



Desert Bugs (Hemiptera: Heteroptera: Thaumastellidae): New records and review of the distribution and habitat of this relict group

PETR KMENT¹, DAWID H. JACOBS^{2,3}, ATTILIO CARAPEZZA⁴, JÜRGEN DECKERT⁵, DAVID A. RIDER⁶ & PÉTER KÓBOR⁷

¹Department of Entomology, National Museum of the Czech Republic, Cirkusová 1740, CZ-193 00 Praha 9 – Horní Počernice, Czech Republic

✉ sigara@post.cz; <https://orcid.org/0000-0002-7026-5691>

²Oppenheimer Generations, Research and Conservation, P.O. Box 61631, Marshalltown, 2107, South Africa

✉ dawidhj@mweb.co.za

³Department of Zoology & Entomology, University of Pretoria, Hatfield, Pretoria 0002, South Africa

⁴University of Palermo; corresponding address: via Sandro Botticelli 15, 90144 Palermo, Italy

✉ attilio.carapezza@unipa.it; <https://orcid.org/0000-0003-3994-1804>

⁵Museum für Naturkunde, Leibniz Institute for Research on Evolution and Biodiversity, Berlin, Germany

✉ Juergen.Deckert@mfn.berlin; <https://orcid.org/0000-0003-4211-4463>

⁶Department of Entomology, North Dakota State University, Fargo, North Dakota, USA

✉ david.rider@ndsu.edu; <https://orcid.org/0000-0002-1989-1873>

⁷Plant Protection Institute, HUN-REN Centre for Agricultural Research, Martonvásár, Hungary

✉ kobor.peter@atk-hun-ren.hu; <https://orcid.org/0000-0003-0266-7303>

Abstract

The known distribution and habitat information of the three described species of the genus *Thaumastella* Horváth, 1896 (Hemiptera: Heteroptera: Pentatomomorpha: Pentatomoidea: Thaumastellidae) are reviewed. In addition a fourth, undescribed species is reported from South Africa (Western Cape). *Thaumastella aradoides* Horváth, 1896, is recorded for the first time from Egypt, Oman, Saudi Arabia, United Arab Emirates, and the states of Khartoum and Sennar in Sudan. Additional records of *Thaumastella namaquensis* Schaefer & Wilcox, 1971, from Namibia (Hardap, ||Kharas) and South Africa (Northern Cape), as well as information on habitat of *Thaumastella namaquensis* and *Thaumastella elizabethae* Jacobs, 1989, are provided. Photographs of the holotypes of the three already described species and their labels are also presented. The distribution of all four species is mapped.

Key words: Hemiptera, Heteroptera, Thaumastellidae, distribution, faunistics, habitat, Afrotropical Region, Palaearctic Region

Introduction

The genus *Thaumastella* Horváth, 1896 (presumably derived from Greek *thaumastos*, meaning wonderful, marvellous), with a single species, *Th. aradoides*, was established by Horváth (1896) based on a single specimen collected by Professor V. Mayet in Biskra, Algeria. Later, two more brachypterous species of *Thaumastella* were described from arid regions of South Africa and Namibia—*Th. namaquensis* Schaefer & Wilcox, 1971, and *Th. elizabethae* Jacobs, 1989 (Schaefer & Wilcox 1971, Jacobs 1989).

About the systematic placement of *Thaumastella* Horváth (1896) wrote: ‘Genus hoc insigne Lygaeidarum verisimiliter subfamiliam novam, in systemate forsitan prope subfamiliam Artheneinarum locandam, efficit. [= This genus belongs probably to a new subfamily of Lygaeidae, being placed in the system probably near the subfamily Artheneinae.]’ In the following decades *Thaumastella aradoides* was mentioned merely in catalogues, being classified in Lygaeidae: Artheneinae (Puton 1899; Oshanin 1906, 1912; Stichel 1959, 1960). Seidenstücker (1960) reported rediscovery of *Th. aradoides* in Iran and provided its detailed and well illustrated redescription based on both sexes. He placed it in a new subfamily, Thaumastellinae Seidenstücker, 1960, based on pentamerous antennae

and plate-like ovipositor. He discussed the problematic systematic placement of the new subfamily but he retained its placement in Lygaeidae. Slater (1964) accepted that placement in his catalogue of Lygaeidae [= Lygaeoidea in its present sense].

Štys (1964) performed a morphological study of both sexes of *Th. aradoides* and as a result elevated Thaumastellinae to family rank and transferred it to Pentatomoidea, considering it the most primitive lineage of the superfamily. Also, Seidenstücker (1964) simultaneously arrived at a similar conclusion, transferring *Thaumastella* to Pentatomoidea, placing it near Cydnidae. This classification was generally accepted in subsequent papers (Cobben 1968, Schaefer & Wilcox 1971, Linnavuori 1977, Schaefer 1981).

On the other hand, Dolling (1981) reduced Thaumastellidae to a subfamily of his broadly conceived Cydnidae (also including Thyreocoridae). Dolling (1981) based his classification on the presence of two shared morphological characters, the strigil on or adjacent to the metathoracic wing vein PCu, and the fringes of bristles at the apices of the coxae (so-called coxal combs). Dolling's (1981) classification was followed by rather few authors (Popov 1986, Schaefer 1988, Gapud 1991, Hoberlandt 1997, Popov & Pinto 2000, Bianchi & Gonçalves 2021), being revived recently by Schuh & Weirauch (2020). On the other hand, most of the other authors adhere to family rank of Thaumastellidae (Afzal & Sahibzada 1988; Henry & Froechner 1988; Jacobs 1986, 1989, 2008; Jacobs *et al.* 1989; Linnavuori 1989, 1993a,b; Zrzavý 1990; Schaefer 1993; Lis 1994, 2006, 2010; Schuh & Slater 1995; Henry 1997, 2009, 2017; Cassis & Gross 2002; Linnavuori & van Harten 2002, 2006; Dejanschi & Péricart 2005; Gogala 2006; Grazia *et al.* 2008; Pluot-Sigwalt & Lis 2008; Kment & Vilímová 2010a,b; Yao *et al.* 2012, 2013; Aukema *et al.* 2013; Ghahari *et al.* 2014; Wu *et al.* 2016; Lis *et al.* 2017; Rider *et al.* 2018; Weirauch *et al.* 2019; Bianchi *et al.* 2021; Hemala *et al.* 2021; Roca-Cusachs *et al.* 2022, Ye *et al.* 2022, Davranoglou *et al.* 2023, Lis 2023, Lis & Domagała 2024, Lis *et al.* 2024). Jacobs (1989) supported the family status of Thaumastellidae by finding m-chromosomes, a character unique in Pentatomoidea but shared with Coreoidea and most of Lygaeoidea (Schaefer 1993, Henry 1997). Recent phylogenetic analyses support the position of Thaumastellidae as a separate family, either sister to all the remaining Pentatomoidea (Wu *et al.* 2016, Lis *et al.* 2017, Weirauch *et al.* 2019, Ye *et al.* 2022) or in the position of Urostylididae + (Thaumastellidae + remaining Pentatomoidea) (Roca-Cusachs *et al.* 2022), though the statistic support was not always significant. Lis (2023) and Lis & Domagała (2024) supported the family rank of Thaumastellidae based on study of molecular apomorphies in the secondary and tertiary structures of length-variable regions (LVRs) of 18S rRNA. In this paper, we keep the family rank of Thaumastellidae.

In this paper, we provide for the first time photographs of the holotypes of the three described *Thaumastella* species, and review all the available published and unpublished distribution records and habitat information for them.

Material and methods

Specimens deposited in the following museums and personal collections were examined:

ACPI	Attilio Carapezza collection, Palermo, Italy;
DARC	David A. Rider collection, North Dakota State University, Fargo, USA;
DHJS	Dawid Jacobs collection, Pretoria, South Africa;
HNHM	Hungarian Natural History Museum, Budapest, Hungary;
MMBC	Moravian Museum, Brno, Czech Republic;
MNHN	Muséum National d'Histoire Naturelle, Paris, France;
NMPC	National Museum of the Czech Republic, Prague, Czech Republic;
TMSA	Ditsong National Museum of Natural History (former Transvaal Museum), Pretoria, South Africa;
ZMHB	Museum für Naturkunde, Berlin, Germany.

