissections were made from dried specimens after separating the abdomen in water, soaking this in cold dilute KOH for 3 hours and then washing in water. If possible, at least three specimens of each species were studied, however, many species considered here are very rare in insect collections. In cases where larger series were studied (e.g. *Clytra laeviuscula*, *Pachybrachis hieroglyphicus*, *Cryptocephalus sericeus*) the shape and arrangement of the rectal sclerites was consistent. All figures presented are drawings of the author except for those taken from Reid (1991, 1994, 1995, 1998, 1999) as indicated in the results section. The nomenclature used here for the kotpresse structures was devised by Erber (1968) and Erber & Schöller (2006).
Abbreviations

**ADS** apodemes of dorsal sclerites  
**AVS** apodeme of ventral sclerite  
**BPD** basal part of dorsal sclerite  
**DCA** dorsal chitininous area  
**DCP** dorsal central plate  
**DFI** dorsal field of the intestine  
**DS** dorsal sclerite  
**DSA** dorsal sclerotised area  
**DSL** dorsal sclerotisation of the lateral fold  
**VBD** ventrally bend part of dorsal sclerite  
**VS** ventral sclerite  
**VSA** ventral sclerotised area  
**VSL** ventral sclerotisation of the lateral fold.

If not otherwise indicated, the specimens are deposited in Matthias Schöller personal collection, Berlin. Letter codens for other collections:

**ANIC** Australian National Insect Collection, Canberra, Australia  
**DEI** Deutsches Entomologisches Institut, Müncheberg, Germany, L. Zerche  
**MLUH** Martin-Luther-Universität Halle/Saale, Wissenschaftsbereich Zoologie, K. Schneider  
**MNHB** Museum für Naturkunde der Humboldt-Universität, Berlin, Germany, J. Frisch and M. Uhlig  
**MRAC** Musée Royal de l’Afrique Centrale Tervuren, Dr. Marc De Meyer  
**NHMB** Naturhistorisches Museum Basel, Switzerland, M. Brancucci and E. Sprecher  
**NMW** Naturhistorisches Museum Wien, Austria, H. Schönmann und H. Schillhammer  
**SMTD** Staatliches Museum für Tierkunde in Dresden, Germany, K. Klass  
**TMSA** Transvaal Museum, Pretoria, Republic South Africa, Ruth Müller.

3. Results

For every taxon, the name is followed by the labelling of the specimen studied and the description of the rectal apparatus. In some cases a note is given e.g. on the systematic placement or external morphological characters. The list follows generally Seeno & Wilcox (1982), but more recently published results on the systematics of Camptosomata (Reid 1991, 1994, 1995, 1998, 1999, Schöller 2000, 2005, 2007) were considered, too.
**Cryptocephalinae Gyllenhal 1813: 582**

**Clytrini Blanchard 1846**

**Clytrina Blanchard 1846**

*Macrolenes dentipes* (Olivier, 1808)
Tunisia, Le Kef, 28.5.1995, Nerger, det. D. Erber
Three dorsal and two ventral sclerites; dorsal apodemes wide, wider than rectum, only base pigmented, inbetween dcp present, dcp transverse, chitinpolster present (Fig. 1); vs at base straight, wider than avs, the latter wider than rectum, apodemes not pigmented, between vs chitinpolster present (Fig. 2).

*Tituboea sexmaculata* (Fabricius, 1781)
Marocco, Ameskroud. 28.1v.1995, leg. Jiri Kadlec
Three dorsal and two ventral sclerites; dorsal apodemes narrow, wider than rectum, inbetween dcp present, dcp apically arcuate and basally with a pair of acute tips, chitinpolster present (Fig. 3); vs at base slightly rounded, a little wider than avs, the latter wider than rectum, between vs chitinpolster present (Fig. 4).

*Barybaena lurida* Lacordaire, 1848
South Africa, Cape Province, Hogsback, 10.-11.12.1956, leg. V. Son&Martin
Three dorsal and two ventral sclerites; dorsal apodemes narrow, wider than rectum, inbetween dcp present, basally deeply incised, chitinpolster present (Fig. 5); vs at base straight, shorter than avs, the latter wider than rectum, between vs chitinpolster present (Fig. 6).

*Barybaena oneili* (Jacoby, 1904)
South Africa, Cape Province, 3 km nw Bonnievale, 1.x.1984, leg. W. Wittmer
Four dorsal and two ventral sclerites; dorsal apodemes wide, triangular, wider than rectum, inbetween a pair of longitudinal ds present, chitinpolster present (Fig. 7); vs at base straight, as wide as avs, the latter wider than rectum, between vs chitinpolster present (Fig. 8).

*Clytra laeviuscula* (Ratzeburg, 1837)
Deutschland, Hessen, Frankfurt a., Sindlingen, 23.vi.1991, auf Salix sp., leg. M. Schöller
Three dorsal and two ventral sclerites; dorsal apodemes large, slightly wider than rectum, inbetween dcp present, dcp apically incised and basally with a pair of acute tips, chitinpolster present (Fig. 9); vs at base straight, wider than avs, the latter wider than rectum, between vs chitinpolster present (Fig. 10).

*Clytrasoma palliatum* (Fabricius, 1801)
Figures 1–12. Kotpresse, dorsal (left), ventral (right): 1, 2: *Macrolenes dentipes*; 3, 4: *Tituboa sexmaculata*; 5, 6: *Barybaena lurida*; 7, 8: *Barybaena oneili*; 9, 10: *Clytra laeviuscula*; 11, 12: *Clytr soma palliatum*. 
Three dorsal and two ventral sclerites; dorsal apodemes narrow, not wider than rectum, inbetween DCP present, DCP apically with a pair of incisions and basally with a pair of acute tips, chitinpolster present (Fig. 11); vs at base rounded, as wide as AVS, the latter wider than rectum, between vs chitinpolster present (Fig. 12).

Coptocephala unicolor (Lucas, 1845)
Italy, Sicily, Messina, Mandanici, 04.06.2006
Three dorsal and two ventral sclerites; dorsal apodemes narrow, slightly wider than rectum, inbetween DCP present, DCP narrow, weakly sclerotised, chitinpolster present (Fig. 13); VS at base rounded, wider than AVS, the latter wider than rectum, between VS chitinpolster present (Fig. 14).
Note: this is a representative of the metallic species

Megalostomina Clavareau, 1913

Megalostomis grossa Foersb., 1921
Three dorsal and two ventral sclerites; dorsal apodemes narrow, arcuate, not wider than rectum, inbetween DCP present, DCP rectangular, basally arcuate, chitinpolster present (Fig. 15); VS at base rounded, wider than AVS, the latter wider than rectum, around VS chitinpolster present (Fig. 16).

