

The cervical sclerites of Mantodea discussed in the context of dictyopteran phylogeny (Insecta: Dictyoptera)

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Abstract. The ventral cervical sclerites, lateral cervical sclerites, and intercervical sclerites of 30 mantodean, 7 “blattarian”, and 4 isopteran species have been studied. This leads to new insights into the dictyopteran ground plan, autapomorphies for several taxa, and the evolution of the mantodean cervical region. It remains unclear if a lack or the presence of one or two ventral cervical sclerites (vcs) has to be assumed for the dictyopteran ground plan. The state of reduction of the vcs in *Phyllocrania* and *Gongylus*, however, supports a close relationship of Empusidae and certain Hymenopodidae. A weak, setae-bearing sclerite (sbs) posterior to the ventral cervical sclerites in *Cryptocercus* is probably autapomorphic. A transverse position of the intercervical sclerites (ics) is a ground plan feature of Dictyoptera and probably autapomorphic for the group. The presence of a groove (lcvg) on the lateral cervical sclerites is also hypothesized as autapomorphic for Dictyoptera with a convergent loss or partial reduction in several “Blattaria” lineages, in Isoptera, and in *Metallyticus*. A midventral fusion of the intercervical sclerites (ics) has probably taken place in the stem species of Mantoidea with a secondary separation in *Theopompella*, *Ameles* and *Empusa*. Two equally parsimonious hypotheses have been found for the evolution of the torus intercervicalis (ticv) with either a single gain in the ground plan of Mantodea except *Mantoida* and several losses within the group, or three separate gains in *Chaeteessa*, *Metallyticus* and the stem-species of Mantoidea with several losses within the latter. The medial groove (icmg) on the intercervicalia is probably autapomorphic for Dictyoptera with independent losses in *Mastotermes*, *Perlamantis*, and *Eremiaphila*. It remains obscure whether in the ground plan of Dictyoptera the posterior part of the intercervicalia is detached, as in Mantodea (sss) and Isoptera (icdpp), or not, as in “Blattaria” (icpp).

Key words. Blattaria, cervical sclerites, Dictyoptera, ground plan characters, Isoptera, Mantodea, morphology, phylogeny.

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1. Introduction

1.1. Systematics of Dictyoptera

Mantodea (praying mantids) is a group of predatory insects with about 2.300 described species (EHRMANN 2002). The taxon Dictyoptera consists of Mantodea together with Isoptera (termites) and “Blattaria” (cockroaches). The monophyly of Dictyoptera is undoubted (KRISTENSEN 1991, 1995; KLASS 1995, 2003; MAEKAWA et al. 1999; BEUTEL & GORB 2001; WHEELER et al. 2001; KJER 2004; TERRY & WHITING 2005), whereas the relationships among these three taxa are still under discussion (THORNE & CARPENTER 1992; DESALLE et al. 1992; BANDI et al. 1995; KLASS 1995, 1997, 1998a,b, 2003; GRANDCOLAS & DELEPORTE 1996; GRIMALDI 1997; LO et al. 2000, 2003; DEITZ et al. 2003; LO 2003; BOHN & KLASS 2003; KLASS

& MEIER 2006). “Blattaria” is most probably paraphyletic (KLASS 1995; LO 2003; KLASS 2003; TERRY & WHITING 2005; KLASS & MEIER 2006), whereas Isoptera and Mantodea are certainly monophyletic groups (HENNIG 1969; AX 1999; EGGLETON 2001; KLASS & EHRMANN 2003; GRIMALDI & ENGEL 2005).

BEIER (1968a) introduced a mantodean classification which is still used with little modification. In the classification by Ehrmann & Roy published in EHRMANN (2002) several “subfamilies” were raised to “family” rank (Liturgusidae, Tarachodidae, Thespididae, Iridopterygidae, Toxoderidae, Sibyllidae) and a new “family” Acanthopidae as well as several new “subfamilies” were created.

However, these changes lack a phylogenetic basis and recent molecular results (SVENSON & WHITING 2004) do not support these groupings. Therefore BEIER's (1968a) traditional classification is favoured in the present work. He proposed a typological classification consisting of 8 "families": Mantoididae, Chaeteessidae, and Metallyticidae with only a single genus each; Amorphoscelidae, Eremiaphilidae, Hymenopodidae, Mantidae, and Empusidae. Recent, mainly morphological works on the phylogeny of Dictyoptera (THORNE & CARPENTER 1992; KLASS 1995, 1997, 1998a,b; DEITZ et al. 2003) only included few mantodean species or used Mantodea as a single terminal taxon. Thus, the phylogenetic relationships within Mantodea are largely unknown and only the basal dichotomies have gained some evidence on a morphological basis (KLASS 1995, 1997) even if they are still under discussion (ROY 1999; GRIMALDI 2003; GRIMALDI & ENGEL 2005). Of all praying mantids, *Mantoida* Newman, 1838 has the most plesiomorphic phallomere complex in the way that several features unique among Mantodea are shared with certain "Blattaria" (KLASS 1995, 1997). It appears to be the sister taxon of the remaining Mantodea (Mantomorpha *sensu* KLASS 1995). However, GRIMALDI (2003) and GRIMALDI & ENGEL (2005), who included a greater part of all known fossil Mantodea as well as the extant taxa in their studies (though no data on the phallomeres), consider *Chaeteessa* Burmeister, 1838 to be the most basal mantid lineage living today due to the lack of a tibial spur and the setae-like spines of the raptorial legs. Both arguments were discussed and rejected by KLASS (1995). ROY (1999) considers *Metallyticus* Westwood, 1835 to be the most basal extant mantid due to plesiomorphic wing characters and the lack of discoidal spines on the raptorial forelegs. According to KLASS (1995) the second dichotomy is probably between *Chaeteessa* and the remaining taxa (Mantidea *sensu* KLASS 1995). The same author favours the view that the third dichotomy consists of *Metallyticus* and the remaining groups (KLASS 1995), the latter of which have not yet been the subject of further phylogenetic investigations until recently. Some morphological characters such as the metathoracic hearing organ ("cyclopean ear") and the elongation of the prothorax may be autapomorphic for a clade Hymenopodidae + Mantidae + Empusidae, which are grouped as Mantoidea by ROY (1999), GRIMALDI (2003), and GRIMALDI & ENGEL (2005). Furthermore, there are some morphological characters that apparently support the monophyly of Empusidae (ROY 2004). However, except for the specialized anteroventral spination of the forefemur ("inner spines"), many of them are also shared with certain Hymenopodidae species, for instance characters of the head (ROY 2004) and of the prosternal region (Wieland, unpubl. data). The asymmetrical subgenital plate of the males is also shared with other mantodean taxa (e.g. *Metallyticus splendidus*, *Tarachodula pantherina*, *Pseudocreobotra wahlbergii*) and even cockroaches (*Ectobius* spp.) (Wieland, pers. obs.; KLASS 1997: 266). Therefore this condition is certainly plesiomorphic.

Results from a phylogenetic reconstruction based on molecular data of 55 mantodean, 5 "blattarian" and 3 isopteran species were recently published by SVENSON & WHITING (2004). Their analysis supports the sister-relationship of *Mantoida* and the remaining Mantodea. However, the analysis does neither include *Chaeteessa* nor *Metallyticus*. Therefore, to date molecular analyses have not yet addressed the relationships among the most primitive groups of Mantodea and the question for the most basal extant mantid needs further discussion. SVENSON & WHITING's (2004) cladogram shows Mantidae, Hymenopodidae and several "subfamilies" *sensu* BEIER (1968a) to be para- or polyphyletic. Empusidae is represented by only a single species (*Gongylus gongylodes*), which comes out to be the sister taxon to a hymenopodid species (*Phyllocrania paradoxa*). This supports a close relationship between the two groups as already proposed by ROY (2004). Eremiaphilidae is not represented in molecular analyses so far.

Morphological characters used for taxonomy that led to previous classifications (e.g. KALTENBACH 1963, 1996, 1998; BEIER 1968a; ROY 1987, 1999) and that were used for the few phylogenetic approaches (e.g. KLASS 1995, 1997; ROY 2004; LOMBARDO & IPPOLITO 2004) come, for instance, from the spination-pattern of the raptorial forelegs, the wing-venation, projections of the vertex, shape and orientation of the supra-anal plate, and the length and shape of the prothorax. Some phylogenetic approaches additionally used the complex skeletomuscular system of the genital organs (KLASS 1995, 1997).

1.2. The sclerotizations of the cervix and their origin within Insecta

The focus in the present work is on the morphology of the cervical sclerites. These sclerites stabilize the soft neck region, which is elongated in most Mantodea living today except for the so-believed most primitive taxa (i.e. *Mantoida*, *Chaeteessa*, *Metallyticus*) and Eremiaphilidae. While *Eremiaphila* is not capable of turning the head as freely as the more derived taxa (Wieland, pers. obs.), the head mobility has not been observed or described in the literature for living specimens of the other three mentioned genera so far.

The three pairs of cervical sclerites studied here (ventral cervical sclerites, lateral cervical sclerites, intercervicalia) can be found in many insect taxa.

The ventral cervical sclerites are probably autapomorphic for Dicondylia because Collembola (SCHALLER 1970), Diplura (MATSUDA 1970), and Protura (JANETSCHKE 1970) do not have them, and they have not been described for Archaeognatha by DENIS (1949), BITSCH (1963), BARLET (1967), and MATSUDA (1970), either. The zygentoman *Lepisma*, however, seems to have two sclerotized ventral cervical sclerites as depicted by CRAMPTON (1917: ps in fig. 1).

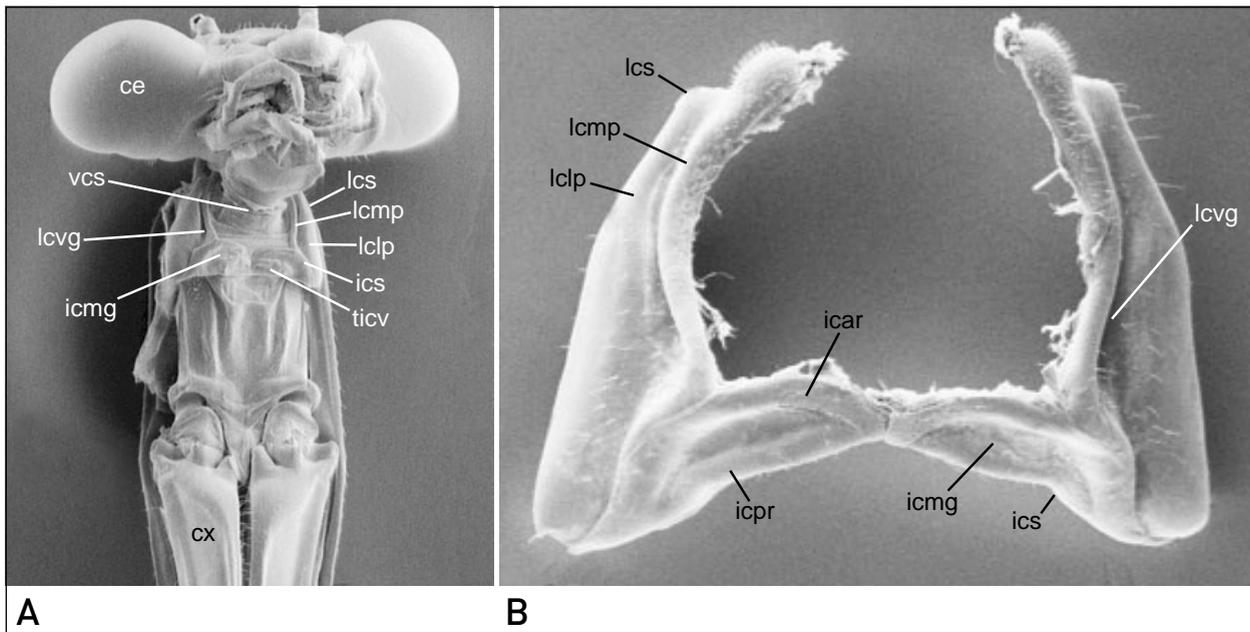


Fig. 1. SEM-images of the ventral prothorax of Mantodea. **A:** *Tenodera* sp., nymph; prothorax, cervical sclerites and head in a ventral view. **B:** *Sphodromantis* sp., ♀, lateral cervical sclerites and intercervicalia (2nd lateral cervical sclerites), surrounding membranes of cervix removed. Orientation: ↑ cranial.

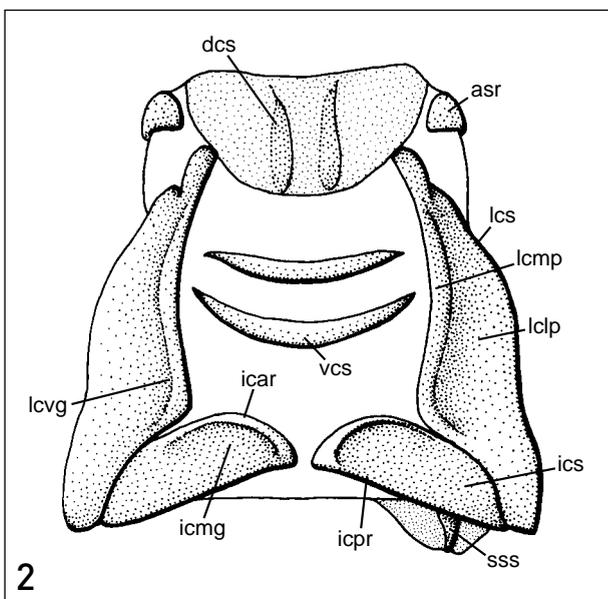


Fig. 2. *Stagmomantis carolina*; cervical sclerites including position of the dorsal cervical sclerites **dcs** and the small slender sclerites **sss**; redrawn and adapted from LEVEREAULT (1936: pl. 11, fig. 7).

The lateral cervical sclerites and intercervicalia most probably have their origin in an undivided laterocervical plate. In many taxa (e.g. Dictyoptera, Embioptera, Phasmatodea) the laterocervical plate is split into lateral cervical sclerites and intercervicalia, which then together are referred to as the laterocervical complex. No such cervical structure has been described for Ellipura and Diplura. The archaeognathan *Lepismachilis* possesses occipital structures (“processus postgénéral” of BARLET

1967: 116, **ag** in fig. 1; “sclérite postlabiale” of BARLET 1967: 116, **pb** in figs. 1, 3) the former of which is probably homologous to the condyle that articulates with the lateral cervical sclerite in many pterygote taxa (MATSUDA 1970: 8). BARLET described a “sclérite anapleurale supérieur” (BARLET 1967: **ap** in fig. 1) that MATSUDA (1970: 7, 8) considered to be homologous to the lateral cervical sclerite of Pterygota due to the probable homology of muscles inserting on the “processus postgénéral” and the “sclérite postlabiale”. However, this structure is a pleural sclerite, therefore the head capsule articulates directly with the propleura without a laterocervical plate being detached from the latter in Archaeognatha and Zygentoma. Detached laterocervical plates, either undivided or split into lateral cervical sclerites and intercervicalia, can be found in many Pterygota and are probably autapomorphic for the group. MATSUDA (1970: 8) distinguished four types of origin for the lateral cervical sclerites. He hypothesized a similarity of origin for Plecoptera, “Blattaria” and “related orders”, and Coleoptera (MATSUDA 1970: 8) suggesting the homology of the lateral cervical sclerites within some lower neopteran taxa. WEIDNER (1982: 154) even assumed a single origin of the laterocervical plate in all hemimetabolous taxa and Coleoptera.

The intercervicalia show different states within Pterygota. WEBER (1924: 81) considered the lack of a laterocervical plate or the presence of a vaguely bordered, triangular and entire laterocervical plate to be plesiomorphic. It remains unclear if the division of the laterocervical plate into lateral cervical sclerites and intercervicalia has a single or a multiple origin.

Most Plecoptera possess an undivided laterocervical plate, which, however, may show a subdivision into two parts in *Eusthenia* (ZWICK 1980: 45).