Label data of Pavel Štys' Sudanese specimens are supplemented by geographical coordinates, additional information, or corrections according to the Štys' field diaries deposited in Moravian Museum, Brno.

The distribution map was created using SimpleMappr (Shorthouse 2010).



FIGURES 1–2. Habitus of *Thaumastella aradoides* Horváth, 1896. 1—holotype ♀ (2.40 mm) and its labels; 2—♀ (2.25 mm) from Saudi Arabia: Wadi Eidabi. (Photos: 1—P. Kóbor, 2—A. Carapezza).

Results

Thaumastella aradoides Horváth, 1896

(Figs 1–2, 9, 11–12)

Thaumastella aradoides Horváth, 1896: 325 (original description). Holotype: ♀, Algeria, Biskra (HNHM—see Péricart 1996: 153; Figs 1–2).

Thaumastella aradoides: Puton (1899): 28 (catalogue); Oshanin (1906): 289 (catalogue, systematic position); Oshanin (1912): 31 (catalogue); Stichel (1959): 324 (catalogue); Stichel (1960): 161 (catalogue); Seidenstücker (1960): 1–4, Figs 1–14 (redescription, morphology, systematic placement, collection circumstances, record); Seidenstücker (1964): 273–278, Figs 9–20 (morphology, systematic placement, collection circumstances, records); Slater (1964): 1498 (catalogue); Štys (1964): 239–248, Figs 1–13 (morphology, systematic placement); Cobben (1968): 78–80, Figs 66“A–C (description of egg); Schaefer (1975): 230, 235 (trichobothria); Linnavuori (1977): 49 (collection circumstances, records); Dolling (1981): 66, 70–71, Figs 16–20 (morphology, systematic placement, record); Schaefer (1981): 232 (morphology); Afzal & Sahibzada (1988): 254 (morphology); Linnavuori (1989): 6 (collection circumstances, record); Zrzavý (1990): 207, 208, 216, 219, 220, [222], Fig. 3e (morphology); Gapud (1991): 872, 878–879, 894 (morphology); Linnavuori (1993a): 142–143, Figs 104p, 105a–h (figures, records); Linnavuori (1993b): 39 (record); Péricart (1996): 153 (type material); Hoberlandt (1997): 182 (collection circumstances, records) [paper omitted in Iranian catalogue by Ghahari *et al.* (2014)]; Linnavuori & van Harten (2002): 181 (record); Derjanschi & Péricart (2005): Pl. IV: Fig. D (habitus drawing); Linnavuori & van Harten (2006): 171 (records); Lis (2006): 117 (Palaeartic catalogue); Pluot-Sigwalt & Lis (2008): 298, 299, 306, 309, Fig. 66 (morphology of spermatheca); Kment & Vilímová (2010a): 6 (record); Kment & Vilímová (2010b): 5, 11, 12, 23, figs 12, 33–34, 101–102 (morphology of metathoracic scent gland efferent system, record); Ghahari *et al.* (2014): 84 (catalogue);

Iran); Lis *et al.* (2017): 482, 484, Figs 1I, 2G (morphology, systematic placement, habitus photo); Rider *et al.* (2018): 135, 185, Fig. 2.16J (systematic placement, habitus photo, record); Lis *et al.* (2024): 4, Fig. 1K, 5, 6, Fig. 2 (morphology, systematic placement, molecular phylogeny).

Type material examined. Holotype: ♀ (Fig. 1), **ALGERIA:** ‘Biskra [printed] // Thaumastella / aradoides Horv’ [handwritten by G. Horváth] (HNHM).

Additional material examined. **ASIA: OMAN:** Al Batinah, 10 km W of Shinas, 24°44′N 56°23′E, 60 m a.s.l., 15.–16.iii.2017, 2 ♂♂ 2 ♀♀, S. Jakl lgt., A. Carapezza det. (ACPI).—**SAUDI ARABIA: Jizan Province:** 10 km SE of Al Eidabi, Wadi Eidabi, 17°09.657′N 42°59.520′E, 139 m a.s.l., 17.iii.2014, 47 ♂♂ 51 ♀♀, A. Carapezza lgt. & det. (Fig. 2, ACPI).—**UNITED ARAB EMIRATES:** Sharjah Desert Park (25°17′N 55°42′E), light trap ([Sample No.] 12374), 2.iii.–1.iv.2007, 1 ♀, A. van Harten lgt., P. Kment det. (NMPC); Wadi Bih (dam) (25°48′N 56°04′E), water trap (12962), 13.xii.2009–8.iii.2010, 2 ♂♂, A. van Harten lgt., P. Kment det. (NMPC); Wadi Safad (25°13′N 56°19′E), light trap (12419), 22.iv.–21.vi.2006, 1 ♂, A. van Harten lgt., P. Kment det. (NMPC). **YEMEN: Abyan Province:** Al Kowd, ix.1999, 1 ♀, van Harten & Haruri leg., A. Carapezza det. (ACPI).—**AFRICA: EGYPT: Giza Governorate:** West Desert Oasis, Bahariya (28°21′5.36″N 28°51′44.6″E), light trap, 30.iv.1996, 1 ♀, W. G. Ulrich lgt., J. Deckert det. (ZMHB). **SUDAN: Al Jazirah:** Meddani [= Wad Madani], Blue Nile, at light, 21.iii.1925, 1 ♀, H. W. Bedford lgt., P. Kment det. (BMNH). **Kassala to Red Sea:** Kassala Prov., Kassala–Haiya, 1.–3.xii.1962, 3 ♀♀, R. Linnavuori lgt. & det., P. Kment revid. (BMNH). **Khartoum:** Khartoum, 26.x.1965, 1 ♂, Omer lgt., P. Kment det. (MMBC); Khartoum ([Sample No.] 28), [15.36°N 32.32°E, University, light trap], 14.ix.1965, 2 ♂♂ 3 ♀♀, P. Štys [on label, S. M. Omer in field diary] lgt. (MMBC); Khartoum (47), [University, light trap], 2.x.1965, 1 ♀, P. Štys [S. M. Omer] lgt., P. Kment det. (MMBC); Khartoum (63), [University, light trap], 26.x.1965, 1 ♂ 2 ♀♀, P. Štys [S. M. Omer] lgt., P. Štys det., P. Kment revid. (1 ♂ 1 ♀ BMNH, 1 ♀ MMBC); Khartoum (463, 466, 467), [University, light trap], 10.x.1966, 41 ♂♂ 115 ♀♀ 8 spec., P. Štys lgt., P. Kment det. (38 ♂♂ 106 ♀♀ 3 spec. MMBC; 4 ♂♂ 6 ♀♀ > NMPC; 4 ♀♀ > MNHN; 5 spec. > DARC [photographed in Rider *et al.* 2018: 185: Fig. 2.16J]) [3 ♂♂ 22 ♀♀ 3 spec. in MMBC, incorrectly labelled as Khartoum-Burri (466)]; Khartoum (479, 480), [University, light trap], 21.x.1966, 11 ♂♂ 14 ♀♀, P. Štys lgt., P. Kment det. (MMBC); Khartoum (1071), 7 [correctly 3].x.1967, 1 ♀, P. Štys lgt., P. Kment det. (MMBC); Khartoum (1072, 1073), [light trap], 3.x.1967, 2 ♂♂ 4 ♀♀, P. Štys lgt., P. Kment det. (MMBC); Khartoum (1111), [University, light trap], 31.x.1967, 2 ♂♂ 1 ♀, P. Štys lgt., P. Kment det. (MMBC); Khartoum-Burri (40), [15.36°N 32.34°E, Pink Palace Hotel, in bed], 20.–27.ix.1965, 1 ♂, P. Štys lgt., P. Kment det. (MMBC); Khartoum-Burri (42), [little garden, at lamp], 27.–30.ix.1965, 2 ♀♀, P. Štys lgt., P. Kment det. (MMBC); Khartoum-Burri (507), [little garden, at light], 2.xi.1966, 1 ♀, P. Štys lgt., P. Kment det. (MMBC); Khartoum-Burri (1065), [at light], 1.–2.[correctly 3].x.1967, 1 ♂, [P. Štys.] N. Williams & M. Hansell lgt., P. Kment det. (MMBC); Shambat (375), [15.40°N 32.32°E, light trap in fields at the University Farm], 22.viii.1966, 1 ♂, P. Štys [on label, Venkatraman & Imam lgt. in field diary] lgt., P. Kment det. (MMBC); Shambat (459), [light trap], 11.x.1966, 1 ♂, P. Štys lgt., P. Kment det. (MMBC); Shambat (496), [light trap], 25.x.1966, 1 ♂, P. Štys lgt., P. Kment det. (MMBC). **Sennar:** Blue Nile Province, Dinder Game Reserve, Galegu (649), [12.36°N 35.02°E, at light], 27.ii.1967, 4 ♂♂ 8 ♀♀, P. Štys lgt., P. Kment det. (MMBC); Dinder Game Reserve, Galegu (657), [at light], 28.ii.1967, 1 ♀, P. Štys lgt., P. Kment det. (MMBC). **White Nile:** Blue Nile Province, El Mellaha (631, 632, 633) [correctly White Nile, Ash Shawal, 13.32°N 32.38°E, light trap], 13.ii.1967, 5 ♂♂ 17 ♀♀, P. Štys lgt. & det., P. Kment revid. (MMBC); Mal aba (637), [13.55°N 32.22°E, sweeping of ruderal vegetation + margin of field with hyacinth bean *Lablab purpureus* subsp. *purpureus*], 14.ii.1967, 1 ♀, P. Štys lgt., P. Kment det. (MMBC).

