The morphology of the metendosternite and the anterior abdominal venter in Chrysomelinae (Insecta: Coleoptera: Chrysomelidae)

Nora Hübler & Klaus-Dieter Klass *

Senckenberg Natural History Collections Dresden, Museum of Zoology, Königsbrücker Landstrasse 159, 01109 Dresden, Germany; Klaus-Dieter Klass [klaus.klass@senckenberg.de] — * Corresponding author

Abstract

The skeletal parts of the metendosternite and of the anteromedian part of the abdominal venter are studied in 39 species of Chrysomelinae (representing tribes Timarchini and Chrysomelini, and 10 of the 12 subtribes of Chrysomelini) and 4 species from Galerucinae, Criocerinae, and Cassidinae. The morphology of these body parts in Chrysomelinae is compared with other cucujiform beetles based on the literature, with a focus on a tenebrionid. The morphology of the metendosternite evidently includes much homoplasy across Cucujiformia including Chrysomelidae, whereby conclusions on the polarity of characters are very limited. The (fairly poor) phylogenetic evidence from the chrysomeline metendosternite is discussed including reflection of the current classification, of the only large-scale molecular-based phylogenetic study of Chrysomelinae, and of phylogenetic evidence from glands and their secretions. Chrysomelinae consistently have a very short metendosternal stalk, the anterior tendon originates far laterally from the furcal arm, and the anterior lamina is limited to the furcal arm or entirely absent (i.e. always absent in the median part of the metendosternite). These features appear as apomorphic compared to the examined Galerucinae, Criocerinae, and Cassidinae and suggest the exclusion of Galerucinae from Chrysomelinae (contra molecular-based results). Metendosternal characters suggest *Phratora* to belong to Chrysomelina, and *Zygogramma* and *Cosmogramma* to be close to Chrysolinina rather than Doryphorina; both is in accord with results derived from DNA sequences and from gland secretions. The two Chrysomelinae genera with reduced hind wings (*Timarcha*, *Crosita*) show simplifications in the metendosternite. It is suggested that some characters may depend on the age of the adults, the development of abdominal hemi-sternites I being one such character.

1. Introduction

Diversity, classification, and phylogeny of Chrysomelinae. Chrysomelidae is among the most diverse families of the Coleoptera-Cucujiformia. Its subfamily Chrysomelinae includes ca. 2000 described species (Farrell 1998) in 176 (Reid 1995; Seeno & Wilcox 1982) or 132 (Daccordi 1994) genera. These have been classified into two tribes, **(1)** Timarchini (only genus *Timarcha* with 4 subgenera) and **(2)** Chrysomelini (Seeno & Wilcox 1982; Daccordi 1994; Riley et al. 2002; Warchalowski 2003).

In Seeno & Wilcox (1982, where M. Daccordi contributed to the classification of Chrysomelinae), Chrysomelini are further divided into the 12 subtribes Barymelina, Doryphorina, Chrysolinina, Monarditina, Chrysomelina, Hispostomina, Dicranosternina, Paropsina, Gonioctenina, Phyllodectina, Phyllocharina, and Entomoscelina; much of this is based on the older system of Weise (1915). Daccordi (1994), however, combined these to 4 subtribes: **(2a)** Chrysolinina (incl. Doryphorina and Monarditina),

(2b) Chrysomelina (incl. Barymelina, Hispostomina, and Phyllodectina), **(2c)** Paropsina (incl. Dicranosternina and Gonioctenina), and **(2d)** Entomoscelina (incl. Phyllocharina) (see Table 3). The classification proposed by STEINHAUSEN (2001), which lists only a few genera occurring in Europe, parallels that of DACCORDI (1994) in some important aspects, but Chrysomelini subtribes are rather ranked as tribes placed besides Timarchini: Doryphorini (including both Chrysolinina and Doryphorina of SEENO & WILCOX 1982), Chrysomelini, Entomoscelini, and Gonioctenini.

Phylogenetic relationships in Chrysomelinae have remained poorly studied, and the above classifications are hardly backboned by phylogenetic reasoning. There are many α-taxonomists working on Chrysomelinae, and there is thus a large amount of data on simple external morphological features, on the genitalia, and on some morphological peculiarities of the adults. Many of these characters are strongly afflicted by homoplasy (see DACCORDI 1994). Characters of larvae (e.g. PATERSON 1931; KIMOTO 1962) and pupae (e.g. REID 1992; STEINHAUSEN 1996) have also received attention and likely bear some phylogenetic evidence. One aspect of interest is the segmental distribution of larval defense glands (which are likely not homologous with somewhat similar structures in Galerucinae-Sermylini: BÜNNIGE & HILKER 2005). There is only a single noteworthy overall morphological treatment: that of RIVNAY (1928) on *Leptinotarsa decemlineata*, which, however, is not very detailed. The limited morphological data on Chrysomelinae has not yet been assembled into a data set for analysing phylogenetic relationships in this group. The few limited attempts to discuss Chrysomelinae phylogeny on a morphological basis are found in DACCORDI (1994) and STEINHAUSEN (2001); discussions on the relationships among particular genera are scattered over the taxonomic literature.

The only phylogenetic study using a decent Chrysomelinae sample is based on DNA sequences: GÓMEZ-ZURITA et al.'s (2007, 2008 *) study on Chrysomelidae phylogeny includes 32 terminal taxa from Chrysomelinae as well as numerous taxa from other chrysomelid subgroups; partial 16S, 18S, and 28S rDNA sequence data were analysed by direct optimisation (the tree resulting for Chrysomelinae from this analysis is shown in Fig. 1 herein), maximum likelihood, and Bayesian methods. This study confirms the basic division between Timarchini and Chrysomelini. Beyond this, the trees obtained by the various analytical methods agree in some parts but also show some striking differences. Evidence from karyological data (see summary in PETITPIERRE 2011) is developing but still limited regarding relationships at the level of the subtribes.

Considerable evidence on phylogenetic relationships in Chrysomelinae comes from work on secretions from the pronotal and elytral glands of the adults (PASTEELS et al. 2003 and references therein). For a limited selection of genera, PASTEELS et al. (2003) report a clear division into three groups based on the main classes of toxic compounds: isoxazolinone glucosides esterified by nitropropanoic acid (group outlined as "Chrysomelina s.str."), cardenolides ("Chrysolinina s.str."), or pentacyclic triterpene saponins ("Doryphorina s.str."). The three classes of compounds are said to require very different biosynthetic pathways, their occurrence appears to be mutually exclusive, and the ability to synthesise them along own metabolic pathways (though partly based on sequestring precursors from plants) is known, among insects, exclusively from the chrysomelines concerned.

Galerucinae (including alticines) is most likely the group closest to Chrysomelinae, but details are contradictory. REID (1995), in most of his morphology-based cladistic analyses, obtained Chrysomelinae and Galerucinae as sister taxa. With a combined morphological-molecular analysis, FARRELL (1998) confirmed the sistergroup relationship between Chrysomelinae and Galerucinae, but only two chrysomeline genera had been sampled (*Chrysomela*, *Phratora*). GÓMEZ-ZURITA et al. (2007, 2008) find both Chrysomelinae and Chrysomelini to be paraphyletic, as a clade comprising all Galerucinae takes a subordinate position within these groups; Timarchini is obtained as the sister taxon of Chrysomelini + Galerucinae. However, none of the nodes relevant to the subordinate position of Galerucinae in Chrysomelinae has strong support. Following GÓMEZ-ZURITA et al. (2007, 2008), the sister group of Chrysomelinae + Galerucinae is a large chrysomelid clade comprising Cryptocephalinae (including also clytrines and chlamisines), Cassidinae (including also hispines), Eumolpinae (including also synetines), Lamprosomatinae, and Spilopyrinae.

It is evident from the above survey that many morphological character systems remain to be studied comparatively in decent samples of Chrysomelinae, and comprehensive morphology-based cladistic analyses remain to be initiated. For such work both a compilation of characters already known (to establish a character matrix) and a search for new phylogenetically informative characters is needed. The metendosternite is one of the few internal cuticular structures frequently used in systematic work on Coleoptera. It is located immediately in front of the ventral transition area between thorax and abdomen.

The metendosternite and the anteroventral part of the abdomen in Chrysomelinae and other beetles. In beetles the posterior ventral sclerite of the metathorax, the sternellum, has become invaginated to form a complex, internally bifurcate apodeme called the metendosternite. Only small parts of the sternellum have remained externally around the origin of the metendosternite (DOYEN 1966: p. 130). The external origin of the metendosternite is located medially between the left and right metacoxae. Internally this large apodeme comprises an unpaired basal stalk (the more external part) and paired furcal arms (the more internal parts). The metendosternite bears a variety of cuticular differentiations such as laminae, ridges,

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* The results in these two papers are identical and based on the same data set.

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Galerucinae (incl. Alticinae)
Doryphora sp. CH-Dor
Proseicela bivittata CH-Dor
Labidomera clivicollis CH-Dor
Leptinotarsa juncta CH-Dor
Desmogramma ljunghi CH-Dor
Chrysolina (Atechna) sp. CH-Chl
Chrysolina femoralis CH-Chl
Chrysolina grossa CH-Chl
Oreina cacaliae CH-Chl
Zygogramma clathrata CH-Dor
Zygogramma suturalis CH-Dor
Calligrapha multipunctata CH-Dor
Calligrapha californica CH-Dor
Cosmogramma patricia CH-Dor
Sphaeratrix sericea CH-Mon
Gonioctena olivacea CH-Gon
Apterocuris sibirica CH-Chm
Paropsis maculata CH-Par
Trachymela sp. CH-Par
Augomela iridea CH-Phd
Plagiodera sp. CH-Chm
Johannica gemellata CH-Phc
Lamprolina sp. CH-Ent
Calomela juncta CH-Phd
Chrysomela mainensis CH-Chm
Linaeidea aena CH-Chm
Plagiodera versicolora CH-Chm
Phratora laticollis CH-Phd
Prasocuris distincta CH-Chm
Phaedon armoraciae CH-Chm
Americanotimarcha cerdo TI
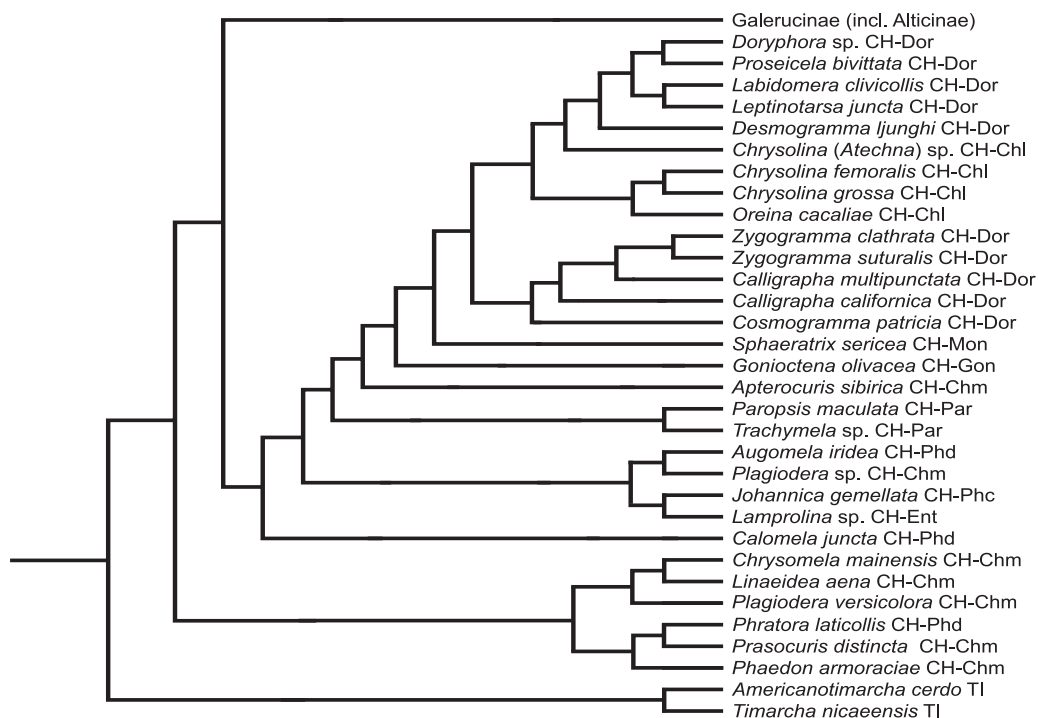*Timarcha nicaeensis* TI

Fig. 1. Molecular-based phylogenetic hypothesis of Chrysomelinae according to Gómez-Zurita et al. (2008: fig. 2; based on 16S, 18S, and 28S rDNA sequence data analysed using direct optimisation), with Galerucinae included as a taxon subordinate in Chrysomelinae. Tribes: TI = Timarchini; CH = Chrysomelini. Subtribes of Chrysomelini: Chl = Chrysolinina; Chm = Chrysomelina; Dor = Doryphorina; Ent = Entomoscelina; Gon = Gonioctenina; Mon = Monarditina; Par = Paropsina; Phc = Phyllocharina; Phd = Phyllodectina; Barymelina, Hispostomina, and Dicranosternina not included. "*Americanotimarcha*" is usually considered a subgenus of *Timarcha* (Seeno & Wilcox 1982; Daccordi 1994).

and delicate tendons of varied shape. These substructures and the metendosternite as a whole serve for the attachment of many muscles connecting different parts of the meso- and metathorax (including the hindlegs) and the 1st abdominal segment (e.g. Evans 1961; Korschelt 1923).

Crowson (e.g. 1938, 1944, 1955) described the metendosternite for many beetles from different subgroups and distinguished several basic types. The structure of the metendosternite was an important character system in his hypotheses on the phylogeny of beetles. Yet, it is also evident from Crowson's descriptions that there are many homoplastic character transformations in metendosternite morphology, as seen from similar metendosternites in distantly related beetle taxa. Many of Crowson's illustrations of the metendosternite are not very instructive, and the same is true for much of the pictorial documentation of this structure found in taxonomic treatments. More detailed descriptions of the metendosternite are only available for a few species of beetles. For Cucujiformia, the major beetle lineage to which the Chrysomelidae belong, the most detailed work is Doyen (1966) on the tenebrionid *Tenebrio molitor*. Somewhat less detailed are McHugh et al.'s (1997) data on the erotylid *Megalodacne heros* and Evans's (1961) on the cryptophagid *Atomaria ruficornis*. In Rivnay's (1928) treatment of *Leptinotarsa decemlineata* (Chrysomelinae) the metendosternite is not mentioned at all.

The anterior ventral part of the abdomen in beetles, especially Polyphaga, is strongly modified as compared to most other insect orders. This mainly concerns a strong reduction and median division of abdominal sternite I, a moderate reduction of sternite II, and the fusion of the latter with sternite III. Sternite III is fully developed and is the most anterior sternite visible from externally without dissection. The sinking of the metacoxae into coxal cavities and the tight closure of the latter around the former are correlated with these sternal modifications.

It is evident from the sparse morphological work on the metendosternite and on the ventral transition area between thorax and abdomen that in this whole region there are some substructures showing variation, and thus probably also some morphological characters potentially informative on phylogenetic relationships in subgroups of beetles. This surely also applies to Chrysomelinae. On the other hand, with the exception of a few drawings by Crowson, a detailed comparative study of this body region in Chrysomelinae is absent (as it is for many other beetle taxa).

Scope of the present study. The main task of this study is to examine the skeletal morphology of the metendosternite and the adjacent part of the abdominal venter in a decent sample of Chrysomelinae species. We additionally include members of Galerucinae, and representatives of two chrysomelid subfamilies that are clearly

Table 1. Species of Chrysomelidae included in this study, with systematic assignment according to Seeno & Wilcox (1982; see Table 3 for assignment according to Daccordi 1994), number of specimens examined (N), condition of hind wings (HW: wde = well developed, red = strongly or completely reduced), and provenance (zoogeographical regions: PAR = Palaearctic, NAR = Nearctic, NTR = Neotropical, ORI = Oriental, ETH = Ethiopian, AUS = Australian regions; country or geographical area added in parentheses); "++" in column "GZ" indicates genera (subgenera for *Timarcha*) that are included in the analysis of Gómez-Zurita et al. (2008), compare Fig. 1. * in column "Species": in Daccordi (1994), *Oreina* is listed as a subgenus of *Chrysolina*, *Desmogramma* as a subgenus of *Strichosa*, and *Hydrothassa* as a subgenus of *Prasocuris*.

Species	Systematic assignment	N	HW	GZ	REGION (Provenance)
Chrysomela (s.str.) saliceti Suffrian, 1851	Chrysomelinae: Chrysomelini: Chrysomelina	3	wde	++	PAR (Hungary)
Chrysomela (Strickerus) cuprea Fabricius, 1775	Chrysomelinae: Chrysomelini: Chrysomelina	3	wde	++	PAR (Germany)
Chrysomela (Pachylina) collaris Linné, 1758	Chrysomelinae: Chrysomelini: Chrysomelina	2	wde	++	PAR (Kasachstan)
Plagiodera versicolora (Laicharting, 1781)	Chrysomelinae: Chrysomelini: Chrysomelina	2	wde	++	PAR (Switzerland)
Hydrothassa glabra (Herbst, 1783) *	Chrysomelinae: Chrysomelini: Chrysomelina	2	wde		PAR (Germany & Greece)
Prasocuris phellandrii (Linné, 1758)	Chrysomelinae: Chrysomelini: Chrysomelina	2	wde	++	PAR (Germany)
Phaedon pyritosus (Rossi, 1792)	Chrysomelinae: Chrysomelini: Chrysomelina	2	wde	++	PAR (Austria)
Phratora vitellinae (Linné, 1758)	Chrysomelinae: Chrysomelini: Phyllodectina	2	wde	++	PAR (Germany)
Gavirga limbatella Stål, 1860	Chrysomelinae: Chrysomelini: Phyllodectina	1	wde		NTR (Peru)
Oidosoma coccinella Fairmaire, 1887	Chrysomelinae: Chrysomelini: Phyllocharina	1	wde		ETH (Tanzania)
Phyllocharis undulata Linné, 1763	Chrysomelinae: Chrysomelini: Phyllocharina	1	wde		ORI (Java)
Entomoscelis suturalis Weise, 1882	Chrysomelinae: Chrysomelini: Entomoscelina	3	wde		PAR (Turkey)
Lamprolina aeneipennis (Boisduval, 1835)	Chrysomelinae: Chrysomelini: Entomoscelina	1	wde	++	AUS (Queensland)
Sphaeratrix latifrons (Gistel, 1857)	Chrysomelinae: Chrysomelini: Monarditina	2	wde	++	ETH (Tanzania & Cameroon)
Humba cyanicollis (Hope, 1831)	Chrysomelinae: Chrysomelini: Chrysolinina	3	wde		PAR (China)
Chrysolina bicolor (Fabricius, 1775)	Chrysomelinae: Chrysomelini: Chrysolinina	2	wde	++	PAR (France)
Chrysolina grossa (Fabricius, 1792)	Chrysomelinae: Chrysomelini: Chrysolinina	2	wde	++	PAR (Italy)
Chrysolina cerealis (Linné, 1767)	Chrysomelinae: Chrysomelini: Chrysolinina	4	wde	++	PAR (Austria, Italy & Russia)
Oreina speciosa (Linné, 1767) *	Chrysomelinae: Chrysomelini: Chrysolinina	3	wde	++	PAR (Germany)
Oreina intricata (Germar, 1824) *	Chrysomelinae: Chrysomelini: Chrysolinina	3	wde	++	PAR (Germany)
Crosita altaica (Gebler, 1823)	Chrysomelinae: Chrysomelini: Chrysolinina	2	red		PAR (Altai Mts.)
Ambrostoma fortunei (Baly, 1860)	Chrysomelinae: Chrysomelini: Chrysolinina	2	wde		PAR (China)
Zygogramma flavotaeniata Stål, 1860	Chrysomelinae: Chrysomelini: Doryphorina	2	wde	++	NTR (Peru)
Zygogramma signatipennis (Stål, 1859)	Chrysomelinae: Chrysomelini: Doryphorina	2	wde	++	NTR (Mexico)
Cosmogramma patricia Erichson, 1847	Chrysomelinae: Chrysomelini: Doryphorina	2	wde	++	NTR (Bolivia)
Proseicela vittata Fabricius, 1781	Chrysomelinae: Chrysomelini: Doryphorina	2	wde	++	NTR (Suriname)
Leptinotarsa decemlineata (Say, 1824)	Chrysomelinae: Chrysomelini: Doryphorina	3	wde	++	PAR (Germany)
Doryphora cincta Germar, 1821	Chrysomelinae: Chrysomelini: Doryphorina	2	wde	++	NTR (Brasil)
Doryphora pyrrhoptera Germar, 1824	Chrysomelinae: Chrysomelini: Doryphorina	2	wde	++	NTR (Brasil)
Desmogramma bivia Germar, 1824 *	Chrysomelinae: Chrysomelini: Doryphorina	2	wde	++	NTR (Brasil & Suriname)
Labidomera clivicollis (Kirby, 1837)	Chrysomelinae: Chrysomelini: Doryphorina	2	wde	++	NAR (Massachusetts)
Dicranosterna picea Olivier, 1807	Chrysomelinae: Chrysomelini: Dicranosternina	1	wde		AUS (New South Wales)
Gonioctena viminalis (Linné, 1758)	Chrysomelinae: Chrysomelini: Gonioctenina	1	wde	++	PAR (Germany)
Gonioctena variabilis (Olivier, 1790)	Chrysomelinae: Chrysomelini: Gonioctenina	2	wde	++	PAR (Spain)
Paropsis marmorea Olivier, 1807	Chrysomelinae: Chrysomelini: Paropsina	1	wde	++	AUS (Queensland)
Paropsides duodecimpustulata (Gebler, 1825)	Chrysomelinae: Chrysomelini: Paropsina	1	wde		PAR (Korea)
Trachymela serpiginosa Erichson, 1842	Chrysomelinae: Chrysomelini: Paropsina	1	wde	++	AUS (Queensland)
Timarcha (Metallotimarcha) metallica (Laicharting, 1781)	Chrysomelinae: Timarchini	3	red		PAR (Alps)
Timarcha (Timarchostoma) goettingensis (Linné, 1758)	Chrysomelinae: Timarchini	2	red		PAR (Germany)
Oides decempunctata (Billberg, 1808)	Galerucinae: Oidini	1	wde	na	PAR (China)
Galeruca tanaceti (Linné, 1758)	Galerucinae: Galerucini	2	wde	na	PAR (Romania)
Lilioceris merdigera (Linné, 1758)	Criocerinae	1	wde	na	PAR (Germany)
Lasiochila rufa (Guérin de Méneville, 1840)	Hispinae	1	wde	na	ORI (Java)

placed outside Chrysomelinae. This work is done in order to explore this body part with the perspective of its use in forthcoming phylogenetic analyses of Chrysomelinae and leaf beetles as a whole. We describe and mostly illustrate the structures under study, identify corresponding (i.e. homologous) elements, and point to preliminary phylogenetic implications. The latter are reflected on current classifications, the phylogenetic study of Gómez-Zurita et al. (2007, 2008), and evidence from glandular secretions.

2.   Material and Methods

The species and specimens we studied are listed in Table 1 *. In the text the genus names alone are used for referring to these species, as long as such reference is unambiguous. The classification of Chrysomelinae follows Seeno & Wilcox (1982), while the taxonomy of European taxa was updated according to Warchalowsky (2003).

Entire specimens were macerated using warm ca. 5% KOH solution, cleaned with distilled water, and transferred into ca. 70% ethanol; the dorsal wall was removed and the wider ventral area giving rise to the metendosternite was cut out. Observations were made under a stereo-microscope using magnifications up to 80 × and different angles of incident light.

Drawings were first made on paper, then scanned, and completed using the graphic computer programmes CorelPhotoPaint vers. 12 (for processing individual illustrations) and CorelDraw vers. 12 (for assembling drawings to plates and for labeling).

The morphological terminology for the substructures of the metendosternite and the surrounding elements (including the anterior parts of the abdomen) is essentially adopted from Doyen's (1966) work on *Tenebrio*, which provides the most detailed description of the body region in question in a cucujiform beetle. This terminology is derived from Crowson's (1938, 1944). For additional structures found in taxa studied herein we either use, as far as available, terms of other authors (such as Crowson 1938, 1944), or we coin new terms. Synonymy for terms used herein and in Doyen (1966) is given in Table 2.

The definition of morphological directions (anterior, posterior, dorsal, ventral) is generally difficult for the metendosternite, which is oblique (directed anterodorsally from its area of origin) and additionally curved. Here we give the directions as inherent in the morphological terms of Doyen (1966). Furthermore, it is also difficult to standardise morphological directions and aspects (in the drawings) across the examined species, because both the inclination of the metendosternite and the relative orientation of many substructures are quite variable among taxa. Related statements in the descriptions must be viewed considering these limitations.

For structures seated upon the furcal arms, the extension alongside the furcal arm is specified as "narrow" vs. "wide", while the extension perpendicular to the main axis of the furcal arm is specified as "long" vs. "short". For instance, a wide, short lamina extends along much of the furcal arm (wide) but hardly projects from it (short).

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* The sample is identical to that in Klass et al. (2011), but *Oreomela clypealis* (Jacobson, 1901) and *Polyspila matronalis* (Erichson, 1847) were here not included.

3.   Abbreviations

The following abbreviations are used in the illustrations and in the text, emphasised by bold print in the latter. Abbreviations used by other authors are occasionally mentioned herein for cross reference; they are also given in bold print.

anla = anterior lamina of metendosternite; **ante** = anterior tendon of metendosternite; **bate** = basal tendon of metendosternite; **dcr** = discrimen (midline ridge) of metaventrite; **fa** = furcal arm of metendosternite; **fal** = outline of lumen of furcal arm (internal part); **icp** = intercoxal process of abdominal venter; **iest** = internal edge of stalk of metendosternite; **if** = internal tip of furcal arm, bearing the following substructures: **if-a** = anterior lobe of internal tip; **if-ar** = anterior ridge of internal tip; **if-at** = delicate tendon on apical edge of internal tip (often split into fringes); **if-dr** = dorsal ridge(s) of internal tip; **if-dt** = dorsal tendinous fringes of internal tip; **if-mr** = median ridge of internal tip; **if-p** = posterior lobe of internal tip; **mcc** = metacoxal cavity, posterodorsal wall formed by abdominal venters I and II; **scr** = sternacostal ridge; **scs** = sternacostal suture; **stI** = abdominal sternite I; **stII** = abdominal sternite II; **stIII** = abdominal sternite III; **stk** = stalk of metendosternite; **tr** = transverse ridge of anterior abdominal venter; **trpf** = median perforation of transverse ridge tr; **tstI** = paired tendons on area of sternite I of abdomen (on rim of metacoxal cavity); **tstII** = paired tendons on sternite II of abdomen; **vebu** = bulb-like ventral pouch in front of ridge tr; **vela** = ventral lamina of metendosternite; **vete** = ventral tendon of metendosternite; **vlf** = midventral longitudinal flange in anterior wall of stalk of metendosternite; **vn3** = metathoracic ventrite; **vri** = ventral ridge of furcal arm distad of tendon vete.
[The ridges **if-ar** and **if-mr** are only labeled in *Timarcha goettingensis*, Fig. 35, and are both ambiguous homologues of either ridge **if-dr** or lobe **if-a** of other species.]