Babiina Clavareau, 1913

Stereoma angularis Lacordaire, 1848
Three dorsal and two ventral sclerites; dorsal apodemes large, wider than rectum, only basally pigmented, inbetween transverse DCP present, DCP basally strongly arcuate, chitinpolster present (Fig. 17); VS at base slightly rounded, shorter than AVS, the latter wider than rectum, margin of VS not pigmented, around VS chitinpolster present (Fig. 18).

Arateina Moldenke, 1981

Aratea costata Lacordaire, 1848
MNHB: Paraguay, Itapua Vega, xii.1954
Three dorsal and two ventral sclerites; dorsal apodemes large, wider than rectum, inbetween transverse rectangular DCP present, chitinpolster present (Fig. 19); VS at base sinuate, shorter than AVS, the latter wider than rectum, between VS chitinpolster present (Fig. 20).
Figures 13–24. Kotpresse, dorsal (left), ventral (right); 13, 14: Coptocephala unicolor; 15, 16: Megalostomis grossa; 17, 18: Stereoma angularis; 19, 20: Aratea costata; 21, 22: Ischiopachys cuprea; 23, 24: Diapericera freudei.
Ischiopachina Clavareau, 1913

*Ischiopachys cuprea* (Fabricius, 1893)  
Venezuela, Maripa, 1.-7.viii. 1992, leg. Hornburg  
Three dorsal and two ventral sclerites; dorsal apodemes large, wider than rectum, only basally pigmented, inbetween transverse DCP present, DCP apically and basally slightly arcuate, chitinpolster present (Fig. 21); VS at base sinuate, shorter than AVS, the latter wider than rectum, margin of AVS not pigmented, around VS chitinpolster present, basally slightly pigmented (Fig. 22).

Eocytrina Monró, 1958

*Diapericera freudei* (Monró, 1958)  
mnhb: Namibia, 80 km SW Rundu Grootfontein-Rundu (18°24’15”S/19°17’41”E), 22.IV.2001, leg. M. Uhlig  
Two dorsal and two ventral sclerites; DS almost reduced to apodemes, long, slightly wider than rectum, DFI with a pair of longitudinal pigmented striae (Fig. 23); VS at base straight, very large, AVS narrow, wider than rectum (Fig. 24).

Cryptocephalini Gyllenhal, 1813  
Pachybrachina Clavareau, 1913

*Acolastus nigrolineatus* (Bryant, 1944)  
Three dorsal and two ventral sclerites; dorsal apodemes narrow, not wider than rectum, inbetween transverse DCP present, basally sinuate in the middle (Fig. 25); VS at base straight, as long as AVS, the latter wider than rectum (Fig. 26).

*Acolastus nama* Schöller, 2006  
Three dorsal and two ventral sclerites; dorsal apodemes narrow, not wider than rectum, inbetween DCP present, apically with a pair of acute tips and apical edges expanded, DSL present (Fig. 27); VS at base rounded, longer than AVS, the latter wider than rectum, pigmented link inbetween VS present, VSL present (Fig. 28).

*Acolastus zurstrasseni* Schöller, 2006  
Three dorsal and two ventral sclerites; dorsal apodemes narrow, not wider than rectum, inbetween DCP present, apically with a pair of arcuate incisions, apical and lateral a pair of pigmented areas, DSL present (Fig. 29); VS at base straight, longer...
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Figures 25–42. Kotpresse, dorsal (left), ventral (right); 25, 26: Acolastus nigrolineatus; 27, 28: Acolastus nama; 29, 30: Acolastus zurstrasseni; 31, 32: Acolastus fausti; 33, 34, 35 (lateral): Acolastus batangensis; 36, 37: Mylassa pectinicornis; 38, 39, 40 (lateral): Pachybrachis hieroglyphicus; 41, 42: Pachybrachis steinhauseni.
than AVS, the latter wider than rectum, pigmented link inbetween VS present, VSL present (Fig. 30).

**Acolastus fausti** (Weise, 1882)
Iran, Elburz Mts., Tehran Prov., 1300 m, Semnan, 22.v.2005, Major leg.
Three dorsal and two ventral sclerites; dorsal apodemes narrow, not wider than rectum, inbetween trapeziform DCP present, DSL present (Fig. 31); VS at base rounded, longer than AVS, the latter wider than rectum, VS present, VSL present (Fig. 32).

**Acolastus batangensis** (Tan, 1992)
China, Yunnan, Daju, 50 km N of Lijiang, 27.-28.v.1992
Three dorsal and two ventral sclerites; dorsal apodemes narrow, not wider than rectum, inbetween quadrate DCP present, DSL present (Fig. 33); VS at base rounded, longer than AVS, the latter wider than rectum (Fig. 34), pigmented link inbetween VS present, VSL present (Fig. 35).

**Mylissa pectinicornis** (Suffrian, 1866)
Chile, Region 1x, South of Melipeuco, 23.1.2004, leg. M. Snizek
One dorsal and two ventral sclerites; dorsal apodemes, DCP present, rectangular, transverse, narrow, not reaching lateral fold, lateral fold widened and bend upwards, especially opposite DCP, to but only weakly sclerotised (Fig. 36); VS at base slightly rounded, wider than AVS, the latter wider than rectum, between VS chitinpolster present, VSL present (Fig. 37).

Note: *Mylissa* was transferred to *Pachybrachina* by Jacobson (1921), but this was not considered by Seeno & Wilcox (1982).

**Pachybrachis hieroglyphicus** (Laicharting, 1781)
Two dorsal and one ventral sclerites; DS short and narrow, linked across dorsal fold by a transparent extension as in *Acolastus nigrolineatus* and *Metallactus mosei*, apodemes large and bend upwards, not wider than rectum, DSL present (Fig. 38); VS is a crosswise band ending in AVS, which are wider than the rectum and bend downwards (Fig. 39, VS not pigmented in the middle, VSL present (Fig. 40).

Note: The same pattern as in *P. hieroglyphicus* has been found in *P. azureus* Suffrian, 1848 (not figured), representative of the subgenus *Chloropachys* Rey, 1883.