Tab. 1. Mantodea investigated. Sex: the sexes given refer to the specimens depicted in this paper. Collections: NHMW = Collection of the Naturhistorisches Museum Wien, Vienna; ZMB = Collection of the Museum für Naturkunde of the Humboldt-University, Berlin; CW = author's collection.

Taxon	Sex	Distribution	Collection
Mantoididae <i>Mantoida maya</i> Saussure & Zehntner, 1894	♂	South and Central America, Florida	CW
Chaeteessidae <i>Chaeteessa caudata</i> Saussure, 1871	♂	South and Central America	NHMW
Metallyticidae <i>Metallyticus splendidus</i> Westwood, 1835	♀	Southeast Asia	CW
Amorphoscelidae Amorphoscelinae <i>Perlamantis allibertii</i> Guérin-Méneville, 1843	♂	Southern Europe, North Africa	NHMW
Paraoxyphilinae <i>Paraoxyphilus verreauxii</i> Saussure, 1870	♂	Australia, Tasmania	NHMW
Eremiaphilidae <i>Eremiaphila braueri</i> Krauss, 1902	♀	Yemen, Sokotra Isl., Jordan, Oman, United Arab Emirates	CW
Hymenopodidae Acromantinae <i>Acanthops</i> sp.	♀	Central and South America	CW
<i>Phyllocrania paradoxa</i> Burmeister, 1838	♂	South and West Africa	CW
Hymenopodinae <i>Creobroter</i> sp.	♀	Southeast Asia	CW
<i>Pseudocreobotra ocellata</i> Palisot, 1805	♀	Central, South and West Africa	CW
Mantidae Liturgusinae <i>Theopompella heterochroa</i> Gerstäcker, 1803	♀	West Africa	NHMW
<i>Humbertiella</i> sp.	♀	Sri Lanka, Southeast Asia	CW
Angelininae <i>Euchomenella heteroptera</i> Haan, 1842	♂	Southeast Asia	NHMW
<i>Leptocola phthisica</i> (Saussure, 1869)	♂	Central and West Africa	ZMB
<i>Stenopyga ziela</i> Roy, 1963	♂	West Africa	ZMB
Amelininae <i>Ameles decolor</i> Charpentier, 1825	♀	Mediterranean	CW
Mantinae <i>Mantis religiosa</i> Linné, 1758	♀	Europe, Asia, Australia, Africa, North America	CW
<i>Mesopteryx alata</i> Saussure, 1870	♀	Southeast Asia, Philippines	NHMW
<i>Tenodera aridifolia</i> (Stoll, 1813)	♂	China, Eastern USA	NHMW
<i>Sphodromantis lineola</i> Burmeister, 1838	♀	Western Africa	CW
Vatinae <i>Oxyopsis gracilis</i> Giglio-Tos, 1914	♂	Paraguay, Bolivia	CW
<i>Heterochaeta strachani</i> (Kirby, 1904)	♀	West Africa	CW
<i>Macrodanuria elongata</i> (Borre, 1838)	♂	West Africa	NHMW
<i>Popa spurca</i> Stål, 1856	♀	South and Oriental Africa	ZMB
Photininae <i>Brunneria borealis</i> Scudder, 1896	♀	Southeast USA	NHMW
<i>Orthoderella ornata</i> Giglio-Tos, 1897	♂	Argentina, Paraguay	ZMB
Toxoderinae <i>Toxodera denticulata</i> Serville, 1837	♀	Java, Sumatra	ZMB
Empusidae Empusinae <i>Gongylus gongylodes</i> Linné, 1758	♀,♂	India, Sri Lanka	CW
<i>Empusa fasciata</i> Brullé, 1832	♀	Turkey, Crete, the Balkans Peninsula, Rhodes	NHMW
Blepharodinae <i>Blepharopsis mendica</i> (Fabricius, 1765)	♂	North Africa, Middle East, Pakistan, India	ZMB

MATSUDA (1970: fig. 67) depicts the lateral cervical complex of *Grylloblatta campodeiformis* as consisting of two plates, the posterior of which he homologises with the intercervical sclerite due to its position and

articulation with the preepisternum (MATSUDA 1970: 167, 168). CRAMPTON (1915: fig. 9), however, depicts *Grylloblatta* with a posterior area of the sclerite being continuous with the anterior part and therefore postulates

Tab. 2. Outgroup species investigated. Sex / caste refers to the specimens depicted herein. All specimens from the author's collection.

Taxon	sex / caste	drawing	original author
“Blattaria”			
Blattidae: Blattinae			
<i>Periplaneta americana</i> (Linné, 1758)	♀	original	
<i>Blatta orientalis</i> (Linné, 1758)	♂	original	
Lamproblattidae			
<i>Lamproblatta albipalpus</i> Hebard, 1919	unknown	original	
“Blattellidae”: Ectobiinae			
<i>Ectobius silvestris</i> (Poda, 1761)	♂	original	
“Blattellidae”: Blattellinae			
<i>Blattella germanica</i> (Linné, 1767)	unknown	redrawn and adapted	MATSUDA (1956)
Blaberidae: Blaberinae			
<i>Blaberus craniifer</i> (Burmeister, 1838)	♀	original	
Cryptocercidae			
<i>Cryptocercus punctulatus</i> Scudder, 1862	♂	original	
Isoptera			
Mastotermitidae			
<i>Mastotermes darwiniensis</i> Froggatt, 1897	soldier	original	
Termitidae: Macrotermitinae			
<i>Macrotermes bellicollis</i> (Smeathman, 1781)	soldier	original	
Termitidae: Nasutitermitinae			
<i>Nasutitermes nigriceps</i> (Haldeman, 1853)	soldier	original	
“Typical termite”	unknown	redrawn and adapted	MATSUDA (1970) after FULLER (1924)

an undivided lateral cervical plate. This has also been shown in simplified drawings by UCHIFUNE & MACHIDA (2005: *cs* in figs. 4b,b',c,c') for *Galloisiana yuasai*.

Studies on the situation in Mantophasmatodea are still due to date.

Embioptera have distinctly separated lateral cervical sclerites and intercervicalia (BITSCH & RAMOND 1970: figs. 4–6; MATSUDA 1970: fig. 51; ROSS 2000: figs. 12b,c, 13; Wieland, pers. obs.).

Phasmatodea have separated lateral cervical sclerites and intercervicalia (BEIER 1968b: figs. 12a,c; BRADLER 1999: figs. 2a–c; TILGNER et al. 1999: fig. 14; Wieland, pers. obs.). JEZIORSKI (1918: 732) mentioned an entire lateral cervical plate for *Carausius morosus* on either side of the cervix. However, a suture of weak sclerotization is discernible between the two sclerites (Wieland, pers. obs.).

Orthoptera are heterogeneous and show both conditions. They may have an undivided plate as, for instance, *Dolichopoda* and *Oecanthus* do (MATSUDA 1970: 169). Some taxa (e.g. *Gryllus*) have incompletely separated lateral cervical sclerites and intercervicalia (MATSUDA 1970: 169; fig. 68a) or entirely separated ones (e.g. *Tetrix*, MATSUDA 1970: fig. 68b). The undivided condition has been assumed to be plesiomorphic in Orthoptera (MATSUDA 1970: 170).

Dictyoptera have distinctly separated lateral cervical sclerites and intercervicalia as shown herein and by several other authors who have studied the dictyopteran cervical region, for instance MARTIN (1916: “Blatt.”); CRAMPTON (1917: Iso., “Blatt.”; 1926: Iso., “Blatt.”,

Mant.; 1927: “Blatt.”); FULLER (1924: Iso.); LEVEREAULT (1936, 1938: Mant.); LA GRECA & RAUCCI (1949: Mant.); MATSUDA (1956: “Blatt.”).

The cervical sclerites of 30 Mantodea species are compared herein with the conditions in selected taxa of “Blattaria” and Isoptera as outgroup representatives, and their usefulness for analyses of the relationships within Mantodea and among the dictyopteran taxa is discussed.

2. Material and Methods

2.1. Techniques

The specimens studied herein were either fixed in ethanol (80%) or dry. The exoskeletal characters were investigated with a binocular microscope (Zeiss Stemi SV 11), without KOH maceration. The structures of interest were drawn in ink with the help of a camera lucida (Zeiss). The SEM-pictures were taken with a LEO 438 VP Microscope. Some pictures from other publications were redrawn and adapted.

2.2. Material

30 species of Mantodea from the collections of the Naturhistorisches Museum Wien, Vienna, the Museum für Naturkunde of the Humboldt-University, Berlin,

and from the author's collection were studied (Tab. 1). Additionally, 7 species of cockroaches and 4 species of termites from the author's collection were investigated as outgroup representatives (Tab. 2).

3. Abbreviations

asr	additional sclerotized region
ce	compound eye
cx	coxa
dcs	dorsal cervical sclerite
icar	anterior rim of intercervical sclerite
icdpp	detached posterior part of intercervical sclerite (Isoptera)
icmg	medial groove of intercervical sclerite
icpp	posterior part of intercervical sclerite, not being detached ("Blattaria")
icpr	posterior rim of intercervical sclerite
ics	intercervical sclerite (2 nd lateral cervical sclerite)
lcdg	dorsal groove of lateral cervical sclerite
lcdp	dorsal part of lateral cervical sclerite
lclp	lateral part of lateral cervical sclerite
lcmp	medial part of lateral cervical sclerite
lcs	lateral cervical sclerite
lcvg	ventral groove of lateral cervical sclerite
sbs	additional setae-bearing sclerotization (<i>Cryptocercus</i>)
sss	small slender sclerite (Mantodea)
ticv	torus intercervicalis
vcs	ventral cervical sclerite

4. Results

4.1. General description of the cervical sclerites

The cervix (neck) of the insects is the largely membranous region spanning between the postoccipital foramen of the head and the cervical foramen of the prothorax (SNODGRASS 1935: 159; LEVEREAULT 1936: pl. 11, figs. 7, 10; BEIER 1968a: fig. 20).

There are five different paired or unpaired types of cervical sclerites in Mantodea (LEVEREAULT 1936: **dCv**, **vCv1** and/or **vCv2**, **ICv1**, **ICv2**, **4** in pl. 11, fig. 7; BEIER 1968a: **Po**, **Cerv_{b,c}**, **ICerv** in fig. 20, dorsal cervical sclerites not depicted), three of which were studied in the present article: ventral cervical sclerites, lateral cervical sclerites, and intercervicalia.

The ventral cervical sclerites (**vcs** in Figs. 1a, 2, 4, 9–33; LEVEREAULT 1936: **vCv** and **vCv2** in pl. 11, fig. 7; BEIER 1968a: **Po** in fig. 20) are one or two unpaired, transverse and slender sclerotizations in the ventromedian part of the cervix. In some mantodean species they are divided at the ventral midline. They are not in contact with any other sclerites. The ventral cervical sclerites can also be

found in "Blattaria" (Figs. 34–40; MARTIN 1916: 75, fig. 3; BEIER 1974: 21, fig. 21) and are said to be present in Termopsidae within Isoptera (WEIDNER 1970: **pg** in fig. 99) – an observation which could not be supported by the study of *Termopsis* sp. (Grimaldi, pers. comm.). *Termopsis*, however, is a fossil genus without any extant species. Further studies on extant Termopsidae are necessary to decide whether the ventral cervical sclerites are actually present in the group.

The lateral cervical sclerites, also named 1st lateral cervical sclerites by several authors (**lcs** in Figs. 1–44; LEVEREAULT 1936: **ICv1** in pl. 11, fig. 7; LA GRECA & RAUCCI 1949: **2c** in fig. 1; BEIER 1968a: **Cerv_b** in fig. 20), are the largest cervicalia and are present as one pair in all three dictyopteran taxa. They are often almost triangular in ventral view and cross the cervix longitudinally on either side of the neck. They articulate anteriorly with the occipital condyles and posteriorly with the intercervicalia (LEVEREAULT 1936: 222). In Mantodea, each bears a deep longitudinal groove **lcvg**, which is only shallow in "Blattaria" and absent in Isoptera (**lcvg** in Figs. 1–33, 35–37, 40). It runs from front to back through the middle of the sclerite. The groove separates a medial part of the lateral cervical sclerite (**lcmp** in Figs. 1–33, 35–37, 40) from a lateral part (**lclp** in Figs. 1–33, 35–37, 40). When **lcvg** is missing or only partly present, **lcmp** and **lclp** can be distinguished only in the area where the groove is present. The part **lcmp** is generally straight or slightly curved and bulged in Mantodea. The part **lclp** is bulged and separated from **lcmp** by **lcvg** in a straight or S-shaped way. When present in "Blattaria", **lcmp** is mostly straight or slightly curved. Isoptera lack a subdivision of the lateral cervical sclerite.

Chaeteessa, *Perlamantis* and *Metallyticus* have a lateral cervical sclerite that appears more or less three-parted. This is due to the three-dimensional structure of the sclerite and a subdivision of the lateral part by another groove: the specific dorsal part (**lcdp** in Figs. 4–6) is separated from the lateral part by a dorsal groove (**lcdg** in Figs. 4–6). In the view chosen herein it projects above the lateral part, thus giving it the tripartite appearance. The groove **lcdg** in *Perlamantis* is only weakly developed. The subdivision in *Metallyticus* is probably not homologous to that of *Chaeteessa* and *Perlamantis* as will be discussed later.

Another pair of cervical sclerites, the intercervicalia, are also called 2nd lateral cervical sclerites by some authors (**ics** in Figs. 1–44; CRAMPTON 1926: **ic** in pl. 12, fig. 28 and pl. 15, fig. 85; LEVEREAULT 1936: **ICv2** in pl. 11, fig. 7; LA GRECA & RAUCCI 1949: **3c** in fig. 1; BEIER 1968a: **ICerv** in fig. 20). They stabilize the ventral membranous area of the cervix and are hinged anteriorly to the lateral cervical sclerites and posteriorly to a pair of cervical sclerites that articulates with the preepisternite in Mantodea (**sss** in Fig. 2; BEIER 1968a: 19; MATSUDA 1970: 157). In Isoptera and "Blattaria" the intercervicalia are directly hinged to the preepisternite + anepisternite (MATSUDA 1970: 154, 143). The central part of each intercervical sclerite bears a groove or hollow of varied shape and orientation (**icmg** in Figs. 1–5, 7, 9–37, 39, 40, 42–44).

The marginal parts of the intercervicalia surrounding the groove **icmg**, especially the anterior and posterior rims (**icar** and **icpr** in Figs. 1b, 2–5, 7, 9–40, 42–44), are more or less bulged. In some Mantodea the posterior rim shows a knob-like, thickened area protruding from **icpr** like a small shelf. It may carry long setae (Wieland, pers. obs.) and is named the torus intercervicalis (**ticv** in Figs. 1a, 4, 5, 9–12, 18–22, 24–28, 30–32) by the author. The other dictyopteran taxa may also have a shallow groove upon the intercervicalia (**icmg** in Figs. 34–37, 39–40, 42–44) but they lack the tori intercervicales.

The dorsal cervical sclerites (**dcs** in Fig. 2) lie in the dorsal neck membrane close to the postocciput and close to the midline without any connection to other sclerites (LEVEREAULT 1936: **dCv** in pl. 11, fig. 7; LA GRECA & RAUCCI 1949: **1c** in fig. 1). They are also present in “Blattaria” (pers. obs. in *Blatta orientalis* and *Blaberis craniifer*) and some Isoptera (e.g. in *Archotermopsis*, WEIDNER 1970: 83).

An additional region on either side of the dorsal cervical sclerites (formally named “additional sclerotized region” **asr** in Fig. 2; LEVEREAULT 1936: **3** in pl. 11, figs. 7, 10; BEIER 1968a: **Cerv_a** in fig. 20) may be slightly sclerotized as in *Stagmomantis carolina* (LEVEREAULT 1936: 222; Fig. 2 herein) or more strongly sclerotized as in *Popa spurca* (Wieland, pers. obs.). These regions carry numerous setae and in the living specimen they come in contact with the underside of the anterior pronotum. Therefore it is possible that they function as mechanoreceptive units for the coordination of head or neck movements.