4.   Morphological descriptions

4.1.   General description for Chrysomelinae

This study treats the metendosternite with all its differentiations and the ventral wall of the abdomen immediately posteriad of it. This includes the metacoxal cavities but not the metacoxae and their articulations. The metendosternite is an inflection of the posterior-most median part of the metathoracic venter, which is sclerotised by the sternellum. In Chrysomelinae (Figs. 2 – 5, 10 – 35) it generally has a very short and wide stalk (**stk**) and distinct, narrow furcal arms (**fa**), though the transition between stalk and furcal arms is fluent. The anterior venter of the abdomen includes the sternites of segments I – III, which are very differently developed.
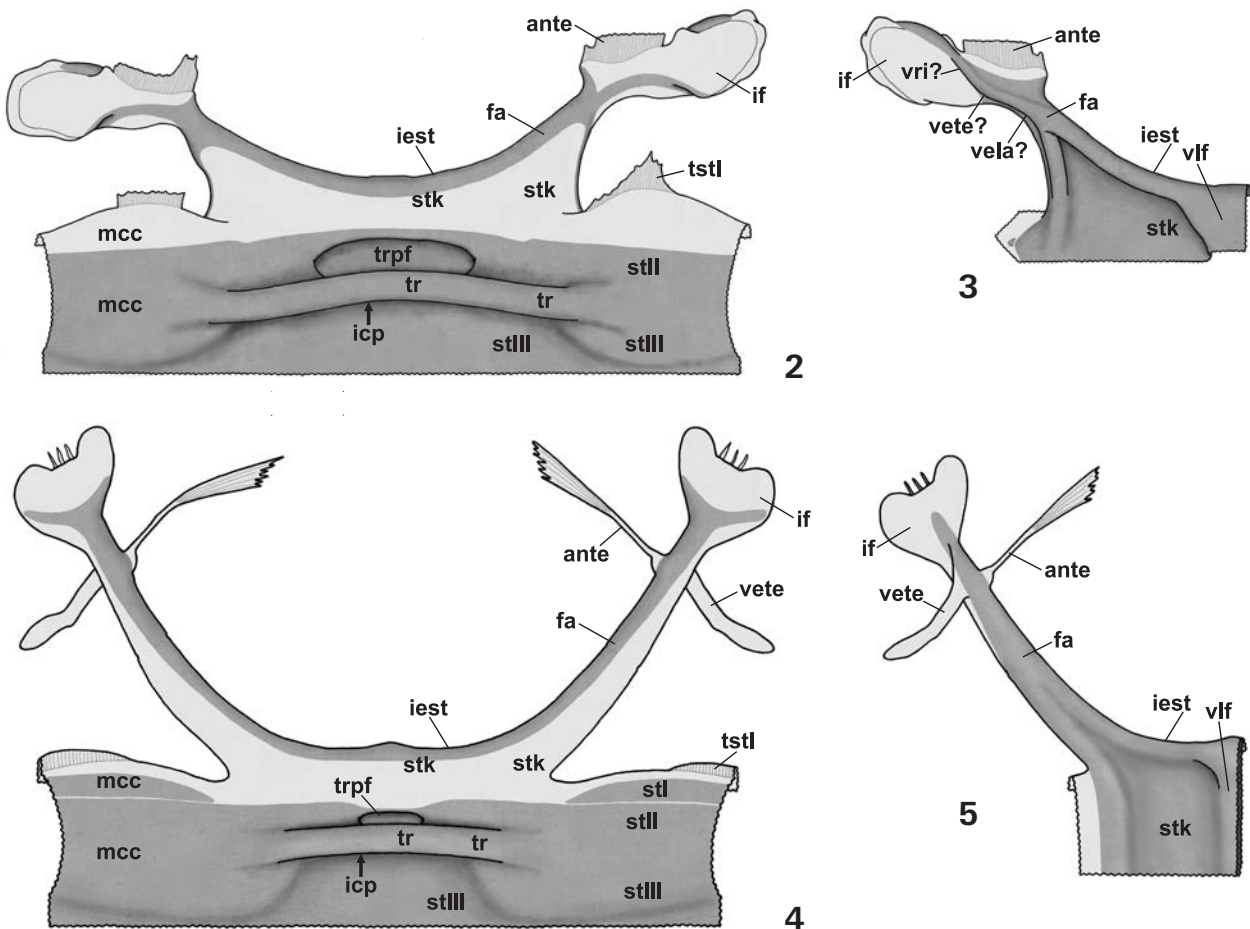
Figs. 2–5. Metendosternite together with anterior-most part of abdominal venter in posterodorsal view (2, 4), and right half of metendosternite in anteroventral view (3, 5). The internal surface of the cuticle (epidermal side) is seen throughout; undulate lines are cutting lines through the cuticle; dark areas in the abdominal part are sclerotised externally in the specimen (i.e. distinctly hardened and usually more or less darkened); dark areas in the metendosternite part simply reflect darkening in the specimen (see section 4.1.). **2**, **3**: *Timarcha metallica*. **4**, **5**: *Doryphora cincta*. (see Figs. 32 and 34 for scale)

Stalk of metendosternite: The anterior wall of the stalk (Figs. 3, 5, 8, 9) is sclerotised extensively; this is the larger, inflected part of the sternellum. Along the midline this sclerotisation is folded inward (i.e. anteriorly) to form the ventral longitudinal flange (**vlf**), which runs vertically along the stalk. Flange **vlf** either meets the transverse sternacostal ridge with its ventral (or: anterior) end, or it obliterates before. The sternacostal ridge (**scr**) is a tranverse infolding upon the posterior part of the metathoracic venter, which is represented by a groove on the external surface, the sternacostal 'suture' (**scs**, the anterior border of the sternellum; Fig. 8). A longitudinal midline infolding, the median internal ridge of the metathoracic venter (discrimen **dcr**), extends anteriorly from the sternacostal ridge; it is continuous with flange **vlf** if this reaches the sternacostal ridge.

The posterior wall of the stalk is shorter than the anterior one, as it does not extend so far ventrally (Figs. 8, 9, compare position of anterior and posterior thick arrows). It is sclerotised only along the internal edge of the stalk (**iest**; Figs. 2, 4, 8), where the sternellum bends from the anterior wall into the posterior wall of the stalk.

Furcal arms of metendosternite: The most internal part of each furcal arm, here called the internal tip (**if**), is more or less strongly widened, its overall shape varying from short to elongate (Figs. 12, 14). It is usually, but with varied distinctness, divided into an anterior lobe (**if-a**) and a posterior lobe (**if-p**) by an apical notch; the lobes are either of similar size, or the posterior one is larger (Figs. 10, 25). The apical edge of the internal tip bears a very thin, laminar tendon (apical tendon **if-at**, e.g. Figs. 14, 16; located in the notch if there is one). This tendon is distinctly thinner than the body of the internal tip, and it is usually divided into a row of densely or loosely (Fig. 4) spaced fringes. The dorsal wall of the internal tip bears a system of mutually continuous ridges (collectively called ridge **if-dr**), which includes a maximum of four parts: The most consistently present part extends along the posterior lobe **if-p** (e.g. Figs. 12, 20); this ridge often projects posteriorly and thus can hide the true posterolateral margin of the posterior lobe (which in addition is often bent ventrally; Fig. 16). The second part curves around the base of the internal tip (e.g. Figs. 10, 33). The third part continues the latter along the (antero)mesal marginal

part of the anterior lobe **if-a** (e.g. Fig. 32), where it can be partly confluent with the (antero)mesal edge of lobe **if-a**. The fourth part continues the part on the posterior lobe proximally to the base of tip **if** or for some distance down the furcal arm (e.g. Figs. 17, 21).

Further proximally the furcal arm can bear various laminar expansions and tendons. The positionally most stable structure is the anterior tendon (**ante**), which originates from the anterior (or: anteromesal) face of the furcal arm, at a varied distance from the internal tip but always from the distal half of the arm, and is often seated upon a small bulge (Figs. 14, 33). Tendon **ante** usually has a very slender, quite cylindrical proximal part; its distal (internal) portion is more widened, flattened, and delicate, and shows a tendency to become split into fringes (called the 'fringy part' of **ante** below). Shortly ventrad of the origin of tendon **ante** the furcal arm occasionally forms a distinct laminar expansion, the anterior lamina **anla** (e.g. Figs. 10, 14). Its length and width vary strongly, it can be curved ventrally to a varied extent, and it can be more closely associated either with the base of tendon **ante** (as in Fig. 11) or tendon **vete** (as in Fig. 12). In most Chrysomelinae, however, lamina **anla** is completely absent (e.g. Fig. 32). Many Chrysomelinae have another laminar expansion extending along the ventral face of the furcal arm, the ventral lamina **vela** (Fig. 10). Internal to lamina **vela** the furcal arm forms a fairly large, usually elongate tendon, the ventral tendon **vete** (Figs. 10, 30), which is nearly always present. It is more massive than the anterior tendon **ante**, and never has a more delicate, fringy distal part. Both lamina **vela** and tendon **vete** can originate from the posteroventral, midventral, or anteroventral face of the furcal arm (often showing covariation in this regard), and tendon **vete** has its origin at a varied distance from the internal tip **if** (Figs. 39–63). When a ventral lamina is present, tendon **vete** usually appears as a strongly lengthened internal part of **vela** (Figs. 10, 39–63), the base of which often curves a bit anteriorly when reaching the base of tendon **vete** (Fig. 51). From the internal base of tendon **vete** a short ridge usually continues towards the anterior lobe of the internal tip, ridge **vri** (Fig. 39). It either obliterates around the base of tip **if** (Fig. 41) or continues alongside the mesal edge of lobe **if-a** (Fig. 39). In many cases the proximal ends of laminae **anla** and **vela** are difficult to define: While the distal part of both is usually discretely projecting from the furcal arm, the proximal part becomes gradually shorter (i.e. lower) and obliterates. Some Chrysomelinae additionally possess a basal tendon **bate**, the base of which extends along the anterodorsal surface of the proximal part of the furcal arm (Fig. 10).

Each furcal arm (**fa**) is essentially an inwardly directed cuticular tube, while the thickness of its cuticle varies strongly along its walls. The lumen (central canal) of the tube is narrow and usually extends inward up to near the base of the internal tip **if**. The outline of the lumen is usually visible inside the furcal arm, and the internal part of this is indicated in many illustrations (**fal**, e.g. Figs. 14, 20). The outline of the canal represents the outer surface of the cuticle forming the furcal arm, while in the drawings Figs. 10–38 the inner surface of the cuticle (which faces the epidermis) is seen throughout. The entire furcal arms can likely be considered as 'sclerotised'. However, sclerotisation is usually limited to a variously deep outer layer of the cuticle, i.e. to the surroundings of the central canal in case of the furcal arm. Most importantly, the substructures of the furcal arm – laminae, tendons, and internal tip – are apparently shaped by a differential thickening of the cuticle towards the body cavity, i.e. they likely consist of massive cuticle largely belonging to the non-sclerotised internal layer. This means it makes little sense to distinguish between sclerotised and membranous parts of the walls and substructures of the furcal arm in the internal views of the metendosternite shown herein. In Figs. 2–5, parts of the furcal arms that appear darker are shown in darker grey (there either the sclerotisation extends deeper into the cuticle, or the non-sclerotised internal layer of the cuticle is thinner or more transparent than in other parts). However, this distinction is not considered in the other drawings, Figs. 10–38 (among which Figs. 32, 34 show the same species as Figs. 2–5). Only near the opening of the metendosternite, i.e. in the stalk area, and outside the metendosternite a distinction between sclerotised and membranous areas of the (non- or weakly thickened) cuticle is applicable. However, this refers to sclerotisation of the external layer of the cuticle, while from the inside only the non-sclerotised internal layer is visible.

Anterior abdominal venter: Behind the posterior wall of the stalk, abdominal territory follows (Figs. 2, 4, 8). The most conspicuous structures seen in an internal view are the cavities of the metacoxae (**mcc**) laterally and a strong transverse ridge (**tr**) medially (Figs. 2, 4).

The metacoxal cavities are inwardly bulged areas of the ventral abdominal wall that embrace the posterior walls of the metacoxae. They are heavily sclerotised in their posterior, more external parts, while their anterior parts are more weakly sclerotised or membranous. Abdominal sternites I (**stI**), II (**stII**) (both medially divided, i.e. hemisternites), and III (**stIII**) contribute to the sclerotisations as indicated in Fig. 4. The presence of hemisternites **stI** shows a wide range in Chrysomelinae: some have a distinct, well darkened and discretely bordered **stI** (Fig. 4; separated by narrow membrane from **stII**), others show no trace of **stI** (Fig. 2). Hemisternites **stII** are always fused to **stIII** (location of border partly unclear) and range from very weak to as strongly sclerotised as **stIII**. Both **stI** and **stII** can be present (as evident from some hardening detected by bending the cuticle) but so weak that their exact outline and separation from each other can hardly be specified.

In a few Chrysomelinae the metacoxal cavities bear tendons: **tstI** on the anterior rim of the coxal cavity (Figs. 2, 4) likely marks the anterior border of abdominal segment I; **tstII** (Fig. 7), located shortly in front of the lateral-most parts of ridge **tr**, marks the anterior border of abdominal segment II (see section 5.1.2.).
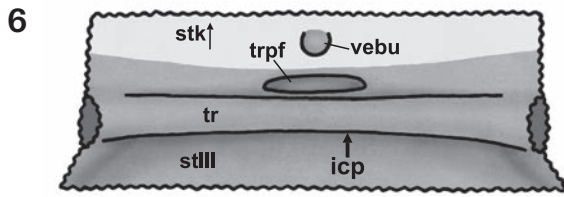
Fig. 6. Ventral wall of anteromedian part of abdomen, in between metacoxal cavities (compare Fig. 4), of *Chrysolina cerealis*, to show sclerotised bulb **vebu**; dorsal view (cuticle thus seen from internally almost throughout); undulate lines are cutting lines through the cuticle (double where the strongly thickened cuticle of ridge **tr** is cut); dark areas are distinctly sclerotised; scale 0.2 mm.
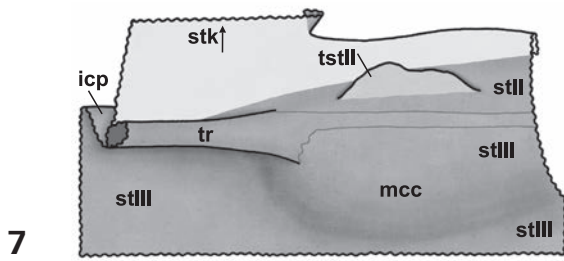
Fig. 7. Ventral wall of right anterior part of abdomen, including middle part and mesal portion of right metacoxal cavity, of *Chryso-mela saliceti*, to show tendon **tstII**; dorsal view (cuticle thus seen from internally almost throughout); undulate lines are cutting lines through the cuticle (double where the strongly thickened cuticle of ridge **tr** is cut); dark areas are distinctly sclerotised; scale 0.2 mm.
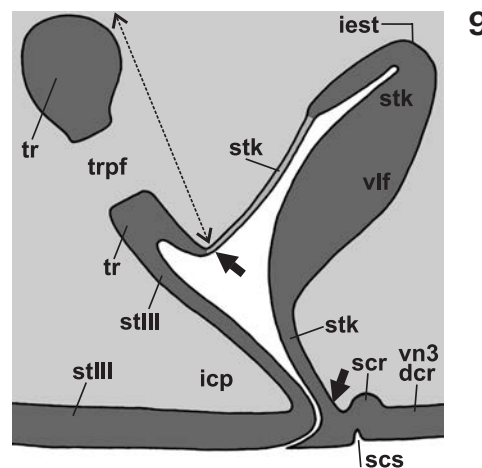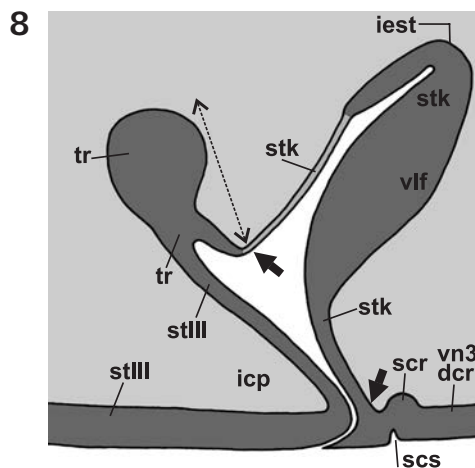
Figs. 8, 9. Mediosagittal section of ventral thorax−abdomen transition area, semi-diagrammatical. The cuticle is shown by double black lines, filled with medium gray if membranous and with dark gray if sclerotised; body cavity filled with light gray, external space white. Thick arrows point to the ventral ends of the anterior and posterior walls of the metendosternal stalk. The dashed arrow indicates the extent of elevation of ridge **tr** from the body wall (with reference to the anterior base of ridge **tr**). **8**: Condition with ridge **tr** moderately elevated and perforation **trpf** absent. **9**: Condition with ridge **tr** strongly elevated and perforation **trpf** present.

The transverse ridge **tr** is formed by inwardly folded plus strongly inwardly thickened cuticle, and it establishes an oblique-vertical wall in between the left and right coxal cavities (compare Figs. 4 and 8). In the middle this wall can be perforated (perforation **trpf** in Figs. 2, 4, 6, 9); the perforation can be of very different size and is limited to the massive internal portion of ridge **tr**, i.e. the portion built of thickened cuticle (Fig. 9). Laterally ridge **tr** obliterates upon the coxal cavities but often continues into a whitish 'seam' (outlined in Fig. 7); this is still thickened cuticle, the whitish appearance results from the thickened internal, non-sclerotised layer of the cuticle. Ridge **tr** likely marks the anterior border of venter III, being its enlarged antecosta.

Immediately behind ridge **tr** the midline body wall is bulged outward and forward to form the intercoxal process (**icp**, belonging to venter III). This abuts against the most proximal anterior wall of the metendosternal stalk (Fig. 8), whereby the ventral thorax-abdomen transition area of the beetle, including the 'entrance' into the metendosternite, is firmly closed between the metacoxae. Occasionally there is a median cuticular thickening or inwardly directed sclerotised bulb-like pouch (**vebu**) in the membrane in front of ridge **tr** (Fig. 6).

It was observed occasionally that in one or several specimens of a species many substructures of the metendosternite were smaller, the perforation **trpf** was smaller, and sternite **stI** was more difficult to recognise (if at all) compared to conspecific specimens. Such specimens often had comparatively pale cuticle (evidently teneral individuals), but as often the cuticle appeared to be fully darkened. We tentatively assume that the specimens concerned were young ones, and that the development of the cuticle is still ongoing during early stages of adult life (see section 5.2.3.).

4.2. Description of Chrysomelinae species

Chrysomela saliceti (Chrysomelina)
Figs. 10, 39 and 7

The internal tip **if** is fairly large and very wide. Its internal (apical) edge is deeply notched, and both the anterior (**if-a**) and the posterior lobe (**if-p**) are well developed. The notched internal edge of **if** bears a delicate tendon (**if-at**, mostly split into fringes). The dorsal ridge **if-dr** is well developed; it extends along the posterior lobe **if-p** and then curves anteriorly around the base of tip **if** and onto the anterior lobe **if-a** (where it is partly confluent with the mesal edge of **if-a**).

A well developed, very long and wide anterior lamina **anla** extends along the anterior (slightly ventral) face of the furcal arm from near the base of the tip **if** down into the stalk region, where it becomes gradually shorter. The free marginal parts of the lamina are curved ventrally so that the lamina has the shape of a trough (open ventrally). The anterior tendon **ante** originates – well remote from the tip region **if** – from the proximal dorsal wall of lamina **anla**; it is moderately long, the fringy part begins at about 1/2 from the base. A small lobe-like tendon **bate** extends along the proximal anterodorsal part of the furcal arm.

A ventral lamina **vela** that is very long distally but gradually becomes shorter proximally arises from the posterior ventral surface of the furcal arm (forming an angle of ca. 120° with lamina **anla**; Figs. 10, 39); proximally it reaches well 2/3 down the furcal arm. The base of the ventral tendon **vete** is limited to the postero- to mid-ventral surface of the furcal arm, well distad of tendon **ante** (Fig. 10) and at the base of tip **if**, and is continuous with the internal part of lamina **vela** (**vela** and **vete** are difficult to differentiate). Tendon **vete** is large and tongue-shaped (with upcurved edges directed anteriorly), directed ventrolaterally from its base and then curved posteriorly. Internally the base of tendon **vete** continues into a ridge **vri** running along the entire anterior lobe **if-a** (Fig. 39).

On the stalk, the ventral flange **vlf** is fairly high but very narrow and weak (i.e., flexible); it obliterates around the ventral end of the stalk and does not reach the sternacostal ridge (which is very low near the midline).

Abdominal sternite II is fused to sternite III (no increased movability in between). No vestige of sternite I was found. Tendon **tstI** is absent. Sternite II bears a large, membranous, almost semicircular tendon **tstII** (Fig. 7). The transverse ridge **tr** is fairly heavy; around the middle it is hardly elevated from the body wall, a perforation **trpf** was absent. In the membrane in front of ridge **tr** there is no particular differentiation.

Chrysomela collaris (Chrysomelina): Very similar to *C. saliceti*, but: Tendon **vete** is wider and thus even more confluent with lamina **vela**.

Chrysomela cuprea (Chrysomelina): Also similar to *C. saliceti*, but: Ridge **if-dr** does not curve anteriorly around the base of tip **if**, but continues from the posterior lobe proximally to end at the base of tip **if** (as in Fig. 12). The anterior lamina **anla** is more strongly directed and curved ventrally from its base; thus the angle between laminae **anla** and **vela** is smaller, ca. 100°. Tendon **ante** is longer (ca. 1.5 ×). Tendon **bate** is vestigial, represented by a low internal ridge. The ventral flange **vlf** was only represented by a low, narrow ridge limited to the internal half of the stalk. Tendon **tstII** is vestigial, only represented by a low internal ridge.

Plagiodera versicolora (Chrysomelina) (Figs. 11, 39): Also similar to *C. saliceti*, but: The internal tip **if** is less deeply notched. The anteromesal edge of lamina **anla** is more distinctly angled proximally. Lamina **anla** is more strongly directed anteriorly; thus the angle between laminae **anla** and **vela** is larger, ca. 150°. Tendon **ante** is longer (ca. 1.4 ×). The origin of tendon **ante** is closer to the free edge of lamina **anla**. Tendon **bate** is absent. The base of tendon **vete** is located a bit further proximally (**vete** was apically twisted in one specimen: Fig. 11). Tendon **tstII** is shorter.

Hydrothassa glabra (Chrysomelina)
Figs. 12, 40

The internal tip **if** is moderately large and very wide. Its internal edge is only slightly notched; while lobes of **if** are thus not clearly separated, the areas corresponding to both the anterior (**if-a**) and the posterior lobe (**if-p**) are well developed. The internal edge of **if** bears a delicate tendon (**if-at**, mostly split into fringes). The dorsal ridge **if-dr** is well developed; it extends along the posterior lobe **if-p** and ends proximally at the base of the internal tip; **if-dr** does not curve anteriorly.

A well developed, long but fairly narrow (altogether tongue-shaped) anterior lamina **anla** originates some distance proximad of the tip **if** from the anteroventral face of the furcal arm (shown by dashes in Fig. 12; in one specimen the origin was rather on the anterior wall of the ventral lamina, see below and inserted scheme in Fig. 12). Lamina **anla** is directed ventrally from its base onward. The anterior tendon **ante** originates – well remote from the tip region **if** – from the anterodorsal face of the furcal arm (seated on a distinct bulge; origin separate from lamina **anla**); it is moderately long, the fringy part begins at about 1/2 from the base. Tendon **bate** is absent.

A ventral lamina **vela** that is very long distally but soon becomes shorter proximally arises from the far posterior ventral surface of the furcal arm (forming an angle of ca. 30° with the ventrally directed lamina **anla**; Figs. 12, 40); proximally it reaches hardly 2/3 down the furcal arm. The base of the ventral tendon **vete** is limited to the postero- to mid-ventral surface of the furcal arm, distad of tendon **ante** and proximad of tip **if**, and is continuous with the internal part of lamina **vela** (**vela** and **vete** are difficult to differentiate). Tendon **vete** is large, tongue-

shaped, and flat, directed (ventro)laterally from its base and hardly curved. Internally the base of tendon **vete** continues into a ridge **vri** running along the proximal part of the anterior lobe **if-a** (Fig. 40).

On the stalk, the ventral flange **vlf** is fairly high but quite narrow and weak; it obliterates around the ventral end of the stalk and does not reach the sternacostal ridge (which is very low near the midline).

Abdominal sternite II is fused to sternite III (no increased movability in between). No vestige of sternite I was found. Tendon **tstI** is absent. Sternite II bears a large, membranous, almost semicircular tendon **tstII** (in the same position as *Chrysomela*, Fig. 7; only low ridges in the one paler specimen). The transverse ridge **tr** is fairly heavy; around the middle it is quite strongly elevated from the body wall, a perforation **trpf** was absent. In the membrane in front of ridge **tr** there is no particular differentiation.

Prasocuris phellandrii (Chrysomelina)
Figs. 13, 41

The internal tip **if** is quite small and moderately wide. Its internal edge is deeply notched, and both the anterior (**if-a**) and the posterior lobe (**if-p**) are well developed. The notched internal edge of **if** bears a delicate tendon (**if-at**, mostly split into fringes). The dorsal ridge **if-dr** is vestigial; it extends along the posterior lobe **if-p**, a continuation from there was not observed.