**Pachybrachis steinhauseni** Schöller, 2005
MNH: Kolumbien, Umg. Cali, 1000 m, Valle de Cauca, 8.8.54, leg. Steinhausen
Two dorsal and one ventral sclerites; DS short and narrow, apodemes large and bend upwards, not wider than rectum, DSL present (Fig. 41); VS is a crosswise band ending in AVS, which are wider than the rectum and bend downwards, VSL present (Fig. 42).
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Metallactus mosei Schöller, 2003
Brazil, Sao Paulo, Boa Esperanca do Sul
One dorsal and one ventral sclerite; ds is a crosswise band ending in ads, which are apically hyaline, and bend upwards, not wider than rectum, dsl present, dca present which is fused across dfi (Fig. 43); vs is a crosswise band ending in avs, which are wider than the rectum and bend upwards (Fig. 44), vs not pigmented in 1/3 of its length, vsl present (Fig. 45).

Ambrotodes elegans (Blanchard, 1851)
Chile, Region viiI, Los Angeles, vecindad El Rincon, 18.x1.2004, leg. K. Renner
Two dorsal and one ventral sclerites; ds short and narrow, apodemes small and bend upwards, not wider than rectum (Fig. 46); vs is a large crosswise band, apically arcuate ending in avs, which are large, wider than the rectum and oriented horizontally (Fig. 47).

Stylosomina Clavareau, 1913
Stylosomus ilicicola Suffrian, 1848
Portugal, Algarve, Amarcao de Pera, 3km E, 50m NN, 10.iv.2004, Fritzlar leg.
Two dorsal and two ventral sclerites; ds nearly reduced to apodemes, apodemes large, wider than the rectum (Fig. 48); vs at base rounded, much wider than avs, the latter are wider than rectum, vsl present (Fig. 49).

Achaenopina Clavareau, 1913
Achaenops dorsalis Suffrian, 1857
South Africa, East Cape, Tsitsikamma nat. park, Storm river mouth, 34°01′S, 23°52′E, 5-11-1999, R. Constantin
Two dorsal and one ventral sclerite; ds large, length about 2 times width, not attached to the broad sclerotisation of the lateral fold (Fig. 50); vs is a large crosswise band, apically with a triangular incision, ending in avs, which are large, wider than the rectum and bend downwards (Fig. 51), above middle of posterior margin of vs chitin polster present, posterior of the ventral band a weakly sclerotised rectangular area present, vsl present (Fig. 52).

Achaenops monstrosus Schöller, 2005
NHMB: Sud Afrika Cape Prov. W. Wittmer, Algeria Cederberg 520/1200m 10.x.1990
Two dorsal and one ventral sclerites; dorsal sclerites slender, with an extension directed towards the dorsal fold, posterior of the dorsal sclerite, a rectangular bent twig of the broad sclerotisation of the lateral fold directed towards the dorsal fold, dorsal fold slightly sclerotised (Fig. 53); vs is a large crosswise band, posterior of which two sclerotised patches are present, and another two sclerotised areas
attached to the anterior and posterior margins of the ventral band, respectively, around vs chitinpolster present, vsl present (Fig. 54).  
Note: This species was described recently again in Clytrini as *Luisia paradoxa* Medvedev & Regalin, 2006.

**Monachulina Cheng, 1913**

*Lexiphanes* sp.  
Paraguay, Kanindeyu: Curuguaty, 17.x.1991, U. Drechsel  
Two dorsal and one ventral sclerites; ds pigmented only at external margin, bend up and folded towards anus, rectally of ds pigmentation of dfi, dsl present (Fig. 55); vs is a crosswise band, ending in large avs, which are wider than the rectum, vs weakly pigmented, vsl present (Fig. 56).

*Adiscus pectoralis* (Pic, 1926)  
China, Yunnan  
Two dorsal and two ventral sclerites; ds sinuate, vbd present, small, apodemes not wider than rectum, rectally of ds pigmentation of dfi, dsl present (Fig. 57); vs at base straight, much wider than avs, the latter are wider than rectum, between vs chitinpolster present; vsl present (Fig. 58).

*Scaphodius striaticollis* (Montrouzier, 1861)  
Nouvelle Caledonie, Noumea, Mont-Dore, 90 m, 11.11.2006, M. Daccordi leg.  
Two dorsal and one ventral sclerites; ds straight, vbd absent, apodemes slightly wider than the rectum, dsl present (Fig. 59); vs is a crosswise band, ending in avs, which are large and wider than the rectum (Fig. 60).

*Ditropidus* sp.  
Two dorsal and one ventral sclerites; ds large, terminating in an acute tip, attaching the pigmented lateral fold, chitin-polster large (Fig. 61); vs is a crosswise band, ending in small avs, which are not wider than the rectum, chitin-polster large, lateral fold broad and bend up (Fig. 62).

*Ditropidus vulpinus* Suffrian, 1859  
Two dorsal and one ventral sclerites; ds large, not attaching lateral fold, chitin-polster large, dsl present (Fig. 63); vs is a crosswise band, ending in small avs, which are not wider than the rectum (Fig. 64).  
Note: this species was described in the genus *Elaphodes*.  

Ditropidella binotata (Lea, 1920)
Two dorsal and one ventral sclerites; DS bend towards colon, VBD absent, apodemes small, VSL present (Fig. 65); VS is a crosswise band, ending in AVS, which are wider than the rectum (Fig. 66) (from Reid, 1998).

Aprionota brandti (Gressitt, 1965)
Irian Jaya, Jayawijaya, Okloma, 30.9.-1.10.1993, 1650-1800m, leg. A. Riedel
Two dorsal and one ventral sclerites; DS straight, narrowing towards apex, apodemes much wider than rectum, bend towards anus, DSA present, long, narrow and directed towards DFI, between DS and DSA chitinous pad, pigmented area basally of DS present, DSI present (Fig. 67); VS is a crosswise band, ending in large AVS, which are wider than the rectum, VSA present, large and apically arcuate, less pigmented but horizontally wrinkled, VSL present (Fig. 68).
Note: This species was described in the genus Coenobius.