Another pair of cervical sclerites in Mantodea (formally named “small and slender sclerites” **sss** in Fig. 2; LEVEREAULT 1936: **4** in pl. 11, fig. 7; LA GRECA & RAUCCI 1949: **4c** in fig. 1; BEIER 1968a: **Cerv_c** in fig. 20) are hidden by the intercervicalia in a fold of the cervix. They intervene between the intercervicalia and the rim of the cervical foramen (LEVEREAULT 1936: **Cer f** in pl. 11, fig. 1) where they articulate with the preepisternum (CRAMPTON 1926: pl. 12, fig. 28, pl. 15, fig. 85; BEIER 1968a: 19). LEVEREAULT (1936: 222) assumes the small sclerites **sss** to be “posterior parts of the margins of the second lateral cervicals” (i.e. intercervicalia). This pair of cervical sclerites cannot be recognized in “Blattaria” but the sclerotizations concerned might be included in the intercervicalia. They can perhaps be derived from a lengthened posterior part (**icpp** in Figs. 34, 36–40) of the intercervicalia in “Blattaria”. In Isoptera the posterior part of the intercervicalia is detached (**icdpp** in Figs. 41–44) but is much larger than in Mantodea. In both Isoptera and “Blattaria” the posterior part of the intercervicalia articulates with the preepisternite (= precoxale) (MARTIN 1916: 75; CRAMPTON 1926: pl. 12, figs. 27, 29, 33, pl. 14, figs. 56–57; MATSUDA 1970: 143; WEIDNER 1970: 83) or the preepisternite + anepisternite of the prothorax (Isoptera, MATSUDA 1970: 154).

The dorsal cervicalia **dcs** and the small slender sclerites **sss** were not studied in detail in the present work. However, the possible origin of the mantodean small slender sclerites within Dictyoptera is discussed.

4.2. Homology of the cervical sclerites in Dictyoptera

The lateral cervical sclerites as well as the intercervicalia are homologous structures in Mantodea, “Blattaria” and Isoptera based on the criteria usually used for homology identification (REMANE 1952). In all Dictyoptera the lateral cervical sclerites articulate anteriorly with the same region of the head capsule and posteriorly with the intercervicalia. The latter, or their detached posterior parts, are hinged to the preepisternum or preepisternal area in this group (MARTIN 1916: 75; CRAMPTON 1926: pl. 12, figs. 27–29, 33, pl. 14, figs. 56–57, pl. 15, fig. 85; MATSUDA 1970: 143, 154; WEIDNER 1970: 83). They stabilize the cervical membrane, and are important insertion points for muscles. The three dictyopteran groups have several cervical muscles in common (MATSUDA 1970: 164 and 57, **op-cv2** or **op-cv3** and **t-cv 2** in fig. 22). Muscles **op-cv2** and **op-cv3** are not distinguishable in Isoptera and “Blattaria” and were not separately recognized in *Mantis religiosa* by LA GRECA & RAUCCI (1949: **8** in fig. 4); however, the two muscles are discrete in *Stagmomantis carolina* (LEVEREAULT 1938). Both **op-cv2** and **op-cv3** arise from the postocciput and are inserted on the anterior and posterior regions of the intercervical sclerite (MATSUDA 1970: 58, fig. 22b; LEVEREAULT 1938: **1a** and **1b** in figs. 2, 3). Muscle **t-cv2** arises from the pronotum and is inserted on the posterior end of the intercervical sclerite (MATSUDA 1970: 58 and fig. 22a; LEVEREAULT 1938: **3** in figs. 2, 3). (MATSUDA does not differentiate between lateral cervical sclerites and intercervicalia in his drawings but depicts them clearly as separated. Therefore the muscle insertions mentioned by him have been changed here to their position on the corresponding separate intercervicalia.)

The ventral cervical sclerites of Dictyoptera lack muscle insertions (MATSUDA 1970: 164–166). However, the sclerites have the same position in the ventral cervix medially between the lateral cervical sclerites and are therefore probably homologous in the three groups.

4.3. The cervical sclerites of Mantodea (Figs. 3–33)

4.3.1. *Mantoida maya* ♂ (Mantoididae, Fig. 3).

There are no ventral cervical sclerites **vcs**. The medial part **lcmp** of the lateral cervical sclerites **lcs** is bulged and slightly curved. The groove **lcvg** is deep. The lateral part **lclp** is bulged as well. The intercervicalia **ics** point medially and are not fused in the midline. The anterior and posterior rims **icar** and **icpr** are only weakly bulged. Therefore the groove **icmg** is only shallow. There is no torus intercervicalis **ticv**.

4.3.2. *Chaeteessa caudata* ♂ (Chaeteessidae, Fig. 4).

One ventral cervical sclerite **vcs** is present, located close to the postmentum. The medial part **lcmp** of the lateral cervical sclerites **lcs** is slightly curved and bulged. Groove **lcvg** is deep. The dorsal part **lcdp** projects above

the lateral part **lclp** from which it is separated by a deep groove **lcdg**, thus the lateral cervical sclerite appears tripartite. The intercervicalia **ics** point medio-cranial and are not fused in the midline. The groove **icmg** is present. The anterior rim **icar** is broad and distinctly bulged, the posterior rim **icpr** is almost plane except for the torus intercervicalis **ticv**.

4.3.3. *Metallyticus splendidus* ♀ (Metallyticidae, Fig. 5). No ventral cervical sclerites **vcs** are present. The medial part **lcmp** of the lateral cervical sclerites **lcs** is bulged and almost straight. Groove **lcvg** is only posteriorly present, therefore the lateral part **lclp** and the medial part **lcmp** are lying anteriorly in the same plane. The groove **lcvg** deepens caudally. The lateral part **lclp** is bulged. The dorsal part **lcdp** is separated from the lateral part **lclp** by the groove **lcdg**, thus giving the impression of a tripartite sclerite. The intercervicalia **ics** are not fused in the midline. The anterior rim **icar** is wide and distinctly bulged and the groove **icmg** is narrow. The posterior rim **icpr** is flat except for the torus intercervicalis **ticv**.

4.3.4. *Perlamantis allibertii* ♂ (Amorphoscelidae: Amorphoscelinae, Fig. 6). No ventral cervical sclerites **vcs** are present. The medial part **lcmp** of the lateral cervical sclerites **lcs** runs slightly diagonally from front to back and is slightly curved. The groove **lcvg** is deep. The lateral part **lclp** is strongly bulged and slopes towards the outer edge. The dorsal part **lcdp** slightly projects above the lateral part **lclp**. The dorsal groove **lcdg** is short and shallow. The intercervicalia **ics** bend such that their lateral halves are orientated medio-cranial whereas the medial halves are transverse. The intercervicalia are widely separated from each other. The thickened margins **icar** and **icpr**, groove **icmg** and the torus intercervicalis **ticv** are missing.

4.3.5. *Paraoxyphilus verreauxii* ♂ (Amorphoscelidae: Paraoxyphilinae, Fig. 7). No ventral cervical sclerites **vcs** are present. The medial part **lcmp** of the lateral cervical sclerites **lcs** is slightly curved and runs diagonally from front to back. The groove **lcvg** is deep. The intercervicalia **ics** are not fused in the midline. The grooves **icmg** run throughout their entire lengths, however, the anterior rim **icar** and the posterior rim **icpr** are only slightly bulged. A torus intercervicalis **ticv** is missing.

4.3.6. *Eremiaphila braueri* ♀ (Eremiaphilidae, Fig. 8). No ventral cervical sclerites **vcs** are present. The cervical sclerites have shifted into the sagittal plane resulting in a short neck. Therefore in ventral view they appear shorter than they actually are. The medial part **lcmp** of the lateral cervical sclerites **lcs** is orientated diagonally from front to back. The groove **lcvg** is narrow and the lateral part **lclp** is bulged. The intercervicalia **ics** are widely separated from each other. The thickened margins **icar** and **icpr**, groove **icmg** and the torus intercervicalis **ticv** are missing.

4.3.7. *Acanthops* sp. ♀ (Hymenopodidae: Acromantinae, Fig. 9). Two weakly sclerotized ventral cervical

sclerites **vcs** are present each of which is and medially split in two parts. The medial part **lcmp** of the lateral cervical sclerites **lcs** is S-shaped. The groove **lcvg** is deep and runs from front to back over the entire sclerite. The lateral part **lclp** is wide and S-shaped. The intercervicalia **ics** are medially fused. Their anterior rims **icar** are bulged and wide. Groove **icmg** is narrow and runs through the entire sclerite. The posterior rim **icpr** is plane except for the weakly developed torus intercervicalis **ticv**.

4.3.8. *Phyllocrania paradoxa* ♂ (Hymenopodidae: Acromantinae, Fig. 10). Two weakly sclerotized ventral cervical sclerites **vcs** are present. The anterior one is subdivided into four small parts, whereas the posterior one is split into two larger parts. The medial part **lcmp** of the lateral cervical sclerites **lcs** is slightly curved. The groove **lcvg** divides the medial part **lcmp** from the S-shaped, bulged lateral part **lclp**. The intercervicalia **ics** are medially fused. The anterior and posterior rims **icar** and **icpr** are equally wide and bulged. The torus intercervicalis **ticv** is slender and only weakly bulged.

4.3.9. *Creobroter* sp. ♀ (Hymenopodidae: Hymenopodinae, Fig. 11). Two ventral cervical sclerites **vcs** are present. The medial part **lcmp** of the lateral cervical sclerites **lcs** is straight. The groove **lcvg** is anteriorly flat and deepens posteriorly. The lateral part **lclp** is bulged but not curved in an S-shaped manner. The intercervicalia **ics** are medially fused. The groove **icmg** is shallow. The anterior rim **icar** is bulged, whereas the posterior one **icpr** is plane, except for the distinct torus intercervicalis **ticv**.

4.3.10. *Pseudocreobotra ocellata* ♀ (Hymenopodidae: Hymenopodinae, Fig. 12). Two weakly sclerotized ventral cervical sclerites **vcs** are present. The medial part **lcmp** of the lateral cervical sclerites **lcs** is slightly curved. The groove **lcvg** is deep and the lateral part **lclp** is bulged and curved in an S-shaped way. The intercervicalia **ics** are medially fused. The anterior rim **icar** is narrow and distinctly bulged, whereas the posterior rim **icpr** is plane except for the small torus intercervicalis **ticv**. The groove **icmg** is shallow.

4.3.11. *Theopompella heterochroa* ♀ (Mantidae: Liturgusinae, Fig. 13). Two ventral cervical sclerites **vcs** are present. The medial part **lcmp** of the lateral cervical sclerites **lcs** is slightly curved. Laterally it is followed by the groove **lcvg** which runs from front to back. The lateral part **lclp** is bulged in an S-shaped way. The intercervicalia **ics** are not fused in the midline. The groove **icmg** is bordered by the anterior and posterior rims **icar** and **icpr**, which are equal in width and slightly bulged. A torus intercervicalis **ticv** is missing.

4.3.12. *Humbertiella* sp. ♀ (Mantidae: Liturgusinae, Fig. 14). Two ventral cervical sclerites **vcs** are present the posterior of which is divided in two parts. The medial part **lcmp** of the lateral cervical sclerites **lcs** is slightly curved. Groove **lcvg** is deep and wide. The lateral part

lclp is bulged and curved in an S-shaped manner. The intercervicalia **ics** are medially fused. Groove **icmg** is present. The anterior rim **icar** is bulged. The posterior rim **icpr** is plane, a torus intercervicalis **ticv** is missing.

4.3.13. *Euchomenella heteroptera* ♂ (Mantidae: Angelinae, Fig. 15). Two ventral cervical sclerites **vcs** are present. The medial part **lcmp** of the lateral cervical sclerites **lcs** is slightly curved. Groove **lcvg** is deep. The lateral part **lclp** is S-shaped and bulged. The intercervicalia **ics** are fused in the midline. The groove **icmg** is surrounded by the rim of the intercervical sclerite **icar** and **icpr** being uniformly wide. A torus intercervicalis **ticv** is missing.

4.3.14. *Leptocola phthisica* ♂ (Mantidae: Angelinae, Fig. 16). Two strongly sclerotized ventral cervical sclerites **vcs** are present. The medial part **lcmp** of the lateral cervical sclerites **lcs** is slightly curved. Groove **lcvg** is deep and narrow. The lateral part **lclp** is curved and bulged. The intercervicalia **ics** are medially fused. The posterior rim **icpr** is slightly wider than the slender anterior rim **icar**. The groove **icmg** is shallow and there is no torus intercervicalis **ticv**.

4.3.15. *Stenopyga ziela* ♂ (Mantidae: Angelinae, Fig. 17). Two ventral cervical sclerites **vcs** are present. The medial part **lcmp** of the lateral cervical sclerites **lcs** is slightly curved. The groove **lcvg** is deep and short. It runs from the anterior quarter to the posterior third of the sclerite. The lateral part **lclp** is curved in an S-shape. The intercervicalia **ics** are medially fused. The anterior rim **icar** is narrow and distinctly bulged, whereas the posterior rim **icpr** is only slightly bulged. Groove **icmg** is extended and shallow, a torus intercervicalis **ticv** is missing.

4.3.16. *Ameles decolor* ♀ (Mantidae: Amelinae, Fig. 18). Two ventral cervical sclerites **vcs** are present, both of which are weakly sclerotized. The medial part **lcmp** of the lateral cervical sclerites **lcs** is almost straight. The groove **lcvg** is flat. The lateral part **lclp** is bulged and straight. The intercervicalia **ics** are medially separated. The anterior rim **icar** is narrow and slightly bulged whereas the posterior rim **icpr** is flat except for the torus intercervicalis **ticv**. Groove **icmg** is shallow.

4.3.17. *Mantis religiosa* ♀ (Mantidae: Mantinae, Fig. 19). Two strongly sclerotized ventral cervical sclerites **vcs** are present. The medial part **lcmp** of the lateral cervical sclerites **lcs** is slightly curved. Groove **lcvg** is deep, and the lateral part **lclp** is bulged in an S-shaped manner. The intercervicalia **ics** are fused in the midline. Groove **icmg** is deep. The anterior rim **icar** is wider and more strongly bulged than the posterior rim **icpr**. A small but distinct torus intercervicalis **ticv** is present.

4.3.18. *Mesopteryx alata* ♀ (Mantidae: Mantinae, Fig. 20). Two ventral cervical sclerites **vcs** are present. The medial part **lcmp** of the lateral cervical sclerites **lcs**

is S-shaped. Groove **lcvg** is deep and the lateral part **lclp** is bulged in an S-shaped manner. The intercervicalia **ics** are medially fused. The anterior rim **icar** is narrow and slightly bulged, the posterior rim **icpr** is plane except for the torus intercervicalis **ticv**.

4.3.19. *Tenodera aridifolia* ♂ (Mantidae: Mantinae, Fig. 21). Two ventral cervical sclerites **vcs** are present. The medial part **lcmp** of the lateral cervical sclerites **lcs** is curved in an S-shape. The groove **lcvg** is deep and runs over the entire length of the sclerite. The lateral part **lclp** is bulged in an S-shaped manner. The intercervicalia **ics** are medially fused. Groove **icmg** is narrow and bulged. The anterior rim **icar** is as wide as the posterior rim **icpr**, which is represented only by the torus intercervicalis **ticv**.

4.3.20. *Sphodromantis lineola* ♀ (Mantidae: Mantinae, Fig. 22). Two heavy ventral cervical sclerites **vcs** are present. The medial part **lcmp** of the lateral cervical sclerites **lcs** is slightly curved and widens posteriorly. The groove **lcvg** is deep. The lateral part **lclp** is bulged in an S-shaped manner. The intercervicalia **ics** are medially fused and have deep grooves **icmg**. The anterior rim **icar** is wider than the posterior rim **icpr**. A slender torus intercervicalis **ticv** is present.