A well developed, long but fairly narrow (altogether tongue-shaped, see inserted picture in Fig. 13) anterior lamina **anla** originates at some distance proximad of the tip **if** from the anterior (slightly ventral) face of the furcal arm. Lamina **anla** is directed (antero)ventrally from its base onward, and curved. The anterior tendon **ante** originates – well remote from the tip region **if** – from the anterodorsal face of the furcal arm (seated on a distinct bulge; origin separate from lamina **anla**); it is very long, the fringy part begins at about 3/4 from the base. Tendon **bate** is absent.

A ventral lamina **vela** that is fairly long distally but soon becomes shorter proximally arises from the postero- to mid-ventral surface of the furcal arm (forming an angle of ca. 70° with the ventrally directed lamina **anla**; Figs. 13, 41); proximally it reaches about 2/3 down the furcal arm. The base of the ventral tendon **vete** is limited to the mid-ventral surface of the furcal arm, distad of tendon **ante** and slightly proximad of tip **if**, and is continuous with the internal part of lamina **vela** (**vela** and **vete** are difficult to differentiate). Tendon **vete** is slender tongue-shaped and flat, directed laterally from its base and moderately curved. Internally the base of tendon **vete** continues into a short ridge **vri** that obliterates at the base of the anterior lobe **if-a** (Fig. 41).

On the stalk, the ventral flange **vlf** is fairly high but quite narrow and weak; it obliterates around the ventral end of the stalk and does not reach the sternacostal ridge (which is very low near the midline).

Abdominal sternite II is fused to sternite III (no increased movability in between). No vestige of sternite I was found. Tendon **tstI** is absent. Sternite II bears a moderately large, membranous, ridge-like tendon **tstII** (in the same position as in *Chrysomela*, Fig. 7). The transverse ridge **tr** is fairly heavy; around the middle it is strongly elevated from the body wall, and there was a fairly large (and high) perforation (ca. 1/3 of minimum distance between coxal cavities). In the membrane in front of ridge **tr** there is no particular differentiation.

Phaedon pyritosus (Chrysomelina)
Figs. 14, 42

The internal tip **if** is moderately large, quite long, and not very wide. Its internal edge is only slightly notched; while lobes of **if** are thus not clearly separated, the areas corresponding to both the anterior (**if-a**) and the posterior lobe (**if-p**) are well developed. The internal edge of **if** bears a delicate tendon (**if-at**, mostly split into fringes). The dorsal ridge **if-dr** is weakly developed; it extends along the posterior lobe **if-p** and ends proximally at the base of the internal tip, where **if-dr** curves a bit anteriorly.

A well developed, long but fairly narrow (altogether tongue-shaped, see inserted picture in Fig. 14) anterior lamina **anla** originates some distance proximad of the tip **if** from the anterior (slightly ventral) face of the furcal arm. Lamina **anla** is directed (antero)ventrally from its base onward. The anterior tendon **ante** originates – well remote from the tip region **if** – from the anterodorsal face of the furcal arm (seated on a distinct bulge; origin separate from lamina **anla**, but very close to its base); it is very long, the fringy part begins at about 2/3 from the base. Tendon **bate** is absent.

A ventral lamina **vela** that is long distally but soon becomes shorter proximally arises from the posterior ventral surface of the furcal arm (forming an angle of ca. 60° with the ventrally directed lamina **anla**; Figs. 14, 42); proximally it reaches well 1/2 down the furcal arm. The base of the ventral tendon **vete** is limited to the postero- to mid-ventral surface of the furcal arm, distad of tendon **ante** and far proximad of tip **if**, and is continuous with the internal part of lamina **vela** (**vela** and **vete** are difficult to differentiate). Tendon **vete** is slender, directed ventrolaterally from its base and moderately curved. Internally the base of tendon **vete** continues into a ridge **vri** that obliterates on the proximal part of the anterior lobe **if-a** (Fig. 42).

On the stalk, the ventral flange **vlf** is fairly high but quite narrow and weak; it obliterates around the ventral end of the stalk and does not reach the sternacostal ridge (which is very low near the midline).

Abdominal sternite II is fused to sternite III (no increased movability in between). No vestige of sternite I was found. Tendon **tstI** is absent. Sternite II bears a vestigial, ridge-like tendon **tstII** (in the same position as in *Chrysomela*, Fig. 7). The transverse ridge **tr** is fairly

heavy; around the middle it is moderately elevated from the body wall, and there was a small perforation (ca. 1/8 of minimum distance between coxal cavities) in one specimen, but a pair (left and right) of tiny perforations in the other. In the membrane in front of ridge **tr** there is no particular differentiation.

Phratora vitellinae (Phyllodectina)
Figs. 15, 43

The internal tip **if** is moderately large and wide. Its internal edge is quite deeply notched, and both the anterior (**if-a**) and the posterior lobe (**if-p**) are well developed. The notched internal edge of **if** bears a delicate tendon (**if-at**, mostly split into fringes). The dorsal ridge **if-dr** is well developed; it extends along the posterior lobe **if-p** and then curves anteriorly around the base of tip **if** and onto the anterior lobe **if-a** (where it is partly confluent with the mesal edge of **if-a**).

A well developed, very long and wide anterior lamina **anla** extends along the anterior (slightly ventral) face of the furcal arm from near the base of the tip **if** down into the stalk region, where it becomes gradually shorter. The free marginal parts of the lamina are curved ventrally so that the lamina has the shape of a narrow trough (open ventrally), and the lamina itself is also curved ventrally. The anterior tendon **ante** originates – well remote from the tip region **if** – from the dorsal wall of lamina **anla**; it is quite long, the fringy part begins at about 2/3 from the base. A small lobe-like tendon **bate** extends along the proximal anterodorsal part of the furcal arm.

A ventral lamina **vela** that is very long distally but soon becomes shorter proximally arises from the posterior ventral surface of the furcal arm (forming an angle of ca. 150° with the base of lamina **anla**; Figs. 15, 43); proximally it reaches well 2/3 down the furcal arm. The base of the ventral tendon **vete** is limited to the postero- to mid-ventral surface of the furcal arm, distad of tendon **ante** and at the base of tip **if**, and is continuous with the internal part of lamina **vela** (**vela** and **vete** are difficult to differentiate). Tendon **vete** is large and tongue-shaped, directed ventrolaterally from its base and then curved posteriorly. Internally the base of tendon **vete** continues into a ridge **vri** running along the entire anterior lobe **if-a** (Fig. 43).

On the stalk, the ventral flange **vlf** is fairly high but very narrow and weak; it obliterates around the ventral end of the stalk and does not reach the sternacostal ridge (which is very low near the midline).

Abdominal sternite II is fused to sternite III (no increased movability in between). No vestige of sternite I was found. Tendon **tstI** is absent. Sternite II bears a large, membranous, almost semicircular tendon **tstII** (a bit further anteriorly than in *Chrysomela*, Fig. 7: close to the anterior margin of **stII**). The transverse ridge **tr** is fairly heavy; around the middle it is hardly elevated from the body wall, a perforation **trpf** was absent. In

the membrane in front of ridge **tr** there is no particular differentiation.

Gavirga limbatella (Phyllodectina)
Figs. 16, 44

The internal tip **if** is fairly large, quite long, and moderately wide. Its internal edge is deeply notched, the posterior lobe (**if-p**) is well developed, the anterior lobe (**if-a**) is smaller. The notched internal edge of **if** bears a delicate tendon (**if-at**, mostly split into fringes). The dorsal ridge **if-dr** is distinct; it extends along the posterior lobe **if-p** (where it almost coincides with the lateral edge of the lobe, which in Fig. 16 is hidden beneath **if-dr**) and then continues proximally for some distance down the furcal arm; **if-dr** does not curve anteriorly.

An anterior lamina **anla** is absent. The anterior tendon **ante** originates – moderately close to the tip region **if** – from the anterior face of the furcal arm (seated on a distinct bulge); it is moderately long, the fringy part begins at about 1/2 from the base. Tendon **bate** is absent.

A fairly short ventral lamina **vela** arises from the anterior ventral surface of the furcal arm (Figs. 16, 44; see section 5.2.1. for the interpretation as **vela** rather than **anla**); proximally it reaches well 2/3 down the furcal arm. The base of the ventral tendon **vete** is limited to the far anterior ventral surface of the furcal arm, slightly distad of tendon **ante** and at the anterior base of tip **if**, and is continuous with the internal part of lamina **vela** (but **vela** is almost obliterate shortly proximad of the base of **vete**: at thick arrow in Fig. 44). Tendon **vete** is long and slender, directed anteriorly from its base, but then strongly curved laterally; its tip is slightly widened and flattened. Internally the base of tendon **vete** continues into a ridge **vri** obliterating on the proximal part of the anterior lobe **if-a** (Fig. 44).

On the stalk, the ventral flange **vlf** is moderately high and quite narrow (but not weak); it obliterates around the ventral end of the stalk and does not reach the sternacostal ridge (which is very low near the midline).

Abdominal sternite II is fused to sternite III (no increased movability in between). No vestige of sternite I was found. Tendons **tstI** and **tstII** are absent. The transverse ridge **tr** is fairly heavy; around the middle it is hardly elevated from the body wall, a perforation **trpf** was absent. In the membrane in front of ridge **tr** there is no particular differentiation.
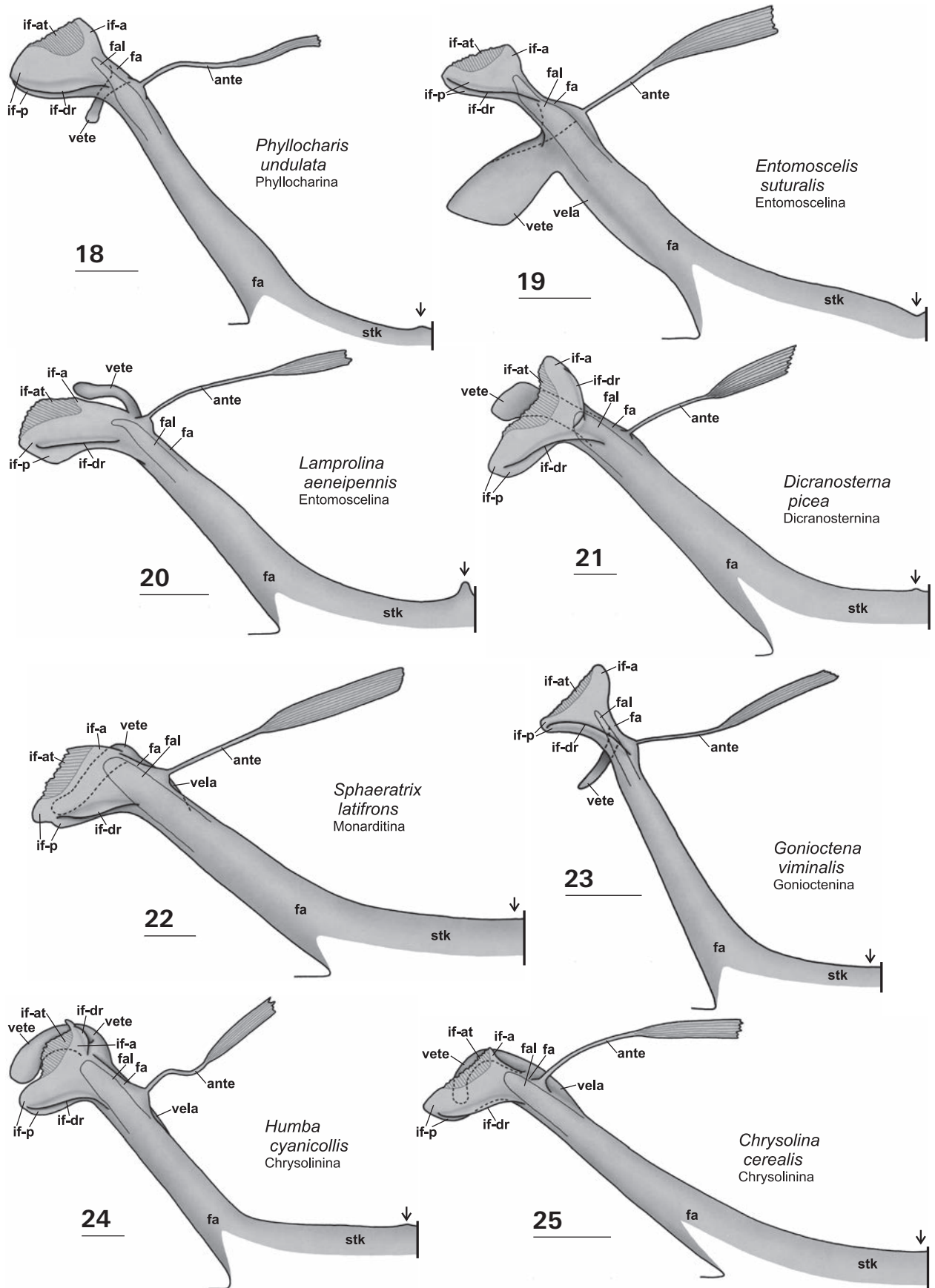
Oidosoma coccinella (Phyllocharina)
Figs. 17, 45

The internal tip **if** is moderately large, quite long, and not very wide. Its internal edge is only slightly notched; while lobes of **if** are thus not clearly separated, the areas corresponding to the anterior (**if-a**) and the posterior lobe (**if-p**) are both well developed (**if-a** is a bit smaller). The internal edge of **if** bears a delicate tendon (**if-at**, mostly
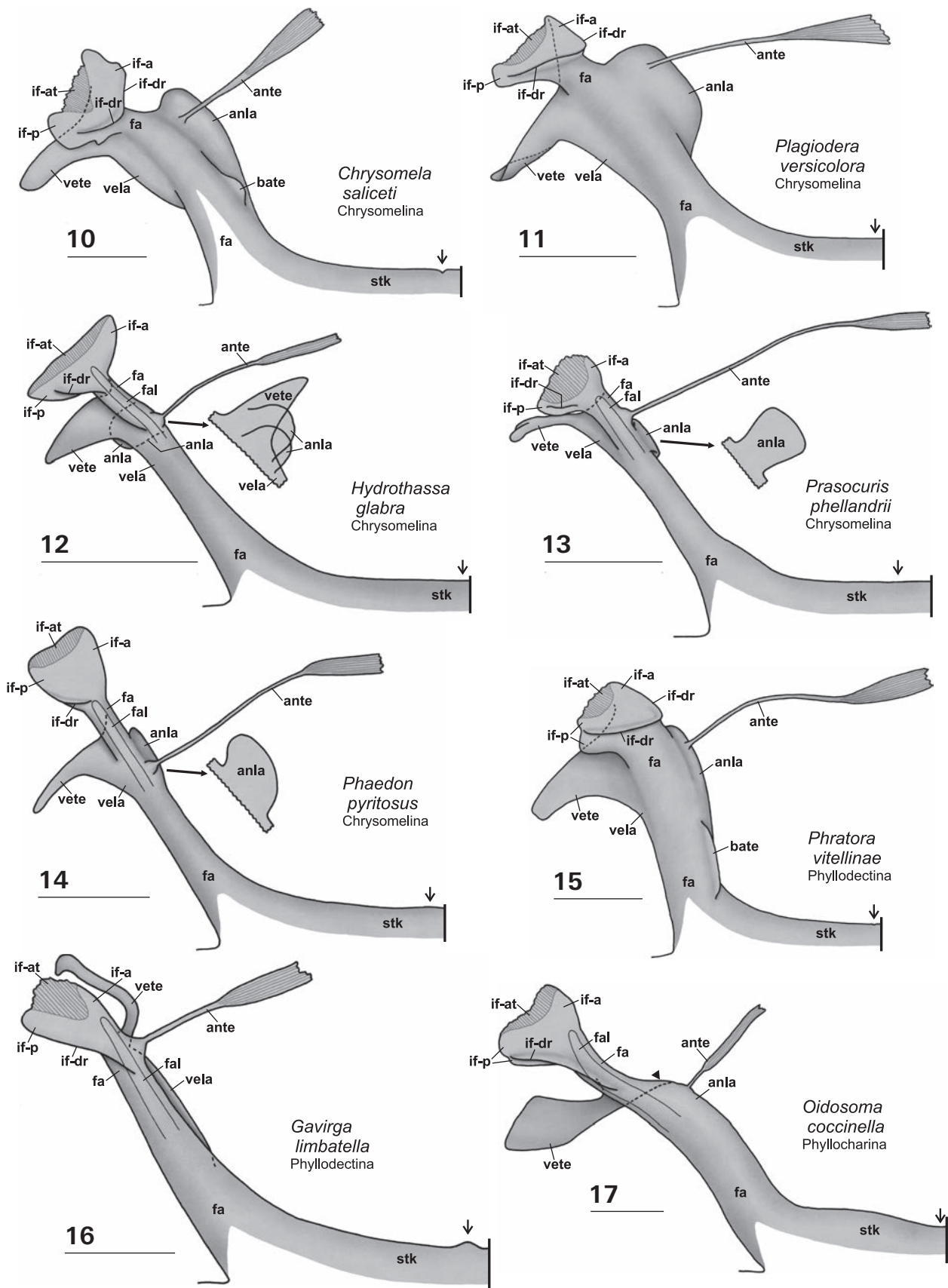
Figs. 10–25. Left half of metendosternite of various Chrysomelini in posterodorsal view (the exact aspect varies slightly depending on the degree of obliqueness of the metendosternite in a species). Near the right margin of each picture, a vertical arrow marks the midline of the body, and a vertical bar marks the end of the illustration; scale = 0.2 mm. Fringed parts of tendons are represented by grey lines. **10**: *Chrysomela saliceti* (Chrysomelina). **11**: *Plagiodera versicolora* (Chrysomelina). **12**: *Hydrothassa glabra* (Chrysomelina). **13**: *Prasocuris*

18: *Phyllocharis undulata* (Phyllocharina). **19**: *Entomoscelis suturalis* (Entomoscelina). **20**: *Lamprolina aeneipennis* (Entomoscelina). **21**: *Dicranosterna picea* (Dicranosternina). **22**: *Sphaeratrix latifrons* (Monarditina). **23**: *Gonioctena viminalis* (Gonioctenina). **24**: *Humba cyanicollis* (Chrysolinina). **25**: *Chrysolina cerealis* (Chrysolinina).

phellandrii (Chrysomelina). **14**: *Phaedon pyritosus* (Chrysomelina). **15**: *Phratora vitellinae* (Phyllodectina). **16**: *Gavirga limbatella* (Phyllodectina). **17**: *Oidosoma coccinella* (Phyllocharina). **18**: *Phyllocharis undulata* (Phyllocharina). **19**: *Entomoscelis suturalis* (Entomoscelina). **20**: *Lamprolina aeneipennis* (Entomoscelina). **21**: *Dicranosterna picea* (Dicranosternina). **22**: *Sphaeratrix latifrons* (Monarditina). **23**: *Gonioctena viminalis* (Gonioctenina). **24**: *Humba cyanicollis* (Chrysolinina). **25**: *Chrysolina cerealis* (Chrysolinina).

26 *Crosita altaica* Chrysolinina

27 *Ambrostoma fortunei* Chrysolinina

28 *Zygogramma signatipennis* Doryphorina

29 *Cosmogramma patricia* Doryphorina

30 *Proseicela vittata* Doryphorina

31 *Leptinotarsa decemlineata* Doryphorina

32 *Doryphora cincta* Doryphorina

33 *Paropsis marmorea* Paropsina
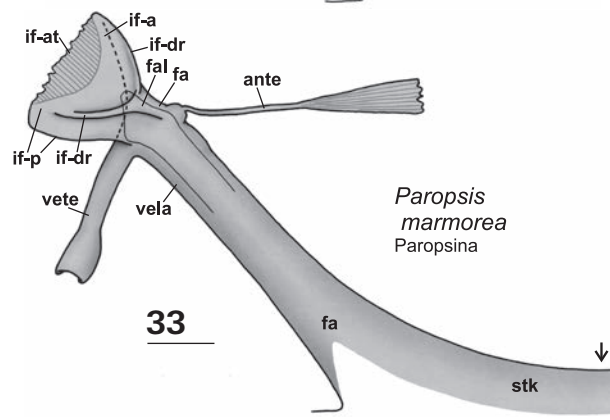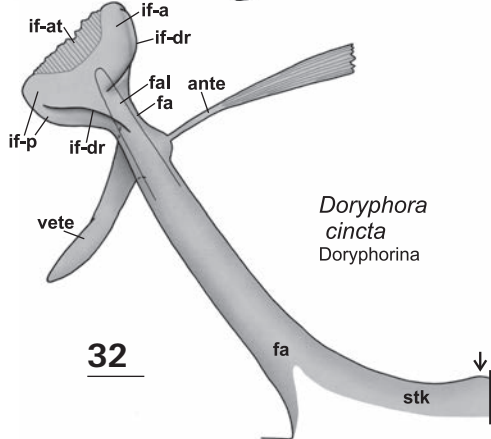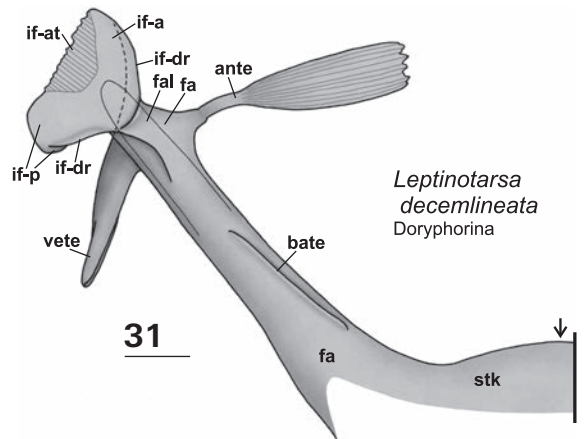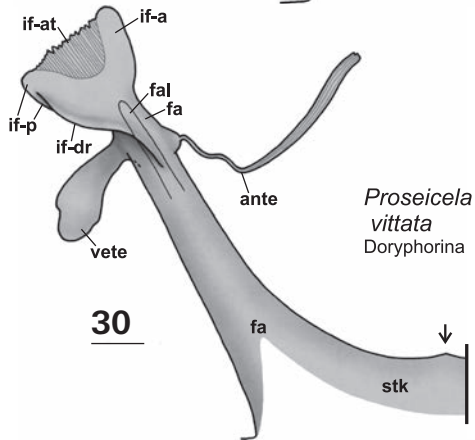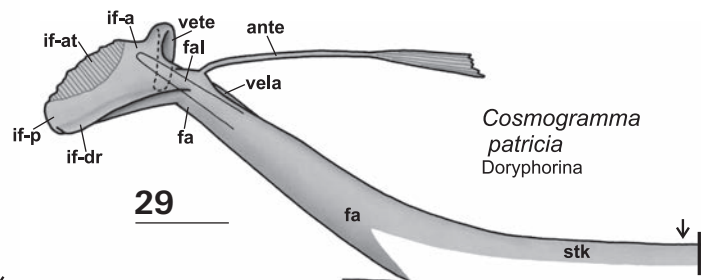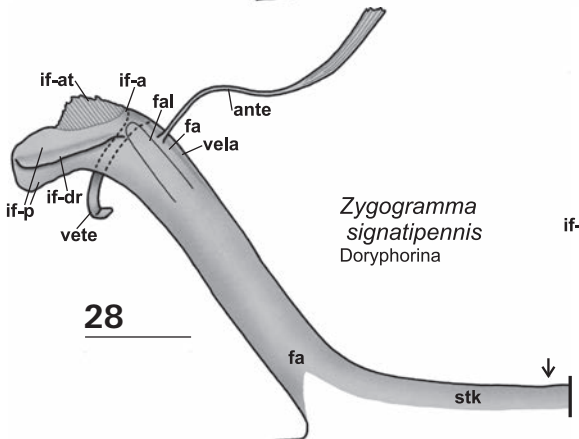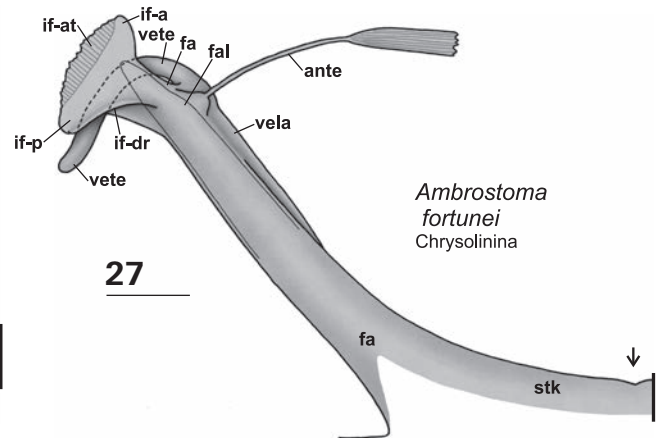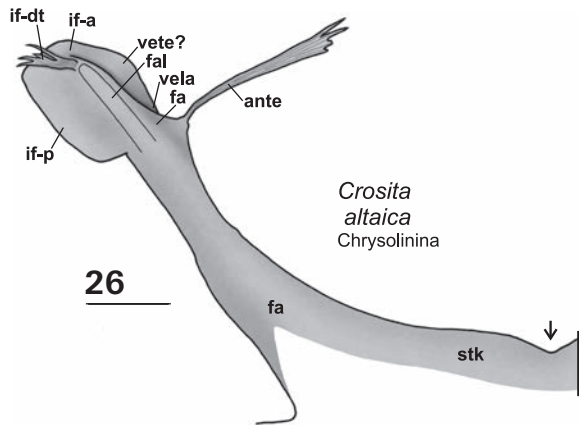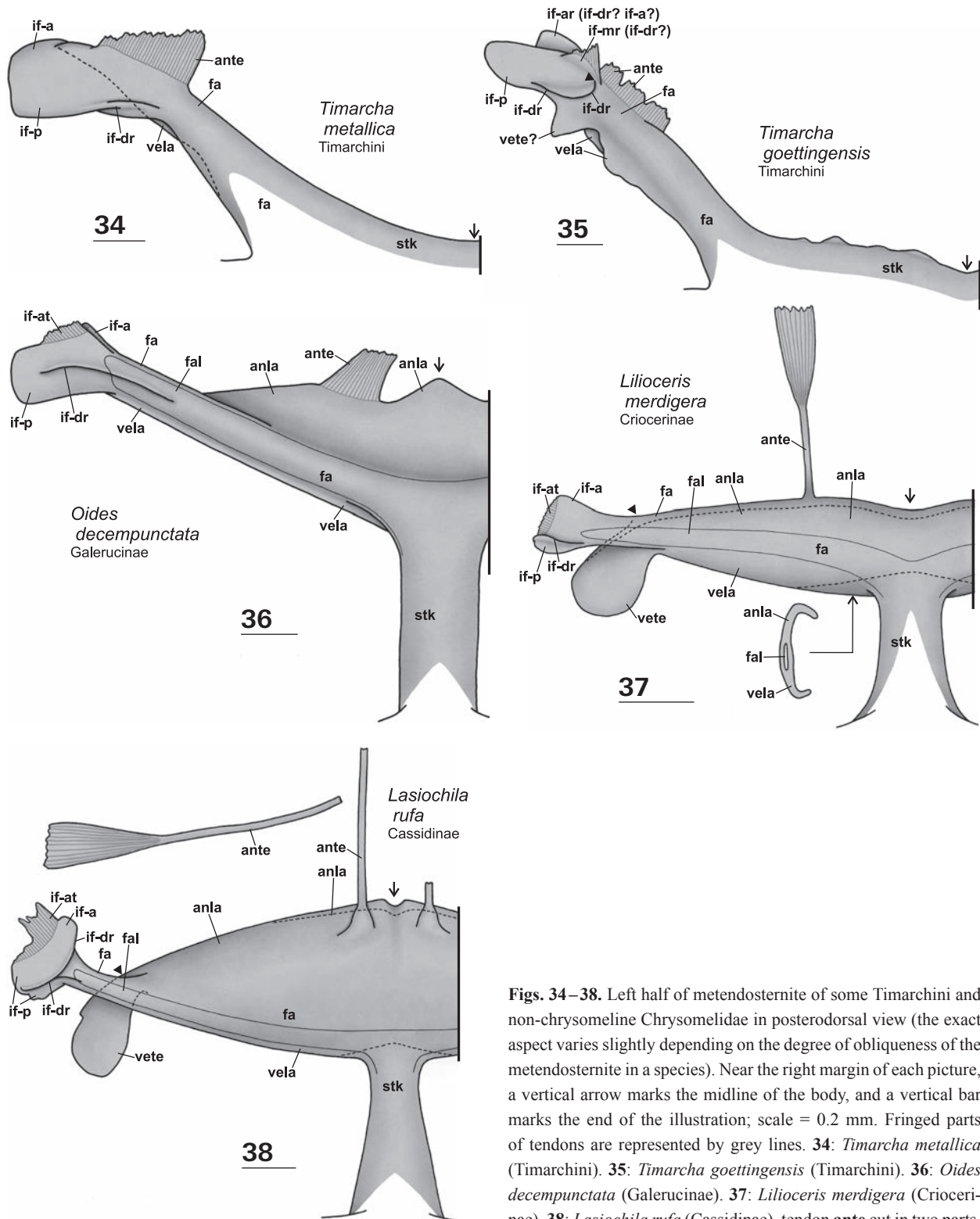
Figs. 34–38. Left half of metendosternite of some Timarchini and non-chrysomeline Chrysomelidae in posterodorsal view (the exact aspect varies slightly depending on the degree of obliqueness of the metendosternite in a species). Near the right margin of each picture, a vertical arrow marks the midline of the body, and a vertical bar marks the end of the illustration; scale = 0.2 mm. Fringed parts of tendons are represented by grey lines. **34**: *Timarcha metallica* (Timarchini). **35**: *Timarcha goettingensis* (Timarchini). **36**: *Oides decempunctata* (Galerucinae). **37**: *Lilioceris merdigera* (Criocerinae). **38**: *Lasiochila rufa* (Cassidinae), tendon **ante** cut in two parts.