Habitat. Very little is known about the biology and habitat of the species. According to Seidenstücker (1964), the species is an Eremian faunal element which occurs in the hot season of the year, swarming in the night, being attracted to light along with cydnids of the genera *Aethus* Dallas, 1851, and *Geotomus* Mulsant & Rey, 1866. Most of the available specimens were collected by light traps (Seidenstücker 1960, 1964; Linnavuori 1977, 1989; Hoberlandt 1997; this paper). Interestingly, the species often co-occurs in the light traps with *Camptocera glaberrima* (Walker, 1872) (Rhyarochromidae) (Seidenstücker 1960, Štys 1964, this paper). Linnavuori (1977, 1989) mentioned it was collected in sandy habitats. Seidenstücker (1960) hypothesized that it lives in epipsammon, an idea shared by Štys (1964), however, we lack any observation to confirm it. Seidenstücker’s (1960) prediction of existence of brachypterous morph of *Th. aradoides* has also not been confirmed, despite the brachypterous morph being the only known form in the three South African species (Schaefer & Wilcox 1971, Jacobs 1989, this paper).

Hoberlandt (1997) summarized the information on its occurrence in Iran as follows: ‘2 ♂♂ and 2 ♀♀ from the vicinity of Kahkom, 20 km SW of Hajiabad, were collected by sweeping. Specimens from all other localities

were collected by light trap mainly in coastal sandy plain (nos 202, 208, 209), dense savanna with tree-like growth with predominant *Prosopis spicigera* [= *P. cineraria*], *Acacia arabica* [= *Vachellia nilotica* subsp. *tomentosa*], *Acacia nubica* [= *Vachellia oerfota* var. *oerfota*], *Tamarix aphylla*, *Salvadora persica*, *Ephedra ciliata*, *Calligonum comosum*, *Calotropis procera*. Collecting places, nos. 215 and 323 represented typical steppe zones.' In the United Arab Emirates, *Th. aradoides* was collected by light or water traps in desert (Sharjah Desert Park) as well as mountainous areas (farms in Wadi Bih and Wadi Safad) (van Harten 2008 and this paper). Both in Oman and Saudi Arabia the collected specimens were attracted to light together with *Camptocera glaberrima* (Walker, 1872) (Heteroptera: Rhyparochromidae); in Oman they were collected in a sandy coastal plain with halophytic vegetation, in Saudi Arabia in an arid sandy area with scanty vegetation (*Vachellia*, *Phragmites*, *Tamarix*) close to a small water course. According to field diaries of P. Štys, all but one of his Sudanese specimens were collected at light (including the one found in a bed); the only exception is one female originating from sample collected by sweeping of ruderal vegetation at margin of a field with hyacinth bean *Lablab purpureus* subsp. *purpureus* (Fabaceae) in Mal'aba (this paper).

Host plant association. There is no evidence of a host plant. In case of the cited plant associations, they refer to surrounding vegetation or cases when the insect was stationary on the plant, i.e., no feeding behavior was observed.

Phenology. Based on the available collecting dates, the adults of *Th. aradoides* may be found all around the year. However, there seems to be differences between the particular regions as the answer to the local climatic conditions. In the Nile basin (South Sudan, Sudan and Eritrea) and Chad the specimens were collected in the following periods: 5.–20.i., 13.–28.ii., 26.–27.iii., 10.–12.v., 20.–22.v., 5.vi., 22.viii., 14.ix.–31.x., 11.xi.–3.xii.; interestingly, the large series of specimens collected in Khartoum and its vicinity by Pavel Štys between 14.ix. and 31.x. has its distinct peak on 10.x. (Seidenstücker 1964; Linnavuori 1977, 1993a; this paper). In Yemen, the specimens were collected from July to October (Linnavuori 1989, 1993a; Linnavuori & van Harten 2002, 2006; this paper), while in the nearby Jizan (Saudi Arabia), it was sampled on 17.iii. (this paper). In the United Arab Emirates and Oman, the specimens were collected on 2.iii.–1.iv., 22.iv.–21.vi., and 13.xii. (this paper), while all the records from the adjacent areas of Iran come from May (Seidenstücker 1960, 1964; Hoberlandt 1997) and those from Baghdad (Iraq) from September (Seidenstücker 1964, Linnavuori 1993b). There is probably more than one generation per year, but their number cannot be estimated based on the available data.

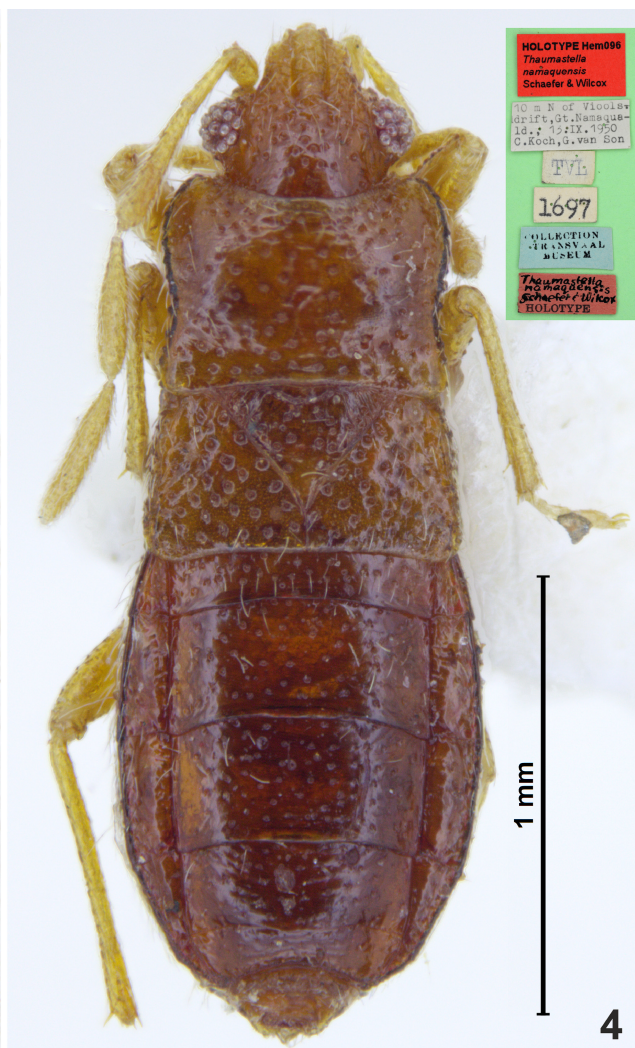
Distribution (Figs 9, 11). **PALAEARCTIC REGION: Algeria** (Horváth 1896); **Iran:** Hormozgan (Hoberlandt 1997, Kment & Vilimová 2010a,b), Kerman (Seidenstücker 1960, 1964; misinterpreted as Sistan & Baluchestan in Ghahari *et al.* 2014); **Iraq** (Seidenstücker 1964, Linnavuori 1993b); **Oman** (new record); **Saudi Arabia** (new record); **United Arab Emirates** (new record); **Yemen** (Linnavuori 1989, 1993a; Linnavuori & van Harten 2002, 2006). **AFROTROPICAL REGION: Egypt** (new record); **Chad** (Linnavuori 1993a); **Eritrea** (Linnavuori 1993a); **South Sudan** (Linnavuori 1977); **Sudan** (Dolling 1981; Rider *et al.* 2018, without exact localities): Al Jazirah (Linnavuori 1977), Kassala (Linnavuori 1977), Khartoum (new record), Red Sea (Linnavuori 1977), River Nile (Linnavuori 1977), Sennar (new record), White Nile (Linnavuori 1977, this paper).—Štys (1964) reported 1 ♂ and 4 ♀♀ from HNHM labelled as Saigon, but considered its provenience from Vietnam as improbable (see also Schaefer & Wilcox 1971).