4.3.21. *Oxyopsis gracilis* ♂ (Mantidae: Vatinae, Fig. 23). Two ventral cervical sclerites **vcs** are present. The medial part **lcmp** of the lateral cervical sclerites **lcs** is curved. The groove **lcvg** is deep. The lateral part **lclp** is bulged in an S-shaped manner. The intercervicalia **ics** are medially fused. The groove **icmg** is shallow but wide. The anterior rim **icar** is only weakly bulged and narrow. The posterior rim **icpr** is almost plane and a torus intercervicalis **ticv** is missing.

4.3.22. *Heterochaeta strachani* ♀ (Mantidae: Vatinae, Fig. 24). One ventral cervical sclerite **vcs** is present. The medial part **lcmp** of the lateral cervical sclerites **lcs** is slightly curved. The groove **lcvg** is deep. The lateral part **lclp** is curved in an S-shaped manner. The intercervicalia **ics** are medially fused. The anterior rim **icar** is strongly bulged, whereas the posterior rim **icpr** is only slightly bulged with only the torus intercervicalis **ticv** distinctly jutting out from it. The groove **icmg** is shallow.

4.3.23. *Macrodanuria elongata* ♂ (Mantidae: Vatinae, Fig. 25). Two heavy ventral cervical sclerites **vcs** are present. The posterior one is much larger than the anterior one. The medial part **lcmp** of the lateral cervical sclerites **lcs** is slightly curved. The groove **lcvg** is deep. The lateral part **lclp** is bulged and slightly curved in an S-shaped way. The intercervicalia **ics** are fused in the midline. Groove **icmg** is shallow. The anterior rim **icar** is as wide as the posterior rim **icpr** which bears a small torus intercervicalis **ticv**.

4.3.24. *Popa spurca* ♀ (Mantidae: Vatinae, Fig. 26). Two ventral cervical sclerites **vcs** are present. The

posterior one is much larger than the anterior one. The medial part **lcmp** of the lateral cervical sclerites **lcs** is slightly curved. Groove **lcvg** is deep and narrow. The lateral part **lclp** is bulged and slightly curved in an S-shape. The heavy intercervicalia **ics** are fused in the middle. The anterior and posterior rims **icar** and **icpr** are wide but not strongly bulging, therefore groove **icmg** is shallow. The posterior rim **icpr** carries a heavy torus intercervicalis **ticv**. The latter is about half as wide as the sclerite itself.

4.3.25. *Brunneria borealis* ♀ (Mantidae: Photinae, Fig. 27). Two ventral cervical sclerites **vcs** are present. The posterior one is split in two, whereas the anterior one is normally built. The medial part **lcmp** of the lateral cervical sclerites **lcs** is curved. The groove **lcvg** is deep. The lateral part **lclp** is bulged and slightly curved. The intercervicalia **ics** are not medially fused and carry a deep groove **icmg**. Their anterior rim **icar** is narrow, but strongly bulged whereas the posterior rim **icpr** bears a distinct torus intercervicalis **ticv**.

4.3.26. *Orthoderella ornata* ♂ (Mantidae: Photinae, Fig. 28). Two ventral cervical sclerites **vcs** are present. Both are medially split in two. The medial part **lcmp** of the lateral cervical sclerites **lcs** is slightly curved. The groove **lcvg** is deep and the lateral part **lclp** is bulged in an S-shaped way. The intercervicalia **ics** are medially fused. They carry a large groove **icmg**. The anterior rim **icar** is wide, whereas the posterior rim **icpr** is plane except for the torus intercervicalis **ticv**.

4.3.27. *Toxodera denticulata* ♀ (Mantidae: Toxoderinae, Fig. 29). A single, large ventral cervical sclerite **vcs** is present. The medial part **lcmp** of the lateral cervical sclerites **lcs** is slightly curved. The groove **lcvg** is deep and runs over the entire sclerite. The lateral part **lclp** is S-shaped. The intercervicalia **ics** are medially fused. The anterior and posterior rims **icar** and **icpr** are narrow and there is no torus intercervicalis **ticv**. Groove **icmg** is large but shallow.

4.3.28. *Gongylus gongylodes* ♂/♀ (Empusidae: Empusinae, Figs. 30, 31). Two ventral cervical sclerites **vcs** are present in the male, whereas in the female only one of them exists. All of them are split medially. In the male the anterior sclerite is split into four small, weakly sclerotized parts, whereas the posterior one is split into two parts. In the female the sclerite is split into two parts as well. It is more strongly sclerotized than in the male. The medial part **lcmp** of the lateral cervical sclerites **lcs** is slightly curved. The groove **lcvg** is deep. The lateral part **lclp** is bulged in an S-shaped manner. The intercervicalia **ics** are medially fused. The anterior rim **icar** is bulged, whereas the posterior rim **icpr** is almost plane except for the slightly protuberant torus intercervicalis **ticv**. The groove **icmg** is distinct and wide.

4.3.29. *Empusa fasciata* ♀ (Empusidae: Empusinae, Fig. 32). A single ventral cervical sclerite **vcs** is present.

The medial part **lcmp** of the lateral cervical sclerites **lcs** is slightly curved. The groove **lcvg** is deep and wide. The lateral part **lclp** is bulged in an S-shaped way. The intercervicalia **ics** approach each other in the middle of the body but do not appear to be connected. The groove **icmg** is shallow. The anterior rim **icar** is bulged, whereas the posterior one **icpr** is plane except for the torus intercervicalis **ticv**.

4.3.30. *Blepharopsis mendica* ♂ (Empusidae: Blepharodinae, Fig. 33). A single ventral cervical sclerite **vcs** is present. The medial part **lcmp** of the lateral cervical sclerites **lcs** is slightly curved. Groove **lcvg** is deep, the lateral part **lclp** is bulged in an S-shaped manner. The intercervicalia **ics** are medially fused. The anterior and posterior rims **icar** and **icpr** are equally wide. The groove **icmg** is shallow and wide and a torus intercervicalis **ticv** is missing.

4.4. The cervical sclerites of “Blattaria” (Figs. 34–44)

4.4.1. *Periplaneta americana* ♀ (Blattidae: Blattinae, Fig. 34). Two strongly sclerotized ventral cervical sclerites **vcs** are present. The lateral cervical sclerites **lcs** are slightly bulged and have a shallow longitudinal groove, which, however, lies far more laterally than the groove **lcvg** in Mantodea and differs strongly from the latter. No distinction between the lateral part **lclp** and the medial part **lcmp** can be recognized. The intercervicalia **ics** are medially separated. Posteriorly they are extended and taper. The posterior part **icpp** is not detached from the intercervicalia. The anterior and posterior rims **icar** and **icpr** are wide. Each sclerite shows a distinct groove **icmg** throughout its entire width.

4.4.2. *Blatta orientalis* ♂ (Blattidae: Blattinae, Fig. 35). Two strongly sclerotized ventral cervical sclerites **vcs** are present. The posterior one is slightly thinner and not as wide as the anterior sclerite. The lateral cervical sclerites **lcs** have strongly curved outer rims. Groove **lcvg** is short and shallow, therefore a separation into the medial part **lcmp** and the lateral part **lclp** is discernible only anteriorly. The intercervicalia **ics** have a shallow groove **icmg** and are posteriorly only slightly extended. They are distinctly separated. The anterior and posterior rims **icar** and **icpr** are wide but only slightly bulged, the posterior part **icpp** is not detached.

4.4.3. *Lamproblatta albipalpus* sex unknown (Lamproblattidae, Fig. 36). Two strongly sclerotized ventral cervical sclerites **vcs** are present. The lateral cervical sclerites **lcs** have a shallow groove **lcvg** separating the lateral part **lclp** from the medial part **lcmp**. The intercervicalia **ics** are medially separated. They have wide anterior and posterior rims **icar** and **icpr** and a shallow groove **icmg**. Posteriorly, they are slightly extended. The posterior part **icpp** is not detached.

4.4.4. *Ectobius silvestris* ♂ (“Blattellidae”: Ectobiinae, Fig. 37). There is a single ventral cervical sclerite **vcs** which is strongly sclerotized. The lateral cervical sclerites **lcs** show a lateral groove which, however, strongly differs from the groove **lcvg** of all other species and therefore is most probably not homologous to the latter. The intercervicalia **ics** have their posterior parts **icpp** being extended but not being detached. The anterior and posterior rims **icar** and **icpr** are slightly bulged. The groove **icmg** is shallow but large.

4.4.5. *Blattella germanica* sex unknown (“Blattellidae”: Blattellinae, Fig. 38). Fig. 38 has been redrawn and adapted from fig. 3 in MATSUDA (1956), which is too schematic to derive much detail from it. Two slender ventral cervical sclerites **vcs** are present. The lateral cervical sclerites **lcs** probably show a slight separation of the medial part **lcmp** and the lateral part **lclp** as can be derived from the anterior portion of the sclerite. The intercervicalia **ics** are separated. A tapering posterior part **icpp** has been drawn by MATSUDA. It is unclear whether it is detached or not. The quality of the anterior and posterior rims **icar** and **icpr** is not discernible, therefore there is no information about the groove **icmg** either.

4.4.6. *Blaberus craniifer* ♀ (Blaberidae: Blaberinae, Fig. 39). There are two strongly sclerotized ventral cervical sclerites **vcs**. A distinction between the medial part **lcmp** and the lateral part **lclp** of the lateral cervical sclerites **lcs** cannot be made. The intercervicalia **ics** are medially separated. The posterior part **icpp** is extended and tapers but is not detached from the intercervical sclerite. The anterior and posterior rims **icar** and **icpr** are slightly bulged. Groove **icmg** is shallow.

4.4.7. *Cryptocercus punctulatus* ♂ (Cryptocercidae, Fig. 40). There are two poorly sclerotized ventral cervical sclerites **vcs** and a weak median, setae-bearing sclerite **sbs** posterior to these. The lateral cervical sclerites **lcs** show a distinct separation between the medial part **lcmp** and the lateral part **lclp** although the groove **lcvg** is shallow. The intercervicalia **ics** are medially separated. They are only slightly extended caudad bearing a small posterior part **icpp** which is not detached. The anterior and posterior rims **icar** and **icpr** are wide but only slightly bulged. The groove **icmg** is shallow.

4.5. The cervical sclerites of Isoptera (Figs. 41–44)

4.5.1. *Mastotermes darwiniensis* soldier (Mastotermitidae, Fig. 41). There are no ventral cervical sclerites **vcs**. The lateral cervical sclerites **lcs** have no groove **lcvg** and therefore no separation between the medial part **lcmp** or the lateral part **lclp**. The intercervicalia **ics** are medially separated and do not have a groove **icmg**. The posterior part **icdpp** is detached and articulates with the remaining part of the intercervical sclerite.

4.5.2. *Macrotermes bellicosus* soldier (Termitidae: Macrotermitinae, Fig. 42). Ventral cervical sclerites **vcs** are missing. The lateral cervical sclerites **lcs** have no groove **lcvg**, therefore there is no subdivision into the medial part **lcmp** and the lateral part **lclp**. The intercervicalia **ics** are medially separated. They have shallow depressions that are probably homologous to the medial grooves **icmg**. The posterior part **icdpp** is detached and articulates with the remaining intercervical sclerite.

4.5.3. *Nasutitermes nigriceps* soldier (Termitidae: Nasutitermitinae, Fig. 43). Ventral cervical sclerites **vcs** are missing. The lateral cervical sclerites **lcs** have no groove **lcvg** to separate the medial part **lcmp** and the lateral part **lclp**. The intercervicalia **ics** are medially separated. The shallow grooves **icmg** are wide. The posterior part **icdpp** is detached and articulates with the remaining intercervical sclerite.

4.5.4. “Typical termite” from MATSUDA (1970) (Fig. 44). Fig. 44 has been redrawn and adapted from fig. 58a in MATSUDA (1970, after FULLER 1924). It is rather schematic but some characters can be recognized in it. Ventral cervical sclerites **vcs** are missing. The lateral cervical sclerites **lcs** have no groove **lcvg** to separate the medial part **lcmp** from the lateral part **lclp**. The intercervicalia **ics** are medially separated. They have shallow and slender depressions **icmg**. The drawing shows the posterior part **icdpp** not being entirely detached from the remaining intercervical sclerite. However, it is impossible to say whether this is true or not because the drawing is too schematic.

5. Discussion and Conclusions

5.1. Comparison and evolution of the cervical sclerites

The phylogenetic relationships among the principal dictyopteran lineages are still under discussion, although the hypothesis of Mantodea being the sister taxon of a “Blattaria” + Isoptera-clade is finding increased support due to morphological and molecular evidence (KLASS 1995; BOHN & KLASS 2003; DEITZ et al. 2003; LO et al. 2003; GULLAN & CRANSTON 2004; SVENSON & WHITING 2004; TERRY & WHITING 2005; GRIMALDI & ENGEL 2005; KLASS & MEIER 2006). One of the most recently published phylogenetic cladograms of Dictyoptera which represents the latest phylogenetic hypothesis (GRIMALDI & ENGEL 2005) has been adapted to the taxon sample used in this study. Characters of the cervical sclerites were mapped on this tree. The results are shown in Figs. 45–50.

5.1.1. The ventral cervical sclerites. In Mantodea the ventral cervical sclerites vary in number and shape. Most of the studied species have two ventral cervical sclerites

(*Acanthops* sp., *Phyllocrania paradoxa*, *Creobroter* sp., *Pseudocreobotra ocellata*, *Theopompella heterochroa*, *Humbertiella* sp., *Euchomenella heteroptera*, *Leptocola phthisica*, *Stenopyga ziela*, *Ameles decolor*, *Mantis religiosa*, *Mesopteryx alata*, *Tenoder a aridifolia*, *Sphodromantis lineola*, *Oxyopsis gracilis*, *Macrodanuria elongata*, *Popa spurca*, *Brunneria borealis*, *Orthoderella ornata*, male of *Gongylus gongylodes*). Some Mantodea species have no ventral cervical sclerites at all (*Mantoida maya*, *Metallyticus splendidus*, *Eremiaphila braueri*, Amorphoscelidae), while others possess a single one (*Chaeteessa caudata*, *Heterochaeta strachani*, *Toxodera denticulata*, *Empusa fasciata*, *Blepharopsis mendica*, female of *Gongylus gongylodes*). The ventral cervical sclerite in *Chaeteessa caudata* likely corresponds to the anterior ventral cervical sclerite considering its position close to the postmentum. In the other species with only one ventral cervical sclerite it is probably the posterior one as deduced from its proximity to the intercervicalia in the posterior cervix.

In some species, the sclerites are quite heavy (*Theopompella heterochroa*, *Humbertiella* sp., *Euchomenella heteroptera*, *Leptocola phthisica*, *Stenopyga ziela*, *Mantis religiosa*, *Mesopteryx alata*, *Tenoder a aridifolia*, *Sphodromantis lineola*, *Oxyopsis gracilis*, *Heterochaeta strachani*, *Macrodanuria elongata*, *Popa spurca*, *Brunneria borealis*, *Orthoderella ornata*, *Toxodera denticulata*, *Empusa fasciata*, *Blepharopsis mendica*), whereas in others the sclerotization is weak (all Hymenopodidae, *Ameles decolor*, *Gongylus gongylodes*). Either one (*Humbertiella* sp., *Brunneria borealis*, female of *Gongylus gongylodes*) or both sclerites can be divided into two or more smaller plates (*Acanthops* sp., *Phyllocrania paradoxa*, *Orthoderella ornata*, male of *Gongylus gongylodes*). In *Phyllocrania paradoxa* and the male of *Gongylus gongylodes*, the anterior sclerite is reduced to four weakly sclerotized, small fragments and the posterior sclerites are divided into two parts.

In “Blattaria” either one (*Ectobius silvestris*) or two ventral cervical sclerites (*Periplaneta americana*, *Blatta orientalis*, *Lamproblatta albipalpus*, *Blaberus craniifer*, *Blattella germanica*, *Cryptocercus punctulatus*) are present that are always entire. They are strongly sclerotized except for those of *Cryptocercus*. Only in this species a slightly sclerotized, setae-bearing area (**sbs**) is present posterior to the ventral cervical sclerites.