← **Figs. 26–33.** Left half of metendosternite of various Chrysomelini in posterodorsal view (the exact aspect varies slightly depending on the degree of obliqueness of the metendosternite in a species). Near the right margin of each picture, a vertical arrow marks the midline of the body, and a vertical bar marks the end of the illustration; scale = 0.2 mm. Fringed parts of tendons are represented by grey lines. **26**: *Crosita altaica* (Chrysolinina). **27**: *Ambrostoma fortunei* (Chrysolinina). **28**: *Zygogramma signatipennis* (Doryphorina). **29**: *Cosmogramma patricia* (Doryphorina). **30**: *Proseicela vittata* (Doryphorina). **31**: *Leptinotarsa decemlineata* (Doryphorina). **32**: *Doryphora cincta* (Doryphorina). **33**: *Paropsis marmorea* (Paropsina).

split into fringes). The dorsal ridge **if-dr** is developed; it extends along the posterior lobe **if-p** and then continues proximally for some distance down the furcal arm; **if-dr** does not curve anteriorly.

A moderately long and very wide anterior lamina **anla** extends along the anterior face of the furcal arm, from near the base of tendon **vete** down into the stalk region; its base is not very clearly set off from the body of the furcal arm. The anterior tendon **ante** originates – far remote from the tip region **if** – from the free edge of lamina **anla**; it is very short, the fringy part starts near its base. Tendon **bate** is absent.

A ventral lamina **vela** is also absent (Fig. 45). The wide base of the ventral tendon **vete** extends across most of the ventral surface of the furcal arm (with an oblique course), shortly distad of the level of tendon **ante** and far proximad of the base of tip **if**. The ventral wall of tendon **vete** continues, around the anteromesal edge of the furcal arm distad of the **ante** origin, into the dorsal wall of lamina **anla** (at arrowhead in Fig. 17). Tendon **vete** is long and of rhombic shape, directed ventrolaterally and a bit anteriorly from its base, and hardly curved (only the tip is bent posteriorly). Internally the base of tendon **vete** does not continue into a ridge **vri** (Fig. 45).

On the stalk, the ventral flange **vlf** is moderately high and quite narrow (but not weak); it becomes lower when approaching the sternacostal ridge, but reaches the ridge.

Abdominal sternite II is fused to sternite III (no increased movability in between); a vestige of sternite I was not clearly observed. Tendons **tstI** and **tstII** are absent. The transverse ridge **tr** is moderately heavy; around the middle it is moderately elevated from the body wall, a perforation **trpf** was absent. In the membrane in front of ridge **tr** there is no particular differentiation.

Phyllocharis undulata (Phyllocharina)
Figs. 18, 46

The internal tip **if** is quite large and moderately wide. Its internal edge is deeply notched, the posterior lobe (**if-p**) is well developed, the anterior lobe (**if-a**) is fairly small. The notched internal edge of **if** bears a delicate tendon (**if-at**, mostly split into fringes). The dorsal ridge **if-dr** is well developed; it extends along the posterior lobe **if-p** and ends proximally at the base of the internal tip; **if-dr** does not curve anteriorly.

An anterior lamina **anla** is absent. The anterior tendon **ante** originates – moderately close to the tip region **if** – from the anterior face of the furcal arm (seated on a distinct bulge); it is moderately long, the fringy part begins at about 1/2 from the base (and is quite narrow). Tendon **bate** is absent.

A ventral lamina **vela** is also absent (Fig. 46). The base of the ventral tendon **vete** is limited to the far anterior ventral surface of the furcal arm, slightly distad of tendon **ante** and at the anterior base of tip **if**. Tendon **vete** is fairly short and slender, directed lateroventrally and slightly anteriorly from its base, and then slightly curved

more posteriorly; its tip is hardly widened or flattened. Internally the base of tendon **vete** continues into a very short and indistinct ridge **vri**.

On the stalk, the ventral flange **vlf** is moderately high and quite narrow (but not weak); it becomes lower when approaching the sternacostal ridge, obliterates, but then ascends again as a very low flange that reaches the ridge.

Abdominal sternite II is fused to sternite III (no increased movability in between); a weakly hardened and darkened sternite I is present in front of sternite II, the two being separated by a fairly narrow, discrete, and weakly curved line of flexibility (similar to Fig. 4). Tendons **tstI** and **tstII** are absent. The transverse ridge **tr** is moderately heavy; around the middle it is moderately elevated from the body wall, a perforation **trpf** was absent. In the membrane in front of ridge **tr** there is no particular differentiation.

Entomoscelis suturalis (Entomoscelina)
Figs. 19, 47

The internal tip **if** is fairly small and moderately wide. Its internal edge is moderately notched, the posterior lobe (**if-p**) is well developed, the anterior lobe (**if-a**) is smaller. The notched internal edge of **if** bears a delicate tendon (**if-at**, mostly split into fringes). The dorsal ridge **if-dr** is weakly developed; it extends along the posterior lobe **if-p** and then continues proximally for a short distance down the furcal arm; **if-dr** does not curve anteriorly.

An anterior lamina **anla** is absent. The anterior tendon **ante** originates – moderately close to the tip region **if** – from the anterior face of the furcal arm (seated on a bulge, which was strongly developed in the specimen shown in Fig. 19, but much smaller in the two other specimens); it is moderately long, the fringy part begins at about 1/2 from the base. Tendon **bate** is absent.

A quite short ventral lamina **vela** arises from the far posterior ventral surface of the furcal arm (Figs. 19, 47); proximally it reaches the base of the furcal arm. The wide base of the ventral tendon **vete** extends across most of the ventral surface of the furcal arm (with an oblique course, but reversed as compared to *Oidosoma*), around and proximad of the level of tendon **ante** and far proximad of the base of tip **if**, and is continuous with the internal part of lamina **vela**. In addition, the anterior part of the **vete** base bends externally to near the base of tendon **ante** (dashed lines in Fig. 19). Tendon **vete** is large and tongue-shaped, directed ventrolaterally from its base, and hardly curved. Internally the base of tendon **vete** continues into a ridge **vri** that does not reach the base of the anterior lobe **if-a** (Fig. 47).

On the stalk, the ventral flange **vlf** is moderately high and quite narrow (but not weak); it becomes very low in the lower part of the stalk, but becomes higher when approaching the sternacostal ridge, which it reaches.

Abdominal sternite II is fused to sternite III (no increased movability in between). A vestigial sternite I

is apparently present in front of sternite II, the two being separated by a narrow but not very discrete, curved line of flexibility. Tendons **tstI** and **tstII** are absent. The transverse ridge **tr** is not very heavy; around the middle it is strongly elevated from the body wall, and there was a small perforation **trpf** (ca. 1/8 – 1/12 of minimum distance between coxal cavities). In the membrane in front of ridge **tr** there is no particular differentiation.

Lamprolina aeneipennis (Entomoscelina)
Figs. 20, 48

The internal tip **if** is large, elongate, and moderately wide. Its internal edge is moderately notched, the posterior lobe (**if-p**) is well developed, the anterior lobe (**if-a**) is much smaller. The notched internal edge of **if** bears a delicate tendon (**if-at**, mostly split into fringes). The dorsal ridge **if-dr** is weakly developed; it extends along the posterior lobe **if-p** and ends proximally at the base of the internal tip; **if-dr** does not curve anteriorly.

An anterior lamina **anla** is absent. The anterior tendon **ante** originates – quite close to the tip region **if** – from the anterior face of the furcal arm (seated on a distinct bulge); it is moderately long, the fringy part begins at about 2/3 from the base. Tendon **bate** is absent.

A ventral lamina **vela** is also absent (Fig. 48). The base of the ventral tendon **vete** is limited to the far anterior ventral surface of the furcal arm, slightly distad of tendon **ante** and slightly proximad of the anterior base of tip **if**. Tendon **vete** is long and slender, directed anteriorly from its base, but then curved a bit ventrally and strongly laterally; its tip is widened and flattened. Internally the base of tendon **vete** continues into a ridge **vri** running along the entire anterior lobe **if-a** (Fig. 48).

On the stalk, the ventral flange **vlf** is very high and quite narrow (but quite stiff); it obliterates abruptly at the ventral end of the stalk and does not reach the sternacostal ridge.

Abdominal sternite II is fused to sternite III (no increased movability in between). No vestige of sternite I was found. Tendons **tstI** and **tstII** are absent. The transverse ridge **tr** is fairly heavy. Around the middle, ridge **tr** is moderately elevated from the body wall, and there was a moderately sized perforation **trpf** (ca. 1/6 of minimum distance between coxal cavities). In the membrane in front of ridge **tr** there is no particular differentiation.

Dicranosterna picea (Dicranosternina)
Figs. 21, 49

The internal tip **if** is large and very wide. Its internal edge is quite deeply notched, the posterior lobe (**if-p**) is well developed, the anterior lobe (**if-a**) is slightly smaller. The notched internal edge of **if** bears a delicate tendon (**if-at**, mostly split into fringes). The dorsal ridge **if-dr** is distinct; it extends along the posterior lobe **if-p**; from there one branch curves anteriorly around the base of tip **if** and

onto the anterior lobe **if-a**; a second branch continues proximally for some distance down the furcal arm.

An anterior lamina **anla** is absent. The anterior tendon **ante** originates – moderately close to the tip region **if** – from the anterior face of the furcal arm (seated on a vestigial bulge); it is moderately long, the fringy part begins at about 1/2 from the base. Tendon **bate** is absent.

A very short, vestigial ventral lamina **vela** arises from the antero- to mid-ventral surface of the furcal arm (Fig. 49, hidden in Fig. 21); proximally it reaches about 1/3 down the furcal arm. The wide base of the ventral tendon **vete** extends across most of the ventral surface of the furcal arm, moderately distad of tendon **ante** and moderately proximad of the base of tip **if** (see dashed lines in Fig. 21), and is continuous with the internal part of lamina **vela**. Tendon **vete** is long and slender (appearing too short in Fig. 21 due to the chosen perspective), directed anterolaterally from its base, and hardly curved; its tip is slightly widened and flattened. Internally the base of tendon **vete** continues into a ridge **vri** running along the proximal part of the anterior lobe **if-a** (Fig. 49).

On the stalk, the ventral flange **vlf** is very high and quite narrow (but fairly stiff) almost down to the sternacostal ridge, but then abruptly obliterates and does not reach the ridge.

Abdominal sternite II is very weak and apparently fused to sternite III. Sternite I was not found. Tendon **tstI** is absent. Tendon **tstII** is represented by a transverse row of delicate tendinous fringes. The transverse ridge **tr** is very heavy; around the middle it is strongly elevated from the body wall, and there was a fairly large perforation **trpf** (2/3 of minimum distance between coxal cavities, which, however, is quite narrow). In the membrane in front of ridge **tr** there is no particular differentiation.

Sphaeratrix latifrons (Monarditina)
Figs. 22, 50

The internal tip **if** is large and moderately wide. Its internal edge is somehow notched, but while the posterior lobe (**if-p**) is well developed, the anterior lobe (**if-a**) is small. The internal edge of **if** bears a delicate tendon (**if-at**, mostly split into fringes). The dorsal ridge **if-dr** is distinct; it extends along the posterior lobe **if-p** and then continues proximally for a short distance down the furcal arm; **if-dr** does not curve anteriorly.

An anterior lamina **anla** is absent. The anterior tendon **ante** originates – fairly close to the tip region **if** – from the anterior face of the furcal arm (seated on a distinct bulge); it is moderately long, the fringy part begins at about 1/2 from the base.

A fairly short ventral lamina **vela** arises from the far anterior ventral surface of the furcal arm (Figs. 22, 50); proximally it reaches about 1/3 down the furcal arm. The base of the ventral tendon **vete** is limited to the far anterior ventral surface of the furcal arm, well distad of tendon **ante** and at the anterior base of tip **if**, and is continuous with the internal part of lamina **vela**. Tendon **vete** is long

and slender, directed anteriorly from its base, then bent ventrally, and then, near its tip, laterally; its middle part is widened. Internally the base of tendon **vete** continues into a very short, indistinct ridge **vri** (Fig. 50).

On the stalk, the ventral flange **vlf** is very high, narrow, and weak almost down to the sternacostal ridge, but then quite abruptly obliterates and does not reach the ridge.

Abdominal sternite II is very weak and apparently fused to sternite III. Sternite I was not found. There is actually hardly any trace of a sclerotisation in front of ridge **tr**. Tendons **tstI** and **tstII** are absent. The transverse ridge **tr** is fairly heavy; around the middle it is strongly elevated from the body wall, and there was a moderately large perforation **trpf** (1/5 of minimum distance between coxal cavities; perforation absent in second specimen, which was apparently teneral). In the membrane in front of ridge **tr** there is no particular differentiation.

Gonioctena viminalis (Gonioctenina)
Figs. 23, 51

The internal tip **if** is fairly small and moderately wide. Its internal edge is only slightly notched; while lobes of **if** are thus not clearly separated, the areas corresponding to both the anterior (**if-a**) and the posterior lobe (**if-p**) are well developed. The internal edge of **if** bears a delicate tendon (**if-at**, mostly split into fringes). The dorsal ridge **if-dr** is well developed; it extends along the posterior lobe **if-p** and then continues proximally for some distance down the furcal arm; **if-dr** does not curve anteriorly.

An anterior lamina **anla** is absent. The anterior tendon **ante** originates – moderately close to the tip region **if** – from the anterior face of the furcal arm (seated on a distinct bulge); it is moderately long, the fringy part begins at about 1/2 from the base. Tendon **bate** is absent.

A very short, ridge-like ventral lamina **vela** arises from the far posterior ventral surface of the furcal arm (Fig. 51, hidden in Fig. 23); proximally it almost reaches the base of the furcal arm. The base of the ventral tendon **vete** is limited to the midventral surface of the furcal arm, slightly distad of tendon **ante** and moderately proximad of the base of tip **if**, and is continuous with the internal part of lamina **vela**. Tendon **vete** is moderately long, slender, directed anteroventrally from its base and then bent ventrally; its tip is hardly widened or flattened. Internally the base of tendon **vete** continues into a ridge **vri** obliterating on the proximal part of the anterior lobe **if-a** (Fig. 51).

On the stalk, the ventral flange **vlf** is moderately high and very narrow (but not weak); it becomes gradually lower when approaching the sternacostal ridge, obliterates, but then ascends again as a very low flange that reaches the ridge.

Abdominal sternite II is fused to sternite III (no increased movability in between). A vestigial sternite I is apparently present in front of sternite II, but not recognisably discrete from it. Tendons **tstI** and **tstII** are absent. The transverse ridge **tr** is moderately heavy; around the

middle it is strongly elevated from the body wall, and there was a moderately large perforation **trpf** (1/4 of minimum distance between coxal cavities). In the membrane in front of ridge **tr** there is no particular differentiation.

***Gonioctena variabilis* (Gonioctenina)**: Same as for *G. viminalis*, but: Tendon **vete** is somewhat wider and flatter. A perforation **trpf** is absent. In the membrane closely in front of ridge **tr** there is an inwardly bulged cuticular thickening reminiscent of the bulb-like pouch **vebu** in *Chrysolina cerealis* (see Fig. 6).

Humba cyanicollis (Chrysolinina)
Figs. 24, 52

The internal tip **if** is fairly large, quite short but wide. Its internal edge is moderately notched, the posterior lobe (**if-p**) is well developed, the anterior lobe (**if-a**) is much smaller. The notched internal edge of **if** bears a delicate tendon (**if-at**, mostly split into fringes). The dorsal ridge **if-dr** is well developed; it extends along the posterior lobe **if-p** and then continues proximally for a short distance down the furcal arm (the posterior-most part of lobe **if-p** is bent ventrally but fully visible beside ridge **if-dr** in Fig. 24); **if-dr** does not curve anteriorly, but there is another, isolated part of ridge **if-dr** upon the anterior lobe **if-a**.

An anterior lamina **anla** is absent. The anterior tendon **ante** originates – quite remote from the tip region **if** – from the anterior face of the furcal arm (seated on a distinct bulge); it is moderately long, the fringy part begins at about 1/2 from the base. Tendon **bate** is absent.

A short ventral lamina **vela** arises from the antero- to mid-ventral surface of the furcal arm (Figs. 24, 52); proximally it almost reaches the base of the furcal arm. The base of the ventral tendon **vete** is limited to the far anterior ventral surface of the furcal arm, well distad of tendon **ante** and on the anterior basal part of tip **if**, and is continuous with the internal part of lamina **vela**. Tendon **vete** is short and wide, directed anteriorly from its base and then evenly and strongly curved ventrally and laterally, and a bit posteriorly; its tip is not widened. Internally the base of tendon **vete** continues into a ridge **vri** running along the entire anterior lobe **if-a** (Fig. 52).

On the stalk, the ventral flange **vlf** is moderately high and quite narrow (and moderately stiff); it becomes very low around the ventral end of the stalk but reaches the sternacostal ridge.

Abdominal sclerotisations anterior to ridge **tr** are too weak for assessing whether sternite II is fused to sternite III. Sternite I is apparently absent. Tendons **tstI** and **tstII** are absent. The transverse ridge **tr** is fairly heavy; around the middle it is moderately elevated from the body wall, and there was a tiny perforation **trpf** (ca. 1/12 of minimum distance between coxal cavities). In the membrane in front of ridge **tr** there is no particular differentiation.

Chrysolina cerealis (Chrysolinina)
Figs. 25, 53

The internal tip **if** is moderately large, short but very wide. Its internal edge is moderately notched, the posterior lobe (**if-p**) is well developed, the anterior lobe (**if-a**) is small. The notched internal edge of **if** bears a delicate tendon (**if-at**, mostly split into fringes). The dorsal ridge **if-dr** is strongly developed; it extends along the posterior lobe **if-p** and then continues proximally for a short distance down the furcal arm (the posterior-most part of lobe **if-p** is bent ventrally and partly hidden beneath ridge **if-dr** in Fig. 25); **if-dr** does not curve anteriorly.

An anterior lamina **anla** is absent. The anterior tendon **ante** originates – fairly close to the tip region **if** – from the anterior face of the furcal arm (seated on a small bulge); it is moderately long, the fringy part begins at about 1/2 from the base. Tendon **bate** is absent.

A fairly short ventral lamina **vela** arises from the far anterior ventral surface of the furcal arm (Figs. 25, 53); proximally it reaches about 1/2 down the furcal arm. The base of the ventral tendon **vete** is limited to the far anterior ventral surface of the furcal arm, slightly distad of tendon **ante** and at the anterior base of tip **if**, and is continuous with the internal part of lamina **vela**. Tendon **vete** is long and slender, directed ventrolaterally and also anteriorly from its base and then evenly curved posteriorly; its tip is slightly widened. Internally the base of tendon **vete** continues into a ridge **vri** running along the proximal part of the anterior lobe **if-a** (Fig. 53).

On the stalk, the ventral flange **vlf** is moderately high and quite narrow (but not weak); it becomes very low around the ventral end of the stalk but reaches the sternacostal ridge.

The weak abdominal sternite II is fused to sternite III (no increased movability in between). No vestige of sternite I was found. Tendons **tstI** and **tstII** are absent. The transverse ridge **tr** is fairly heavy; around the middle it is strongly elevated from the body wall, and there was a moderately large perforation **trpf** (1/4–1/6 of minimum distance between coxal cavities). In the membrane in front of ridge **tr** there was no particular differentiation in one specimen (male) but a tiny, bulb-like, sclerotised pouch **vebu** in the other (female, Fig. 6). When the abdomen is fully appressed to the thorax (achieved by artificial movement in the dissected specimen), the bulb is inserted into the perforation **trpf** (which is considerably wider than the bulb).

Chrysolina bicolor (Chrysolinina) (Fig. 53): Same as for *C. cerealis*, but: Lamina **vela** reaches a bit further down the furcal arm. Tendon **vete** is somewhat shorter and wider. There is no bulb **vebu** in front of ridge **tr** (males examined).

Chrysolina grossa (Chrysolinina) (Fig. 53): Same as for *C. cerealis*, but: The anterior lobe **if-a** of tip **if** is even less developed. Lamina **vela** reaches a bit further down the furcal arm. Tendon **vete** is somewhat shorter and wider,

and a bit more strongly curved. There is no bulb **vebu** in front of ridge **tr** (including the examined female). In one specimen, sternite I was represented by one small distinctly darkened and hardened patch per side, located in the most anterodorsal wall of the metacoxal cavity.

Oreina speciosa (Chrysolinina) (Fig. 54): Same as for *C. cerealis*, but: Tendon **vete** has its origin slightly further remote from tip **if** and closer to **ante**, is directed ventrally and somewhat laterally from its base, but hardly or not at all anteriorly; it is distinctly curved (posterolaterally) thereafter, and is longer and more slender. Lamina **vela** is of similar extension. Flange **vlf** is less high and becomes very low further dorsally. Perforation **trpf** is very small to moderately sized. There is no bulb **vebu** in front of ridge **tr** (one male and two females examined). Sternite I is represented by a moderately sized, distinctly darkened and hardened patch that is hinged upon the anterior margin of sternite II.