Most of the known localities of *Th. aradoides* are concentrated in three distinct areas: i) the Nile basin in South Sudan, Sudan and Eritrea; ii) Yemen and the adjacent Jizan province of the Saudi Arabia, and iii) areas around the Strait of Hormuz in the UAE, Oman and Iran. There are four exceptions—isolated localities Biskra in southern outskirts of Atlas Mts. (Algeria), Farcha near N'Djamena east of Chad Lake (Chad), West Desert Oasis (Egypt), and Baghdad on Tigris River (Iraq). Although the known localities are situated in Eremian region, the species apparently avoids the central desert areas of the Sahara, Arabian Peninsula and eastern Iran (Fig. 12).

***Thaumastella elizabethae* Jacobs, 1989**

(Fig. 3, 9–10, 13)

Thaumastella elizabethae Jacobs, 1989: 302–314, Figs 1–3, 5, 7–9, 11–16, 19–20, 22–23, 25–26, 28–32, 35–36 (original description, morphology, karyotype). Holotype: ♂, South Africa, Namaqualand, Farm Wiedouw, nr. Vanrhynsdorp, 31°44'S 18°46' (TMSA).



FIGURES 3–5. Habitus of South African *Thaumastella* species. 3—*Th. elizabethae* Jacobs, 1989, holotype ♂ and its labels; 4—*Th. namaquensis* Schaefer & Wilcox, 1971, holotype ♂ and its labels; 5—living specimen of *Th. namaquensis*, Namibia, Gellap, 9.ix.2008. (Photos: 3–4—D. H. Jacobs, 5—J. Deckert).

Thaumastella elizabethae: Jacobs *et al.* (1989): 459–463 (composition of metathoracic scent gland secretion); Kerzhner *et al.* (2004): 17 (list of karyotypes); Grazia *et al.* (2008): 6, 8, 11, 23–26, 28–31 (phylogenetic analysis); Yao *et al.* (2012): 3 (phylogenetic analysis); Yao *et al.* (2013) 66–68 (phylogenetic analysis); Wu *et al.* (2016): 756–757 (phylogenetic analysis); Lis *et al.* (2017): 485, 490–492 (phylogenetic analysis); Rider *et al.* (2018): 135 (morphology, biology); Roca-Cusachs *et al.* (2022): 41 (phylogenetic analysis); Bianchi *et al.* (2021): 414, 416, 418 (molecular phylogeny); Lis (2023): 3–13 (secondary and tertiary structures of length-variable regions of 18S rRNA, phylogenetic position); Lis & Domagała (2024): 3, 7–8, 11–17, 19 (secondary and tertiary structures of length-variable regions of 18S rRNA, phylogenetic position).

Thaumastella elisabethae [incorrect subsequent spelling]: Pluot-Sigwalt & Lis (2008): 299, 305 (spermatheca).

Type material examined. Holotype: ♂ (Fig. 3), **SOUTH AFRICA: Western Cape:** ‘Farm Wiedouw / nr. VANRHYSNDORP / S31.44 E18.46 / 7–9. ix. 1986 / D.H. Jacobs [printed] // *Thaumastella / elizabethae* ♂ [handwritten] / HOLOTYPE No. [printed in red; original type label, white with wide red frame] // HOLOTYPE Hem727 / *Thaumastella / elizabethae* / Jacobs ♂ [printed; red type label added by museum]’ (TMSA). Allotype: ♀, same data as holotype (TMSA). Paratypes: 10 ♂♂ 19 ♀♀: same data as holotype (DHJS, TMSA); 5 ♂♂ 10 ♀♀, same data as holotype but 18–21.ix.1984 (TMSA).

Habitat and host plant. A few specimens of *Th. elizabethae* were originally collected under a large stone at the foot of the Gifberg mountain near Vanrhynsdorp in southern Namaqualand. In September 1986, many specimens were collected in the late afternoon while feeding on fallen seeds of *Pharnaceum aurantium* (DC) Druce (Aizoaceae) which grow on an embankment at the edge of a cultivated field. Under nearby stones many more specimens were present. The small seeds of *P. aurantium* are hard and disc-shaped with a diameter of about 0.6–0.7 mm. The stylets of *Th. elizabethae* could only penetrate the seed at its edge and probably with difficulty. Many specimens were seen walking with a seed still attached to their stylets so that the seed was dragged at the side of the thorax. Even when disturbed they seem unable to free their stylets quickly and ran with the seeds still attached to them. Some specimens were observed entering small holes some distance away from any visible stones (Jacobs 1989).

Phenology. Adults were collected in September (Jacobs 1989).

Distribution (Figs 9, 10). **AFROTROPICAL REGION: South Africa:** Western Cape (Jacobs 1989, Jacobs *et al.* 1989). *Thaumastella elizabethae* is only known from its type locality.

***Thaumastella namaquensis* Schaefer & Wilcox, 1971**

(Figs 4–5, 9–10, 13)

Thaumastella namaquensis Schaefer & Wilcox, 1971: 207–213, Figs 1–4 (original description, morphology, habitat, distribution).

Holotype: ♂, Namibia: 10 miles N of Vioolsdrift, Gt. Namaqualand (TMSA).

Thaumastella namaquensis: Schaefer (1975): 230, 235 (trichobothria); Jacobs (1986): 142–144 (habitus drawing, habitat); Jacobs (1989): 302, 305–314 (differential diagnosis, morphology, karyotype, habitat, distribution); Jacobs (2008): 142–144 (habitus drawing, habitat); Jacobs *et al.* (1989): 459–463 (composition of metathoracic scent gland secretion); Kerzhner *et al.* (2004): 17 (list of karyotypes); Grazia *et al.* (2008): 6, 8, 11, 13, 23–26, 28–31, Figs. 8 (morphology, phylogenetic analysis); Pluot-Sigwalt & Lis (2008): 299, 305 (spermatheca); Wu *et al.* (2016): 756–757 (phylogenetic analysis); Lis *et al.* (2017): 485, 490–492 (phylogenetic analysis); Rider *et al.* (2018): 135 (biology); Weirauch *et al.* (2019): 74, 78, 81–82, 93–94, Fig. 3 (phylogenetic analysis, habitus photo); Bianchi *et al.* (2021): 414, 416, 418 (molecular phylogeny); Rocca-Cusachs *et al.* (2022): 41 (phylogenetic analysis).

Type material examined. Holotype: ♂ (Fig. 4), **NAMIBIA:** ‘10 m N of Viools- / drift, Gt. Namaqua- / ld.; 13:IX.1950 / C. Koch, G. van Son [printed]; TVL [printed] / 1697 [printed] / COLLECTION / TRANSVAAL / MUSEUM [printed, pale blue label] / *Thaumastella / namaquensis / Schaefer & Wilcox* [handwritten] / HOLOTYPE [printed, red original type label] // HOLOTYPE Hem096 / *Thaumastella / namaquensis / Schaefer & Wilcox* [printed; red type label added by museum]’ (TMSA). Paratypes: 2 ♂♂ 2 ♀♀, same data as holotype (TMSA).

