



## Thoracic scent efferent system of the Tessaratomidae *sensu lato* (Hemiptera: Heteroptera: Pentatomoidea) with implication to the phylogeny of the family

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### Table of contents

Abstract .....	1
Introduction .....	2
Material and methods .....	4
Terminology .....	6
Results .....	13
Oncomerinae .....	13
Tessaratominae .....	23
Tessaratomina .....	26
Eusthenina .....	35
Prionogastrini .....	37
Sepinini .....	37
Natalicolinae .....	39
Platyatina .....	42
Cladistic analysis .....	42
Discussion .....	42
Morphology of external scent efferent system .....	42
Polarization of characters .....	46
Phylogeny and relationships of Tessaratomidae <i>sensu lato</i> .....	48
Function of the metathoracic scent apparatus .....	50
Acknowledgements .....	51
References .....	51

### Abstract

We studied the cuticular structures associated with the opening of the adult metathoracic scent glands in the family Tessaratomidae. The terminology previously used for these structures in the Tessaratomidae and Pentatomoidea is briefly reviewed and most suitable terms are selected (i.e., metathoracic scent apparatus, internal and external scent efferent system, internal orifice, vestibule, ostiole, ostiolar groove, peritreme, auricle, spout, groove, ruga, disc, peritremal lobes, evaporatorium, mycoid surface, mushroom body, bridge, alveole, trabeculae, and peritremal surface). We examined and illustrated external scent efferent system of 40 species from 33 genera belonging to all three subfamilies of Tessaratomidae *sensu lato*, i.e. Tessaratominae, Natalicolinae, and Oncomerinae. Three basic types were recognized: i) Oncomerinae – ostiole slightly removed laterally from the position between coxal acetabula, oval, ostiolar groove not developed or very short, peritreme in form of spout attached anterolaterally to the ostiole; ii) Tessaratomidae *sensu stricto* (= Tessaratominae + Natalicolinae) – ostiole situated between acetabula, strongly incised mesad, thus vestibule distally opened in two planes (ventrally and laterally) as ostiolar groove, peritreme in form of anterior and posterior peritremal lobes surrounding the ostiolar groove; and iii) Platyatina (*Platyatus ambiguus* Bergroth, 1892) – ostiole shifted near to lateral metapleural margin, ostiolar groove reduced, situated between two flat, reniform processes (median and lateral lobe). A polarity of these structures is suggested: the type i) of Oncomerinae is regarded as plesiomorphic

(shared with Urostylididae, Dinidoridae, etc.); the type iii) of Platytatina is homologized with type ii) of Tessaratominae *sensu stricto*; the type ii) is unique within Pentatomoidea and considered as an autapomorphy. The information content of the characters of the external scent efferent system and metathoracic spiracle for a phylogenetic hypothesis of relationships within Pentatomoidea is tested by cladistic analyses. We found some apomorphies helping to define Tessaratomidae and Plataspidae, most of the characters, however, seem to be homoplasious at family level. The results of the cladistic analyses further support the monophyly of Dinidoridae + Tessaratomidae *sensu lato* and that of Tessaratomidae *sensu stricto*, while the relationships of Oncomerinae and Tessaratomidae *sensu stricto* as well as the relationships among the family-group taxa within Tessaratomidae *sensu stricto* need further studies.

**Key words:** Heteroptera, Pentatomoidea, Tessaratomidae, Tessaratominae, Natalicolinae, Oncomerinae, morphology, terminology, cuticular structures, metathoracic scent glands, anagenesis

## Introduction

The Tessaratomidae was first established as a subfamily within Pentatomidae by Stål (1865, 1870, as Tessaratomida), and later generally accepted as a distinct family (e.g., Dupuis 1953; Leston 1955; Kumar 1962, 1969a,b, 1974a; Kumar & Ghauri 1970; Štys & Kerzhner 1975; Nuamah 1982; Rolston *et al.* 1993; Schaefer 1993; Schuh & Slater 1995; Sinclair 2000a,b; Cassis & Gross 2002; Li *et al.* 2005, 2006a,b; Rider 2006; Grazia *et al.* 2008; etc.). Currently, Tessaratomidae includes about 240 species in 37 genera (Rolston *et al.* 1993), most of them being large and colourful insects. Stål (1870) divided the Tessaratomidae into five sections, recently accepted as subfamilies or tribes. The higher classification of the family was subsequently discussed and modified by Horváth (1900), Leston (1955), Kumar (1962, 1969a,b, 1974a), and Kumar & Ghauri (1970). The recently accepted classification of the family Tessaratomidae *sensu lato* (divided into subfamilies Natalicolinae, Oncomerinae, and Tessaratominae), has been summarized by Rolston *et al.* (1993). An alternative opinion based on a cladistic analysis in Ph.D. thesis by Sinclair (1989) remains unpublished (see Grazia *et al.* 2008). A historical overview of the classification of the Tessaratomidae *sensu lato* is given in Table 1.

Most of the papers published on the Tessaratomidae deal with alpha and beta taxonomy (e.g., Kumar 1962, 1964, 1969a,b, 1974a; Kumar & Ghauri 1970; Moizudin *et al.* 1992; Sinclair 2000a,b; Magnien 2008; Magnien *et al.* 2008). Since there is no recent revision or complex analysis of the Tessaratomidae, its phylogeny and internal relationships are still poorly known. Leston (1953, 1954a, 1958) suggested that Tessaratomidae represents one of the most ancestral pentatomoidean taxa, probably closest to the family Phloeidae. This opinion was followed by some other authors, e.g. McDonald (1966) and Gross (1975). Gapud (1991) considered the Tessaratomidae as a sister group of Dinidoridae based on two synapomorphies (exposed spiracles on abdominal segment II and greatly enlarged paratergites 9). Quite a different opinion, Tessaratomidae being closely related to Pentatomidae, thus both families representing the most advanced Pentatomoidea, was defended by Singh-Pruthi (1925) and Southwood (1956). Tsai *et al.* (2004) placed Tessaratomidae close to Dinidoridae, Cydnidae, and Scutelleridae based on similarities in the morphology of the male genitalia (aedeagus). Leston (1953, 1954a,b, 1955) even suggested a close relationship of the Tessaratomidae with the superfamily Coreoidea.

Recently, DNA sequences of several different genes were used to elucidate the phylogenetic relationships among pentatomoidean families (Dai 2006; Dai & Zheng 2004, 2005; Li *et al.* 2005, 2006a,b; Grazia *et al.* 2008; Hua *et al.* 2008) (see Discussion for more details). Grazia *et al.* (2008) performed analyses based on 57 morphological characters and four gene regions, including a total evidence analysis of all their data, producing the most robust hypothesis on the pentatomoidean phylogeny so far published. The analysis recognized the Tessaratomidae as a monophyletic taxon, closely related to Dinidoridae (Grazia *et al.* 2008); this result was supported also by Li *et al.* (2005, 2006a,b). The monophyly of the Tessaratomidae *sensu lato* was previously questioned by Kumar (1969a) and especially Sinclair (1989), whose opinion about the Oncomerinae deserving a family status was accepted by Schaefer (1993), but later abandoned by Sinclair (2000a,b) himself. The relationships of the family-group taxa within the Tessaratomidae still remain unresolved, as the available phylogenetic analyses included DNA sequences representing only one or two species of only Tessaratominae: Tessaratomini (Dai & Zheng 2004; Li *et al.* 2005, 2006a) or Oncomerinae