Isnus sp.
Indonesia, C. Sulawesi, Kab. Dongala, Toro, 1°30’S, 120°02’E, alt. 750-1000m, fogging, leg. M. Bos, cacao plantation, planted Fabac., shade, off T. cacao, 18.iv.2005
Two dorsal and one ventral sclerites; DS straight, apodemes slightly wider than rectum, bend up, DSA present, broad, narrowing apically and directed towards DFI, between DS and DSA chitinous pad, pigmented area basally of DS present, DSI present (Fig. 69); VS is a crosswise band, ending in AVS, which are wider than the rectum, VSA present, large and apically arcuate, one chitinous pad attached basally of VS and one trapeziform pad rectally of VSA (Fig. 72), between this pad and lateral fold an arcuate pigmentation present, VSI present (Fig. 73).
Note: The same pattern was detected in the Afrotropical species Isnus niger Weise.

Coenobius triangulum Suffrian, 1857
Two dorsal and one ventral sclerites; DS straight, narrowing towards apex, apodemes wider than rectum, bend up, DSA present, long, narrow and directed towards DFI, between DS and DSA chitinous pad, DSI present (Fig. 71); VS is a crosswise band, ending in AVS, which are wider than the rectum, VSA present, large and apically arcuate, one chitinous pad attached basally of VS and one trapeziform pad rectally of VSA (Fig. 72), between this pad and lateral fold an arcuate pigmentation present, VSI present (Fig. 73).
Note: This is the generic type species of Coenobius.

Coenobius discoideus Schöller, 1999
Congo Belge: Ruanda, Lac Ngando (Volc. Karisimbi) 2400 m. 9-iii-1935 G.F. de Witte
Two dorsal and one ventral sclerites; DS straight, narrowing towards apex and directed towards DFI, apodemes not wider than rectum, VBD present, DSA present, long, widening towards apex and directed towards DFI, inner margin weaker pigmented, DSI present (Fig. 74); VS is a crosswise band, ending in AVS, which are
Figures 67–81. Kotpresse, dorsal (left), ventral (right); 67, 68: Aprionota brandti; 69, 70: Isnus sp.; 71, 72, 73 (lateral): Coenobius triangulum; 74, 75: Coenobius discoideus; 76, 77: Coenobius burgeoni; 78, 79: Cryptocephalus (Cryptocephalus) decemmaculatus; 80, 81: Cryptocephalus (Cryptocephalus) ajeschae.
wider than the rectum, vsA present, weakly pigmented, large and rectangular, vsL present (Fig. 75).

**Coenobius burgeoni** Pic, 1930  
**MRAC:** Haut-Uélé: Moto -1923, L. Burgeon  
Two dorsal and one ventral sclerites; ds straight, narrowing towards apex, apodemis wider than rectum, bend up, vBD present, dSA present, long, narrow and directed towards dfI, dsI present (Fig. 76); vs is a crosswise band, ending in avS, which are wider than the rectum, vsA present, very large and subquadrate, vsL present (Fig. 77).

**Cryptocephalinida Gyllenhal, 1813**

**Cryptocephalus** (**Cryptocephalus**) *decemmaculatus* (Linnaeus, 1758)  
**SMTD:** Germany, Saxonia  
Two dorsal and one ventral sclerites; ds transverse, vBD present (Fig. 78); vs is a crosswise band ending in avS, which are wider than the rectum; vsA present, wide, half width of vs (Fig. 79).  
Note: this is the generic type species of *Cryptocephalus*.

**Cryptocephalus** (**Cryptocephalus**) *ajescae* Schöller, 2006  
Two dorsal and one ventral sclerites; ds sinuose, vBD present, vs is a crosswise band, less pigmented at middle, ending in avS, which are wider than the rectum (Fig. 80); vsA present, short, less than half width of vs (Fig. 81).

**Cryptocephalus** (**Cryptocephalus**) *colmanti* Pic, 1929  
**MRAC:** Congo  
Two dorsal and one ventral sclerites; ds sinuose, vBD present, vs is a crosswise band, ending in avS, which are wider than the rectum (Fig. 82); vsA present, but weakly pigmented, long, half width of vs (Fig. 83).

**Cryptocephalus** (**Chrysocryptocephalus**) *sericeus* (Linnaeus, 1758)  
Deutschland, Brandenburg, Uckermark, Eichhof bei Lychen, 14.VII.2006, leg. M. Schöller  
Two dorsal and one ventral sclerites; ds transverse, narrowed toward apex, vBD present (Fig. 84); vs is a crosswise band ending in avS, which are little wider than the rectum; vsA present, small, one third width of vs (Fig. 85).

**Cryptocephalus** (**Anteriscus**) *reinecki* Weise, 1904  
**MNHB:** R.S. Africa, 28.i.1994, 27°30’S 31°20’E, Natal: Itala Game Reserve, leg. F. Koch
Figures 82–95. Kotpresse, dorsal (left), ventral (right); 82, 83: *Cryptocephalus* (*Cryptocephalus*) *colmanti*; 84, 85: *Cryptocephalus* (*Cryptocephalus*) *sericeus*; 86, 87: *Cryptocephalus* (*Anteriscus*) *reinecki*; 88, 89: *Cryptocephalus* (*Asionus*) *reitteri*; 90, 91: *Cryptocephalus* (*Bertiellus*) *lopatini*; 92, 93: *Cryptocephalus* (*Burlinius*) *nitzidicollis*; 94, 95: *Cryptocephalus* (*Burlinius*) *nubigena*. 
Two dorsal and one ventral sclerites; DS transverse, VBD present, a pair of strongly pigmented patches within the DCA present (Fig. 86); VS is a crosswise band ending in AVS, which are wider than the rectum; VSA present, short (Fig. 87).

Note: Anteriscus was described as a subgenus of Cryptocephalus by Weise, but most authors subsequently treated it as a proper genus or a subgenus of Melixanthus.

Cryptoleptus (Asionus) retteri Weise, 1882
Croatia, 30 km SE Knin, 43°51’N 16°29’E, 25.5.2005, 450 m, leg. M. Z. Halada
Two dorsal and one ventral sclerites; DS transverse, DSA present, short, at one level with DS (Fig. 88); VBD absent, but lateral fold strongly pigmented ventrally, DFI with a pair of longitudinal sclerotisations; VS is a crosswise band ending in AVS, which are wider than the rectum; VSA absent (Fig. 89).