Isoptera do not possess ventral cervical sclerites except for Termopsidae (WEIDNER 1970). WEIDNER describes the sclerite as a fusion product of the “postgulae” (WEIDNER 1970: **pg** in fig. 99). *Termopsis* sp., however, has no such sclerite (Grimaldi, pers. comm. 2005; see also 4.1.). The ventral cervical sclerite perhaps present in recent Termopsidae is probably homologous to the anterior ventral cervical sclerite of the other Dictyoptera due to its position close to the postmentum as indicated by WEIDNER (1970).

Conclusions: The number of ventral cervical sclerites **vcs** varies in Dictyoptera: 1 (only [some] Termopsidae) or 0 in Isoptera, 1 or 2 in “Blattaria”, and 0, 1, or 2 in

Mantodea. Embiidina have 2 **vcs** (CRAMPTON 1926; BITSCH & RAMOND 1970; MATSUDA 1970; ROSS 2000). Phasmatodea have 0 (BEIER 1968b; MATSUDA 1970; BRADLER 1999) or 1 **vcs** (Wieland, pers. obs.), which is probably not homologous to the **vcs** of the other taxa (Bradler, pers. comm. 2006). Orthoptera have 0–2 **vcs** (MARTIN 1916; BEIER 1955, 1972; Wieland, pers. obs.) and Dermaptera have 2 **vcs**, the posterior of which may be fused with the presternite in some species (MATSUDA 1970; GÜNTHER & HERTER 1974; CRAMPTON 1926). Grylloblattodea (CRAMPTON 1915; MATSUDA 1970) and Mantophasmatodea (Wieland, pers. obs.) lack ventral cervical sclerites.

Assuming that the ventral cervical sclerites can be lost or gained individually (as the possession of a single **vcs** in several taxa implicates) the gain or loss of two **vcs** needs two individual evolutionary steps for explanation. Therefore three similarly parsimonious scenarios are imaginable for the evolution of the ventral cervical sclerites in Dictyoptera: The lack of ventral cervical sclerites, the possession of one and the possession of two **vcs** in the ground plan of Dictyoptera implicate scenarios which need an identical number of evolutionary steps. The relationships within Lower Neoptera are still highly controversial to date. Molecular studies (e.g. TERRY & WHITING 2005) lead to groupings that find only few or even no morphological support (e.g. Xenonomia = Mantophasmatodea + Grylloblattodea) and that are often only weakly supported by additional molecular data (e.g. CAMERON et al. 2006). From the morphological standpoint, too, the relationships between Lower Neoptera are highly controversial and still far from being resolved. Therefore a decision about the presence or absence of the ventral cervical sclerites in the ground plan of Dictyoptera with respect to outgroup taxa would be highly speculative. Further studies of a wide range of neopteran taxa may help to decide on this problem.

The additional setae-bearing sclerite (**sbs**) of *Cryptocercus* may be autapomorphic for the genus. It is located posterior to the second ventral cervical sclerite. Its function is unclear. Some cockroaches have the anterior part of the basisternite being protruded or even detached. This situation was observed in a “Blattid” by CRAMPTON (1926: **ps** in pl. 12, fig. 33) and in *Ectobius lapponicus* by MARTIN (1916: **prs** in pl. 3, fig. 9), which could be confirmed by the present author. MARTIN (1916: 70 and **prs** in pl. 3, fig. 9) described it as “presternite in the process of becoming detached from the verasternite” (= basisternite). This situation cannot be found in *Blatta orientalis* and *Periplaneta americana* (Wieland, pers. obs.). It remains unclear whether the small sclerite anterior to the basisternite in *Blaberus craniifer* (CRAMPTON 1926: pl. 12, fig. 27; Wieland, pers. obs.) is homologous to the presternite. The protruded or detached anterior part of the basisternite of *Ectobius* and other cockroaches, however, cannot be homologised with the mentioned sclerotization in *Cryptocercus* because the latter lies anterior to the intercervicalia whereas the presternite is located posterior to them. Therefore its origin remains unclear.

5.1.2. The lateral cervical sclerites. In most of the mantodean species the lateral cervical sclerites are almost identical. They appear to be divided into a medial part (**lcmp**) and a lateral part (**lclp**) by a groove (**lcvg**). The medial part **lcmp** is slender and either nearly straight (*Metallyticus splendidus*, *Creobroter* sp., *Ameles decolor*, *Sphodromantis lineola*, *Macrodanuria elongata*), curved in an S-shaped manner (*Mantoida maya*, *Chaeteessa caudata*, *Eremiaphila braueri*, *Acanthops* sp., *Tenodera aridifolia*, *Mesopteryx alata*, *Blepharopsis mendica*) or medially slightly curved laterad or mesad (*Perlamantis allibertii*, *Paraoxyphilus verreauxii*, *Phyllocrania paradoxa*, *Pseudocreobotra ocellata*, *Theopompella heterochroa*, *Humbertiella* sp., *Euchomenella heteroptera*, *Leptocola phthisica*, *Stenopyga ziela*, *Mantis religiosa*, *Oxyopsis gracilis*, *Heterochaeta strachani*, *Popa spurca*, *Brunneria borealis*, *Orthoderella ornata*, *Toxodera denticulata*, *Gongylus gongylodes*, *Empusa fasciata*).

The groove **lcvg** either runs cranio-caudally through the entire sclerite (*Mantoida maya*, *Chaeteessa caudata*, *Perlamantis allibertii*, *Paraoxyphilus verreauxii*, *Eremiaphila braueri*, Hymenopodidae, Mantidae, Empusidae) or is present only in the caudal part of the sclerite, (*Metallyticus splendidus*). In some species, **lcvg** is narrow (*Mantoida maya*, *Chaeteessa caudata*, *Metallyticus splendidus*, *Perlamantis allibertii*, *Paraoxyphilus verreauxii*, *Eremiaphila braueri*, *Creobroter* sp., *Brunneria borealis*). In the remaining species studied here the groove is more or less wide.

The part **lclp** is often S-shaped (all Hymenopodidae except *Creobroter* sp.; all Mantidae except *Leptocola phthisica*, *Ameles decolor* and *Brunneria borealis*; all Empusidae).

In some species **lcs** appears tripartite (*Chaeteessa caudata*, *Metallyticus splendidus*, *Perlamantis allibertii*). In other specimens the drawings of which seem to show tripartite lateral cervical sclerites (*Mantoida*, *Paraoxyphilus*, *Eremiaphila*) the outer part projecting above the lateral part **lclp** is part of the cervical membrane. In *Metallyticus*, the lateral part **lclp** is medially strongly bulged and flattens laterally. Therefore the tripartite appearance is due to the aberrantly shaped lateral part, and both dorsal part **lcdp** and dorsal groove **lcdg** strongly differ from the situation in the other two species. In *Perlamantis*, a short and shallow dorsal groove **lcdg** partly separates the lateral part **lclp** in two parts. The groove **lcdg** is distinct and deep in *Chaeteessa*. It separates the dorsal part **lcdp** from the lateral part **lclp**. The tripartite appearance of the lateral cervical sclerites **lcs** in *Metallyticus* and the two other species is certainly not homologous. The different shapes of the lateral part of the lateral cervical sclerites of *Chaeteessa* and *Perlamantis* make it difficult to homologise the dorsal parts **lcdp** and the dorsal grooves **lcdg** of the two species. Furthermore, both specimens were dry and rather old, therefore it is imaginable that the structures mentioned are artefacts caused by desiccation. Therefore, further studies with alcohol-preserved specimens are indispensable.

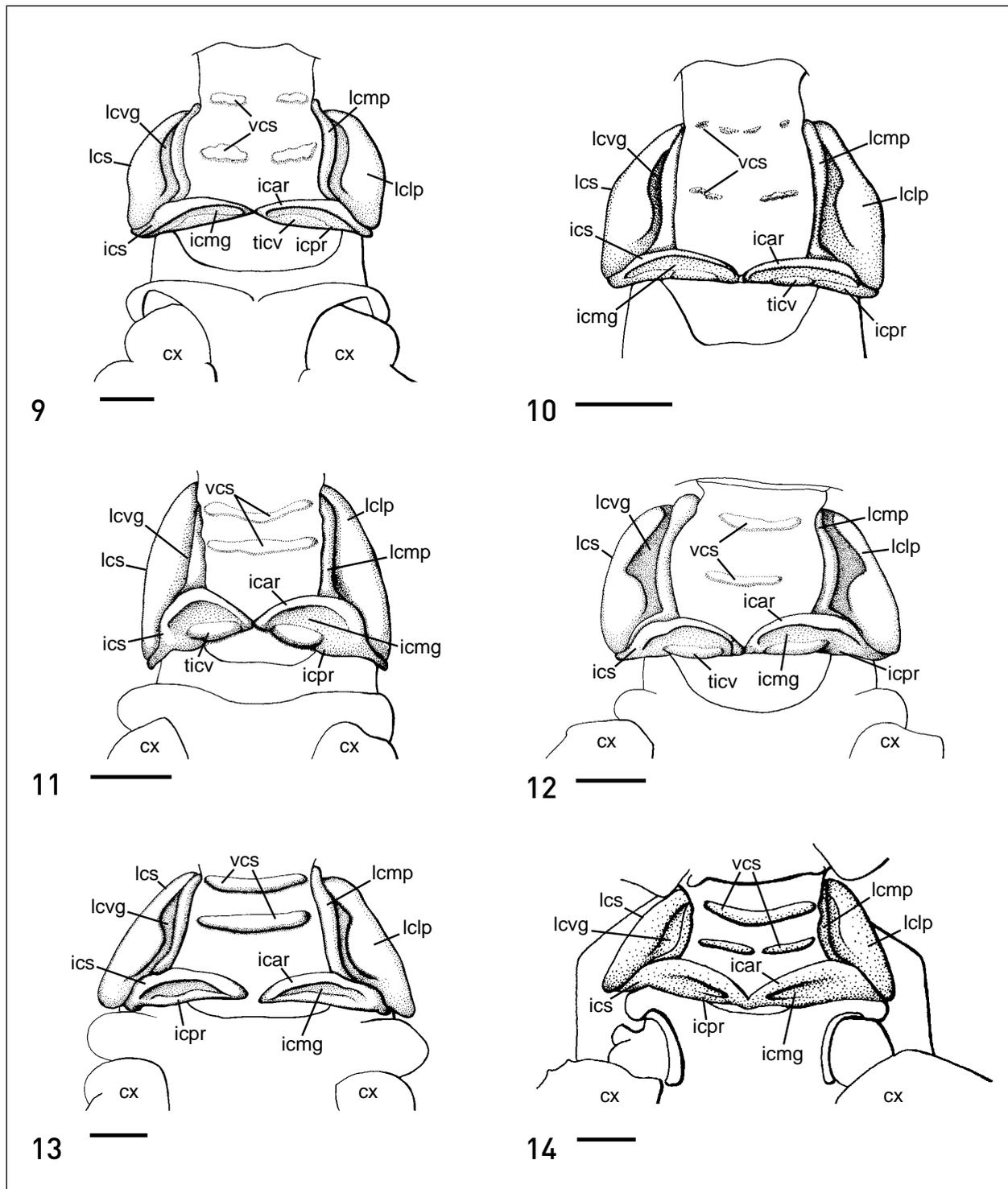
Within “Blattaria” several species show a groove **lcvg** (*Lamproblatta*, *Blatta*, *Cryptocercus*), while in two

species such a groove is entirely absent (*Periplaneta*, *Blaberus*). In *Blatta* **lcvg** is present only in the anterior part of the lateral cervical sclerite. The situation in *Ectobius* and *Blattella* remains unclear. Because of its proximity to the lateral edge of the sclerite, the groove **lcvg** in *Ectobius* is probably only a lateral indentation that is quite different from the lateral cervical groove of other taxa and therefore probably not homologous to it. The depiction of *Blattella* taken and adapted from MATSUDA (1956: fig. 3 Fig. 38 in the present paper) is too schematic to discern such a groove.

In Isoptera there is no groove **lcvg** and therefore no border between **lcmp** or **lclp** on the lateral cervical sclerites. The sclerites are slightly bulged.

Conclusions: The lateral cervical sclerites are large in all three dictyopteran groups. They are slender anteriorly and become wider posteriorly. All Mantodea studied here have a groove **lcvg** on the lateral cervical sclerite, which some cockroach species and none of the termites studied in the present work possess. If the phylogenetic relationships according to GRIMALDI & ENGEL (2005) are accepted, the groove **lcvg** has to be assumed for the dictyopteran ground plan (Fig. 46). It is probably an autapomorphy for Dictyoptera, as other Lower Neoptera do not have it (Wieland, pers. obs. in several different taxa of Plecoptera, Embioptera, Phasmatodea, Orthoptera s.str., and Dermaptera). Four independent partial or entire losses of **lcvg** have to be postulated for this hypothesis: in *Periplaneta*, the “Blattellidae”-Blaberidae group, Isoptera, and *Metallyticus*.

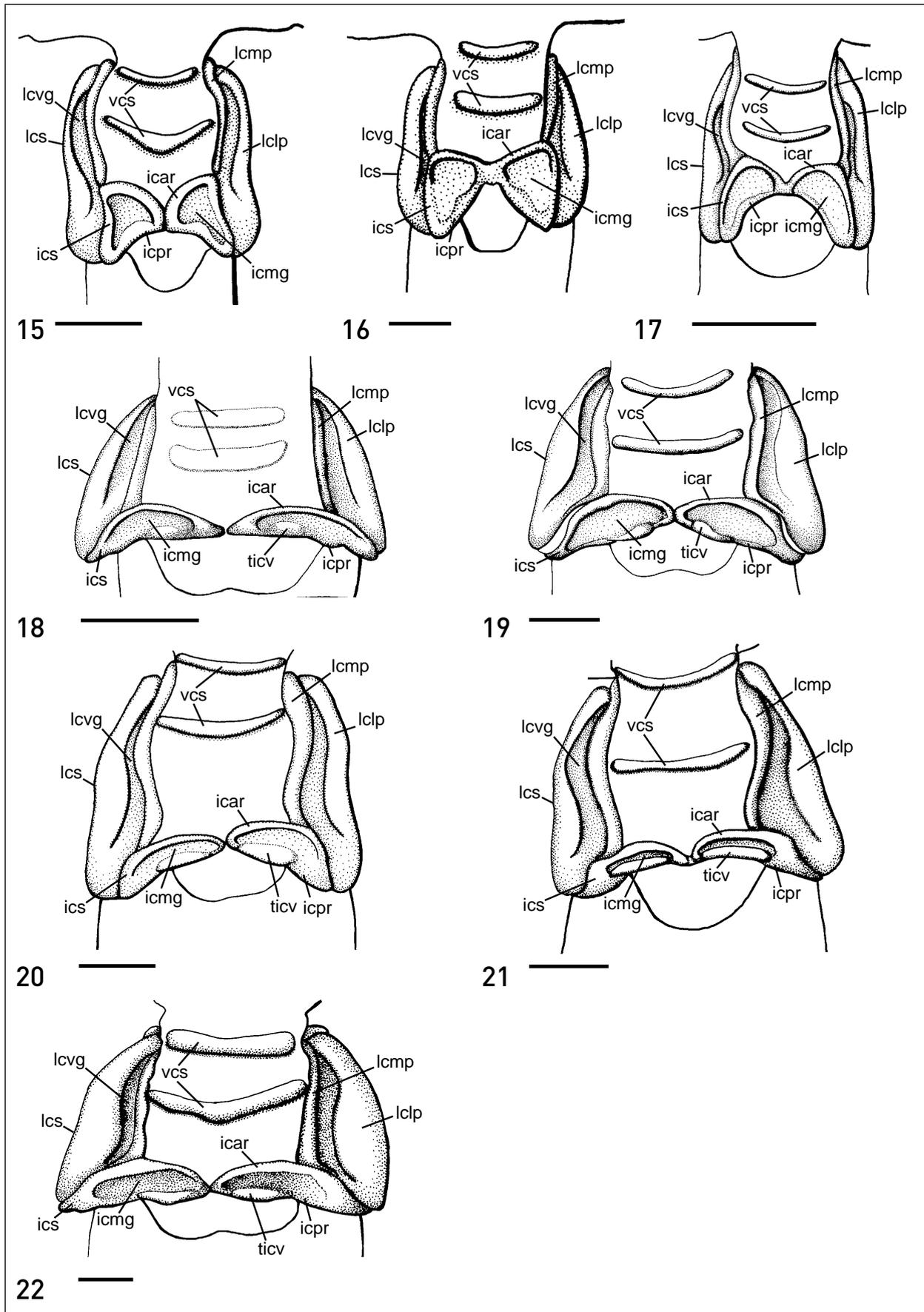
5.1.3. The intercervicalia. The intercervicalia (**ics**) are similar in most of the investigated Mantodea and are usually orientated transversely. Only in *Chaeteessa* and *Metallyticus* they point medio-cranial. This, however, may be an artefact caused by desiccation of the specimens at hand. The shape of the intercervicalia differs in the species investigated. They are slender (*Mantoida maya*, *Perlamantis allibertii*, *Paraoxyphilus verreauxii*, *Eremiaphila braueri*, *Acanthops* sp., *Phyllocrania paradoxa*, *Theopompella heterochroa*, *Humbertiella* sp., *Ameles decolor*, *Tenodera aridifolia*, *Orthoderella ornata*, *Gongylus gongylodes*, *Empusa fasciata*, and *Blepharopsis mendica*), may have an oval shape (*Chaeteessa caudata*, *Metallyticus splendidus*, *Pseudocreobotra ocellata*, *Creobroter* sp., *Mantis religiosa*, *Mesopteryx alata*, *Sphodromantis lineola*, *Heterochaeta strachani*, *Macrodanuria elongata*, *Popa spurca*) or are almost as long as wide (*Euchomenella heteroptera*, *Leptocola phthisica*, *Stenopyga ziela*, *Oxyopsis gracilis*, *Brunneria borealis*, *Toxodera denticulata*). They are mostly lentil-shaped or triangular, with all transitions. The anterior (**icar**) and posterior rims (**icpr**) may be bulged and enclose a central groove (**icmg**) between them. Rim **icpr** is often partly or entirely thickened, forming a transverse, knob-like protuberance, the torus intercervicalis (**ticv**). Its shape varies greatly in Mantodea and all transitions can be found. It can be distinct and more or less heavy (*Creobroter* sp., *Ameles*