Oreina intricata (Chrysolinina) (Fig. 54): Same as for *C. cerealis*, but: Tendon **vete** has its origin slightly further remote from tip **if** and closer to **ante**, is directed ventrally from its base, hardly anteriorly and not at all laterally; it is only slightly curved (posteriorly) thereafter, and its tip is more strongly widened. Lamina **vela** is of similar extension but slightly shorter. Flange **vlf** is less high and becomes very low further dorsally. Perforation **trpf** is very small. There is no bulb **vebu** in front of ridge **tr** (two females examined). Sternite I is represented by a moderately sized, distinctly darkened and hardened patch that is hinged upon the anterior margin of sternite II.
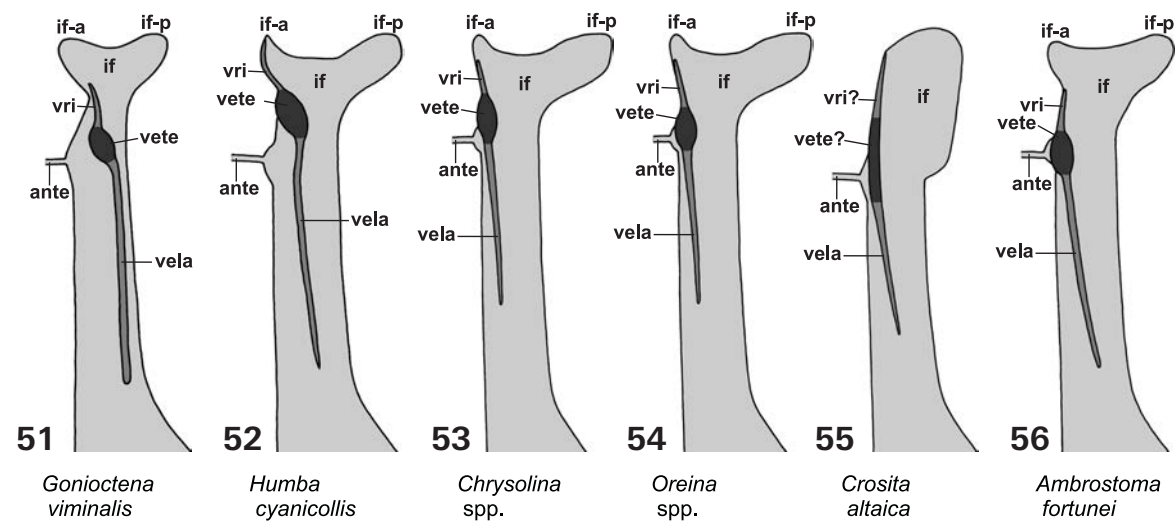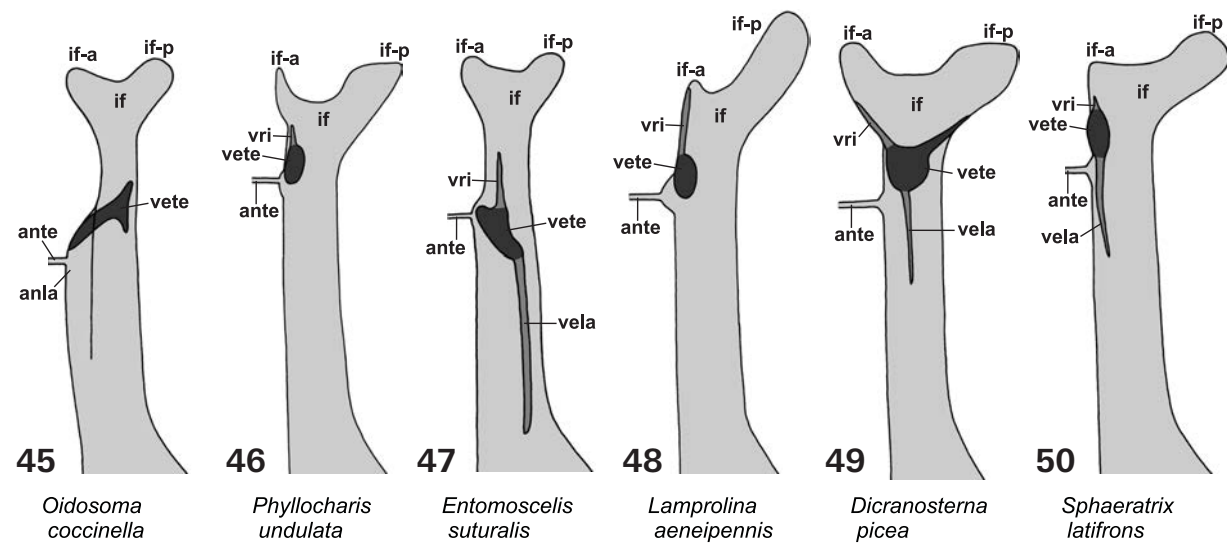
Crosita altaica (Chrysolinina)
Figs. 26, 55; hind wings reduced

Altogether very aberrant. The internal tip **if** is quite large, elongate but narrow (but see below for a potential integration of tendon **vete** into tip **if**). The internal edge of **if** is slightly convex rather than notched; lobes **if-a** and **if-p** of **if** are thus not distinguished, and the relative size of the areas corresponding to them cannot be assessed (also due to the possible inclusion of **vete**). Along the internal edge of **if** there is no delicate tendon (**if-at**); however, a group of fringes (**if-dt**) originates from the disc of **if**, next to the internal end of the furcal arm lumen (**fal**). A dorsal ridge **if-dr** is absent.

An anterior lamina **anla** is absent. The anterior tendon **ante** originates – quite remote from the tip region **if** – from the anterior face of the furcal arm (seated on a large bulge); it is short, the fringy part begins at or near the base. Tendon **bate** is absent.

A fairly short ventral lamina **vela** arises from the anterior ventral surface of the furcal arm (Fig. 55, hidden in Fig. 26); proximally it reaches well 1/2 down the furcal arm. An individualised tendon **vete** is absent; however, lamina **vela** continues distally into the apparent anteromesal edge of tip **if**, and **vete** (plus ridge **vri**?) may

39 *Chrysomela* spp. *Plagiodera versicolora*

40 *Hydrothassa glabra*

41 *Prasocuris phellandrii*

42 *Phaedon pyritosus*

43 *Phratora vitellinae*

44 *Gavirga limbatella*

45 *Oidosoma coccinella*

46 *Phyllocharis undulata*

47 *Entomoscelis suturalis*

48 *Lamprolina aeneipennis*

49 *Dicranosterna picea*

50 *Sphaeratrix latifrons*

51 *Gonioctena viminalis*

52 *Humba cyanicollis*

53 *Chrysolina* spp.

54 *Oreina* spp.

55 *Crosita altaica*

56 *Ambrostoma fortunei*

Figs. 39–63. Left furcal arm of metendosternite of various Chrysomelini in ventrolateral and slightly anterior view, semi-diagrammatical. The exact aspect varies slightly among the illustrations; it was attempted to realise a view directed perpendicular on the internal tip **if**, and with the tendon **ante** directed exactly to the left. Shape and proportions of substructures of the furcal arm are only considered to a limited extent (therefore no scale is given). Medium gray marks the base of the ventral lamina **vela** upon the furcal arm and the base of the ventral ridge **vri** on the internal tip, dark gray marks the base of the ventral tendon **vete** upon the furcal arm (note that the bases of all three elements, if present, are continuous with each other, and in the specimens the borders between the bases of **vela**, **vete**, and **vri** are less clear-cut than indicated in the illustrations). The width of the base of lamina **vela** as shown in the illustrations approximately reflects the length of lamina **vela**. **39**: *Chrysomela* spp. and *Plagiodera versicolora* (Chrysomelina). **40**: *Hydrothassa glabra* (Chrysomelina). **41**: *Prasocuris phellandrii* (Chrysomelina). **42**: *Phaedon pyritosus* (Chrysomelina). **43**: *Phratora vitellinae* (Phyllodectina). **44**: *Gavirga limbatella* (Phyllodectina). **45**: *Oidosoma coccinella* (Phyllocharina). **46**: *Phyllocharis undulata* (Phyllocharina). **47**: *Entomoscelis suturalis* (Entomoscelina). **48**: *Lamprolina aeneipennis* (Entomoscelina). **49**: *Dicranosterna picea* (Dicranosternina). **50**: *Sphaeratrix latifrons* (Monarditina). **51**: *Gonioctena viminalis* (Gonioctenina). **52**: *Humba cyanicollis* (Chrysolinina). **53**: *Chrysolina* spp. (Chrysolinina). **54**: *Oreina* spp. (Chrysolinina). **55**: *Crosita altaica* (Chrysolinina). **56**: *Ambrostoma fortunei* (Chrysolinina). **57**: *Zygogramma signatipennis* (Doryphorina). **58**: *Cosmogramma patricia* (Doryphorina). **59**: *Proseicela vittata* (Doryphorina). **60**: *Leptinotarsa decemlineata* (Doryphorina). **61**: *Doryphora* spp. and *Desmogramma bivia* (Doryphorina). **62**: *Labidomera clivicollis* (Doryphorina). **63**: *Paropsis marmorea* and *Trachymela serpiginosa* (Paropsina).

thus have been integrated into tip **if**, representing its anteromesal portion.

On the stalk, the ventral flange **vlf** is very high and quite narrow (and moderately stiff); it gradually obliterates well before the sternacostal ridge, but close to the latter it arises again to reach it as a low ridge.

Abdominal sclerotisations anterior to ridge **tr** are too weak for assessing whether sternite II is fused to sternite III. Sternite I is apparently absent. Tendons **tstI** and **tstII** are absent. The transverse ridge **tr** is quite narrow; around the middle it is moderately elevated from the body wall, there was no perforation **trpf**. In the membrane in front of ridge **tr** there is no particular differentiation.

Ambrostoma fortunei (Chrysolinina)
Figs. 27, 56

The internal tip **if** is moderately large, quite short but wide. Its internal edge is hardly notched; while lobes of **if** are thus not clearly separated, the areas corresponding to both the anterior (**if-a**) and the posterior lobe (**if-p**) are well developed – especially the latter. The internal edge of **if** bears a delicate tendon (**if-at**, mostly split into fringes). The dorsal ridge **if-dr** is distinct; it extends along the posterior lobe **if-p** and then continues proximally for a short distance down the furcal arm (the distal posterior-most part of lobe **if-p** is bent ventrally and hid-

den beneath ridge **if-dr** in Fig. 27); **if-dr** does not curve anteriorly.

An anterior lamina **anla** is absent. The anterior tendon **ante** originates – quite remote from the tip region **if** – from the anterior face of the furcal arm (seated on a distinct bulge); it is moderately long, the fringy part begins at about 2/5 from the base. Tendon **bate** is absent.

A fairly short ventral lamina **vela** arises from the far anterior (distal part) to slightly anterior (proximal part) ventral surface of the furcal arm (Figs. 27, 56); proximally it reaches well 1/2 down the furcal arm. The base of the ventral tendon **vete** is limited to the far anterior ventral surface of the furcal arm, at the level of tendon **ante** and well proximad of the anterior base of tip **if**, and is continuous with the internal part of lamina **vela**. Tendon **vete** is long and slender, directed anterolaterally and a bit ventrally from its base and then evenly and moderately curved posterolaterally; its tip is not widened. Internally the base of tendon **vete** continues into a ridge **vri** obliterating at the base of the anterior lobe **if-a** (Fig. 56).

On the stalk, the ventral flange **vlf** is moderately high and quite narrow (and moderately stiff); it gradually obliterates in the ventral-most part of the stalk and does by far not reach the sternacostal ridge.

Abdominal sclerotisations anterior to ridge **tr** are too weak for assessing whether sternite II is fused to sternite III. Sternite I is apparently absent. Tendons **tstI** and **tstII** are absent. The transverse ridge **tr** is quite narrow; around the middle it is moderately elevated from the body wall, and there was a small perforation **trpf** (ca. 1/6 of minimum distance between coxal cavities). In the membrane in front of ridge **tr** there is no particular differentiation.

Zygogramma signatipennis (Doryphorina)
Figs. 28, 57

The internal tip **if** is fairly large, short but very wide. Its internal edge is moderately notched, the posterior lobe (**if-p**) is well developed, the anterior lobe (**if-a**) is very small. The notched internal edge of **if** bears a delicate tendon (**if-at**, mostly split into fringes). The dorsal ridge **if-dr** is strongly developed; it extends along the posterior lobe **if-p** (near its middle) and continues proximally to the base of the internal tip; **if-dr** does not curve anteriorly.

An anterior lamina **anla** is absent. The anterior tendon **ante** originates – fairly close to the tip region **if** – from the anterior face of the furcal arm (not seated on a distinct bulge); it is moderately long, the fringy part begins at well 1/2 from the base. Tendon **bate** is absent.

A short ventral lamina **vela** arises from the far anterior ventral surface of the furcal arm (Figs. 28, 57); proximally it reaches about 1/2 down the furcal arm. The base of the ventral tendon **vete** is limited to the far anterior ventral surface of the furcal arm, slightly distad of tendon **ante** and on the anterior basal part of tip **if**, and is continuous with the internal part of lamina **vela**. Tendon **vete** is long and slender, directed ventrolaterally from its base and then evenly curved posteriorly; its tip is not widened

but especially strongly curved. Internally the base of tendon **vete** continues into a short ridge **vri** running along the anterior lobe **if-a** (Fig. 57).

On the stalk, the ventral flange **vlf** is moderately high and quite narrow (but not weak); it becomes very low around the ventral end of the stalk but reaches the sternacostal ridge.

The weak abdominal sternite II is fused to sternite III (no increased movability in between). No vestige of sternite I was found. Tendons **tstI** and **tstII** are absent. The transverse ridge **tr** is moderately heavy; around the middle it is moderately elevated from the body wall, and there was a small perforation **trpf** (ca. 1/5 – 1/8 of minimum distance between coxal cavities). In the membrane in front of ridge **tr** there is no particular differentiation.

***Zygogramma flavotaeniata* (Doryphorina)**: Same as for *Z. signatipennis*, but: Lamina **vela** is even shorter, vestigial.

Cosmogramma patricia (Doryphorina)
Figs. 29, 58

The internal tip **if** is fairly large, short but very wide. Its internal edge is moderately notched, the posterior lobe (**if-p**) is well developed, the anterior lobe (**if-a**) is small. The notched internal edge of **if** bears a delicate tendon (**if-at**, mostly split into fringes). The dorsal ridge **if-dr** is strongly developed; it extends along the posterior lobe **if-p** and then continues proximally for a short distance down the furcal arm; **if-dr** does not curve anteriorly.

An anterior lamina **anla** is absent. The anterior tendon **ante** originates – quite close to the tip region **if** – from the anterior face of the furcal arm (seated on a wide bulge); it is moderately long, the fringy part begins at about 2/3 from the base. Tendon **bate** is absent.

A short, vestigial ventral lamina **vela** arises from the far anterior ventral surface of the furcal arm (Figs. 29, 58); proximally it reaches hardly 1/2 down the furcal arm. The base of the ventral tendon **vete** is limited to the far anterior ventral surface of the furcal arm, well distad of tendon **ante** and on the anterior basal part of tip **if**, and is continuous with the internal part of lamina **vela**. Tendon **vete** is long and slender, directed anteroventrally from its base and then evenly curved posteriorly; its tip is hardly widened. Internally the base of tendon **vete** does not continue into a ridge **vri** (Fig. 58).

On the stalk, the ventral flange **vlf** is fairly high and quite narrow (but not weak); it becomes very low around the ventral end of the stalk but reaches the sternacostal ridge.

The weak abdominal sternite II is fused to sternite III (no increased movability in between). No vestige of sternite I was found. Tendons **tstI** and **tstII** are absent. The transverse ridge **tr** is moderately heavy; around the middle it is moderately elevated from the body wall, and there was no perforation **trpf**. In the membrane in front of ridge **tr** there is no particular differentiation.

Proseicela vittata (Doryphorina)
Figs. 30, 59

The internal tip **if** is large and moderately wide. Its internal edge is very deeply notched, both the posterior lobe (**if-p**) and the anterior lobe (**if-a**) are well developed, though the latter is slightly smaller. The notched internal edge of **if** bears a delicate tendon (**if-at**, mostly split into fringes). The dorsal ridge **if-dr** is well developed; it extends along the posterior lobe **if-p** and then continues proximally for some distance down the furcal arm; **if-dr** does not curve anteriorly.

An anterior lamina **anla** is absent. The anterior tendon **ante** originates – moderately close to the tip region **if** – from the anterior face of the furcal arm (seated on a distinct bulge); it is moderately long, the fringy part begins at about 1/3 from the base (and is quite narrow). Tendon **bate** is absent.

A very short, vestigial ventral lamina **vela** arises from the postero- to mid-ventral surface of the furcal arm (Fig. 59, hidden in Fig. 30); proximally it reaches about 1/2 down the furcal arm. The base of the ventral tendon **vete** is limited to the postero- to mid-ventral surface of the furcal arm, at the level of tendon **ante** and well proximad of the base of tip **if**, and is continuous with the internal part of lamina **vela**. Tendon **vete** is moderately long, slender basally but widened distally, directed ventrolaterally from its base, and then curved posteriorly. Internally the base of tendon **vete** does not continue into a ridge **vri** (Fig. 59).

On the stalk, the ventral flange **vlf** is fairly high, very narrow, and weak (flexible); it obliterates in the ventral-most part of the stalk and does by far not reach the sternacostal ridge.

Abdominal sternite II is fused to sternite III. A very weakly hardened and darkened sternite I is present in front of sternite II, the two being separated by a fairly narrow, discrete, and weakly curved line of flexibility. Tendons **tstI** and **tstII** are absent. The transverse ridge **tr** is fairly heavy; around the middle it is moderately elevated from the body wall, and there was no perforation **trpf**. In the membrane in front of ridge **tr** there is no particular differentiation.

Leptinotarsa decemlineata (Doryphorina)
Figs. 31, 60

The internal tip **if** is large and very wide. Its internal edge is deeply notched, both the posterior lobe (**if-p**) and the anterior lobe (**if-a**) are well developed, though the latter is slightly smaller. The notched internal edge of **if** bears a delicate tendon (**if-at**, mostly split into fringes). The dorsal ridge **if-dr** is well developed; it extends along the posterior lobe **if-p**; from there one branch curves anteriorly around the base of tip **if** and onto the anterior lobe **if-a**; a second branch continues proximally for some distance down the furcal arm.

An anterior lamina **anla** is absent. The anterior tendon **ante** originates – quite close to the tip region **if** –

from the anterior face of the furcal arm (seated on a large bulge); it is quite short, the fringy part begins at about 1/4 from the base. A very short but wide tendon **bate** was present in one specimen (Fig. 31), absent in the others.

A short ventral lamina **vela** arises from the mid-ventral surface of the furcal arm (Fig. 60, hidden in Fig. 31); proximally it reaches about 2/3 down the furcal arm. The base of the ventral tendon **vete** is limited to the mid-ventral surface of the furcal arm, at the level of tendon **ante** and slightly proximad of the base of tip **if**, and is continuous with the internal part of lamina **vela**. Tendon **vete** is long, slender basally but widened distally (and slightly grooved mesally), directed ventrally and a bit laterally from its base, and almost straight. Internally the base of tendon **vete** continues into a ridge **vri** running along the entire anterior lobe **if-a** (Fig. 60).

On the stalk, the ventral flange **vlf** is fairly high, very narrow, and weak (flexible); it obliterates in the ventral-most part of the stalk and does by far not reach the sternacostal ridge.

Abdominal sternite II is fused to sternite III. A weakly hardened and darkened sternite I is present in front of sternite II, the two being separated by a fairly narrow, discrete, and weakly curved line of flexibility. Tendons **tstI** and **tstII** are absent. The transverse ridge **tr** is fairly heavy; around the middle it is moderately elevated from the body wall, and there was a small perforation **trpf** (ca. 1/8 of minimum distance between coxal cavities). In the membrane in front of ridge **tr** there is no particular differentiation.

Doryphora cincta (Doryphorina)
Figs. 4, 5, 32, 61

The internal tip **if** is large and very wide. Its internal edge is quite deeply notched, both the posterior lobe (**if-p**) and the anterior lobe (**if-a**) are well developed, though the latter is slightly smaller. The notched internal edge of **if** bears a delicate tendon (**if-at**, mostly split into fringes). The dorsal ridge **if-dr** is weakly developed (but with some variation); it extends along the posterior lobe **if-p**; from there one branch curves anteriorly around the base of tip **if** and onto the anterior lobe **if-a**; a second branch continues proximally to the base of the internal tip.

An anterior lamina **anla** is absent. The anterior tendon **ante** originates – moderately close to the tip region **if** – from the anterior face of the furcal arm (seated on a distinct bulge); it is quite short, the fringy part begins at about 1/3 from the base. Tendon **bate** is absent.

A ventral lamina **vela** is also absent (Fig. 61). The base of the ventral tendon **vete** is limited to the postero- to mid-ventral surface of the furcal arm, at the level of tendon **ante** and well proximad of the base of tip **if**. Tendon **vete** is fairly long, slender basally but widened distally (and slightly grooved laterally), directed ventrally and a bit laterally from its base, and then curved posteriorly. Internally the base of tendon **vete** continues into a

ridge **vri** that obliterates at the base of the anterior lobe **if-a** (Fig. 61).

On the stalk, the ventral flange **vlf** is quite low, narrow, and weak (flexible; Fig. 5); it obliterates in the ventral-most part of the stalk and does by far not reach the sternacostal ridge.

Abdominal (Fig. 4) sternite II is fused to sternite III. A weakly hardened and darkened sternite I is present in front of sternite II, the two being separated by a fairly narrow, discrete, and weakly curved line of flexibility. Tendon **tstI** was found in a vestigial condition (Fig. 4), but this was clear only in one of the two specimens. Tendon **tstII** is absent. The transverse ridge **tr** is not very heavy; around the middle it is strongly elevated from the body wall, and there was a moderately large perforation **trpf** (1/3–1/5 of minimum distance between coxal cavities). In the membrane in front of ridge **tr** there is no particular differentiation.

Doryphora pyrrhoptera **(Doryphorina)** (Fig. 61): Same as for *D. cincta*, but: The ventral flange **vlf** is much higher in its upper part. No vestiges of tendon **tstI** found.

Desmogramma bivia **(Doryphorina)** (Fig. 61): Same as for *D. cincta*, but: The dorsal ridge **if-dr** along the posterior lobe and furcal arm is stronger (almost as shown for *Leptinotarsa* in Fig. 31). The ventral flange **vlf** was much higher in its upper part in one specimen, but low as in *D. cincta* in the other. No vestiges of tendon **tstI** found. Perforation **trpf** was ca. 1/4 of minimum distance between coxal cavities.

Labidomera clivicollis **(Doryphorina)** (Fig. 62): Same as for *D. cincta*, but: There is a very short, vestigial ventral lamina **vela** (same extension along ventral face of furcal arm as in *Leptinotarsa*). Internally the base of tendon **vete** does not continue into a ridge **vri** (Fig. 62). The ventral flange **vlf** was much higher in its upper part in one specimen, but low as in *D. cincta* in the other. No vestiges of tendon **tstI** found. Ridge **tr** is only weakly elevated from the body wall, and there was no perforation **trpf**.

Paropsis marmorea (Paropsina)
Figs. 33, 63

The internal tip **if** is large and moderately wide. Its internal edge is deeply notched, both the posterior lobe (**if-p**) and the anterior lobe (**if-a**) are well developed, though the latter is slightly smaller. The notched internal edge of **if** bears a delicate tendon (**if-at**, mostly split into fringes). The dorsal ridge **if-dr** is well developed; it extends along the posterior lobe **if-p**; from there one branch curves anteriorly around the base of tip **if** and onto the anterior lobe **if-a** (where it is partly confluent with the edge of the lobe); a second branch continues proximally for a short distance down the furcal arm.

An anterior lamina **anla** is absent. The anterior tendon **ante** originates – moderately close to the tip region

if – from the anterior face of the furcal arm (seated on a distinct bulge); it is moderately long, the fringy part begins at well 1/2 from the base. Tendon **bate** is absent.

A very short, vestigial ventral lamina **vela** arises from the far posterior ventral surface of the furcal arm (Figs. 33, 63); proximally it reaches well 1/2 down the furcal arm. The wide base of the ventral tendon **vete** extends across most of the ventral surface of the furcal arm (with an oblique course, same orientation as in *Entomoscelis*, Fig. 47), around and distad of the level of tendon **ante** and slightly proximad of the base of tip **if**, and is continuous with the internal part of lamina **vela**. Tendon **vete** is long and slender, directed ventrally from its base; its tip is slightly curved posteriorly, slightly widened, and deeply grooved on the ventral side. Internally the base of tendon **vete** continues into a strong ridge **vri** running along the entire anterior lobe **if-a** (Fig. 63, dashed line in Fig. 33).

On the stalk, the ventral flange **vlf** is moderately high, very narrow, and fairly weak; it becomes very low around the ventral end of the stalk but reaches the sternacostal ridge.

The very weak abdominal sternite II is fused to sternite III. No trace of sternite I was found. There is actually hardly any trace of a sclerotisation in front of ridge **tr**. Tendons **tstI** and **tstII** are absent. The transverse ridge **tr** is fairly heavy; around the middle it is moderately elevated from the body wall, a perforation **trpf** was absent. In the membrane in front of ridge **tr** there is no particular differentiation.

Trachymela serpiginosa **(Paropsina)**: Same as for *P. marmorea*, but: Tendon **vete** is terminally less curved (but also grooved).

Paropsides duodecimpustulata **(Paropsina)**: Same as for *P. marmorea*, but: The origin of tendon **ante** on the furcal arm is slightly further proximally. The ventral lamina **vela** is slightly longer. Tendon **vete** is terminally less curved (and hardly grooved), but more strongly and evenly curved (posteriorly) along its entire length. Ridge **vri** only reaches the base of the anterior lobe **if-a**. Flange **vlf** obliterates around the ventral end of the stalk and does not reach the sternacostal ridge.

Timarcha metallica (Timarchini)
Figs. 2, 3, 34; hind wings reduced

Altogether very aberrant. The internal tip **if** appears proportionately very large (but see below), elongate but fairly narrow, but is not clearly set off from the furcal arm. The internal edge of **if** is blunt rather than notched, occasionally a bit irregularly shaped (Fig. 2 right side), and it lacks a delicate apical tendon **if-at**. It is unclear to what extent the areas corresponding to the posterior lobe (**if-p**) and the anterior lobe (**if-a**) are represented in the tip. Tip **if** bears a faint ridge-like elevation, which likely represents the **if-dr** part upon the posterior lobe.

A wide, delicate, and partly fringy tendon in the transition area of tip **if** and the furcal arm likely represents the anterior tendon **ante**. Tendon **bate** and (probably) lamina **anla** are absent. A ridge running along the ventral side of the transition area between internal tip and furcal arm might represent a poorly developed lamina **vela**, a vestigial tendon **vete**, and the ventral ridge **vri** (Fig. 3). Note that the territories of **vete?** and **ante** should belong to the furcal arm proper, while the internal tip **if** starts apicad of these elements.

On the stalk, the ventral flange **vlf** is fairly low and wide (Fig. 3); it becomes still lower around the ventral end of the stalk but reaches the sternacostal ridge. The lateral and anterior edges of the metendosternite are thickened and somewhat folded ventrally (Fig. 3); the anterior bars (along the edge **iest**) join the **vlf** flange medially, and the lateral and anterior bars unite upon the furcal arm. In other Chrysomelinae the same areas are at most slightly swollen (Fig. 5).

Abdominal (Fig. 2) sternite II is fused to sternite III (no increased movability in between). No trace of sternite I was found. Tendon **tstI** is represented by a row of tendinous fringes of varied length. Tendon **tstII** is absent. The transverse ridge **tr** is fairly heavy; around the middle it is strongly elevated from the body wall, and there was a wide perforation **trpf** (almost 1/2 of minimum distance between coxal cavities). In the membrane in front of ridge **tr** there is no particular differentiation.

Timarcha goettingensis (Timarchini)
Fig. 35; hind wings reduced

Altogether very aberrant. The internal tip **if** is large and wide (anterior half, bearing the ridge labeled **if-ar**, bent underneath posterior half and not seen in Fig. 35). While both the areas representing the posterior lobe (**if-p**) and the anterior lobe (**if-a**) are well developed, the internal edge of **if** is convex rather than notched, and it lacks a delicate apical tendon **if-at**. Tip **if** bears three dorsal ridges, all fairly high and distinct. The one running along the proximal part of the posterior lobe and then curving anteriorly to separate the internal tip from the furcal arm proper is clearly ridge **if-dr** (compare Fig. 33). Ridge **if-mr** in the central dorsal wall bears a delicate fringy tendon; it may correspond to the **if-dr** part continuing onto the anterior lobe (compare Fig. 33). However, this identification may be more likely for the large, lobe-like ridge **if-ar** upon the anteromesal margin of the anterior lobe **if-a**, though this may alternatively represent the strongly upcurved edge of the anterior lobe. (Due to their ambiguous identification, the two latter ridges are given names of their own, but potential homologies are included in the labeling of Fig. 35.) All three ridges almost meet (but do not connect) in a single point at the base of **if** (arrowhead in Fig. 35).