Cryptoleptus (Bertiellus) lopatini L. Medvedev, 1978
Afghanistan, 3000 m, Bamgan Gardandewal, Helmond Riv., vi.1971 (Paratype)
Two dorsal and one ventral sclerites; DS transverse, rectangular; VBD absent, but lateral fold strongly pigmented ventrally (Fig. 90), VS is a crosswise band more weakly sclerotised at middle ending in AVS, which are wider than the rectum; VSA absent (Fig. 91).

Cryptoleptus (Burlinius) nitidicollis Wollaston, 1864
DEI: Anaga, El Pijaral, 800-850m, Laurisilva, 4.vii.1995, leg. Zerche
Two dorsal and one ventral sclerites; DS transverse, VBD present, DSA present but weakly sclerotised; LFI pigmented apical of DS (Fig. 92); VS is a crosswise band ending in AVS, which are wider than the rectum; VSA present, wide, more than half width of VS (Fig. 93) (From Erber & Schöller 2006).

Note: the same pattern can be found in Cryptocephalus (Burlinius) meridibrunneus Schöller, 2002 from tropical Africa.

Cryptoleptus (Burlinius) nubigena Franz, 1982
Tenerife
Two dorsal and one ventral sclerites; DS transverse, VBD present, DSA absent (Fig. 94); VS is a crosswise band ending in AVS, which are wider than the rectum; VSA present but weakly sclerotised, wide, more than half width of VS (Fig. 95) (From Erber & Schöller 2006).

Cryptoleptus (Disopus) pini pini (Linnaeus, 1758)
SMTD: Dresden-Rockwitz, 28.08.1910
Two dorsal and one ventral sclerites; DS transverse, VBD present, DSA absent (Fig. 96); VS is a crosswise band ending in AVS, which are wider than the rectum; VSA present, short, less than half width of VS (Fig. 97).
Note: C. pini is the subgeneric type species.
Figures 96–107. Kotpresse, dorsal (left), ventral (right); 96, 97: *Cryptocephalus* (*Disopus*) *pini*; 98, 99: *Cryptocephalus* (*Heterichnus*) *carinthiacus*; 100, 101: *Cryptocephalus* (*Lamellosus*) *laevicollis*; 102, 103: *Cryptocephalus* (*Protophysus*) *wehnkei*; 104, 105: *Cryptocephalus* (*Canthostethus*) *schreibersii*; 106, 107: *Cryptocephalus* (*Cerodens*) *emiliae*. 
Cryptocephalus (Heterichnus) carinthiacus carinthiacus Suffrian, 1848
Helvetia, Champex vs, 1500/1800m, 13./23.7.1969, W. Wittmer
Two dorsal and one ventral sclerites; DS transverse, VBD present, chitinpolster pigmented (Fig. 98); VS is a crosswise band ending in AVS, which are wider than the rectum; VSA present, wide, half width of VS, LFI pigmented apical and basal of VS (Fig. 99).

Cryptocephalus (Lamellosus) laevicollis Gebler, 1830
Slovakia, Plesivec, 26.5.1994, Moravec P.
Two dorsal and one ventral sclerites; DS transverse, DSA present, long, bent distally; VBD absent, LFI pigmented basal and apical of DS (Fig. 100); VS is a crosswise band ending in AVS, which are wider than the rectum; VSA present, wide, almost half width of VS (Fig. 101).

Cryptocephalus (Protophysus) wehnkei Weise, 1882
Turcia, m. Prov. Adana, Hasanbeyli/Nurdagi Gec., 37°07’14”N, 36°34’30”E, 24.-26.V. 2002, 8-1100m, leg. A. Weigel
Two dorsal and one ventral sclerites; DS sinuose, VBD present, DSA present, slender (Fig. 102); VS is a crosswise band, ending in AVS, which are wider than the rectum; VSA absent (Fig. 103).

Note: C. schreibersii is the subgeneric type species.

Cryptocephalus (Canthostethus) schreibersii Suffrian, 1852
Two dorsal and two ventral sclerites; DS transverse, VBD absent, apodemes wider than the rectum (Fig. 104); VS at base rounded, as wide as at AVS, the latter are wider than the rectum, between VS chitinpolster present; VSA absent; all sclerites weakly pigmented (Fig. 105).
Note: C. schreibersii is the subgeneric type species.

Cryptocephalus (Cerodens) emiliae Burlini, 1954
Marocco, Ifrane, 20.VIII.1963, leg. A. Warchalowski
Two dorsal and one ventral sclerites; DS straight, VBD present, a pair of narrow sclerites posterad of DS present, DSL present (Fig. 106); VS is a crosswise band, ending in AVS, which are slightly wider than the rectum; VSA present (Fig. 107).
Note: C. emiliae is the subgeneric type species.

Cryptocephalus subgenus incertae sedis
Cryptocephalus moliroensis Clavareau, 1913
Africa, Moliro, J. Duvivier 1894
Two dorsal and two ventral sclerites; DS transverse, VBD present, dorsal sclerotisation of the lateral fold present (Fig. 108); VS at base straight, as wide as at AVS, the latter are wider than the rectum, between VS chitinpolster present; VSA present,
Figures 108–120. Kotpresse, dorsal (left), ventral (right); 108, 109: Cryptocephalus moliroensis; 110, 111: Madacryptus ebenus; 112, 113: Madacryptus euchlorus; 114, 115, 116 (lateral): Jaxartiolus baeckmannianus; 117, 118: Melixanthus sp. (Borneo); 119, 120: Melixanthus intermedius.
tall, twice as wide as long, wider than one ventral sclerite, ventral sclerotisation of the lateral fold present (Fig. 109).

**Madacryptus ebenus** (Fairmaire, 1897)
Madagascar, Anleitra
Two dorsal and two ventral sclerites; **ds** reduced to apodemes, ventrally bend, much wider than rectum, dorsal sclerotisation of the lateral fold present apically and basally of **ds** (Fig. 110); **vs** at base slightly rounded, a little less wide as at **avs**, the latter are wider than the rectum, between **vs** chitin polster present; **vs** absent; all sclerites weakly pigmented (Fig. 111).

**Madacryptus euchlorus** (Dohrn, 1884)
Two dorsal and two ventral sclerites; **ds** large, narrow, apodemes wider than **ds** and with an apical twig, much wider than rectum, sclerotisation of **dfi** present, **dsl** present basally of **ds** (Fig. 112); **vs** large, transverse, at base slightly rounded, as wide as **avs**, the latter are wider than the rectum, between **vs** chitinpolster present; **vsa** absent; **vsl** present; all sclerites strongly pigmented (Fig. 113).