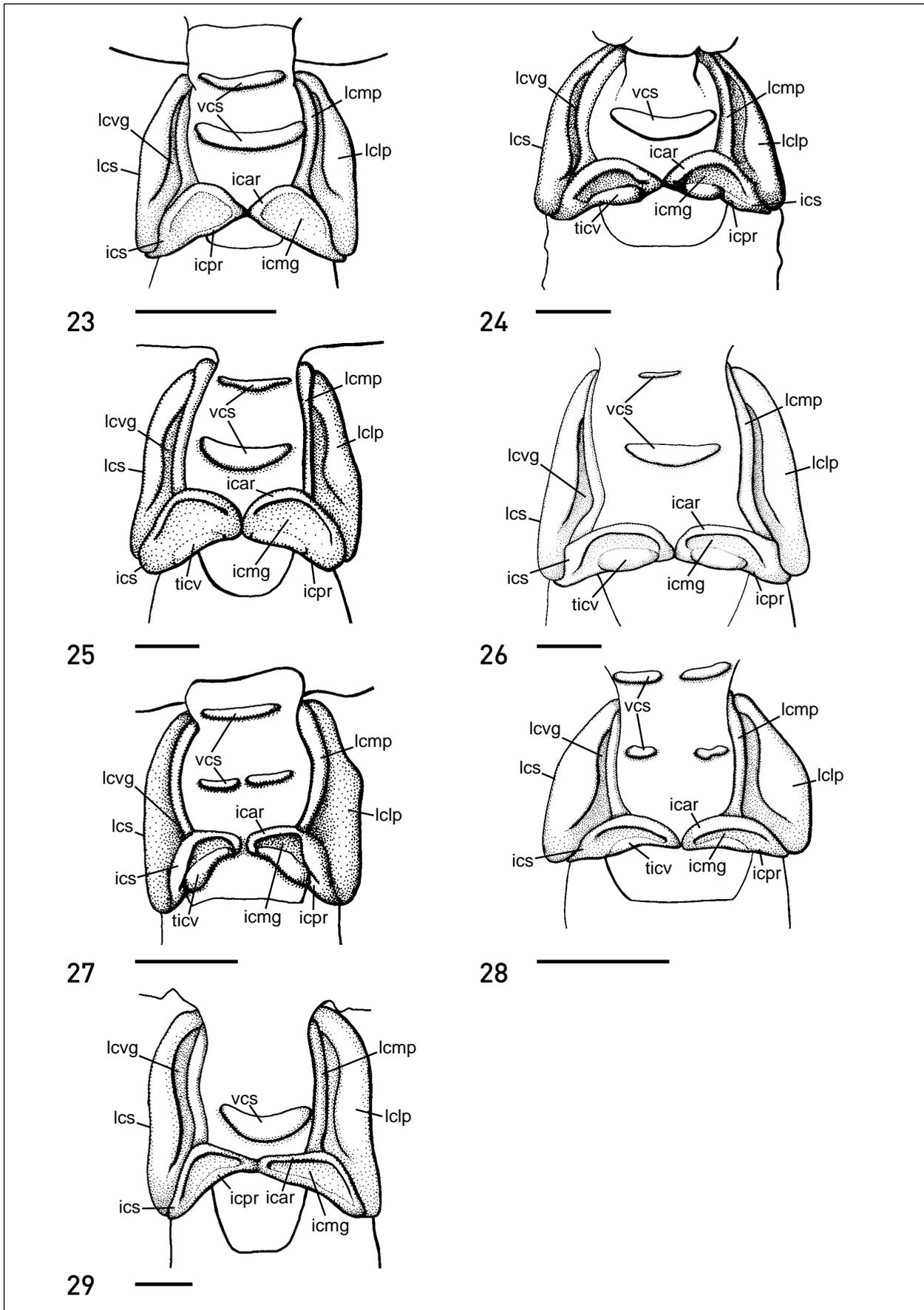
Figs. 9–14. The cervical sclerites of Hymenopodidae and Mantidae: Liturgusinae. **9:** *Acanthops* sp., ♀ (Hymenopodidae: Acromantinae). **10:** *Phyllocrania paradoxa*, ♂ (Hymenopodidae: Acromantinae). **11:** *Creobroter* sp., ♀ (Hymenopodidae: Hymenopodinae). **12:** *Pseudocreobotra ocellata*, ♀ (Hymenopodidae: Hymenopodinae). **13:** *Theopompella heterochroa*, ♀ (Mantidae: Liturgusinae). **14:** *Humbertiella* sp., ♀ (Mantidae: Liturgusinae). Orientation: ↑ cranial. (Scale bar: 1 mm)

The intercervicalia are medially separated in “Blattaria”. All species with the exception of *Blatta orientalis* possess intercervicalia that are more or less elongated caudad (**icpp**) without the often tapering posterior part being detached. All cockroach species except for *Blattella*, according to the schematic drawing in MATSUDA (1956: fig. 3; Fig. 38 herein), have a groove **icmg**. None of the species studied has a torus intercervicalis.

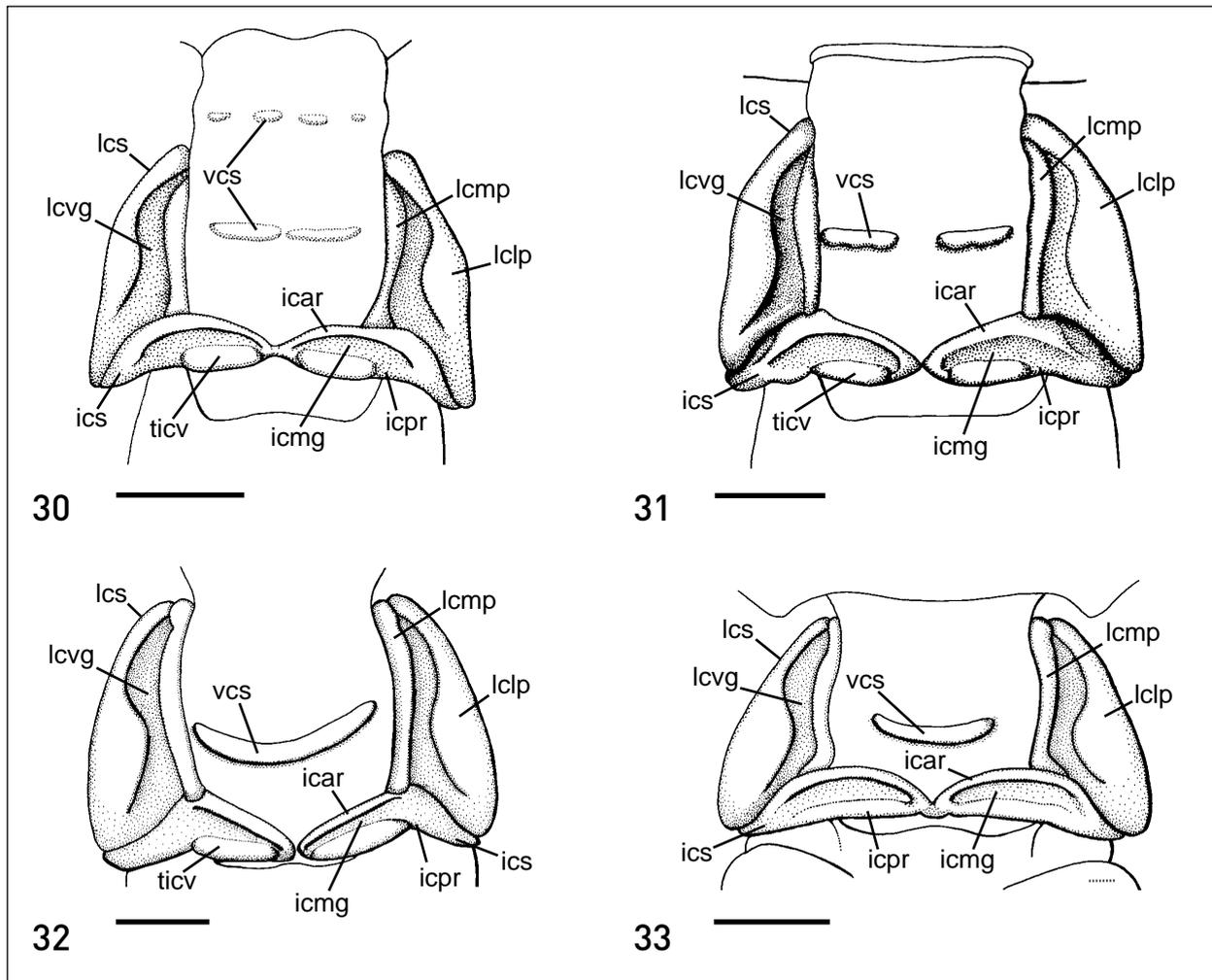
The transverse intercervicalia are medially separated in all Isoptera. *Nasutitermes*, *Macrotermes* and the “typical termite” adapted from MATSUDA (1970: fig. 58a, after FULLER 1924; Fig. 44 herein) show a very shallow central depression representing **icmg**, whereas *Mastotermes* lacks a groove **icmg** on the intercervicalia. All Isoptera studied have a detached posterior part of the intercervicalia (**icdpp**) that articulates with the



Figs. 15–22. The cervical sclerites of Mantidae: Angelinae, Amelinae and Mantinae. **15:** *Euchomenella heteroptera*, ♂ (Mantidae: Angelinae). **16:** *Leptocola phthisica*, ♂ (Mantidae: Angelinae). **17:** *Stenopyga ziela*, ♂ (Mantidae: Angelinae). **18:** *Ameles decolor*, ♀ (Mantidae: Amelinae). **19:** *Mantis religiosa*, ♀ (Mantidae: Mantinae). **20:** *Mesopteryx alata*, ♀ (Mantidae: Mantinae). **21:** *Tenodera aridifolia*, ♂ (Mantidae: Mantinae). **22:** *Sphodromantis lineola*, ♀ (Mantidae: Mantinae). Orientation: ↑ cranial. (Scale bar: 1 mm)



Figs. 23–29. The cervical sclerites of Mantidae: Vatinae, Photininae and Toxoderinae. **23:** *Oxyopsis gracilis*, ♂ (Mantidae: Vatinae). **24:** *Heterochaeta strachani*, ♀ (Mantidae: Vatinae). **25:** *Macrodanuria elongata*, ♂ (Mantidae: Vatinae). **26:** *Popa spurca*, ♀ (Mantidae: Vatinae). **27:** *Brunneria borealis*, ♀ (Mantidae: Photininae). **28:** *Orthoderella ornata*, ♂ (Mantidae: Photininae). **29:** *Toxodera denticulata*, ♀ (Mantidae: Toxoderinae). Orientation: ↑ cranial. (Scale bar: 1 mm)



Figs. 30–33. The cervical sclerites of Empusidae. **30:** *Gongylus gongylodes*, ♂ (Empusidae: Empusinae). **31:** *Gongylus gongylodes*, ♀ (Empusidae: Empusinae). **32:** *Empusa fasciata*, ♀ (Empusidae: Empusinae). **33:** *Blepharopsis mendica*, ♂ (Empusidae: Blepharodinae). Orientation: ↑ cranial. (Scale bar: 1 mm)

anterior part. None of the species has a torus intercervicalis.

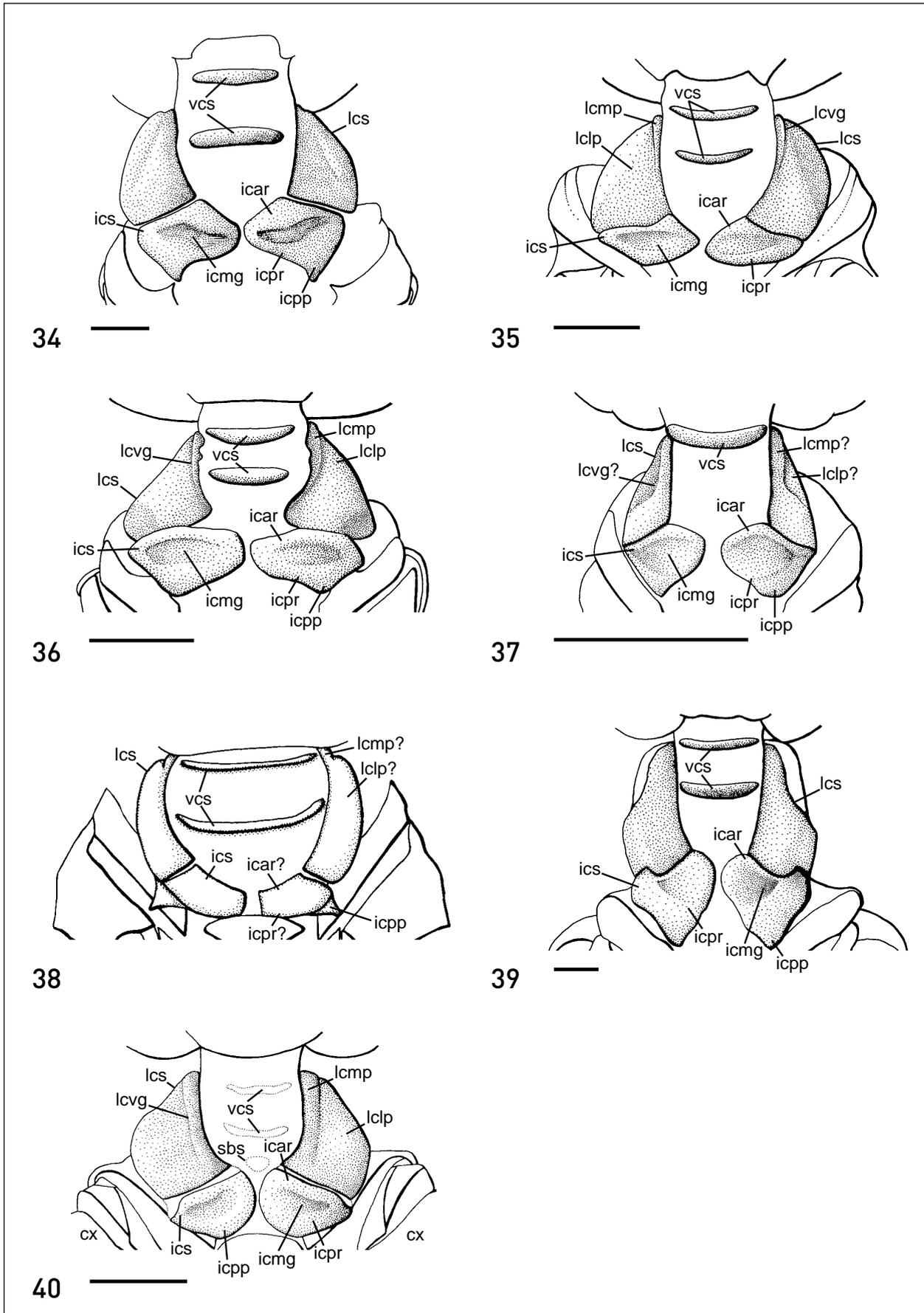
Conclusions: There are fundamental similarities in the shape of the intercervicalia throughout Dictyoptera. They are transverse and closely approach each other at the midline in all three taxa, or may be even fused as in most Mantodea studied herein. This orientation of the sclerites is most probably a ground plan autapomorphy of Dictyoptera because no other taxa within the lower Neoptera have it (Wieland, pers. obs. in several different taxa of Plecoptera, Embioptera, Phasmatodea, Orthoptera s.str., and Dermaptera).