Additional material examined. NAMIBIA: Hardap Region: S.W.Afr., Naukluft, Felseneck reserve, 24.21°S 16.04°E, light collection, 24.x.1974, E-Y: 416, 1 ♀, Endrödy-Younga lgt., D. H. Jacobs det. (TMSA). ||**Kharas Region:** Keetmanshoop Dist.: Gellap Agr. Exp. Station, 26°24′42.2″S 18°00′45.0″E, 1080 m a.s.l., 16.–23.x.2002, pitfall trap E6, BIOTA, 1 ♀, A. Hoffmann lgt., J. Deckert det. (ZMHB); Keetmanshoop Distr. Gellap Ost, 1100 m a.s.l., 26°24′26″S 18°00′38″E, 24.x.2002, 6 ♂♂ 6 ♀♀, 9.ix.2008, 8 ♂♂ 1 ♀, J. Deckert lgt. & det. (Fig. 5, ZMHB); Keetmanshoop Distr.: Gellap Ost 3, 23 km NW Keetmanshoop, dwarf shrub savannah (Nama-Karoo), BIOTA 10.005.2001.7.05.572, 26°24′06.4″S 18°00′38.6″E, 10 pitfall traps, 5.–10.iv.2001, 12.00–12.00, 5 ♂♂ 3 ♀♀, M. Uhlig & E. Marais lgt., J. Deckert det. 2003 (ZMHB); ditto, BIOTA 10.005.2001.7.11.1005, 26°24′06″S 18°00′38″E, singling, 7.iv.2001: 13.30, 32 °C, 12 ♂♂ 1 ♀, J. Deckert lgt. & det. 2003 (ZMHB); BIOTA 10.005.2001.7.11.1005, 26°24′06″S 18°00′38.2″E, singling, 7.iv.2001: 10:30, 6 ♂♂ 3 ♀♀, J. Deckert lgt. & det. 2003 (ZMHB); ditto, BIOTA 10.000.2001.7.11.1001, 26°24′26.5″S 18°00′34.2″E, singling, 7.iv.2001: 10:30, 3 ♂♂ 1 ♀, J. Deckert lgt., D. H. Jacobs det. (DHJS); BIOTA 10.049.2001.7.11.551, 26°24′18.5″ 18°00′25.5″E, singling, 8.iv.2001: 12.30, 30 °C, 2 ♂♂, Uhlig, Ebert & Deckert lgt., J. Deckert or D. H. Jacobs det. (1 ♂ DHJS, 1 ♂ ZMHB); Keetmanshoop Distr.: Nabaos 7 (Nuwe Fontein), 24 km NW Keetmanshoop, dwarf shrub savannah (Nama-Karoo), BIOTA 11.031.2001.7.05.571, 26°23′38.1″S 17°59′50.0″E, 10 pitfall traps, 5.–10.iv.2001, 16.00–10.00, 1 ♂ 1 ♀, M. Uhlig

& E. Marais lgt., J. Deckert det. 2003 (ZMHB); ditto, BIOTA 11.031.2001.7.05.298, 26°23'45.8"S 17°59'47.5"E, pitfall traps, 4.–8.iv.2002, 1 ♀, M. Uhlig lgt., J. Deckert det. (ZMHB); S.W. Afr., S Namib, Rosh-Pinah, 27.53°S 16.50°E, from under stones, 21.ix.1973, 1 ♀, Endrödy-Younga lgt., D. H. Jacobs det. (TMSA). **SOUTH AFRICA: Northern Cape:** S. Afr.; Richtersveld, Hellskloof, 4 km N, 28.17°S 16.59°E, 26.ix.1991, E-Y: 2798, from under stones, 9 ♂♂ 9 ♀♀, Endrödy-Younga lgt., D. H. Jacobs det. (TMSA); S. Afr.: Richtersveld, Hellskloof, 28.20°S 16.59°E, 7.ix.2001; E-Y: 3414, under stones & ground, 9 ♂♂ 5 ♀♀, SATM staff leg., D. H. Jacobs det. (TMSA); S. Afr., Richtersveld, Ganakom Riv. Valley, 28.26°S 17.12°E, 5.ix.1976; E-Y: 1221, ground trap with faeces bait, 35 days; 1 ♂, Endrödy-Younga lgt., D. H. Jacobs det. (TMSA); ditto, E-Y: 1221, from under stones, 1 ♂ 3 ♀♀, Endrödy-Younga lgt., D. H. Jacobs det. (TMSA); S. Afr., Richtersveld, Ekstienfonteinval (= Eksteenfontein valley ?), 28.47°S 17.12°E, 28.ix.1991; E-Y: 2804, from under stones, 1 ♀, Endrödy-Younga lgt., D. H. Jacobs det. (TMSA); Anenous Pass nr. Steinkopf, 29°13'S 17°37'E, 1.x.2002, 3 ♂♂, D. Jacobs & M. Stiller lgt., D. H. Jacobs det. (DHJS); RSA: Northern Cape Province, Steinkopf, 29°16'31"S 17°44'43"E, 11.ix.2008, 5 ♂♂ 4 ♀♀, J. Deckert lgt., J. Deckert & D. H. Jacobs det. (2 ♂♂ 2 ♀♀ DHJS, 3 ♂♂ 2 ♀♀ ZMHB); Steinkopf, roadside, 800 m a.s.l., 29°16'58.980"S 17°44'56.880"E, 11.ix.2008, 3 ♂♂ 4 ♀♀, J. Deckert lgt. & det. (ZMHB); nr. Spektakel Pass, 29°41'S 17°39'E, 16.ix.1984, 8 ♀♀, D. H. Jacobs lgt. & det. (DHJS); nr. Spektakel Pass, Namaqualand, 29.42°S 17.42°E, 7.iv.1985, 2 ♂♂ 6 ♀♀, D. H. Jacobs lgt. & det. (DHJS); Farm Deurdrift nr. Springbok (Figs 6–7), 29.45°S 17.56°E, 6.–13.iv.1985, 15 ♂♂ 22 ♀♀, D. H. Jacobs lgt. & det. (DHJS); ditto, 13.–17.ix.1984, 2 ♂♂ 10 ♀♀, D. H. Jacobs lgt. & det. (2 ♂♂ 10 ♀♀ DHJS, 2 ♂♂ 2 ♀♀ BMNH); S. Afr., Namaqualand, Springbok, 18 km, 29.47°S 19.50°E [error on label, should be 17.50°E], 26.viii.1977; E-Y: 1334, ground traps with faeces bait, 61 days; 2 ♀♀, Endrödy-Younga lgt., D. H. Jacobs det. (TMSA); S. Afr., Namaqualand, Mesklip, 29.49°S 17.52°E, 26.viii.1977; E-Y: 1335, ground traps, 61 days, 1 ♀, Endrödy-Younga lgt., D. H. Jacobs det. (TMSA); S. Afr., Namaqualand, Springbok, Mesklip, 29.49°S 17.52°E, 30.viii.1976; E-Y: 1184, ground traps with meat bait, 43 days, 2 ♂♂ 6 ♀♀, Endrödy-Younga lgt., D. H. Jacobs det. (TMSA). S. Africa (16), Hester Malan N. R., 10 mls. E Springbok, under cut lucerne [*Medicago sativa*, Fabaceae], 7.–8.i.1972, 1 ♂, Southern African Exp. 1972-1, W. Dolling det., P. Kment revid. (BMNH).

Habitat. Sweet, in Schaefer & Wilcox (1971), provided the following description of the habitat at Springbok: ‘This area is delimited as the biotic Province of Little Namaqualand, with low precipitation which falls chiefly during the winter months. The low vegetation is correspondingly largely a karoo flora with some Cape elements; the period of major biotic activity is early spring. The collecting site was a bouldery hillside with a sunny northwest exposure and a slope of about 20°. Kokerboom [= Quiver] trees (*Aloe dichotoma* Masson [= *Aloidendron dichotomum*; Asphodelaceae]) occurred on top of the hill. The perennial plants consisted primarily of succulent Euphorbiaceae and *Mesembryanthemum* [Aizoaceae] and at this time, many drying and dying ephemerals, mostly Asteraceae. Grasses were very infrequent and large areas of bare sandy soil were present. *Thaumastella* was found just underground in small chambers about 1" by 5" [= 25.4–127 mm] in soft sandy soil along the margin of a boulder. Five or six bugs were found together in a group and two were found singly. The thaumastellids were very lygaeid-like in their movements and were initially taken to be a *Plinthisus* [Stephens, 1829, Rhyparochromidae] or a small blissine [Blissidae]. In the laboratory, the thaumastellids spent most of the time hiding as a group under a flake of bark. The insects fed readily on sunflower, and peanut and some small seeds from the habitat, and grew fairly fat, swelling the abdominal conjunctiva. Although the insects lived for three months in the laboratory, no mating was observed and no eggs were laid. This suggests that the insects were in reproductive diapause and may have already completed their life cycle by mid-September’ (Sweet in Schaefer & Wilcox 1971).