**Jaxartiolus baeckmannianus** Jacobson, 1922
Uzbekistan
Three dorsal and one ventral sclerites; **ds** is a crosswise band, longest and acute at middle, **vbd** absent, apodemes large and strongly bent upwards, a pair of dorsal sclerotised areas present, **dsl** strong (Fig. 114); **vs** is a crosswise band ending in large **avs** which are wider than the rectum and strongly bend downwards (Fig. 115); **vsa** present, short, width one third of **vs** (Fig. 116).
Note: this is the generic type species.

**Melixanthus** sp.
**NMW:** Borneo
Two dorsal and one ventral sclerites; **ds** sinuose, **vbd** absent, apodemes large (Fig. 117); **vs** is a crosswise band, less pigmented at middle, ending in **avs**, which are not wider than the rectum, **vsl** present, **vsa** absent (Fig. 118).

**Melixanthus** sp. **nr. intermedius**
**NMW:** Sumatra
Two dorsal and one ventral sclerites; **ds** sinuose, **vbd** absent, apodemes relatively small (Fig. 119); **vs** is a crosswise band, less pigmented at middle, ending in **avs**, which are not wider than the rectum, **vsa** absent (Fig. 120).
Note: *M. intermedius* is the generic type species.
Lophistomus conradti (Reineck, 1915)

**MNHB**: Usamgebiet, Besum, 11.-20.6.1914, S. Tessmann

Two dorsal and one ventral sclerites; ds sinuose, vbd absent, dsa present, slender, dsl present (Fig. 121); vs is a crosswise band, ending in avs, which are wider than the rectum and bend downwards; vsa absent (Fig. 122).

Mecostethus hispaeformis (Suffrain, 1866)
MLUH: Brazil
Two dorsal and two ventral sclerites; DS transverse, reaching lateral fold which is regularly widened and bend upwards, but only weakly sclerotised, VBD absent (Fig. 123); VS at base rounded, slightly wider than AVS, the latter are wider than the rectum, between VS chitinpolster present, VS weakly pigmented, VSL present (Fig. 124).

Mecostethus carneolus (Perty, 1832)
Two dorsal and two ventral sclerites; DS transverse, with a pointed tip at middle, reaching lateral fold which is much widened and bend upwards, especially close to DS, but only weakly sclerotised, VBD absent (Fig. 125); VS at base rounded, wider than AVS, the latter are wider than the rectum, between VS chitinpolster present (Fig. 126).

Mecostethus constricticollis (Jacoby, 1889)
Two dorsal and two ventral sclerites; DS transverse, reaching lateral fold which is regularly widened and bend upwards, but only weakly sclerotised and narrow, VBD absent (Fig. 127); VS at base rounded, slightly wider than AVS, the latter are wider than the rectum, between VS chitinpolster present, VS weakly pigmented, VSL absent (Fig. 128).
Note: This species was described recently again as Aulacothoracicus costaricensis Watts, 2005

Diachus auratus (Fabricius, 1801)
California, Paraiso, 7.V.1928
Two dorsal and one ventral sclerites; DS slightly sinuose, VBD absent (Fig. 129); VS is a crosswise band, ending in AVS, which are wider than the rectum, VSL present, VSA absent (Fig. 130).

Triachus atomarus LeConte, 1880
Two dorsal and two ventral sclerites; DS straight, VBD absent (Fig. 131); VS straight, AVS wider than the rectum, slightly wider than base of sclerite, VSL absent, VSA absent (Fig. 132).

Subtribe incertae sedis

Arnomus brouni Sharp, 1876
New Zealand
Two dorsal and one ventral sclerites; DS reaching lateral fold, with a narrow posteriorly directed extension, apodemes not wider than rectum, VBD present, long,
vs a transverse band, apodemes only slightly broader than vs and wider than rectum,DSA absent (Fig. 134) (from Reid, 1991).

*Semelvillea parva* Reid, 1991
Australia
Three dorsal and one ventral sclerites; Ds longitudinal, posteriorly directed, attached to the strongly sclerotised lateral fold, DFI sclerotised, bearing a longitudinal
median sclerite which is not attached to ds (Fig. 135); vs a transverse band, apodemes broad, not wider than rectum (Fig. 136), dsa present, narrow and wide, 2/3 width of vs (Fig. 137) (from Reid, 1991).

_Semelvillea tasmaniae_ Reid, 1991

ANIC: Tasmania, Hartz Mountains Nat. Park, 800m, on _Nothofagus cunninghami_, 7.xii.1986, P.B. McQuillan

Two dorsal and one ventral sclerites; ds straight, rectangular, reaching lateral fold, apodemes not wider than rectum, vbd present (Fig. 138); vs a transverse band, apodemes broad, laterally expanded and wider than rectum, dsa absent (Fig. 139) (from Reid, 1991).

_Platycolaspis pubescens_ Reid, 1994

Museum of Victoria, Melbourne: Australia, Victoria, Barwon Heads, 4.Nov.44, leg. E. Smith

Two dorsal and one ventral sclerites; ds broad, straight, triangular, reaching lateral fold, apodemes wider than rectum (Fig. 140); vs a transverse band, apodemes broad, laterally expanded and wider than rectum, dsa present, but only partly pigmented (Fig. 141) (from Reid, 1994).

_Platycolaspis australis_ Jacoby, 1908

Two dorsal and one ventral sclerites; ds broad, strongly narrowing towards apex, slightly bend posterad, reaching lateral fold, apodemes wider than rectum (Fig. 142); vs a transverse band, apodemes broad and wider than rectum, dsa present, wide, 2/3 width of vs (Fig. 143) (from Reid, 1994).

_Chloroplisma viridis_ Saunders, 1847

Australia

Two dorsal and no ventral sclerites; ds acute triangular, reaching lateral fold, apically a pair of triangular chitinpolster present, dsl present (Fig. 144); ventral chitinpolster present, large, lateral fold pigmented, widened and bend upwards (Fig. 145).

_Aporocera_ (Aporocera) sp.

N.S.-Wales

Two dorsal and no ventral sclerites; ds narrow, acute triangular, reaching lateral fold (Fig. 146); ventral chitinpolster present, large, lateral fold much widened and bend upwards (Fig. 147).