The torus intercervicalis **ticv** is neither present in “Blattaria” and Isoptera nor in several Mantodea. If the phylogenetic hypothesis after GRIMALDI & ENGEL (2005) reflects the relationships correctly, two most parsimonious assumptions can be postulated for the evolution of the torus intercervicalis (Fig. 47). a) **ticv** is autapomorphic for Mantodea except *Mantoida* (Mantomorpha *sensu* KLASS 1995); it has been reduced independently in Amorphoscelidae, *Eremiaphila*, *Blepharopsis*, *Theopompella*, *Humbertiella*, *Euchomenella*, *Leptocola*, *Steno-*

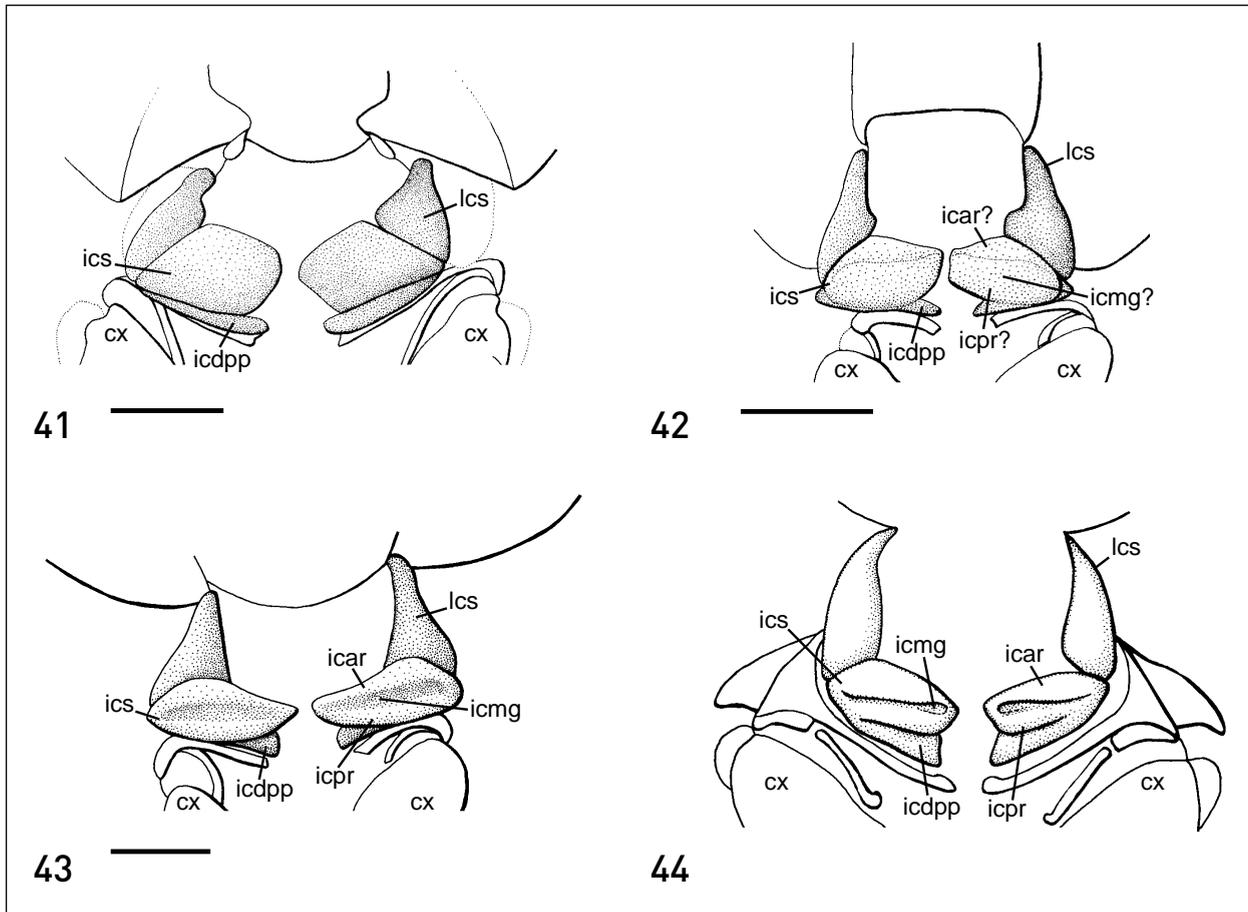
pyga, *Oxyopsis*, and *Toxodera*. b) **ticv** is autapomorphic for Mantoidea; it has been acquired independently in *Chaeteessa* and *Metallyticus* and was reduced in *Blepharopsis*, *Theopompella*, *Humbertiella*, *Euchomenella*, *Leptocola*, *Stenopyga*, *Oxyopsis*, and *Toxodera*. As Mantoidea is phylogenetically not resolved at the present, no decision can be made about the evolution of this character.

The groove **icmg** of the intercervicalia is present throughout Dictyoptera (Fig. 48). Only some species of Isoptera (*Mastotermes darwiniensis*) and Mantodea (*Perlamantis allibertii*, *Eremiaphila braueri*) do not have it. The most parsimonious assumption is the presence of the groove in the ground plan of Dictyoptera and a loss in the Isoptera and Mantodea listed above. It is probably autapomorphic for Dictyoptera because the other lower neopteran taxa do not have it (Wieland, pers. obs. in several different taxa of Plecoptera, Embioptera, Phasmatodea, Orthoptera s.str., and Dermaptera).

The intercervicalia are medially not fused in the “Blattaria” and Isoptera investigated herein and depicted in the literature. The intercervicalia of most of the investigated Mantodea are probably medially fused with exception



Figs. 34–40. The cervical sclerites of “Blattaria”. **34:** *Periplaneta americana*, ♀ (Blattidae: Blattinae). **35:** *Blatta orientalis*, ♂ (Blattidae: Blattinae). **36:** *Lamproblatta albipalpus*, sex unknown (Lamproblattidae). **37:** *Ectobius silvestris*, ♂ (“Blattellidae”: Ectobiinae). **38:** *Blattella germanica*, sex unknown (“Blattellidae”: Blattellinae), redrawn and adapted from MATSUDA (1956: fig. 3). **39:** *Blaberus craniifer*, ♀ (Blaberidae: Blaberinae). **40:** *Cryptocercus punctulatus*, ♂ (Cryptocercidae). Orientation: ↑ cranial. (Scale bar: 1 mm)



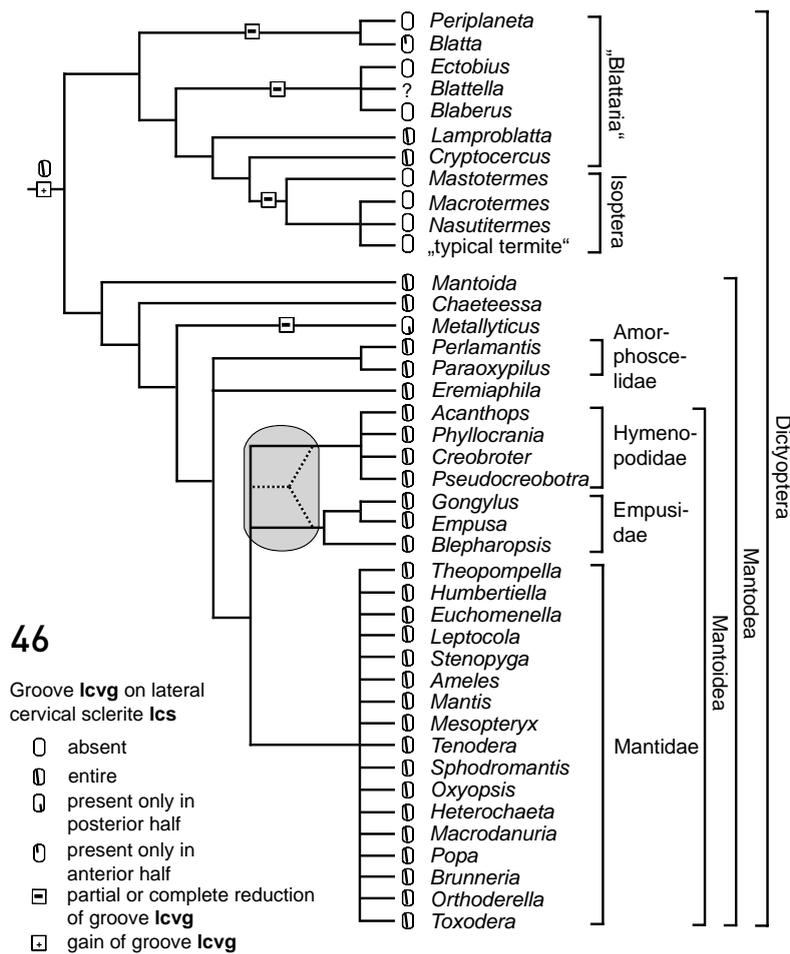
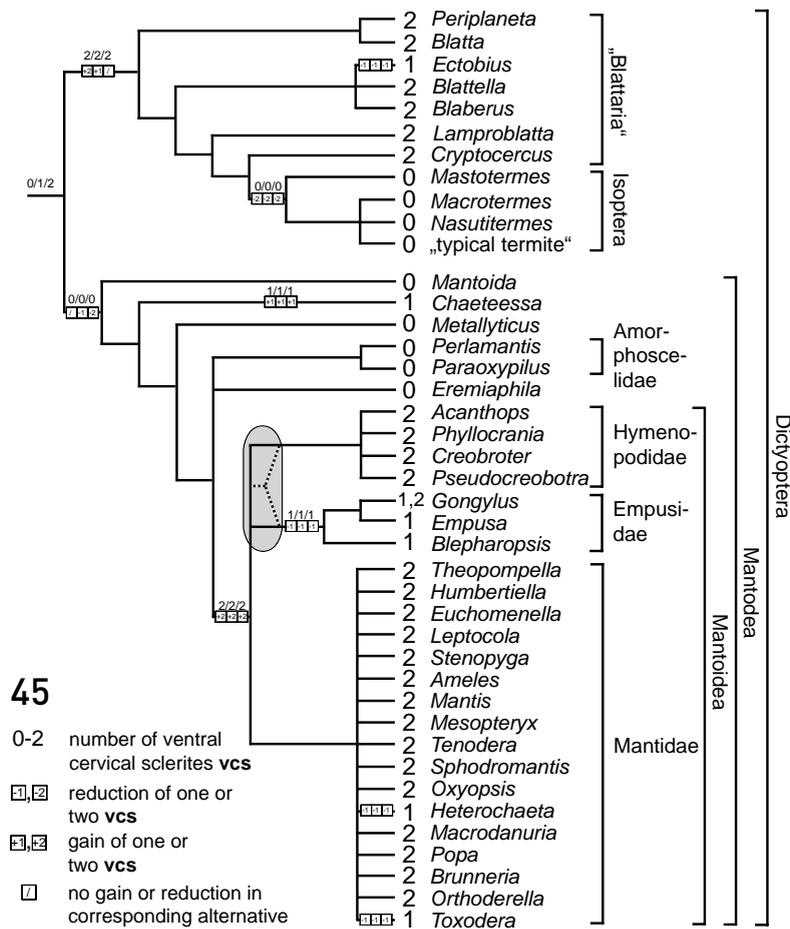
Figs. 41–44. The cervical sclerites of Isoptera. **41:** *Mastotermes darwiniensis*, soldier (Mastotermitidae). **42:** *Macrotermes bellicosus*, soldier (Termitidae: Macrotermitinae). **43:** *Nasutitermes nigriceps*, soldier (Termitidae: Nasutitermitinae). **44:** “Typical termite”, redrawn and adapted from MATSUDA (1970: fig. 58a, after FULLER 1924). Orientation: ↑ cranial. (Scale bar: 0,5 mm)

of few species (*Mantoida*, *Chaeteessa*, *Metallyticus*, *Perlamantis*, *Paraoxypilus*, *Eremiaphila*, *Ameles*, *Theopompella*, *Empusa*) in which the intercervicalia are separated or do not seem to have a rigid interconnection. As the intercervicalia are separated in the closest relatives of Mantodea and in species with many plesiomorphic characters, the fusion of the sclerites most probably took place within Mantodea (Fig. 49) where it can probably be interpreted as an autapomorphy of Mantoidea. It remains unclear whether the separation of the intercervical sclerites in *Ameles*, *Theopompella*, and *Empusa* is plesiomorphic or secondary. Therefore this character needs further investigation with alcohol-preserved specimens that allow a dissection.

Isoptera possess a detached posterior part of the intercervicalia (**icdpp**) that may be homologous to the small slender sclerites in Mantodea (LEVEREAULT 1936: 222, 4 in pl. 11, figs. 7, 10; BEIER 1968a: **Cerv**_c in fig. 20; **sss** in Fig. 2). “Blattaria” have the posterior part of the intercervicalia (**icpp**) caudally elongated but not detached from the rest of the sclerite. All the mentioned sclerotizations bear the articulation with the thoracic sclerites. Two similarly parsimonious hypotheses are possible (Fig. 50). The first one assumes an un-detached posterior part (**icpp**) in the dictyopteran ground plan with two independent separations in the stem species of

Mantodea and of Isoptera. The second would propose a detached posterior part (**icdpp**) in the ground plan of Dictyoptera. This hypothesis also needs two evolutionary events for explanation. The posterior part is entirely fused with the remaining part of the intercervical sclerite in the stem species of “Blattaria” + Isoptera, and a secondary separation occurred at the base of Isoptera. A detached posterior part of the intercervicalia could not be confirmed for any other of the Lower Neoptera (Wieland, pers. obs. in several different taxa of Plecoptera, Embioptera, Phasmatodea, Orthoptera s. str., and Dermaptera), therefore the probability of an un-detached posterior part in the dictyopteran ground plan may be higher. However, more investigations on the situation in Lower Neoptera have to be undertaken before one of the hypotheses gains more support.