A wide, delicate, and partly fringy tendon extending along the distal half of the anterior surface of the furcal arm proper likely represents the anterior tendon **ante**.

Tendon **bate** and (probably) lamina **anla** are absent. A group of laminar expansions on the far posteroventral face of the furcal arm may represent lamina **vela** and tendon **vete**, as labeled in Fig. 35.

On the stalk, the ventral flange **vlf** is fairly low and wide; it becomes still lower around the ventral end of the stalk but reaches the sternacostal ridge. The lateral and anterior edges of the metendosternite show the same condition as in *T. metallica* (see Fig. 3).

Abdominal sternite II is fused to sternite III (no increased movability in between). A vestigial sternite I is apparently present in front of sternite II, the two being separated by a very narrow, discrete, and curved line of flexibility. Tendon **tstI** is represented by a row of short tendinous fringes. Tendon **tstII** is absent. The transverse ridge **tr** is fairly heavy; around the middle it is hardly elevated from the body wall, a perforation **trpf** was absent. In the (short) membrane in front of ridge **tr** there is no particular differentiation.

4.3. Description of outgroup taxa

Fully winged representatives of the chrysomelid subfamilies Galerucinae, Cassidinae, and Criocerinae were examined. In all, the metendosternite differs strongly from that in Chrysomelinae, mainly due to the consistent presence of a long, slender, tubular stalk (**stk**) and of large anterior laminae (**anla**) also extending across the midline. The width of the lumen of the furcal arm (**fal**) varies a bit, but like in Chrysomelinae the lumen ends internally at the base of the internal tip **if**.

Oides decempunctata (Galerucinae)
Fig. 36

The internal tip **if** is moderately large, short but fairly wide. Its internal edge is not notched; while lobes of **if** are thus not clearly separated, the area corresponding to the posterior lobe (**if-p**) is strongly developed, whereas that corresponding to the anterior lobe (**if-a**) is vestigial. The mesal part of the internal edge of **if** bears a delicate tendon (**if-at**, mostly split into fringes). The dorsal ridge **if-dr** is well developed; it extends along lobe **if-p** and then down along the furcal arm for some distance; **if-dr** does not curve anteriorly.

In its proximal 2/3 the furcal arm bears a long and wide anteriorly directed laminar expansion, the anterior lamina **anla**, which becomes gradually longer towards the midline, where (upon the stalk **stk**) the **anla** of the two sides are medially confluent along their entire length and additionally are prolonged at midline. The anterior tendon **ante** is placed on the anterior edge of lamina **anla**, far mesally and thus also far remote from the tip **if**. As in *Timarcha* it is wide, short, delicate, and partly fringy. Tendon **bate** is absent.

The ventral lamina **vela** is vestigial, likely represented by a very short, ridge-like expansion along the entire posterior (slightly ventral) face of the furcal arm. The mesal part of lamina **vela** extends onto the ventral side of the stalk. There is no trace of a ventral tendon **vete**.

The median ventral flange **vlf** is fairly narrow and moderately stiff. It continues throughout the ventral (anterior) wall of the stalk and the lamina **anla** (up to its median prolongation), is very high in the area of **anla** and where the left and right furcal arm lumina meet, is much lower along the stalk proper, but gradually becomes higher again on its way down to the sternacostal ridge, which it reaches.

In the anterior abdomen many of the differentiations found in Chrysomelinae are absent (compare Figs. 2–9). Metacoxal cavities **mcc** and a ridge **tr** are not developed at all (and a perforation **trpf** is thus also absent). A tiny, low median bulge might represent a vestige of the intercoxal process **icp**. In the anterior ventral sclerotisation of the abdomen no borders between sternites II and III (and I, if present: difficult to assess due to the paucity of landmarks) can be recognised. Two pairs of wide ridge-like tendons on the anterior margin of the sclerotisations might represent either **tstI** (more likely: see *Galeruca* below) or **tstII** – but not both as they are located at the same anteroposterior level.

Galeruca tanaceti (Galerucinae)

The metendosternite is altogether similar to that in *Oides*, but: The most striking difference is the near-complete absence of the anterior lamina **anla**. The tendons **ante** arise from the anterior face of the furcal arm, at the same mesolateral level as in *Oides*, and they show the same condition as in *Oides*. The tip **if** is more elongate, and the posterior lobe **if-p** bent ventrally (thus seemingly reduced in a posterodorsal perspective). The posterior face of the furcal arm bears numerous short tendinous fringes rather than some short lamina **vela**; only the most mesal part of **vela** (next to the stalk) is present as a lamina.

The stalk is slightly wider and shorter than in *Oides*. The ventral flange **vlf** is fairly high in the upper part of the stalk but becomes gradually lower on its way to the sternacostal ridge, which it does not reach.

The anterior abdomen has metacoxal cavities **mcc** and an intercoxal process **icp**, but both are less discretely shaped as in all Chrysomelinae. Ridge **tr** is absent, as in *Oides*, but lateral ribbons of slight cuticular thickening (appearing whitish) are located as the lateral continuations of **tr** are in Chrysomelinae (Fig. 7) and provide orientation in the delimitation of sternites II and III (sternite I being absent). Two pairs of small, delicate tendons shortly in front of the sclerite margin clearly represent **tstI** (which may then also be more likely for the tendons in *Oides*).

Lilioceris merdigera (Criocerinae)
Fig. 37

The internal tip **if** is small, short and narrow. Its internal edge is only slightly notched; while lobes of **if** are thus not clearly separated, the areas corresponding to the posterior lobe (**if-p**) and anterior lobe (**if-a**) are of similar size (though **if-a** is a bit smaller). The internal edge of **if** bears a delicate tendon (**if-at**, mostly split into fringes). The dorsal ridge **if-dr** is well developed on the internal portion of the posterior lobe but becomes very low and obliterates towards the base of **if**; **if-dr** does not curve anteriorly.

In its proximal 4/5 the furcal arm bears an anteriorly directed laminar expansion, the anterior lamina **anla**, which becomes gradually longer towards the midline, where (upon the stalk **stk**) the **anla** of the two sides are medially confluent along most of their length. The entire anterior edge of **anla** is narrowly folded ventrally (dashed line and cross section in Fig. 37). The anterior tendon **ante** is placed on the anterior face of lamina **anla**, far mesally and thus also far remote from the tip **if**. As in most Chrysomelinae it is long and slender, the internal half being wider and fringy. Tendon **bate** is absent.

The ventral lamina **vela** is represented by a moderately long laminar expansion along the entire posterior (slightly ventral) face of the furcal arm (longest around the middle of the arm). In its mesal part lamina **vela** is bent anteroventrally, and this fold also traverses the midline across the ventral wall of the stalk (dashed line and cross section in Fig. 37). The ventral wall of the furcal arm well proximad of the base of **if** bears a large, lobe-like ventral tendon **vete**; in its proximal part the lateral edges are bent ventrally and **vete** is thus widely groove-shaped. The base of tendon **vete** extends obliquely (orientation as in *Entomoscelis*, Fig. 47) across the entire ventral face of the furcal arm. The anterolateral (ventrally curved) edge of **vete** continues into the (likewise ventrally curved) anterior edge of lamina **anla** (dashed line in Fig. 37). The posteromesal edge of **vete** continues into the posterior edge of lamina **vela**. Accordingly, the upper surface of tendon **vete** is narrowly directly continuous with that of lamina **anla** (at arrowhead in Fig. 37; compare arrowhead in Fig. 17 of *Oidosoma*) and with that of lamina **vela**.

The median ventral flange **vlf** is fairly narrow and moderately stiff. It continues throughout the ventral (anterior) wall of the stalk and the lamina **anla** (its upper part thus forming a vertical midline connection of the downward-bent edges of laminae **anla** and **vela**), is very high almost down to the sternacostal ridge, but then it obliterates and does not reach the ridge.

The anterior abdomen is very similar to that in Chrysomelinae (compare Figs. 2–9). There are discretely bordered metacoxal cavities **mcc**, a large, discrete intercoxal process **icp**, and a heavy transverse ridge **tr**. The ridge is strongly elevated around the midline and has a very large perforation **trpf** (wider than minimum distance between coxal cavities). Sternite II is fused to sternite III,

an isolated sternite I was not found. A wide, ridge-like tendon on the anterior margin of sternite II most likely represents **tstII** (but is placed further anterolaterally than in *Chrysomela*, compare Fig. 7).

Lasiochila rufa (Cassidinae)
Fig. 38

The internal tip **if** is moderately large, short but very wide. Its internal edge is only slightly notched; while lobes of **if** are thus not clearly separated, the areas corresponding to the posterior lobe (**if-p**) and anterior lobe (**if-a**) are of similar size (though **if-a** is a bit smaller). The internal edge of **if** bears a delicate tendon (**if-at**, mostly split into fringes). The dorsal ridge **if-dr** is very low; it extends along the posterior lobe **if-p**; from there one branch curves anteriorly around the base of tip **if** and onto the anterior lobe **if-a**; a second branch continues proximally for a short distance down the furcal arm.

In its proximal 4/5 the furcal arm bears an anteriorly directed laminar expansion, the anterior lamina **anla**, which becomes gradually longer towards the midline, where (upon the stalk **stk**) the **anla** of the two sides are medially confluent along their entire length. Around the middle the anterior edge of **anla** is very narrowly folded ventrally (dashed line in Fig. 38). The anterior tendon **ante** is placed on the distal dorsal wall of lamina **anla** (upon a bulge), very close to the midline and thus also far remote from the tip **if**. It is long and slender, the internal 1/5 being wider and fringy. Tendon **bate** is absent.

The ventral lamina **vela** is vestigial, likely represented by a very short, ridge-like expansion along the entire posterior (slightly ventral) face of the furcal arm. In its mesal part lamina **vela** is bent anteroventrally, and this fold also traverses the midline across the ventral wall of the stalk (dashed line in Fig. 38). The ventral wall of the furcal arm well proximad of the base of **if** bears a large, lobe-like ventral tendon **vete**. The base of tendon **vete** extends obliquely (orientation as in *Entomoscelis*, Fig. 47) across the entire ventral face of the furcal arm except for the posterior-most part. The anterolateral edge of **vete** continues into the anterior edge of lamina **anla**. The posteromesal edge of **vete** ends on the posteroventral face of the the furcal arm wall and is not continuous with the edge of lamina **vela**. Accordingly, the upper surface of tendon **vete** is narrowly directly continuous with that of lamina **anla** (at arrowhead in Fig. 38) but not with that of lamina **vela**.

The median ventral flange **vlf** is fairly narrow and moderately stiff. It continues throughout the ventral (anterior) wall of the stalk and the lamina **anla** (its upper part thus forming a vertical midline connection of the downward-bent edges of laminae **anla** and **vela**), is high in its upper half, then almost obliterates, then becomes higher again and eventually reaches the sternacostal ridge.

The anterior abdomen is very similar to that in Chrysomelinae (compare Figs. 2–9). There are discretely bordered metacoxal cavities **mcc**, a large but quite narrow,

discrete intercoxal process **icp**, and a heavy transverse ridge **tr**. The ridge is strongly elevated around the midline and has a very small perforation **trpf** (ca. 1/5 of minimum distance between coxal cavities – while the cavities are close together). Sternite II is fused to sternite III, an isolated sternite I was not found. Tendons resembling **tstI** and **tstII** are absent.

5. Discussion

5.1. Comparison with previous morphological work

We want to embed our morphological results on the metendosternite and anterior-most abdominal venter in Chrysomelinae into a wider systematic context of Coleoptera-Cucujiformia. The body parts in question are depicted to the greatest detail found among cucujiform beetles in Doyen's (1966: mainly figs. 45–48, 55–58) treatment of *Tenebrio molitor* (Tenebrionidae), which thus is our major source for comparison (Table 2 compares the similar terminologies used herein and in Doyen 1966).

The metendosternite has been widely considered in the literature, but most illustrations are quite superficial. We use Crowson's (1938, 1944, 1955) contributions, which cover a great variety of cucujiforms, but in which most drawings are simple sketches with the meaning of many of the lines being obscure. In addition, we refer to Doyen & Tschinkel (1982; Tenebrionidae) and Tomaszewska (2000; Endomychidae), who have contributed extensive data on the metendosternite in particular families. McHugh et al.'s (1997) work on the morphology of *Megalodacne heros* (Erotylidae) also provides some data on the metendosternite.

With regard to the anterior abdominal venter, Evans's (1961) contribution on *Atomaria ruficornis* (Cryptophagidae, including the musculature) occasionally yields important supplementary information, while this part of the body has otherwise been largely neglected in the literature (including McHugh et al. 1997).

5.1.1. Metendosternite

In *Tenebrio* the internal tip of the furcal arm (**if**; "membranous tip" in Doyen 1966: figs. 45–48) is not at all widened and lacks any differentiations. This is in strong contrast to the strongly widened and highly differentiated internal tip (with apical notch, tendon **if-at** and ridge **if-dr**) of Chrysomelinae (e.g. Figs. 10, 23). However, the illustrations for a variety of Tenebrionidae in Doyen & Tschinkel (1982: figs. 25–31) show that there is much

Table 2. Synonymic list of morphological terms used in this paper and in Doyen (1966). For Doyen's terms reference to illustrations is partly given from which the usage of a term is evident.

Abbreviation	This paper: Chrysomelinae	Doyen (1966): *Tenebrio*
fa	furcal arm	furcal arm
fal	lumen of furcal arm	furcal invagination in figs. 45, 47
stk	stalk of metendosternite	stalk of metendosternite
anla	anterior lamina	anterior flange in fig. 46
ante	anterior tendon	anterior tendon in fig. 45
vela	ventral lamina	lamina
vete	ventral tendon	[absent]
bate	basal tendon	[absent]
if	internal tip of furcal arm	"membranous tip" of furcal arm in fig. 45
if-a	anterior lobe of internal tip	[absent]
if-p	posterior lobe of internal tip	[absent]
if-at	delicate tendon on apical edge of internal tip	[absent]
if-dr	dorsal ridge(s) on internal tip	[absent]
if-dt	dorsal tendinous fringes of internal tip	[absent]
vlf	ventral flange in anterior wall of stalk	"ventral longitudinal flange" in fig. 47
scr	sternacostal ridge	sternacostal ridge in fig. 47
scs	sternacostal suture	sternacostal suture
dcr	discrimen	"median ridge / groove" in figs. 44, 47
vn3	metathoracic ventrite	metasternum
vebu	bulb-like pouch in front of ridge tr	[absent]
icp	intercoxal process (of abdomen III)	intercoxal process in fig. 56
mcc	metacoxal cavity	metacoxal cavity
stl	abdominal (hemi-)sternite I	abdominal sternite I
stlI	abdominal (hemi-)sternite II	abdominal sternite II
stlII	abdominal sternite III	abdominal sternite III
tstl	paired tendons on area of sternite I of abdomen	likely corresponding to "antecostal suture" in fig. 56
tstlI	paired tendons on sternite II of abdomen	[absent]
tr	transverse ridge of anterior abdominal venter	[absent]
trpf	median perforation of transverse ridge tr	[absent]

variation in the structuring of the internal tip **if**, which is often widened and may even bear a ridge like **if-dr** in Chrysomelinae (e.g. Fig. 11). Unfortunately, these illustrations are not detailed enough for closer comparison.

Tenebrio has a wide, short "anterior flange" which extends along the proximal two thirds of the anterior surface of the furcal arm and likely corresponds with the anterior lamina **anla** present in some Chrysomelinae (Figs. 10–15; it is unclear whether the left and right **anla** meet at midline, as in Figs. 36–38). The anterior tendon **ante** of *Tenebrio* is distinct and shaped as a long ribbon, and it originates near the internal tip **if**, as in Chrysomelinae. However, in contrast to the Chrysomelinae possessing a lamina **anla** (Figs. 10–15), tendon **ante** is not placed on or next to it since in *Tenebrio* **anla** obliterates far proximad of the base of **ante**.

On the posteroventral surface of the furcal arm, *Tenebrio* has another distinct lamina, which corresponds with the ventral lamina **vela** found in the same position in many Chrysomelinae (e.g. Figs. 10, 11; see section 5.2.1. for the identification of lamina **vela** in cases where it is located further anteriorly). However, there is no trace of a tendon associated with this lamina, such as tendon **vete**, which is so distinct in most Chrysomelinae (Figs.

10–33) and is present even if lamina **vela** is vestigial or absent (e.g. Figs. 32, 61).

The stalk (**stk**) of the metendosternite in *Tenebrio* is much longer and narrower than in Chrysomelinae (similar as in Figs. 36–38), which have an extremely short and wide stalk by comparison with most beetles. The ventral longitudinal flange **vlf** of *Tenebrio* is high and clearly reaches the sternacostal ridge (**scr**), as in some Chrysomelinae.

Some of the less conspicuous structures that Doyen (1966: figs. 45, 48) reports for *Tenebrio* were not found in Chrysomelinae: the two "transverse flanges" per side that cut across the anterior and ventral laminae on the anteroventral face of the furcal arm, and the pair of "ventral processes" of the stalk, which seem to be lateral branches of the median **vlf** flange (both structures not clearly depicted).

According to the illustrations in Crowson (1938, 1944, 1955), the shape and structuring of the metendosternite vary enormously in Cucujiformia. There is much variation even within certain families, and Chrysomelidae is among these (e.g. Crowson 1938). There are chrysomelids where, in contrast to Chrysomelinae, the stalk is long and narrow, the anterior and ventral laminae

are both extensive, the anterior tendons **ante** originate next to the midline, and the internal tip **if** is hardly widened. Almost every possible character of the metendosternite is variable in Chrysomelidae, and there are many different combinations. Our own limited data on non-chrysomeline Chrysomelidae (Figs. 36–38) together with those on Chrysomelinae confirm this.

Endomychidae is another family for which an enormous range of variation has been documented for the metendosternite. TOMASZEWSKA (2000: figs. 508–540) shows the same points of variation as seen in Chrysomelidae: The stalk can be long or short (figs. 526, 534); tendon **ante** can originate next to the midline or far distally on the furcal arm (figs. 511, 518); tendon **vete** can be large or absent (figs. 514, 537) and originate posteriorly or anteriorly (figs. 536, 534); the internal tip **if** can be apically widened or not (figs. 509, 520), and notched or not (figs. 515, 536); lamina **anla** seems to be extensive in some endomychids but absent in others (figs. 526, 538). For Tenebrionidae DOYEN & TSCHINKEL (1982: p. 138) state that the metendosternite encompasses "virtually the entire range of variation in the Cucujoidea".

On the other hand, very similar metendosternites can occur in members of different cucujiform families. For instance, the curculionid *Baris* (CROWSON 1944: fig. 84) and the endomychid *Panamomus* (TOMASZEWSKA 2000: fig. 512) both have a metendosternite that in most characters (as far as recognisable in the illustrations) resembles that in the chrysomeline *Doryphora* (Figs. 4, 32).

In conclusion, cucujiform beetles show both much plasticity and much homoplasy in the characters of the metendosternite. This situation makes the attempt appear almost useless to use metendosternite characters for the reconstruction of phylogenetic relationships among cucujiform taxa of and above subfamily level. Yet, metendosternite morphology may be more useful for phylogenetic work on subgroups of lower rank.

5.1.2. Anterior-most abdominal venter

Tenebrio (DOYEN 1966: figs. 54–58) has a pair of discrete oval-shaped (hemi-)sternites I (**stI**) located in the anterodorsal portion of the metacoxal cavities (as in Fig. 4). In Chrysomelinae there is a wide range regarding the presence of sternites I, occasionally including intra-specific variation. The one extreme, found in few chrysomelines, is a fairly clear-cut hardened, slightly brownish patch that is clearly separated by more flexible membrane from the sclerotisation of sternite II (**stII**) behind it (**stI** in *Doryphora*, Fig. 4). This sclerite, however, is always much weaker than sternites III and (usually) II. The other extreme, found in the majority of chrysomelines, is that the area of sternite I is neither harder nor darker than the neighbouring membrane, i.e. **stI** is entirely absent. For *Atomaria*, isolated remains of sternite I are reported to be absent (EVANS 1961: fig. 38).

In *Tenebrio* the anterior margin of sternite I, which is next to the anterior rim of the metacoxal cavity (compare

mcc in Fig. 4), forms an "antecostal suture" (DOYEN 1966: fig. 56), which is rather an internal ridge (see longitudinal section fig. 58 therein). This ridge bears the posterior attachment of a muscle coming from the metendosternite (a ventral longitudinal muscle of the metathorax; DOYEN 1966: figs. 57, 58) and is thus plausibly part of the antecosta of abdominal venter I, marking its anterior border. Tendon **tstI**, which is present in Timarchini but usually not in Chrysomelini (Figs. 2, 4), is located in the same position as the ridge in *Tenebrio* and is here interpreted as its (internally expanded) homologue. In Chrysomelinae, however, sternite I does not reach as far anteriorly as to include the **tstI** area (Fig. 4). Then, in Chrysomelinae, as compared to *Tenebrio*, (at least) the anterior part of sternite I has become membranous, sternite I being relatively smaller. However, this has to be tested by a study of the musculature in Chrysomelinae.

In *Tenebrio* sternite II is, like in Chrysomelinae (sclerotisation **stII** in Fig. 4), fully fused to abdominal sternite III (sclerotisation **stIII** in Fig. 4) and occupies the part of the posterodorsal wall of the metacoxal cavities that follows behind the **stI** area (see DOYEN 1966: figs. 55, 56, 58). No ridge- or tendon-like differentiation is reported to be seated on sternite II of *Tenebrio*, but its anterior part bears the posterior attachment of a muscle coming from the ridge on sternite I (a ventral longitudinal muscle of abdominal segment I; DOYEN 1966: figs. 57, 58); the attachment marks the anterior border of abdominal venter II. Sternite II is also undifferentiated in most Chrysomelinae, but some others have a tendon **tstII** (Fig. 7) in the area where in *Tenebrio* the muscle is attached. Tendon **tstII** is thus plausibly part of the antecosta of sternite II (see longitudinal section DOYEN 1966: fig. 58). The part of **stII** anteriad of **tstII** is its antesternal part.

For *Tenebrio* neither a ridge traversing the abdominal venter at the level of the metacoxal cavities nor any kind of perforation, such as ridge **tr** and perforation **trpf** in Chrysomelinae (Figs. 2, 4), is reported. For *Atomaria*, however, EVANS (1961: fig. 38) shows a transverse ridge in that position, which on the metacoxal cavity reaches further laterally than ridge **tr** in Chrysomelinae. Its median part show positional correspondence with ridge **tr** (Figs. 2, 4). However, no details are given for the median part in *Atomaria*, so it is unclear whether its ridge is elevated and perforated. Ridge **tr** is in the right position to represent the ventromedian part of the antecosta of abdominal segment III.

Tenebrio and *Atomaria* have an intercoxal process **icp** similar to that in Chrysomelinae. It is elevated from the ventral abdominal wall posteriad of ridge **tr** (see Fig. 8; or from the corresponding area in *Tenebrio*: DOYEN 1966: figs. 55, 56) and based on the above interpretation of ridge **tr** clearly belongs to abdominal venter III.

RIVNAY's (1928) description of the anterior abdominal venter in *Leptinotarsa decemlineata* is very brief. In contrast to him we did find a vestigial abdominal sternite I in the same species. In addition, while RIVNAY (1928) considers sternite II also to be absent (though he admits it might be fused to sternite III), we note that by compari-

son with *Tenebrio* this should be represented by part of the sclerotisation in the posterodorsal wall of the metacoxal cavities (Fig. 4; entirely ascribed to sternite III by RIVNAY 1928).

5.2. Homology, characters, and phylogenetic implications in Chrysomelinae

5.2.1. Homology of metendosternal laminae

The identification of potentially homologous (at the primary level) elements or simply of corresponding parts in the metendosternites of the Chrysomelinae and non-chrysomeline species here studied is mostly evident (as expressed by labeling in the illustrations), including the anterior tendon **ante**. However, there is one major homology problem involving the anterior lamina **anla**, the ventral lamina **vela**, and the ventral tendon **vete**, which show much variation in Chrysomelinae concerning their presence, position, and interrelations.

Tendons **vete** are plausibly homologous in all Chrysomelinae. While the base of tendon **vete** can be variously limited to the far posterior (e.g. Figs. 14, 33 and 42, 63) or to the far anterior (e.g. Figs. 20, 25 and 48, 53) ventral side of the furcal arm, there are also cases showing an intermediate midventral position (e.g. Fig. 60) or an extension of the base of **vete** across most of the ventral side of the furcal arm (*Oidosoma*, *Entomoscelis*, and *Dicranosterna*; Figs. 45, 47, 49). Homology of **vete** is additionally supported by the usual distal continuation of its base into a ridge **vri** that targets the posterior lobe **if-p** of the internal tip – irrespective of the anteroposterior level of the base of **vete** (e.g. Figs. 42, 53).

In the cases where the furcal arm bears two laminae, one anteriorly and one posteriorly (Figs. 39–43), these are unambiguously identified as laminae **anla** and **vela**, respectively, and considering each of them as homologous across the taxa concerned is uncontroversial (at the primary level of hypothesising homology). In cases where only a single lamina is present in a far posteroventral postion on the furcal arm (e.g. Figs. 51, 63), the identification of this as lamina **vela** is also uncontroversial, lamina **anla** then being absent. In cases where a single lamina is present in a far anteroventral position (e.g. Figs. 53, 57), this could straightforwardly be identified as a lamina **anla** – while we prefer to interpret it as lamina **vela** (see descriptions and labeling in illustrations). This needs to be explained. Concerned are *Chrysolina*, *Oreina*, *Ambrostoma*, and *Crosita* from Chrysolinina, *Gavirga* from Phyllodectina, *Sphaeratrix* from Monarditina, as well as *Zygogramma* and *Cosmogramma* from Doryphorina (but see below for a revision of the latter assignment) (Figs. 16, 22, 25, 27–29 and 44, 50, 53, 54, 56–58; note that the lamina labeled "**vela**" is well visible anteromesad of the furcal arm in

the former group of figures, which is indicative of its far anterior position).