_Aporocera_ (Loxopleurus) sp.

Queensland, Brisbane, Hacker

No dorsal and no ventral sclerites; a dorsal transverse chitinpolster present, lateral fold triangularly widened and bend upwards (Fig. 148); a ventral transverse chitinpolster present, lateral fold extended (Fig. 149).
Formation of the extrachorion in Camptosomatan leaf beetles

Figures 154–166. Kotpresse, dorsal (left), ventral (right); 154, 155: Melatia metallica; 156, 157: Chlamisus pavoninus; 158, 159: Chlamisus sublaevicollis; 160, 161: Chlamisus indicus; 162, 163: Chlamisus pumicata; 164, 165, 166 (lateral): Pseudolychnopaes africanaus.
Cadmus (Cadmus) crucicollis Boisduval, 1835
Australia, South Australia, South Mt. Lofty Ranges, 30°SE Adelaide, Scott Creek Conservation Park, 18.12.1999, Hands & Hendrich leg.
Two dorsal and two ventral sclerites; ds transverse, not reaching lateral fold, large chitinpolster present around ds, dsl present (Fig. 150); vs at base slightly rounded, wider than Avs, the latter are not wider than the rectum, between vs chitinpolster present, vs not strongly pigmented, lateral fold much widened and bend upwards (Fig. 151).

Cadmus (Lachnabothra) braccatus (Klug, 1824)
Two dorsal and no ventral sclerites; ds rectangular, bend posteriorly, reaching lateral fold, large chitinpolster present between ds, dsl present (Fig. 152); ventral chitinpolster present, large, lateral fold extended and bend upwards (Fig. 153) (from Reid, 1999).

Melatia metallica (Gressitt, 1965)
Two dorsal and no ventral sclerites; ds narrow, gradually widening towards apex, not reaching lateral fold, large chitinpolster present around ds (Fig. 154); ventral chitinpolster present, large, lateral fold much widened and bend upwards (Fig. 155) (from Reid, 1998).

Chlamisini Chapuis, 1874

Chlamisus pavoninus Lacordaire, 1848
MNHB: Mexico, Comitan
Two dorsal and two ventral sclerites; ds narrow, transverse, located at the anterior margin of the chitinpolster, not reaching lateral fold, chitinpolster large, dsl present, lateral fold bend upwards (Fig. 156); vs narrow, slightly bend anteriorly, not wider than the rectum, around vs large chitinpolster present, vsl present (Fig. 157).
Note: This is a species with smooth, pubescent dorsal surface.

Chlamisus sp. nr. sublaevicollis Jacoby, 1889
Mexico (Puebla), Petlalcingo, Highway 190, 9.8.1998, leg. S. Gottwald
Two dorsal and two ventral sclerites; ds transverse, located at the centre of the chitinpolster, reaching lateral fold, df1 with strong sclerotisations (Fig. 158); vs slightly bend anteriorly, slightly wider than the rectum, around vs large chitinpolster present which is posteriorly wrinkled, vsl present (Fig. 159).
Note: This is a species with sculptured, nodulose dorsal surface.
*Chlamisus indicus* (Jacoby, 1901)
Nepal Central, Bagmati Zone, Kathmandu valley, Lalitpur Distr., Godawan Phulchoki, 2200–2700 m, 17.vi.1996, P.Čechosky, leg.
Two dorsal and one ventral sclerites; ds lengthwise sickle-shaped, narrow, located close to df1, not reaching lateral fold, chitinpolster large, dsl present (Fig. 160); vs large but narrow at centre, wider than the rectum, around vs large chitinpolster present, vsl present (Fig. 161).
*Chlamisus* sp. near *pumicata* (Lacordaire, 1848)
Zimbabwe, centr., 60 km sw of Gweru, (Shangani env.), 2.-3.12.1998., leg. S. Bečvár
Two dorsal and two ventral sclerites; ds reduced to the apodemes, i. e. located at the lateral margins of the chitinpolster, chitinpolster very large (Fig. 162); vs transverse, wider than the rectum, around vs chitinpolster present (Fig. 163).
Note: The external morphology is more similar to the Asian species of *Chlamisus* than to the Neotropical species.

**Lamprosomatinae Lacordaire, 1848**

**Neochlamysini Monró, 1958**

*Pseudolychnophaes africanus* (Jacoby, 1882)

**MNHb**: South Africa, north: Cape Province, Quaggafontein, 13.ix.2003, leg. Willers
Two dorsal and no ventral sclerites; ds apically rounded, bend posteriorly, in-between large chitinpolster present, lateral fold bend upwards (Fig. 164); a ventral transverse chitinpolster present (Fig. 165) which is stronger pigmented laterally (Fig. 166).

**Sphaerocharini Clavareau, 1913**

*Sphaerocharis marginicollis* (Guérin, 1844)

**MNHb**: Brazil
Two dorsal and no ventral sclerites; ds apically acute, attached to lateral fold, a linear pigmentation parallel to dfi present, lateral fold bend upwards (Fig. 167); a ventral transverse chitinpolster present (Fig. 168), lateral fold bend upwards (Fig. 169).

**Lamprosomatini Bedel, 1891**

*Xenoomorphus africanus* Weise, 1882

**SMTD**: South Africa, Western Cape Province, Kleinmond, 34,333°S 19,026°E, 30.viii. 2003, leg. K.-D. Klass
Two dorsal and two ventral sclerites; ds apically rounded, bend posteriorly, in-between large chitinpolster present (Fig. 170); vs triangular, narrow, attached to the lateral fold which is triangularly widened and bend upwards (Fig. 171), large chitinpolster present (Fig. 172).

*Oomorphoides tonkinensis* Chûjo, 1935
No dorsal and no ventral sclerites; a dorsal transverse chitinpolster present, lateral fold bend upwards (Fig. 173); a ventral trapeziform chitinpolster present, lateral fold extended and bend upwards (Fig. 174).

*Lamprosoma* sp.
Paraguay, NP Serrania San Luis, 21.-23.1.2001, leg. Mrácek
No dorsal and no ventral sclerites; a large dorsal chitinpolster present, lateral fold widened, bend upwards and posteriorly extended into a lengthwise twig (Fig. 175); ventral chitinpolster present, large, lateral fold much widened and bend upwards (Fig. 176).

Eumolpinae Hope, 1840

*Eupales ulema* Germar, 1813
No dorsal and no ventral sclerites; a dorsal transverse chitinpolster present (Fig. 177) (from Reid 1998).