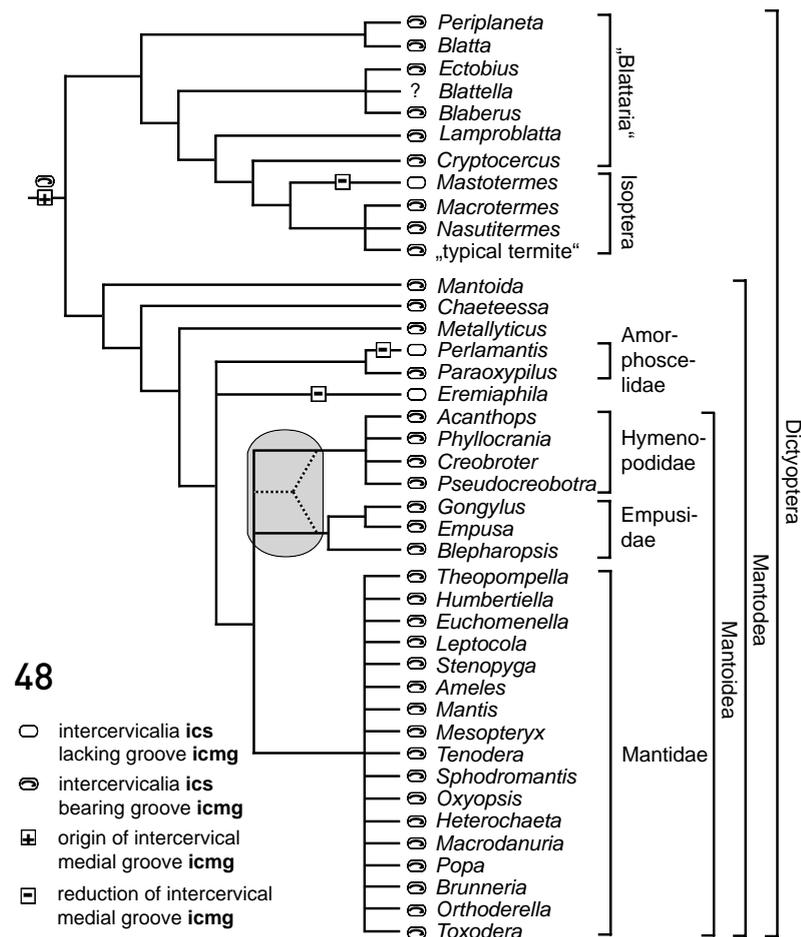
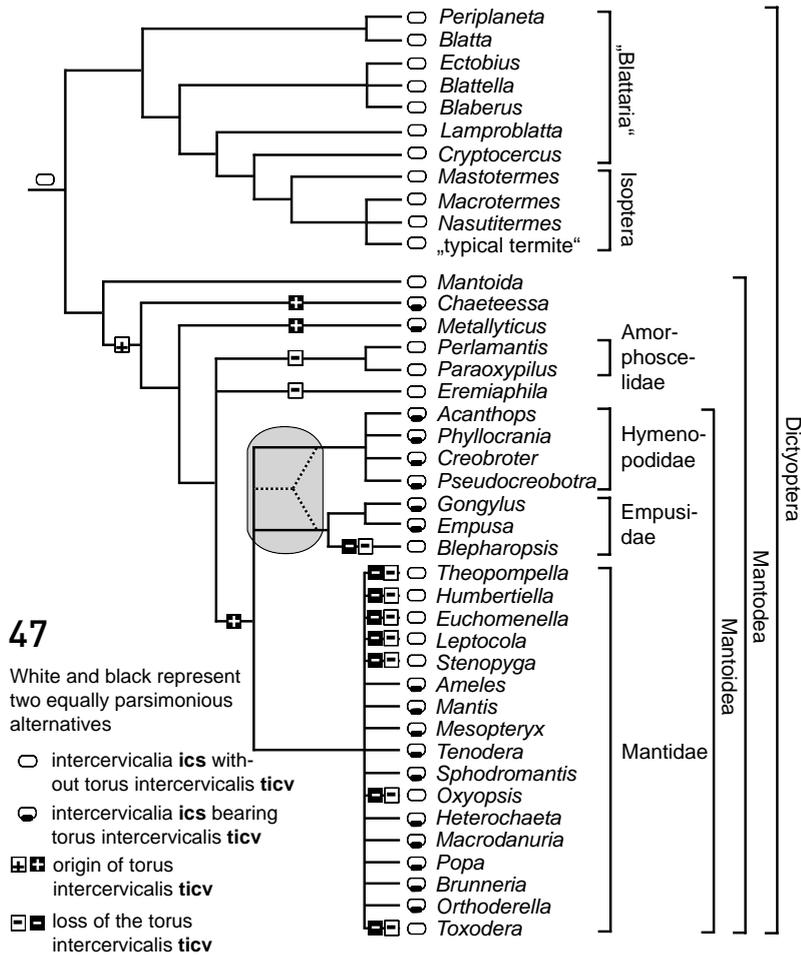
In either case **icdpp** of Isoptera and the **sss** of Mantodea have been separated from the intercervicalia independently. However, as far as their position posterior to the intercervicalia and their posterior articulation with the preepisternum is concerned, **icpp** of “Blattaria”, **icdpp** of Isoptera, and **sss** of Mantodea are probably homologous as sclerotizations.



Figs. 45–50. Phylogenetic trees of Dictyoptera adapted from GRIMALDI & ENGEL (2005). Only the taxa used in this study are included. Some of the characters studied herein are mapped onto the tree in the most parsimonious way. The positions of *Chaeteessa* and *Mantoida* have been switched due to morphological evidence by KLASS (1995, 1997). Mantidae, Hymenopodidae and Empusidae form the Mantoidea *sensu* ROY (1999), GRIMALDI (2003) and GRIMALDI & ENGEL (2005). Possible synapomorphic characters are the metathoracic hearing organ and an elongated prothorax being 2–20 times longer than wide. Empusidae is depicted as a monophyletic group based on the morphological characters discussed by ROY (2004). A possible synapomorphic character for the Hymenopodidae species is the posteroventral spination of the foretibiae (i.e. “external tibial spines”) standing closely together and being laid down. Empusidae share a specialized 1-3-1 pattern of anteroventral spines on the forefemur (“inner spines”) which is probably autapomorphic for the group. A close relationship between Empusidae and Hymenopodidae has been postulated by ROY (2004). Empusidae may be the sister group to Hymenopodidae according to the small taxon sample of TERRY & WHITING (2005). SVENSON & WHITING (2004) however, who used a slightly larger taxon sample for the two groups, showed Hymenopodidae to be paraphyletic with *Phyllocrania* being the sister taxon of *Gongylus*. However, both analyses only use a small number of species of either taxon. By morphological means the monophyly of Hymenopodidae and its relationship with Empusidae remains unresolved. As the results of the analyses mentioned above are contradictory and not sufficiently supported by a large taxon sample of the two groups, both phylogenetic scenarios are presented in the cladograms (grey boxes).

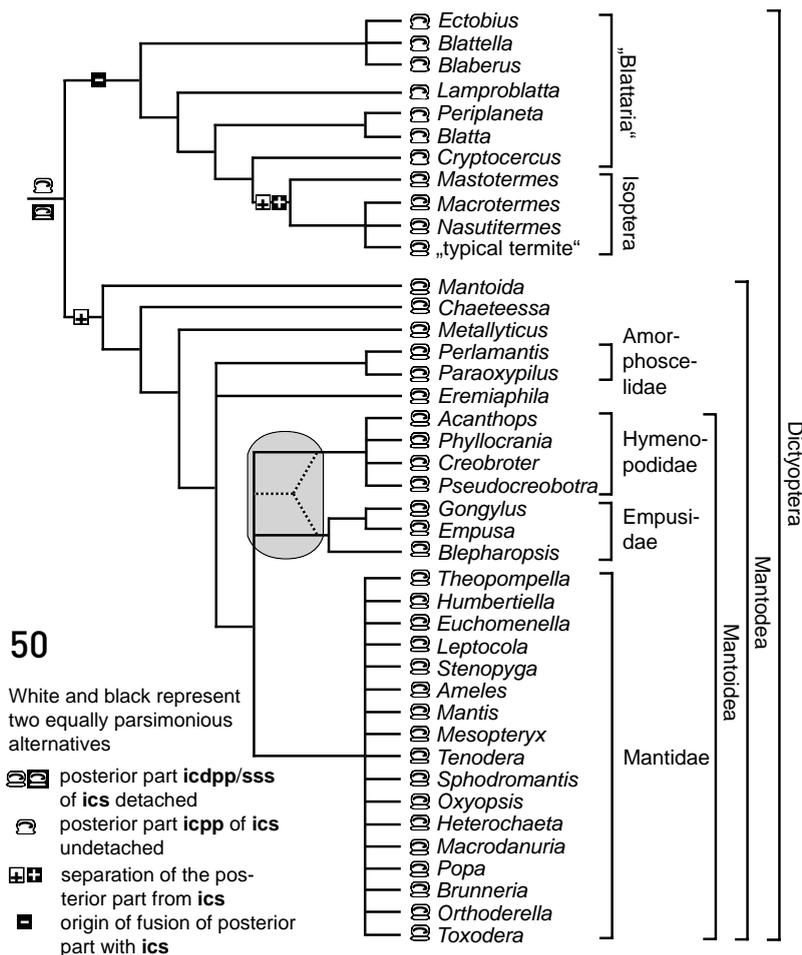
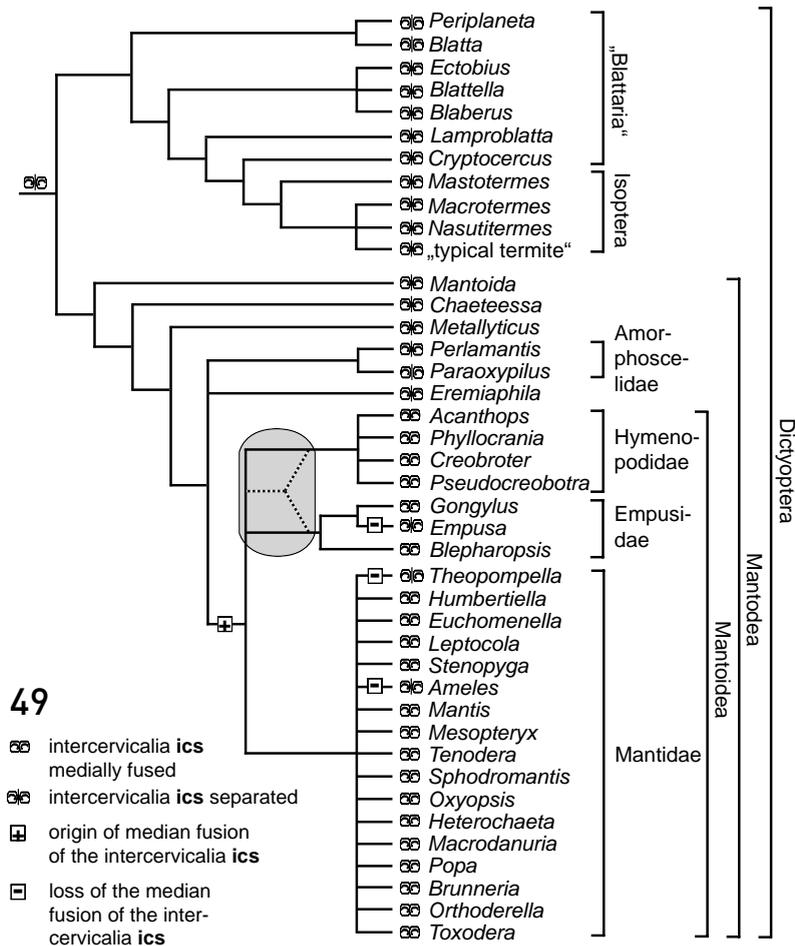
45: Three similarly parsimonious scenarios for the evolution of the ventral cervical sclerites (vcs) in Dictyoptera, written one behind the other.

46: Possible evolution of the ventral groove of the lateral cervical sclerites (lcvg) visually separating the sclerite lcs into a medial (lcmp) and a lateral part (lclp).



47: Distribution of the torus intercervicalis (ticv) within Dictyoptera and two equally parsimonious alternatives for its evolution, given in white and black.

48: Evolution of the intercervical medial groove (icmg) in Dictyoptera.



49: Most parsimonious hypothesis of the inter-cervicalia (ics) becoming medially fused.

50: Two similarly parsimonious scenarios for the evolution of a detached posterior part (icpp of “Blattaria” / icdpp of Isoptera / sss of Mantodea) of the inter-cervicalia, given in white and black.

5.2. Phylogenetic implications

The morphological characters studied in the present paper provide an insight into a small character complex that might be of some value for phylogenetic research. The structure of the cervical sclerites provided new autapomorphies for Dictyoptera (transverse orientation of the intercervicalia; presence of a groove **icmg** on the intercervicalia; presence of a groove **levg** on the lateral cervical sclerites) as well as possible autapomorphies for Mantoidea (medial fusion of the intercervicalia) and *Cryptocercus* (presence of a weakly sclerotized, setae-bearing sclerite **sbs** anterior to the intercervicalia). A study of further taxa of other lower neopteran lineages might illuminate the ground plan of Dictyoptera more precisely and could perhaps also provide information about the sister taxon of Dictyoptera.

Some implications for the internal mantodean relationships arise from the data. The monophyly of Empusidae has been assumed by ROY (1999, 2004) and others. The only character that strongly supports the monophyly is the specialized anteroventral spination of the raptorial forelegs. Other characters, such as the process of the vertex, the anterior medial spine on the frontal shield (i.e. “scutellum”) and the asymmetrical subgenital plate of the males are shared by all Empusidae but can also be found in several Hymenopodidae (ROY 2004; Wieland, unpubl. data). The asymmetrical subgenital plate is also present in *Metallyticus splendidus*, *Tarachodula pantherina*, *Pseudocreobotra wahlbergii*, and in many Blattaria (KLASS 1997) and is therefore evidently plesiomorphic (Wieland, pers. obs.). The shape of the male antennomeres bearing one or two processes is also shared by other mantids than Hymenopodidae (e.g. *Vates*). Nevertheless, a close relationship of Empusidae and Hymenopodidae can be assumed (ROY 2004) and is also supported by the first molecular-based phylogenetic hypothesis for Mantodea (SVENSON & WHITING 2004). Although the loss of ventral cervical sclerites is certainly strongly homoplastic, a close relationship of Empusidae and certain Hymenopodidae may be assumed when, for

instance, comparing the strong and complex similarity of the reduction of the **vcs** of *Phyllocrania* (Fig. 10) and the male of *Gongylus* (Fig. 30).

The monophyly of Mantoidea as assumed by ROY (1999), GRIMALDI (2003) and GRIMALDI & ENGEL (2005) has found support herein due to the medial fusion of the intercervicalia (**ics**) in most of the taxa studied. Further autapomorphies supporting the group that have been stated by other authors (e.g. GRIMALDI 2003; GRIMALDI & ENGEL 2005) are the prothorax being 2–20 times as long as wide, and the presence of a metathoracic hearing organ described by YAGER & HOY (1986) and YAGER (1999).

There are great problems with the homologization of a number of structures within Mantodea because there is most probably a high degree of homoplasy (e.g. the lamellar enlargement of the pronotum in several mantodean lineages, see ROY 1999). It is still unclear whether structures such as the head processes of Empusidae and certain Hymenopodidae, showing a high morphological resemblance, have an independent origin or may be synapomorphic. Furthermore, there may be the possibility of “reversal” evolution, for instance in the presence of a short prothorax in some of the so-believed basal mantodean lineages. The prothorax of Amorphoscelidae, for example, has usually been considered as primarily short (BEIER 1968a; ROY 1999), while based on their molecular data SVENSON & WHITING (2004: 364) interpret the prothorax of the amorphoscelid subgroup Paraoxypilinae as secondarily shortened.

The phylogenetic hypothesis used for the discussion of the evolution of the structures studied herein is certainly not satisfactory. The mantodean tree, for instance, is poorly resolved. The molecular results (SVENSON & WHITING 2004) implicate a high degree of non-monophyly in the existing classification of Mantodea as proposed, for example, by BEIER (1968a), EHRMANN (2002), GRIMALDI (2003), and GRIMALDI & ENGEL (2005). It is therefore inevitable to compile large morphological character sets for a phylogenetic analysis based on morphological data. Correspondingly the molecular approach with a wide taxon sample has to be intensively expanded.

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