Discussing this issue requires a view on non-chrysomelines. In the chrysomelids *Lilioceris* and *Lasiochila* (Figs. 37, 38) and in the erotylid *Megalodacne* (McHUGH et al. 1997: fig. 33) a wide tendon **vete** originates from the entire width of the furcal arm (reminiscent of *Oidosoma*, *Entomoscelis*, and *Dicranosterna*), and the dorsal surfaces of **vete** and **anla** are even narrowly continuous on the anterior face of the furcal arm (arrowhead in Figs. 37, 38; dorsal surface bent ventrally in *Lilioceris*) – a condition also indicated in *Oidosoma* (arrowhead in Fig. 17). In *Lilioceris* the dorsal surfaces of **vete** and **vela** are also narrowly continuous on the posterior face of the furcal arm. The situation in *Lilioceris* can be viewed as laminae **anla** and **vela** continuing into each other around the furcal arm, like a collar, the lateral, bending part of this being a wide tendon **vete**. It is this entire collar structure that Crowson calls "lamina" (= **anla** + **vete** + **vela**; e.g. CROWSON 1938: plt. 1 fig. 1 of the lymexylid *Hylecoetus*), and he considers a complete, wide collar as a plesiomorphic condition (for Coleoptera, which may be true or not).

In all Chrysomelinae the part of the collar bending around the furcal arm is incomplete (see, for instance, Figs. 11, 39 of *Plagiodera*, where lamina **anla** and the **vete**-**vela**-complex are not connected around the ventral face of the furcal arm); hence some reduction must have occurred. A few chrysomelines have at least retained an almost-full-width-origin of tendon **vete** (*Oidosoma*, *Entomoscelis*, and *Dicranosterna*). It is conceivable that in different other subgroups the (already partly reduced) bending part of the collar has either **(1)** become further reduced to its posterior part, where tendon **vete** is associated with lamina **vela**, or **(2)** become further reduced to its anterior part, where tendon **vete** is associated with lamina **anla**. The occurrence of transformation (1) is quite clear for the cases where both laminae **anla** and **vela** are present (e.g. Fig. 11 of *Plagiodera*, with **vete** associated with **vela** but not with **anla**). For the critical taxa listed above (*Chrysolina* etc.), transformation (2) could well be true, their single lamina then being **anla** (scenario A). Alternatively, the interpretation of the lamina of these critical taxa as **vela** would imply that their morphology is also based on transformation (1), followed by a further transformation **(3)**: a shift of lamina **vela** to the anterior, into the position taken by lamina **anla** in other taxa (scenario B). The latter scenario is supported by intermediate conditions: Among Chrysolinina, the far anterior position of the entire lamina in *Chrysolina* and *Oreina* (Figs. 53, 54) is contrasted by a bending of the proximal part of the lamina to the posterior in *Ambrostoma* (Fig. 56) and by an overall further posterior (mid-ventral) position of the entire lamina in *Humba* (Fig. 52). We thus interpret the single lamina in the critical taxa as **vela**, although with some doubt remaining.

Transformations (1) and (2) inherent in scenario A are mutually exclusive apomorphies. This scenario would thus agree best with a phylogenetic hypothesis where the critical taxa (those having only a far anteriorly located lamina)

form the sister group of a clade comprising most of the other chrysomelines. According to scenario B, transformation (1) is a plesiomorphy also applying to the critical taxa, while these additionally share transformation (3) as an apomorphy (transformation (2) has not occurred). This scenario would be supported if the critical taxa formed a subordinate clade of Chrysomelini (while the relationship indicated for scenario A would also be possible). Unfortunately, the phylogenetic relationships proposed by GÓMEZ-ZURITA et al. (2007, 2008), shown in Fig. 1, do not provide support to either of the two scenarios.

5.2.2. Correlation with hindwing reduction

It is well known that generally in beetles a strong reduction of the hind wings can go along with simplifications in the pterothoracic segments, which also involve the metendosternite (e.g. DOYEN & TSCHINKEL 1982: p. 138 for Tenebrionidae). In our sample, the *Timarcha* species (Figs. 34, 35) and *Crosita* (Fig. 26) are the only representatives with strongly reduced hind wings; they are probably only distantly related (Table 1). These 'wingless' species show some simplifications in the metendosternite that are in contrast to all other Chrysomelinae.

(1) The apical edge of the internal tip **if** is slightly convex rather than notched, and it lacks a delicate fringy tendon **if-at**. It is noteworthy, however, that some tendinous fringes are present on the dorsal surface of the internal tip in *Timarcha goettingensis* (seated on ridge **if-mr**) and in *Crosita* (**if-dt**) (Figs. 26, 35).

(2) The ventral tendon **vete** is reduced to some extent, but apparently in different ways: *Crosita* has an indistinct ventral lamina **vela** along the far anterior ventral surface of the furcal arm (Figs. 55) – in the same position as **vela** in other Chrysolinina (Figs. 53, 54). In the latter this is correlated with a far anterior position of tendon **vete**. This suggests that in *Crosita* vestiges of tendon **vete** (if not completely absent) have been integrated into the anteromesal distal part of the furcal arm (as labeled in Fig. 26; compare Fig. 25). In *Timarcha goettingensis* (Fig. 35) laminar projections on the posteroventral surface of the furcal arm likely represent lamina **vela** and tendon **vete** (as labeled in Fig. 35). These elements would then be in the same posteroventral position as in species from Chrysomelina (Figs. 10–14). A low ridge in the same part of the furcal arm of *Timarcha metallica* (Figs. 3, 34) can then probably be interpreted as a vestige of lamina **vela** and tendon **vete**.

(3) The anterior tendon **ante** is very wide and short in the two *Timarcha* species (Figs. 34, 35), which is in strong contrast to the long and proximally very slender condition of **ante** in all 'winged' Chrysomelinae (e.g. Fig. 19). *Crosita* (Fig. 26) also has a long tendon **ante** with a slender basal part. However, this basal part as well as the entire tendon are shorter than in all other Chrysomelini, which could be seen as some tendency towards the condition of **ante** in *Timarcha*. These differences concerning tendon **ante**, however, are not necessarily correlated with

hindwing reduction, since tendons **ante** of the galerucine *Oides* (Fig. 36) closely resemble those in *Timarcha*.

(4) The internal tip **if** of *Crosita* lacks a ridge **if-dr** (Fig. 26), which is present at least on the posterior lobe **if-p** in all 'winged' Chrysomelinae (e.g. Fig. 19). *Timarcha metallica* (Fig. 34) has a potential vestige of ridge **if-dr**, and in *T. goettingensis* (Fig. 35) **if-dr** is even well developed.

Points (1)–(4) show that also in Chrysomelinae strong hindwing reduction is correlated with simplifications in the metendosternite. In the taxa concerned there are both similar and different modifications. Similar parallel simplifications of the metendosternite may be due to similar changes in the thoracic musculature (reduction of tendon **vete**) or to an overall shortening of the hindwing-bearing segment (shortening of tendon **ante**; compare MCHUGH et al. 1997: fig. 3).

5.2.3. Character incongruence and potential age-dependence of characters

It is commonplace that the cuticular cover of the body is still developing in teneral beetles. We hypothesise that processes of this kind can still be ongoing in more mature adults, concerning internal thickening, sclerotisation, and perhaps resorption of cuticle. We also hypothesise that with regard to these processes there may well be shifts in the timing among different species (or among different specimens of a species). Then a particular structure may be found more rarely or (on average) in a less complete condition in the one species (where it is formed later) but more often or in a more complete condition in another (where it is formed earlier). We have no direct evidence on all this, which would require studies on some particular species using adults of different age. However, the following findings may tentatively be considered as pointing this way:

(1) The presence of abdominal sternite I (**stI**; Fig. 4) shows a fairly chaotic distribution over the examined species (character 15 in Table 3), with intra-specific variation at least in *Chrysolina grossa*. Furthermore, the degree of hardening and darkening of **stI** varies strongly across the species where **stI** was found, and there is also much intra-specific variation in this regard (not specified in the above descriptions). This may suggest that the sclerotisation of **stI** continues in adults, with inter-specific differences in its timing.

(2) The presence of the perforation **trpf** in the ridge **tr** (Figs. 2, 4) also shows a fairly chaotic distribution over the examined species (see character 16 in Table 3), with two cases of absence versus presence in members of the same genus (*Gonioctena*, *Timarcha*), and with intra-specific variation at least in *Sphaeratrix latifrons*. In addition, the size of **trpf** shows much intra-specific variation. The ontogenetic development of the perforation **trpf** could be similar as hypothesised in KLASS et al. (2011) for the median perforation in the wall in between the mesocoxal cavities. We tentatively propose that the

perforation can grow (and possibly even originate) during adult life by continued resorption of cuticle.

(3) The body part here studied includes many structures that are formed by strong internal thickening of the cuticle. For instance, the elements seen in an internal view of the furcal arms (as in Figs. 10–38), such as laminae **anla** and **vela**, tendon **vete**, and the entire internal tip **if** with its substructures, fall in this category. (Note that the external surface of the cuticle in this area is represented by the outline of the central canal **fal** in e.g. Fig. 16.) Although we did not report details in the descriptions, we occasionally found these elements developed to a fairly different degree in different specimens of the same species.

We submit that the findings in (1)–(3) can be interpreted in the way that the characters concerned simply show enormous irregular variation among and within species. However, the options of ongoing modification of cuticular elements in adults and of a different timing of such processes in different species would provide a simple explanation for the (then only apparent) irregularity. These possibilities should be kept in mind when scoring characters for phylogenetic studies. For instance, the distribution of the presence of **stI** over chrysomeline species would straightforwardly imply several parallel losses or re-appearances of **stI** in Chrysomelinae. However, the different matrix entries for different species could to some (unknown) extent be influenced by focal examination of either younger or older individuals combined with inter-specific differences in the timing of the sclerotisation of **stI**.

5.2.4. Uniformity in Chrysomelinae and the position of Galerucinae

The Chrysomelinae species here studied show a few features of the metendosternite that are uniformly present throughout the group: **(1)** The stalk (**stk**) is always very short and very wide, no matter whether winged or wingless (only *Crosita* and *Timarcha*, Figs. 26, 34, 35) taxa are considered. **(2)** The anterior tendon **ante** always originates from the distal half of the furcal arm (maximal proximal extension shown in Fig. 17), and **(3)** it is always fairly long, with a very slender proximal part (except in the wingless *Timarcha*). **(4)** The anterior lamina **anla** never reaches the median part of the metendosternite but is either limited to the furcal arm (maximal proximal extension shown in Fig. 10, or perhaps Fig. 17 with **anla** hardly distinct) or is (more usually) absent. **(5)** The tendon **vete** is very distinct (except in the wingless *Crosita* and *Timarcha metallica*), and longer than wide at its base. **(6)** The internal tip of the furcal arm **if** is always widened compared to the part of the furcal arm proximad of it, and **(7)** it bears a delicate apical tendon **if-at** (except in the wingless taxa) and **(8)** a dorsal ridge **if-dr** on its posterior lobe or part (except in the wingless *Crosita*).

In contrast to Chrysomelinae, the galerucines *Oides* (Fig. 36) and *Galeruca* have **(1')** a much longer and narrower stalk and show **(2')** a far mesal origin of tendon **ante**. *Oides* furthermore has **(4')** a lamina **anla** that extends to the midline to connect with **anla** of the other side (while in *Galeruca* lamina **anla** is altogether vestigial). In these features the galerucines agree with the criocerine *Lilioceris* (Fig. 37) and the cassidine *Lasiochila* (Fig. 38), which are clearly outgroup taxa to Chrysomelinae. While there are generally strong limitations regarding the polarisation of metendosternite characters within Cucujiformia (see section 5.1.1.), it appears secure to consider features (1'), (2'), and (4') of Galerucinae plesiomorphic compared to features (1), (2), and (4) of Chrysomelinae. These features thus suggest that Chrysomelinae is monophyletic under the exclusion of Galerucinae. This contradicts the molecular-based hypotheses of GÓMEZ-ZURITA et al. (2007, 2008: figs. 2–4, i.e. all tree-building methods) (see Fig. 1; we note that these authors do not discuss conflicts between their results and morphological data).

Chrysomelinae are also quite uniform with regard to the morphology of the anterior abdominal venter (Figs. 2, 4, 8, 9). This includes the constant presence of distinct metacoxal cavities **mcc**, a distinct intercoxal process **icp**, and a distinct transverse ridge **tr**. This complies with conditions in *Lilioceris* and *Lasiochila*. The simplifications seen in the anterior ventral abdomen of the two examined Galerucinae species are part of a generally more loosely built, somewhat 'malacodermatan'-type body structure found in many members of this group. *Oides* and *Galeruca* differ strongly in the extent of this development: Metacoxal cavities **mcc**, the intercoxal process **icp**, and the ridge **tr** are absent or highly vestigial in *Oides*, whereby the ventral closure of the thoraco-abdominal border is very incomplete. All these elements, however, are developed in *Galeruca*, though not as discrete as in Chrysomelinae, *Lilioceris*, and *Lasiochila*. Comparison with the three latter taxa and many other cucujiform beetles (including *Tenebrio*) shows that this simplification in Galerucinae is apomorphic and thus would not be in conflict with Galerucinae being subordinate in Chrysomelinae.

5.2.5. Variation in Chrysomelinae: list of characters

In the following the main characters are listed for which variation was found among different Chrysomelinae. The distribution of character states over the examined taxa is given in Table 3. The states are indicated by short abbreviations reminding of their definition. For use in a phylogenetic analysis, the different abbreviations used in a character simply need to be replaced by ciphers 0, 1, 2 etc. However, use in phylogenetic work should be done very cautiously: In many characters the transition between states is fluent; while extreme conditions are very distinct, the assignment of intermediate conditions to particular states is often quite subjective. In addition, some characters could well be age-dependent (see section 5.2.3.) and our report of a state in a species might be

biased by this (i.e. reflect a mixture of species-specificity and age-specificity).

Ch1 Size proportion between anterior and posterior lobes, **if-a** and **if-p**, of internal tip of furcal arm: **if-a** and **if-p** of similar size [***sim***] (e.g. Figs. 12, 30); **if-a** and **if-p** of slightly different size, with **if-a** somewhat smaller [***sdi***] (e.g. Fig. 16); **if-a** and **if-p** of very different size, with **if-a** much smaller [***vdi***] (e.g. Fig. 25). – Character problematic due to fluent transition of states and because the size ratio may variously depend on the expansion / reduction of the lobes or of the notch separating them.

Ch2 Distinctness of notch between anterior and posterior lobes, **if-a** and **if-p**, of internal tip of furcal arm: distinct [***dis***] (e.g. Figs. 16, 25, 32); hardly developed [***hde***] (e.g. Figs. 12, 23); absent [***abs***] (e.g. Figs. 26, 34). – Character problematic due to fluent transition of states and to possible interdependence with the general shape of the tip area **if** (short versus elongate).

Ch3 Presence of a part of ridge **if-dr** that traverses anteroposteriorly across the furcal arm, thus separating the dorsal surface of the internal tip from the more proximal part of the furcal arm: present [***prs***] (e.g. Figs. 10, 21, 33); absent [***abs***] (e.g. Figs. 14, 24). – This part of the ridge is always continuous with the part on the posterior lobe of the internal tip, and also with the part on the anterior lobe if such a part is present. – Character possibly age-dependent.

Ch4 Antero-posterior level of origin of tendon **vete** on ventral face of furcal arm: on (far) anterior ventral face only [***ant***] (e.g. Figs. 16, 27, 29 and 44, 56, 58); on middle to posterior ventral face only [***pos***] (e.g. Figs. 11, 23, 30, 31 and 39, 51, 59, 60); extending from far anterior to posterior ventral face [***eap***] (e.g. Figs. 17, 19 and 45, 47). – Character problematic due to fluent transition of states and because it is difficult to assess the position of **vete** in context with variation of neighbouring parts and variation in the shape and width of the furcal arm. However, the extreme conditions of the character are very distinct.

Ch5 Presence of ventral lamina **vela** on furcal arm: present, including vestigial conditions [***prs***] (e.g. Figs. 10 and 39); absent [***abs***] (e.g. Figs. 20 and 48). – It appears impossible to define further states for different degrees of development of lamina **vela**, because variation is too fluent and overlapping with the degree of confluency between **vela** and tendon **vete** (high degree in e.g. Figs. 14, 15). Character still problematic since vestigial presence versus absence of **vela** is difficult to judge in cases where **vela** is short and its base not distinctly set off from the furcal arm.

Ch6 Antero-posterior level of base of lamina **vela** on furcal arm: far anteriorly [***fan***] (e.g. Figs. 16, 25 and 44, 53); intermediate [***ime***] (e.g. Fig. 49, 52, 60); far posteriorly [***fpo***] (e.g. Figs. 10, 12 and 39, 40). – Only applicable to taxa having [prs] in character 5. – Character problematic due to fluent transition of states and because it is difficult to assess the position of **vela** in context with variation in the shape and width of the furcal arm. However, the extreme conditions of the character are very distinct.

Ch7 Development of anterior lamina **anla** on furcal arm: well developed, long (wide or fairly narrow) [***wdl***] (e.g. Figs. 10, 13 and 39, 41); well developed, short (and wide) [***wds***] (Figs. 17 and 45); absent [***abs***] (e.g. Figs. 18, 22 and 46, 50). – A fairly clear-cut unproblematic character with our sample.

Ch8 Position of origin of anterior tendon **ante** relative to lamina **anla**: in dorsal wall of lamina **anla** [***dwa***] (e.g. Figs. 11, 15, 17); dorsad of base of lamina **anla** [***dba***] (e.g. Fig. 14). – Only applicable to taxa having [wdl] or [wds] in character 7. – Character a bit problematic due to fluent transition of states.

Ch9 Shape of anterior tendon **ante**: slender (at least in a short proximal part) and long [***sl***] (e.g. Figs. 10, 17, 29, 31); wide and short (essentially widest at base) [***ws***] (e.g. Fig. 34). – A clear-cut unproblematic character with our sample.

Ch10 Presence of basal tendon **bate** in dorsal wall of furcal arm: present [***prs***] (e.g. Figs. 10, 15, 31); absent [***abs***] (e.g. Figs. 11, 16, 30). – A clear-cut unproblematic character with our sample (though with one case of intra-specific polymorphism).

Ch11 Extension of ventral midline flange **vlf** of metendosternite to the anterior: developed throughout and reaching internal transverse ridge **scr** [***rch***]; obliterating anteroventrally and not reaching internal transverse ridge **scr** [***obl***]; obliterating but then rising again and reaching internal transverse ridge **scr** [***orc***]. – See Fig. 8 for this character. – Character a bit problematic due to fluent transition of states.

Ch12 Presence of bulb-like invagination **vebu** behind posterior base of metendosternite: present [***prs***] (Fig. 6); absent [***abs***] (Figs. 2, 4). – A clear-cut unproblematic character with our sample. However, there seems to be sexual dimorphism, with **vebu** only being present in females.

Ch13 Presence of tendon **tstI** upon metacoxal cavity: present [***prs***] (Figs. 2, 4); absent [***abs***] (Fig. 7). – A fairly clear-cut unproblematic character with our sample.

Ch14 Presence of tendon **tstII** upon metacoxal cavity: present [***prs***] (Fig. 7); represented by a row of delicate tendinous fringes [***fri***]; absent [***abs***] (Figs. 2, 4). – A clear-cut unproblematic character with our sample.

Ch15 Presence of abdominal (hemi-)sternite **stI** upon metacoxal cavity: present [***prs***] (Fig. 4); absent [***abs***] (Fig. 2). – Character problematic due to fluent transition of states (**stI** often extremely weak), and possibly age-dependent.

Ch16 Presence of perforation **trpf** in abdominal transverse ridge **tr**: present [***prs***] (Figs. 2, 4, 6, 9); absent [***abs***] (Fig. 8). – A clear-cut character with our sample, but possibly age-dependent.

5.2.6. Implications on the phylogeny of Chrysomelinae

Due to the overall high degree of homoplastic evolution in the metendosternite of Cucujiformia and Chrysomeli-

Table 3. Matrix of characters and states defined in section 5.2.5. The states are indicated by short abbreviations reminding of their definition (instead of ciphers; see text). '?' represents ambiguous conditions (no state can be assigned due to aberrant morphology of the area in question). '–' represents inapplicability of a character (no state can be assigned due to the clear absence of the character-bearing element). '(pol)' = polymorphic means that all defined states of a character were found in the taxon. 'SyPo' = systematic position of taxon abbreviated: SyPo1 according to SEENO & WILCOX (1982), SyPo2 according to DACCORDI (1994), see Table 1 and Introduction for complete taxon names.

Species	SyPo1	SyPo2	1 if-a : if-p	2 if notch	3 if-dr trav.	4 vete posit.	5 vela devel.	6 vela posit.	7 anla devel.	8 ante posit.	9 ante shape	10 bate pres.	11 vlf exten.	12 vebu pres.	13 tstl pres.	14 tstll pres.	15 stl pres.	16 trpf pres.
Chrysomela (s.str.) saliceti	CH-Chm	CH-Chm	sim	dis	prs	pos	prs	fpo	wdl	dwa	sl	prs	obl	abs	abs	prs	abs	abs
Chrysomela (Strickerus) cuprea	CH-Chm	CH-Chm	sim	dis	abs	pos	prs	fpo	wdl	dwa	sl	prs	obl	abs	abs	prs	abs	abs
Chrysomela (Pachylina) collaris	CH-Chm	CH-Chm	sim	dis	prs	pos	prs	fpo	wdl	dwa	sl	prs	obl	abs	abs	prs	abs	abs
Plagiodera versicolora	CH-Chm	CH-Chm	sim	dis	prs	pos	prs	fpo	wdl	dwa	sl	abs	obl	abs	abs	prs	abs	abs
Hydrothassa glabra	CH-Chm	CH-Chm	sim	hde	abs	pos	prs	fpo	wdl	dba	sl	abs	obl	abs	abs	prs	abs	abs
Prasocuris phellandrii	CH-Chm	CH-Chm	sim	dis	abs	pos	prs	fpo	wdl	dba	sl	abs	obl	abs	abs	prs	abs	prs
Phaedon pyritosus	CH-Chm	CH-Chm	sim	dis	abs	pos	prs	fpo	wdl	dba	sl	abs	obl	abs	abs	prs	prs	prs
Phratora vitellinae	CH-Phd	CH-Chm	sim	dis	prs	pos	prs	fpo	wdl	dwa	sl	prs	obl	abs	abs	prs	abs	abs
Gaviga limbatella	CH-Phd	CH-Chm	sdi	dis	abs	ant	prs	fan	abs	–	sl	abs	obl	abs	abs	abs	abs	abs
Oidosoma coccinella	CH-Phc	CH-Ent	sim	dis	abs	eap	abs	–	wds	dwa	sl	abs	rch	abs	abs	abs	abs	abs
Phyllocharis undulata	CH-Phc	CH-Ent	sdi	dis	abs	ant	abs	–	abs	–	sl	abs	orc	abs	abs	abs	prs	abs
Entomoscelis suturalis	CH-Ent	CH-Ent	sdi	dis	abs	eap	prs	fpo	abs	–	sl	abs	rch	abs	abs	abs	prs	prs
Lamprolina aeneipennis	CH-Ent	CH-Ent	vdi	dis	abs	ant	abs	–	abs	–	sl	abs	obl	abs	abs	abs	abs	prs
Sphaerotrix latifrons	CH-Mon	CH-Chl	vdi	dis	abs	ant	prs	fan	abs	–	sl	abs	obl	abs	abs	abs	abs	(pol)
Humba cyanicollis	CH-Chl	CH-Chl	vdi	dis	abs	ant	prs	ime	abs	–	sl	abs	rch	abs	abs	abs	abs?	prs
Chrysolina bicolor	CH-Chl	CH-Chl	vdi	dis	abs	ant	prs	fan	abs	–	sl	abs	rch	?	abs	abs	abs	prs
Chrysolina grossa	CH-Chl	CH-Chl	vdi	dis	abs	ant	prs	fan	abs	–	sl	abs	rch	abs	abs	abs	(pol)	prs
Chrysolina cerealis	CH-Chl	CH-Chl	vdi	dis	abs	ant	prs	fan	abs	–	sl	abs	rch	prs	abs	abs	abs	prs
Oreina speciosa	CH-Chl	CH-Chl	vdi	dis	abs	ant	prs	fan	abs	–	sl	abs	rch	abs	abs	abs	abs	prs
Oreina intricata	CH-Chl	CH-Chl	vdi	dis	abs	ant	prs	fan	abs	–	sl	abs	rch	abs	abs	abs	prs	prs
Crosita altaica	CH-Chl	CH-Chl	?	abs	abs	?	prs	fan	abs	–	sl	abs	orc	abs	abs	abs	prs	abs
Ambrostoma fortunei	CH-Chl	CH-Chl	sdi	hde	abs	ant	prs	fan	abs	–	sl	abs	obl	abs	abs	abs	abs	prs
Zygogramma flavotaeniata	CH-Chl	CH-Dor	vdi	dis	abs	ant	prs	fan	abs	–	sl	abs	rch	abs	abs	abs	prs	prs
Zygogramma signatipennis	CH-Dor	CH-Chl	vdi	dis	abs	ant	prs	fan	abs	–	sl	abs	rch	abs	abs	abs	abs	prs
Cosmogramma patricia	CH-Dor	CH-Chl	vdi	dis	abs	ant	prs	fan	abs	–	sl	abs	rch	abs	abs	abs	abs	abs
Proseicela vittata	CH-Dor	CH-Chl	sim	dis	abs	pos	prs	ime	abs	–	sl	abs	obl	abs	abs	abs	prs	abs
Leptinotarsa decemlineata	CH-Dor	CH-Chl	sim	dis	prs	pos	prs	ime	abs	–	sl	(pol)	obl	abs	abs	abs	abs	abs
Doryphora cincta	CH-Dor	CH-Chl	sim	dis	prs	pos	abs	–	abs	–	sl	abs	obl	abs	ves	abs	prs	prs
Doryphora pyrrhoptera	CH-Dor	CH-Chl	sim	dis	prs	pos	abs	–	abs	–	sl	abs	obl	abs	abs	abs	prs	prs
Desmogramma bivia	CH-Dor	CH-Chl	sim	dis	prs	pos	abs	–	abs	–	sl	abs	obl	abs	abs	abs	prs	abs
Labidomera clivicollis	CH-Dor	CH-Chl	sim	dis	prs	pos	prs	ime	abs	–	sl	abs	obl	abs	abs	abs	prs	abs

Table 3 continued.