Jacobs (1989) described the habitat and bionomics of *Th. namaquensis* as follows: At Springbok (Figs 6–7) most of the specimens were collected under fairly large stones in cavities which are exposed when the stones are removed. Single specimens were also collected on the ground near the stones, especially at dusk, but individuals of *Th. namaquensis* seemed reluctant to leave their sheltered environment. Even night visits, to the spots where they were abundant produced no individuals above-ground. It is possible that they live on seeds that are accumulated by the wind against the stones and very seldom leave their shelters. Although they were found at scattered spots they seemed to be especially abundant where a few suitable stones were present in or near old or existing sheep and goat kraals, despite different species of plants were present in the kraals at Deurdrift and Spektakelberg. It is possible that the manure and moisture supplied by the sheep and goats could maintain better seed-producing vegetation in this arid region to the advantage of the bugs which are almost certainly seed-eating.



FIGURES 6–7. Habitat of *Thaumastella namaquensis* Schaefer & Wilcox, 1971, South Africa, Farm Deurdrift near Springbok. (Photos: D. H. Jacobs).



FIGURE 8. Landscape where an undescribed *Thaumastella* species was collected near Beaufort West in the Karroo, South Africa. (Photo: D. H. Jacobs).

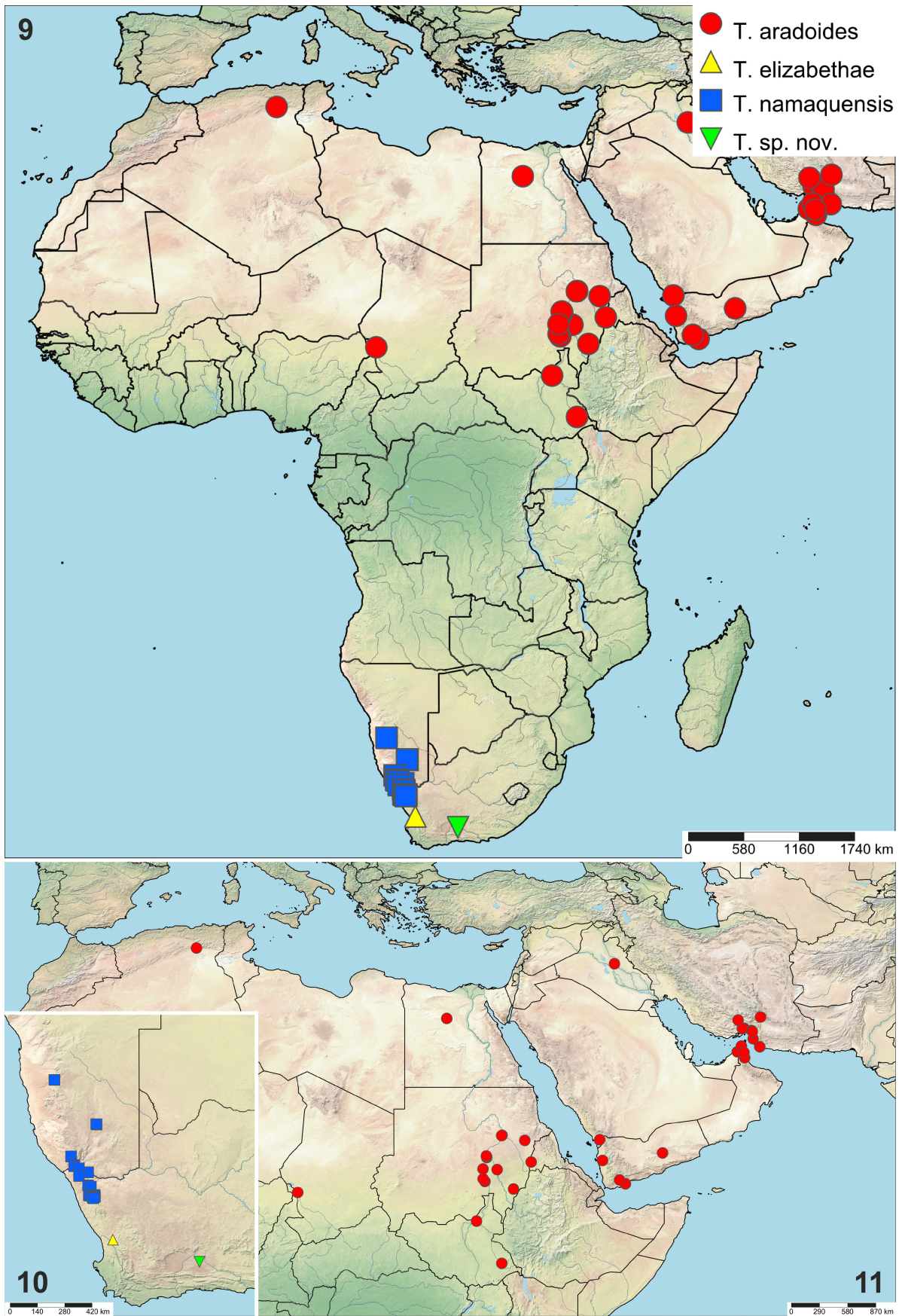
Jürgen Deckert and colleagues collected *Th. namaquensis* in Namibia with pitfall traps filled with ethylene glycol on two different locations, one was heavily grazed by sheep and goats (Nabaos) while in the other (Gellap Ost) there were no sheep or goats, but instead, there was a better developed vegetation where more specimens were found (J. Deckert, pers. observ.).

A few of the specimens were collected by means of ground traps, some of them baited by faeces or meat; it remains a question if these events were merely an accident or that *Thaumastella* is occasionally using such diet as it is known in many other Pentatomomorpha species (e.g., Payne *et al.* 1968, Adler & Wheeler 1984, Booth 1990, Chérot *et al.* 1998, Voigt 2001, López *et al.* 2009, Baz *et al.* 2010, Ekanem & Dike 2010, Eger *et al.* 2015, Valcárcel & Goula 2018).