(Synetinae Edwards, 1953)

*Syneta adamsi* Baly, 1877
No dorsal and no ventral sclerites; a dorsal trapeziform chitinpolster present (Fig. 178) (from Reid 1998).

4. Discussion

Based on the similarity of the pattern of rectal sclerites, all species studied can be assigned to one of the following four groups. The group Clytrini + *Acolastus* + *Mylassa* is characterised by two ventral and three dorsal sclerites, one being a central dorsal plate. The dorsal fold of the intestine is absent, only the two lateral folds are present. The dorsal central plate could be a fusion of sclerotisations of the dorsal fold of the intestine. In this case, the dorsal sclerites would have been reduced to its apodemes. Small such sclerotisations can be found in *Cryptocephalus* (*Asianus*) *reitteri*, *Scaphodius* sp. and *Chlamisus* sp. All other Camptosomata show three folds, i.e. one dorsal and two lateral folds. The presence of a dorsal central plate should be considered as an apomorphic character in phylogenetic studies.

Another common pattern are one ventral and two dorsal sclerites. The generic type species of *Cryptocephalus*, *Lophistomus* and *Melixanthus*, as well as a large number of species in these genera bear one ventral and two dorsal sclerites with a ventrally bend part of the dorsal sclerites present. In *Cryptocephalus*, an additional ventral sclerotised area is frequently present, i.e. the ventral band is doubled. In the species of the subgenera *Asianus*, *Bertiellus* and *Lamellosus* studied, no ventrally bend part of the dorsal sclerites was found. The group *Coenobius* + *Isinus* + *Aprionota* is characterised by one ventral and two dorsal sclerites, with strongly developed branches of the dorsal sclerites directed towards anus. The Neotropical Monachulina *Lexiphanes* have one ventral and two dorsal sclerites, too, but with ventral apodemes being large and dorsal sclerites bend up and in caudal direction in a characteristic way, followed by linear sclerotisations directed towards the dorsal fold. Moreover, one ventral and two dorsal sclerites were recorded from *Diachus*, *Jaxartiolus*, *Scaphodius*, *Ditropidus*, *Ditropidella*, *Ambrotodes*,
Platycolaspis, Semelvillea and Arnomus. Achaenops spp. have one ventral and two dorsal sclerites, too, but the dorsal sclerites are not reaching the sclerotised lateral fold. The presence of a ventral band should be considered as an apomorphic character in phylogenetic studies, because it is considered to be a fusion of a pair of formerly independent ventral sclerites. The branches of the dorsal sclerites in Coenobius and allies should be considered as an apomorphic character as well, because these are additional structures which are likely to be linked with a special arrangement of associated muscles.

Five taxa studied show two ventral and two dorsal sclerites, a pattern supposed to represent a plesiomorphic character state in taxa with rectal sclerites. In Stylosomus, these four sclerites resemble those observed in Clytrini in shape. The shape of the ventral sclerites in Cryptocephalus moliroensis, C. (Canthostethus) schreibersii, Mecostethus spp. and Triachus sp. is generally as in Cryptocephalus s. str., but the sclerites are not fused. Weak sclerotisation of the central part of the ventral band was found in Cryptocephalus ajeschae and Melixanthus spp., so different degrees of fusion of the ventral sclerites can be observed. The shape of the dorsal sclerites is of more interest in these species, being quite different from the typical shape found in Cryptocephalus spp. in C. (Canthostethus) schreibersii and Mecostethus spp. A peculiarity of Mecostethus is the lateral fold which is sclerotised and bend upwards. The pair of ventral sclerites found in Madacryptus, recently split of Cryptocephalus (Schöller, 2007), differ from Cryptocephalus s. str. in being broader and wider than the rectum.

A different pattern can be found in the species-rich group Cadmus + Melatia + Aporocera + Chlamisini + Lamprosomatinae. A large ventral chitinpolster with or without two ventral sclerites is present, and a large dorsal chitinpolster with or without two dorsal sclerites, often the lateral fold is broadened and bend up. The last-mentioned character should be considered apomorphic in phylogenetic studies.

Sclerotised rectal plates are unique to the Cryptocephalinae (Erber 1968, Reid 1995) and Lamprosomatinae as has been shown here. A crucial question for the use of kotpresse characters for phylogenetic research is the interpretation of the absence of sclerotised rectal plates in certain taxa. The absence of sclerotised rectal plates in Eumolpinae (including Synetinae) is considered here to be a plesiomorphic state, i.e. members of this group never had rectal plates. For certain members of Australian Cryptocephalinae and most Lamprosomatinae, this hypothesis is doubtful. As many derived characters can be found in the species under question (e.g. unbordered suture, deep canthus etc.) it is more likely that sclerotised rectal plates were reduced. However, more studies are needed to substantiate this hypothesis, especially the biomechanical implications of the strong sclerotisation of the lateral fold that is usually associated with the absence of sclerotised rectal plates in this group.

The findings generally support the hypothesis of De Monte (1957) postulating the existence of different ‘types’ of rectal apparatus within Camptosomata.
However, these ‘types’ do not reflect exactly the four Camptosomatan subfamilies as they were recognised in 1957, *i.e.* Clytrinae, Cryptocephalinae, Chlamisininae and Lamprosomatiniae. Further studies are necessary to evaluate the full diversity of this character complex. This is especially the case for the Lamprosomatiniae. De Monte (1957) thought the rectal apparatus of Lamprosomatiniae consists of delicate chitinpolster only. The species studied here showed the presence of extensions of the lateral fold as well as the presence of dorsal and ventral sclerites. The findings of this study support the traditional classification treating Cryptocephalinae and Lamprosomatiniae as a monophyletic group. However, the similar pattern found for the two groups Clytrini + *Acolastus* + *Mylassa*, and *Cadmus* + *Melattia* + *Aporocera* + Chlamisinii + Lamprosomatiniae should encourage future cladistic analysis to determine the position of these taxa within the Camptosomatata.

In all taxa, the pattern of rectal glands and microsculpture like spines and scales of the chitinpolster could provide another set of characters as suggested by Erber (1968). Some further information on these characters was provided by Reid (1991, 1994). In conclusion, the pattern of rectal sclerites provide most likely a valuable character set for phylogenetic studies on Camptosomatata.

References