Species	SyPo1	SyPo2	1 if-a : if-p	2 if notch	3 if-dr trav.	4 vete posit.	5 vela devel.	6 vela posit.	7 anla devel.	8 ante posit.	9 ante shape	10 bate pres.	11 vlf exten.	12 vebu pres.	13 tstl pres.	14 tstll pres.	15 stl pres.	16 trpf pres.
Dicranosterna picea	CH-Dic	CH-Par	sdi	dis	prs	eap	prs	ime	abs	–	sl	abs	obl	abs	abs	fri	abs	prs
Gonioctena viminalis	CH-Gon	CH-Par	sim	hde	abs	pos	prs	fpo	abs	–	sl	abs	orc	abs	abs	abs	prs	prs
Gonioctena variabilis	CH-Gon	CH-Par	sim	hde	abs	pos	prs	fpo	abs	–	sl	abs	orc	prs	abs	abs	abs	abs
Paropsis marmorea	CH-Par	CH-Par	sim	dis	prs	eap	prs	fpo	abs	–	sl	abs	rch	abs	abs	abs	abs	abs
Paropsides duodecimpustulata	CH-Par	CH-Par	sim	dis	prs	eap	prs	fpo	abs	–	sl	abs	obl	abs	abs	abs	abs	abs
Trachymela serpiginosa	CH-Par	CH-Par	sim	dis	prs	eap	prs?	fpo	abs	–	sl	abs	rch	abs	abs	abs	prs	prs
Timarcha metallica	Tl	Tl	?	abs	abs	?	prs?	fpo?	abs?	–	ws	abs	rch	abs	prs	abs	abs	abs
Timarcha goettingensis	Tl	Tl	?	abs	prs	pos?	prs?	fpo?	abs?	–	ws	abs	rch	abs	prs	abs	?	abs
Oides decempunctata	Galeruc	Galeruc	vdi	abs	abs	–	prs	fpo	wdl	dwa	ws	abs	rch	abs	prs?	abs	abs	abs
Galeruca tanaceti	Galeruc	Galeruc	vdi	abs	abs	–	prs	fpo	wds	dwa	ws	abs	obl	abs	prs	abs	abs	abs
Lilioceris merdigera	Criocer	Criocer	sim	hde	abs	eap	prs	fpo	wdl	dwa	sl	abs	obl	abs	abs	prs	abs	prs
Lasiochila rufa	Cassid	Cassid	sim	hde	prs	eap	prs	fpo	wdl	dwa	sl	abs	rch	abs	abs	abs	abs	prs

dae (see section 5.1.1.) there is for hardly any character unambiguous outgroup comparison for Chrysomelinae, not even within Chrysomelidae. Characters of the anterior abdominal venter also appear to be considerably homoplastic. Thus, it usually remains unclear to a varied extent whether similarities shared between particular taxa are shared apomorphies or plesiomorphies. Homoplasy correlated with hindwing reduction (section 5.2.2.) and the possible age-dependence of some characters (section 5.2.3.) are special aspects increasing the problems in the phylogenetic evaluation.

Yet, in the following we try to extract, with these limitations in mind, phylogenetic evidence from metendosternal and antero-abdominal morphology in Chrysomelinae. As a background of our evaluation we use the classification in SEENO & WILCOX (1982) rather than that in DACCORDI (1994). Neither classification is backboned by much phylogenetic reasoning, and the 12 subtribes of Chrysomelini outlined in the former are comprised to 4 subtribes in the latter (see columns SyPo1 vs. SyPo2 in Table 3). We reflect our phylogenetic implications mainly on GÓMEZ-ZURITA et al.'s (2007, 2008) phylogenetic hypotheses based on Direct Optimisation (DO; shown in Fig. 1), Maximum Likelihood (ML), and MrBayes (MB), which show some differences of particular interest. In addition we consider the more fragmentary phylogenetic evidence from glands and the compounds of their secretions (e.g. KIMOTO 1962; PASTEELS et al. 2003). Our evaluation will be limited to Chrysomelini, since not much can be concluded from the modified metendosternite of the wingless Timarchini. We proceed in 5 steps.

(1) *Chrysomela*, *Plagiodera*, *Prasocuris*, *Phaedon* (Chrysomelina) and *Phratora* (Phyllodectina) are members of a clade which is strongly supported in all analyses of GÓMEZ-ZURITA et al. (2007, 2008; see Fig. 1) and is the sister group of the remaining Chrysomelini (not considering Galerucinae). Members of these taxa plus *Hydrothassa* (Chrysomelina; not included in GÓMEZ-ZURITA et al. 2007, 2008) show a long, well developed lamina **anla** (character 7; Figs. 10–15, 39–43), which is unique for Chrysomelinae, but likely plesiomorphic by comparison with *Oides*, *Lilioceris*, and *Lasiochila* (Figs. 36–38). The presence in all these taxa of a tendon **tstII** on the abdominal venter (character 14; Fig. 7) is also unique within Chrysomelinae (not considering the sparse tendinous fringes in *Dicranosterna*), but the presence of a potential homologue in *Lilioceris* makes the polarity of this character ambiguous. The far posterior location of the bases of lamina **vela** and tendon **vete** (characters 4 and 6) in the listed taxa is most likely plesiomorphic, and also not unique in Chrysomelinae. This clade in GÓMEZ-ZURITA et al. (2007, 2008; Fig. 1) is thus overall plausible from the morphological perspective, but it is difficult to support by unambiguous apomorphies. The inclusion of *Phratora* in this group is of particular interest, as it is assigned to Phyllodectina by SEENO & WILCOX (1982; rather than to Chrysomelina), *Gavirga* being another member of that subtribe. However, *Phratora* has a metendoster-

nite in all respects very similar to that in *Chrysomela* and *Plagiodera* (Figs. 10, 11, 15), which is suggestive of a close relationship of these taxa and supports the placement of *Phratora* in Chrysomelina. In contrast, the metendosternite of *Gavirga* (Fig. 16) shows many characters suggestive of a placement near Chrysolinina (see below, step (4)). Unfortunately, *Gavirga* has not been sampled by GÓMEZ-ZURITA et al. (2007, 2008).

Our morphological results thus agree with the previous molecular results regarding a well-defined group Chrysomelina that also includes *Phratora* (but not *Gavirga*). This furthermore agrees with results on glandular secretions of the adults (PASTEELS et al. 2003): *Phratora* and the abovelisted Chrysomelina share isoxazolinone glucosides esterified by nitropropanoic acid as the major compound (unknown for *Gavirga*). Moreover, Chrysomelina and *Phratora* show a characteristic equipment with glands in the larvae: nine serial pairs of thoracic and abdominal exsertile defensive glands (see PASTEELS et al. 2003: p. 271; "glanduliferous group" of genera in KIMOTO 1962).

(2) Within the Chrysomelina, a clade *Chrysomela* + *Phratora* is supported by the presence of a tendon **bate** on the proximal dorsal face of the furcal arm (character 10; Figs. 10, 15), of which otherwise only some vestige was found in one *Leptinotarsa* specimen. This character agrees with striking apomorphic similarities of these two genera in the biochemistry of gland secretions (KIRSCH et al. 2011). On the other hand, a clade *Prasocuris* + *Hydrothassa* + *Phaedon* + *Phratora* (Figs. 12–15) is supported by a stronger ventral bending of lamina **anla** than found in *Chrysomela* and *Plagiodera* (Figs. 10, 11). This might be considered an apomorphy by comparison with *Oides*, *Lilioceris*, and *Lasiochila* (Figs. 36–38) and would agree with the clade (*Phratora* + *Prasocuris*) + *Phaedon* in all analyses of GÓMEZ-ZURITA et al. (2007, 2008; see Fig. 1; *Hydrothassa* not included therein).

Only *Prasocuris*, *Phaedon*, and *Hydrothassa* show a very narrow, tongue-like condition and an extreme ventral bending of lamina **anla**, and the base of tendon **ante** is in a position dorsad of the base of lamina **anla** (rather than in the dorsal wall of **anla**; character 8). By comparison with *Oides*, *Lilioceris*, and *Lasiochila* (Figs. 36–38) as well as *Oidosoma* (Fig. 17; the only chrysomeline taxon outside Chrysomelina that has a lamina **anla**) these features appear as three apomorphies suggesting *Prasocuris*, *Phaedon*, and *Hydrothassa* to form a clade (under exclusion of *Phratora*). This, however, is inconsistent with the analyses of GÓMEZ-ZURITA et al. (2007, 2008; see Fig. 1).

(3) All other Chrysomelini sampled herein (i.e. all not included in the Chrysomelina discussed in steps (1) and (2)) share the (near-)absence of lamina **anla** (character 7), which appears as an apomorphy and is consistent with the monophyly of Chrysomelini under exclusion of Chrysomelina in all analyses of GÓMEZ-ZURITA et al. (2007, 2008; see Fig. 1) (irrespective of a consideration of

Galerucinae). As the only taxon, *Oidosoma* has retained a lamina **anla** (Figs. 17, 45), but this is much shorter and much less distinctly set off from the furcal arm than in Chrysomelina and the chrysomelid outgroup taxa.

Concerning the relationships within this possible Chrysomelini-minus-Chrysomelina clade (CmC in the following), metendosternite morphology is indicative of a basal dichotomy between *Oidosoma* (Phyllocharina) and the remainder due to the retention of some trace of lamina **anla** only in *Oidosoma* (character 7; Fig. 17). *Oidosoma* has also retained a full-width origin of tendon **vete** on the ventral face of the furcal arm, which by comparison with *Lilioceris* and *Lasiochila* (Figs. 37, 38) is plesiomorphic, and which in CmC is additionally found in *Dicranosterna*, *Entomoscelis*, and all Paropsina (character 4). These three taxa may thus form the following offshoots in the basal part of the CmC tree. These two characters 4 and 7 alone, however, are by far not convincing. Unfortunately, of all these taxa only Paropsina (*Paropsis* and *Trachymela*) are represented in GÓMEZ-ZURITA et al. (2007, 2008). These do, in the DO-based tree, indeed form a clade that originates from a very deep dichotomy within CmC; of the taxa examined herein only *Lamprolina* (see below, step (4)) has a deeper origin.

(4) For sorting the CmC taxa remaining after step (3), there is a group of near-congruent features that suggest a clade composed of chrysomelines from various subtribes. *Chrysolina*, *Oreina*, *Ambrostoma*, and *Crosita* from Chrysolinina, *Gavirga* from Phyllodectina, *Sphaeratrix* from Monarditina, and *Zygogramma* and *Cosmogramma* from Doryphorina (Figs. 16, 22, 25, 27–29 and 44, 50, 53, 54, 56–58) share a far anterior position of lamina **vela** and tendon **vete** (characters 4 and 6; these taxa show the distinctive extremes of these characters, as mentioned above in the character definitions; position of tendon **vete** unclear for *Crosita*, see section 5.2.2.). As discussed in section 5.2.1. (scenarios A versus B), this is clearly an apomorphic condition, either consisting in a shift of **vela** and **vete** to the anterior (interpretation here followed; transformation (3) in 5.2.1.), or consisting in a special type of reduction of the bending part of the 'collar' in the lamina system (transformation (2) in 5.2.1., "**vela**" of these taxa then rather being **anla**). In *Humba* (Chrysolinina; Figs. 24, 52), *Lamprolina* (Entomoscelina; Figs. 20, 48), and *Phyllocharis* (Phyllocharina; Figs. 18, 46) tendon **vete** shows the same apomorphic position as in the aforementioned taxa; lamina **vela**, however, is located a bit less far anteriorly in *Humba*, and is absent in *Lamprolina* and *Phyllocharis*. Nearly the same set of taxa shares a strong difference in size between the anterior and posterior lobes (**if-a**, **if-p**) of the internal tip (character 1, state [vdi]), with lobe **if-a** being much smaller (often nearly absent). Such a condition is otherwise not found in Chrysomelinae. In *Gavirga*, *Phyllocharis*, and *Ambrostoma*, however, this size difference is less distinct (state [sdi]) – present only to an extent also found in *Entomoscelis* and *Dicranosterna* (see step (3) for these

taxa) among the remaining Chrysomelinae. The polarity of character 1 is conflicting considering the chrysomelid outgroup taxa (Figs. 36 – 38). In sum, the characters here considered may tentatively support a clade comprising *Chrysolina*, *Oreina*, *Humba*, *Ambrostoma*, *Crosita*, *Gavirga*, *Sphaeratrix*, *Zygogramma*, *Cosmogramma*, *Lamprolina*, and *Phyllocharis*.

In some of the taxa included in this grouping the base of tendon **vete** is located far distally and is especially closely associated with the anterior part of the internal tip **if**: *Chrysolina*, *Oreina*, *Humba*, *Sphaeratrix*, *Zygogramma*, *Cosmogramma* (and perhaps *Crosita*; Figs. 22, 24, 25, 28, 29). This may favour an especially close relationship among these taxa.

Neither the larger nor the smaller one of these two assemblages of genera (both of which include the Doryphorina *Zygogramma* and *Cosmogramma*) is reflected in GÓMEZ-ZURITA et al.'s (2007, 2008) DO analysis, since the remaining Doryphorina (see below, step (5)) are subordinate in the apical part of the tree, and *Lamprolina* is far remote from the other taxa of this assemblage. However, the ML and MB analyses of GÓMEZ-ZURITA et al. (2008: figs. 3, 4) show a clade *Chrysolina + Oreina + Zygogramma + Cosmogramma + Sphaeratrix* (clade poorly supported; *Humba* and *Crosita* not included in their sample), which is sister to the remaining Doryphorina. In addition, the above grouping of genera agrees with results on glandular secretions of the adults (PASTEELS et al. 2003): *Chrysolina*, *Oreina*, *Ambrostoma*, *Zygogramma*, and *Cosmogramma* (as well as *Calligrapha* and *Stilodes*, which were not sampled herein) share cardenolides as the major compound (no data for *Humba*, *Crosita*, *Gavirga*, *Sphaeratrix*, *Lamprolina*, and *Phyllocharis*). The inclusion of *Zygogramma* and *Cosmogramma* is noteworthy, as the other Doryphorina show different secretions (see below, step (5)). There is thus overall considerable support for the grouping of genera outlined in step (4), but for a clear picture the molecular, biochemical, and morphological data sets need additional sampling.

(5) The only CmC taxa of our sample that remain after steps (3) and (4) are *Gonioctena* (Gonioctenina; Fig. 23) as well as *Doryphora*, *Proseicela*, *Labidomera*, *Leptinotarsa*, and *Desmogramma* (Doryphorina; Figs. 30 – 32). All these taxa have similar metendosternites (especially the various Doryphorina), with similarly sized lobes **if-a** and **if-p**, with tendon **vete** and lamina **vela** (as far as present) having their bases mid- or posteroventrally, and with the base of tendon **vete** not closely associated with the internal tip. However, there is no feature that might support a close relationship among these taxa, or for a subset of them. In the morphology of the metendosternite the Doryphorina show much overall resemblance with Paropsina (Figs. 33, 63), which, however, appear to be more plesiomorphic in the positioning of the bases of lamina **vela** and tendon **vete**, see step (3) above.

In all analyses of GÓMEZ-ZURITA et al. (2007, 2008) the Doryphorina *Doryphora*, *Proseicela*, *Labidomera*, *Leptinotarsa*, and *Desmogramma* together form a strongly supported clade (see Fig. 1). In addition, there is a corresponding grouping of Doryphorina genera regarding glandular secretions of the adults (PASTEELS et al. 2003): *Leptinotarsa*, *Labidomera*, and *Desmogramma* (as well as *Platyphora*, not sampled herein and in GÓMEZ-ZURITA et al. 2007, 2008) share cardenolides as the major compound (no data for *Doryphora* and *Proseicela*). This is at least not in conflict with our results on the metendosternite, which is very similar in these Doryphorina.

Neither the metendosternite nor the anterior abdominal venter have been considered very valuable character systems with regard to the reconstruction of phylogenetic relationships in cucujiform beetles. We also see many problems in this regard in Chrysomelinae, as explained above, and we would not assume that the morphological evidence included in the above discussions in steps (1) – (5) could be taken to propose a phylogenetic hypothesis. Nevertheless, steps (1) – (5) show that in the metendosternite of Chrysomelinae the distribution of the states of some characters across the species here examined is not simply arbitrary. Some characters indeed bear useful phylogenetic information. This is shown by the above cases where details of the metendosternite suggest the same phylogenetic relationships as a previous molecular study and evidence from glandular secretions. Metendosternite morphology may thus well contribute to clarifying phylogenetic relationships in beetle subgroups of low rank, including Chrysomelinae.

5.2.7. Conclusions on the classification of Chrysomelinae

According to the results in GÓMEZ-ZURITA et al. (2007, 2008), PASTEELS et al. (2003), and this paper, the classification of Chrysomelini into subtribes in SEENO & WILCOX (1982) only partly holds. *Chrysolina*, *Oreina*, *Ambrostoma*, *Humba*, and perhaps also the wingless *Crosita* are well placed in the same subtribe, Chrysolinina, according to all available evidence from metendosternite, molecules, and gland secretions. *Doryphora*, *Proseicela*, *Labidomera*, *Leptinotarsa*, and *Desmogramma* are convincingly assembled in another subtribe, Doryphorina, according to all these data sources. Evidence from metendosternite, molecules, and gland secretions, however, unanimously suggests to transfer *Zygogramma* and *Cosmogramma* from Doryphorina to Chrysolinina. The metendosternites in the three genera of Paropsina we studied – *Paropsis*, *Paropsides*, and *Trachymela* – are very similar. This agrees with the strongly supported clade *Paropsis + Trachymela* in GÓMEZ-ZURITA et al. (2007, 2008; *Paropsides* not sampled) and with outlining Paropsina as a subtribe (no data on glandular secretions). From three further subtribes we sampled two genera each: Entomoscelina with *Entomoscelis* and *Lamprolina*; Phyllocharina with *Oidosoma* and *Phyllocharis*; and Phyllodectina with *Phratora* and *Gavirga*. In all three cases the two sampled members show a very

different structure of the metendosternite, which is inconsistent with their assignment to the same subtribe. Since only one (Entomoscelina, Phyllodectina) or none (Phyllocharina) of the genera here sampled is included in Gómez-Zurita et al.'s (2007, 2008) sample, and evidence on glandular secretions is only present for *Phratora*, the results cannot be compared. In case of Phyllodectina, the transfer of *Phratora* to Chrysomelina is supported by all available evidence.

The lumping of Chrysomelini subtribes in Daccordi (1994) – with Chrysomelina, Chrysolinina, Entomoscelina, and Paropsina – has solved some problems but also has retained or created others (as also evident from Pasteels et al. 2003). With the inclusion of Phyllodectina in **Chrysomelina**, *Phratora* is now adequately classified with *Chrysomela* and its relatives, but *Gavirga*, with a very different metendosternite, also is and might be misplaced. The inclusion of Doryphorina and Monarditina in **Chrysolinina** has associated *Zygogramma* and *Cosmogramma* as well as *Sphaeratrix* with their putative closest relatives, the genera around *Chrysolina*, but the remaining Doryphorina around *Leptinotarsa*, with different metendosternite and glandular toxines, have also been shifted to this subtribe. Nevertheless, in this case the results of Gómez-Zurita et al. (2007, 2008) suggest that these groups around *Chrysolina* and *Doryphora* together form one of the major clades within Chrysomelini. Grouping Phyllocharina into **Entomoscelina**, i.e. combining *Oidosoma* and *Phyllocharis* as well as *Entomoscelis* and *Lamprolina* in a subtribe, seems to associate genera having fairly plesiomorphic features (*Oidosoma*, *Entomoscelis*) with others resembling the group around *Chrysolina* in some aspects (*Phyllocharis*, *Lamprolina*), and thus appears to continue the possibly artificial nature of the two groups included. However, this topic requires molecular and glandular data from additional members of this Entomoscelina s.l. On the inclusion of Dicranosternina (with *Dicranosterna*) and Gonioctenina (with *Gonioctena*) in **Paropsina** not much can be said from the perspective of the metendosternite; some of Gómez-Zurita et al.'s (2007, 2008) results (ML and MB trees) weakly support *Gonioctena* and Paropsina to be placed together in a major lineage of Chrysomelini (*Dicranosterna* not sampled).

6. Acknowledgements

7. References

Bünnige M., Hilker M. 2005. Do "glanduliferous" larvae of Galerucinae (Coleoptera: Chrysomelidae) possess defensive glands? A scanning electron microscopic study. – Zoomorphology **124**: 111–119.

Crowson R.A. 1938. The metendosternite in Coleoptera: a comparative study. – Transactions of the Royal Entomological Society London **87**: 397–415 + plates.

Crowson R.A. 1944. Further studies on the metendosternite in Coleoptera. – Transactions of the Royal Entomological Society London **94**: 273–310 + plates.

Crowson R.A. 1955. The Natural Classification of the Families of Coleoptera. – London, Nathaniel Lloyd and Co., 187 pp.

Daccordi M. 1994. Notes for phylogenetic study of Chrysomelinae, with descriptions of new taxa and a list of all known genera (Coleoptera: Chrysomelidae, Chrysomelinae). Pp. 60–84 in: Furth D.G. (ed.), Proceedings of the Third International Symposium on the Chrysomelidae, Beijing, 1992. – Backhuys, Leiden, 150 pp.

Doyen J.T. 1966. The skeletal anatomy of *Tenebrio molitor* (Coleoptera: Tenebrionidae). – Miscellaneous Publications of the Entomological Society of America **5**(3): 103–150.

Doyen J.T., Tschinkel W.R. 1982. Phenetic and cladistic relationships among tenebrionid beetles (Coleoptera). – Systematic Entomology **7**: 127–183.

Evans M.E.G. 1961. The musculature and reproductive systems of "*Atomaria ruficornis*" (Marsham) (Coleoptera: Cryptophagidae). – Transactions of the Royal Society of Edinburgh **64**(14): 297–399.

Farrell B.D. 1998. "Inordinate fondness" explained: why are there so many beetles. – Science **281**(5376): 555–559.

Gomez-Zurita J., Hunt T., Kopliku F., Vogler A.P. 2007. Recalibrated tree of leaf beetles (Chrysomelidae) indicates independent diversification of angiosperms and their insect herbivores. – PLoS ONE **4**(e360): 1–8.

Gomez-Zurita J., Hunt T., Vogler A.P. 2008. Multilocus ribosomal RNA phylogeny of the leaf beetles (Chrysomelidae). – Cladistics **24**: 34–50.

Kimoto S. 1962. A phylogenetic consideration of Chrysomelinae based on immature stages of Japanese species (Coleoptera). – Journal of the Faculty of Agriculture, Kyushu University **12**(2): 67–88 + 1 plate.

Kirsch R., Vogel H., Muck A., Vilcinskas A., Pasteels J.M., Boland W. 2011. To be or not to be convergent in salicin-based defence in chrysomeline leaf beetle larvae: evidence from *Phratora vitellinae* salicyl alcohol oxidase. – Proceedings of the Royal Society B, doi:10.1098/rspb.2011.0175.

Klass K.-D., Rentsch J., Rulik B., Hübler N. 2011. The mesothoracic intercoxal perforation in Chrysomelinae and its evolutionary significance (Insecta: Coleoptera: Chrysomelidae). – Zoologischer Anzeiger **250**: 89–101.

Korschelt E. 1923. Bearbeitung einheimischer Tiere, erste Monographie: Der Gelbrand, *Dytiscus marginalis* L. Erster Band. vi + 863 pp. – Wihelm Engelmann, Leipzig.

McHugh J.V., Marshall C.J., Fawcett F.L. 1997. A study of adult morphology in *Megalodacne heros* (Say) (Coleoptera: Erotylidae). – Transactions of the American Entomological Society **123**(4): 167 – 223.

Pasteels J.M., Termonia A., Daloze D., Windsor D.M. 2003. Distribution of toxins in chrysomeline leaf beetles: possible taxonomic inferences. Pp. 261 – 275 in: Furth D.G. (ed.), Proceedings of the Fifth International Symposium on the Chrysomelidae, Iguacu, 2000. – Pensoft Publishers.

Paterson N.F. 1931. Studies on the Chrysomelidae II. The bionomics and comparative morphology of the early stages of certain Chrysomelidae. – Proceedings of the Zoological Society **3**: 879 – 949.

Petitpierre E. 2011. Cytogenetics, cytotaxonomy and chromosomal evolution of Chrysomelinae revisited (Coleoptera, Chrysomelidae). – ZooKeys **157**: 67 – 79.

Reid C.A.M. 1992. Descriptions of the pupae of nine genera of Australian paropsine Chrysomelinae. – Proceedings of the Linnean Society of New South Wales **113**(4): 311 – 337.

Reid C.A.M. 1995. A cladistic analysis of subfamilial relationships in the Chrysomelidae *sensu lato* (Chrysomeloidea). Pp. 559 – 631 in: Pakaluk J., Slipinski S.A. (eds.), Biology, Phylogeny, and Classification of Coleoptera: papers celebrating the 80th birthday of Roy A. Crowson, vol. 2. – Muzeum i Instytut Zoologii PAN, Warsaw. Pp. i – vi + 559 – 1092.

Riley E.G., Clark S.M., Flowers R.W., Gilbert A.J. 2002. 124. Chrysomelidae Latreille 1802. Pp. 617 – 691 in: Arnett R.H.Jr., Thomas M.C., Skelly P.E., Frank J.H. (eds.), American Beetles vol. 2. – CRC Press, Boca Raton etc.

Rivnay E. 1928. External morphology of the Colorado potato beetle (*Leptinotarsa decemlineata* Say). – Journal of the New York Entomological Society **36**: 125 – 141 + plates.

Seeno T.N., Wilcox J.A. 1982. Leaf beetle genera. – Entomography **1**: 1 – 221.

Steinhausen W.R. 1996. Vergleichende Morphologie der Puppen der Blattkäfer-Unterfamilie Chrysomelinae (Col., Chrysomelidae). – Entomologische Nachrichten und Berichte **40**(2): 89 – 98.

Steinhausen W.R. 2001. Integrierte Systematik bei Blattkäfern (Coleoptera, Chrysomelidae, Chrysomelinae). – Entomologische Blätter **97**(2/3): 225 – 236.

Tomaszewska K.W. 2000. Morphology, phylogeny and classification of adult Endomychidae (Coleoptera: Cucujoidea). – Annales Zoologici **50**: 449 – 558.

Warchalowski A. 2003. Chrysomelidae – The Leaf-Beetles of Europe and the Mediterranean Area. – Natura Optima Dux Foundation, Warsaw.

Weise J. 1915. Übersicht der Chrysomelini. – Deutsche Entomologische Zeitschrift **1915**(4): 434 – 436.