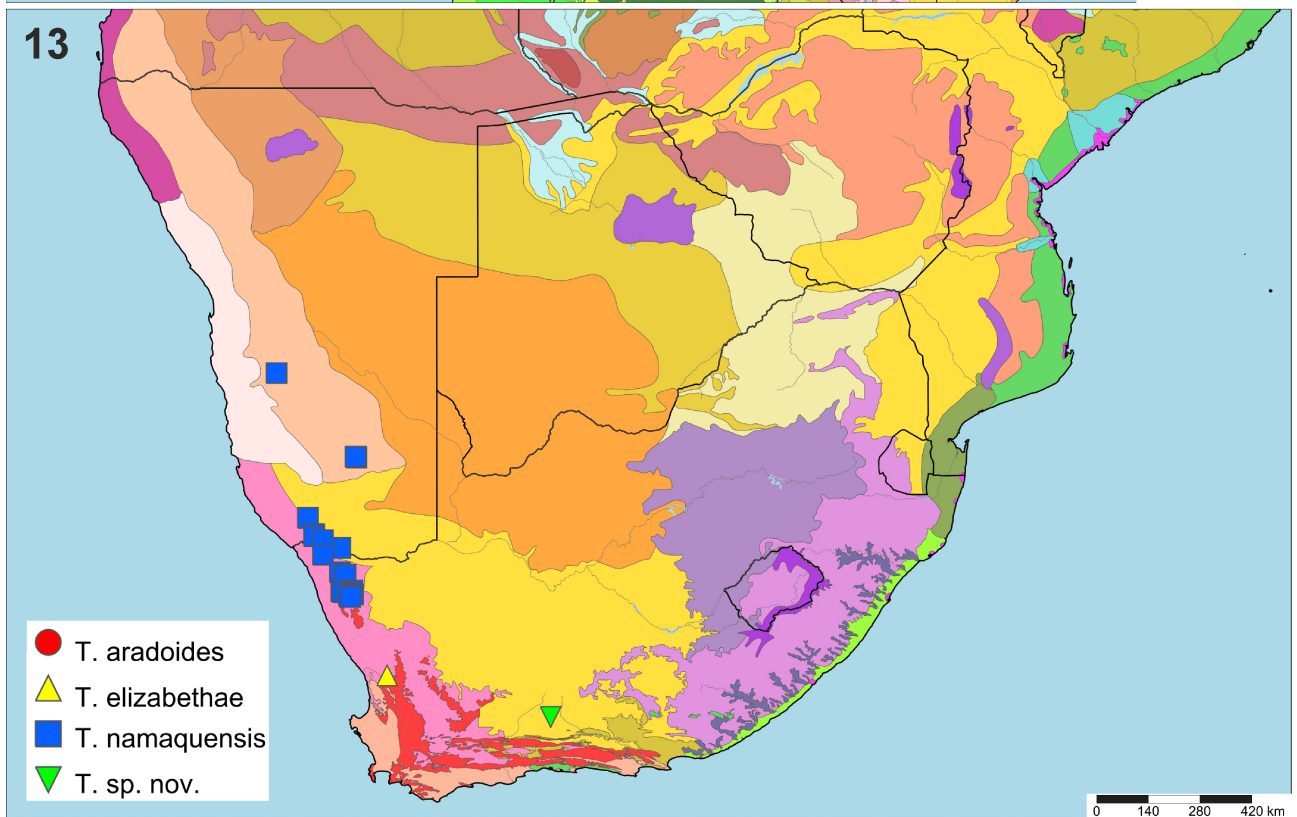
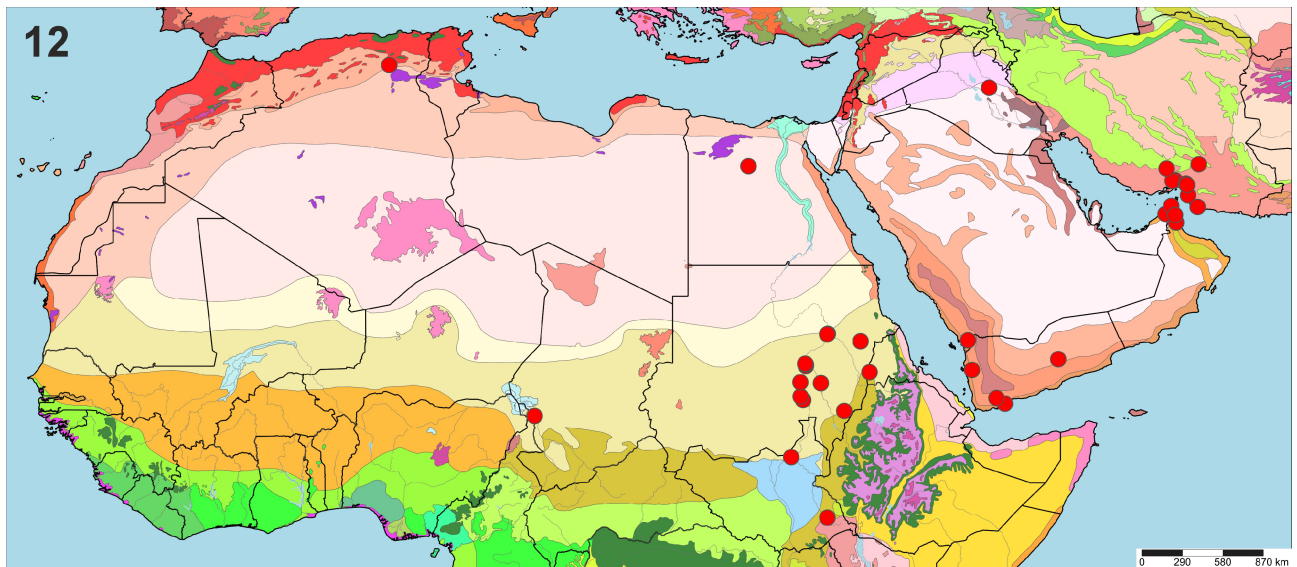
Phenology. Collected regularly in April and August to October (Schaefer & Wilcox 1971, Jacobs 1989, this paper), with exception of a single specimen found in January (this paper). Although August to September is the time of year when most of the plants of this winter rainfall area produce flowers and seeds, thaumastellid nymphs were only found during April. Nymphs of all stages were found together with the adults (Jacobs 1989). The collection dates are probably not a true reflection on when the species occur or are active but the result of the fact that most collecting in Namaqualand is done in August to October when most plants grow and actively flower. Most probably the bugs are around all year round, but are less active and mostly underground and under stones in the winter.

Distribution (Figs 9, 10). **AFROTROPICAL REGION: Namibia:** Hardap, ||Kharas (Schaefer & Wilcox 1971, this paper), **South Africa:** Northern Cape (Schaefer & Wilcox 1971, Jacobs 1989, Jacobs *et al.* 1989, this paper).

According to Schaefer & Wilcox (1971), the type series of *Th. namaquensis* is from Vioolsdrift, near the Orange River near the southern end of the Namib Desert, which is a very dry area (1.5 in. [= 38.1 mm] annual rainfall) with scant vegetation. The specimens collected near Springbok, about 75 miles [= 120.7 km] south of Vioolsdrift, comes from a little less dry area (8–10 in. [= 203.2–254 mm] annual rainfall). The annual average precipitation in Gellap Ost is about 150 mm per year (Berger *et al.* 2010).



FIGURES 9–11. Distribution maps of *Thaumastella* species: 9—general view; 10—detailed distribution of *Th. aradoides* Horváth, 1896 in North Africa and Near East; 11—detailed distribution of *Th. elizabethae* Jacobs, 1989, *Th. namaquensis* Schaefer & Wilcox, 1971 and *Thaumastella* sp. nov. in Namibia and South Africa.



FIGURES 12–13. Comparison of distribution of *Thaumastella aradoides* Horváth, 1896 (12) and the South African species of *Thaumastella* (13), *Th. elizabethae* Jacobs, 1989, *Th. namaquensis* Schaefer & Wilcox, 1971 and *Thaumastella* sp. nov., compared to ecoregions according to Shorthouse (2010).

Thaumastella new species

(Figs 9–10, 13)

Material examined. SOUTH AFRICA: Western Cape: about 45 km SSE of the town Beaufort West, 1 ♂ 1 ♀, unbaited pitfall traps, D. Jacobs lgt. & det. (DHJS). This species has the general facies of *Th. elizabethae*, but the male genital capsule shows significant differences.

Habitat. The locality where it was collected is more or less 400 km ESE of the type locality of *Th. elizabethae*. It is situated in the Gamka Karoo of the Lower Karoo Bioregion of the Nama Karoo Biome (Mucina & Rutherford

2006). It is a dry part of the Karoo with an annual rainfall of about 170 mm. The vegetation of the area can be classified as Stony plains vegetation (Fig. 8). This community occurs on stony footslopes away from mountains. Tall shrubs are sparsely scattered in a lower matrix of Karoo bushes. The canopy cover is sparse (about 30%). The cover is dominated by *Ruschia spinosa* [Aizoaceae] and *Pentzia incana* [Asteraceae]. Other characteristic species are *Euphorbia stellispina* [Euphorbiaceae], *Hermannia desertorum* [Malvaceae], *Limeum aethiopicum* [Limeaceae] and *Pteronia adenocarpa* [Asteraceae] (D. Jacobs, pers. observ.).

Distribution (Figs 9, 10). South Africa: Western Cape (this paper).

Note. The new species will be described later by D. Jacobs.

TABLE 1. Published and new localities of *Thaumastella aradooides* Horváth, 1896, *Th. elizabethae* Jacobs, 1989, *Th. namaquensis* Schaefer & Wilcox, 1971, and *Th. sp. nov.* with their geographical coordinates. If not given on labels or in original publications, coordinates were traced in GoogleMaps, except Iranian localities by Hoberlandt (1997), which were specified by Hoberlandt (1981, 1983), the UAE localities listed by van Harten (2008), and the Sudanese localities accepted from P. Štys's field diaries.

Country	State / Province	Locality	Coordinates	References
<i>Thaumastella aradooides</i> Horváth, 1896				
Algeria	Biskra	Biskra	34°51'26"N 5°45'10"E	Horváth (1896), Seidenstücker (1964)
Chad	Chari-Baguirmi	Farcha	12°07'03"N 14°59'00"E	Linnavuori (1993a)
	or Hadjer-Lamis		12°25'40"N 15°13'14"E	
Egypt	Giza	Bahariya	28°21'5.36"N 28°51'44.6"E	this paper
Eritrea	Gash-Barka	Tessenei [= Teseney]	15°06'31"N 36°39'18"E	Linnavuori (1993a)
Iran	Hormozgan	Abbassi [= Bandar Abbas], Bagh-e Tang, 6 km W of Geno [= Genu], 50 km N of Bandar Abbas (loc. no. 323)	27°27'N 56°18'E	Hoberlandt (1997)
	Hormozgan	Abbassi, Bilai (loc. no. 209)	26°29'N 57°09'E	Hoberlandt (1997)
	Hormozgan	Abbassi, Issin [= Isin], south slopes of Kuhha-ye Geno [= Genu] 45 km NW of Bandar Abbas (loc. no. 198)	27°25'N 56°09'E	Hoberlandt (1997)
	Hormozgan	Abbassi, Shahvar, 12 km NW of Minab (loc. no. 202)	27°14'N 57°01'E	Hoberlandt (1997)
	Hormozgan	Abbassi, Minab (loc. no. 203)	27°09'N 57°05'E	Hoberlandt (1997), Kment & Vilímová (2010a,b)
	Hormozgan	Abbassi, 16 km N of Jask (loc. no. 208)	25°44'N 57°46'E	Hoberlandt (1997)
	Hormozgan	7 km W of Kahkom, 20 km SW of Hajiabad (loc. no. 215)	28°12'N 55°46'E	Hoberlandt (1997)
	Kerman	Djibroft [= Jiroft]: Anbar-Abad [= Anbarabad]	28°28'51"N 57°50'05"E	Seidenstücker (1960, 1964)
Iraq	Baghdad	Baghdad	33°24'08"N 44°20'59"E	Seidenstücker (1964), Linnavuori (1993b)
Oman	Al Batinah	10 km W of Shinas	24°44'N 56°23'E	this paper
Saudi Arabia	Jizan	10 km SE of Al Eidabi, Wadi Eidabi	17°09'39"N 42°59'31"E	this paper

.....continued on the next page

TABLE 1 (Continued)

Country	State / Province	Locality	Coordinates	References
South Sudan		Kapoeta → Boma	4°46'30"N 33°35'24"E → 6°12'52"N 34°23'34"E	Linnavuori (1977)
		Malakal	9°38'44"N 31°36'58"E	Linnavuori (1977)
Sudan	Al Jazirah	Wad Medani [= Wad Madani]	14°14'24"N 33°18'36"E	Linnavuori (1977)
	Kassala → Red Sea	Kassala → Haifa [= Haiya]	15°31'44"N 36°24'53"E → 18°20'22"N 36°23'04"E	Linnavuori (1977)
	Khartoum	Khartoum	15°21'36"N 32°19'12"E	this paper
	Khartoum	Khartoum-Burri	15°21'36"N 32°20'24"E	this paper
	Khartoum	Shambat	15°24'0"N 32°19'12"E	this paper
	River Nile	Ed Damer [= Ad-Dāmar]	17°34'53"N 33°58'09"E	Linnavuori (1977)
	River Nile	Hudeiba	17°33'00"N 33°55'59"E	Seidenstücker (1964)
	Sennar	Dinder Game Reserve, Galegu	12°21'36"N 35°01'12"E	this paper
	White Nile	Ash Shawal [incorrectly as El Mellaha]	13°19'12"N 32°22'48"E	this paper
	White Nile	Mal aba [= Mal'abah]	13°33'00"N 32°13'12"E	this paper
	White Nile	Wad es Zaki [= Wad Alzaky]	14°27'43"N 32°12'25"E	Linnavuori (1977)
United Arab Emirates	Fujairah	Wadi Safad	25°13'N 56°19'E	this paper
	Ras al-Khaimak	Wadi Bih (dam)	25°48'N 56°04'E	this paper
	Sharjah	Sharjah Desert Park	25°17'N 55°42'E	this paper
Yemen	Abyan	Al Kowd [= Al Kawd]	13°05'00"N 45°22'00"E	Linnavuori & van Harten (2002, 2006)
	Al Hudaydah	Al Kadan	15°15'04"N 43°15'00"E	Linnavuori & van Harten (2006)
	Hadhramaut	Seyun [= Seiyun]	15°56'38"N 48°47'52"E	Linnavuori & van Harten (2006)
	Lahij → Dhale	Lahej-Dhala [= Lahij-Dhale/Ad Dali] road	13°03'34"N 44°53'02"E → 13°42'28"N 44°43'29"E	Linnavuori (1989, 1993a)
<i>Thaumastella elizabethae</i> Jacobs, 1989				
South Africa	Western Cape	at Gifberg, Farm Wiedouw, nr. Vanrhynsdorp	31°44'S 18°46'E	Jacobs (1989), Jacobs <i>et al.</i> (1989)
<i>Thaumastella namaquensis</i> Schaefer & Wilcox, 1971				
Namibia	Hardap	Naukluft, Felsenneck reserve.	24°21'S 16°04'E	Jacobs (1989, in map), this paper
	Kharas	10 miles N of Violsdrif	28°37'12"S 17°37'26"E	Schaefer & Wilcox (1971)
	Kharas	Gellap Agr. Exp. Station	26°24'42.2"S 18°00'45.0"E	this paper
	Kharas	Gellap Ost	26°24'26"S 18°00'38"E	this paper
	Kharas	Gellap Ost 3, 23 km NW Keetmanshoop	26°24'06"S 18°00'38"E	this paper
	Kharas	Gellap Ost 3, 23 km NW Keetmanshoop	26°24'06"S 18°00'38.2"E	this paper

.....continued on the next page

TABLE 1 (Continued)

Country	State / Province	Locality	Coordinates	References
	Kharas	Gellap Ost 3, 23 km NW Keetmanshoop	26°24'06.4"S 18°00'38.6"E	this paper
	Kharas	Gellap Ost 3, 23 km NW Keetmanshoop	26°24'18.5"S 18°00'25.5"E	this paper
	Kharas	Gellap Ost 3, 23 km NW Keetmanshoop	26°24'26.5"S 18°00'34.2"E	this paper
	Kharas	Nabaos 7 (Nuwe Fontein), 24 km NW Keetmanshoop	26°23'38.1"S 17°59'50.0"E	this paper
	Kharas	Nabaos 7 (Nuwe Fontein), 24 km NW Keetmanshoop	26°23'45.8"S 17°59'47.5"E	this paper
	Kharas	S. Namib, Rosh-Pinah	27°53'S 16°50'E	Jacobs (1989, in map), this paper
South Africa	Northern Cape	Richtersveld, 4 km N Hellskloof	28°17'S 16°59'E	this paper
	Northern Cape	Richtersveld, Hellskloof	28°20'S 16°59'E	this paper
	Northern Cape	Richtersveld, Ganakom Riv. valley	28°26'S 17°12'E	this paper
	Northern Cape	Richtersveld, Ekstienfontein valley	28°47'S 17°12'E	this paper
	Northern Cape	Anenous Pass, nr. Steinkopf	29°13'S 17°37'E	this paper
	Northern Cape	Steinkopf	29°16'31"S 17°44'43"E	this paper
	Northern Cape	Steinkopf	29°16'58.980"S 17°44'56.880"E	this paper
	Northern Cape	1 mile E of Springbok	29°39'52"S 17°55'05"E	Schaefer & Wilcox (1971)
	Northern Cape	nr. Spektakel Pass	29°41'S 17°39'E	this paper
	Northern Cape	Spektakelberg Pass, ca. 30 km W of Springbok	29°42'S 17°42'E	Jacobs (1989), Jacobs <i>et al.</i> (1989)
	Northern Cape	Farm Deudrift near Springbok	29°45'S 17°56'E	Coordinates incorrect in Jacobs (1989), this paper
	Northern Cape	Namaqualand, 18 km S Springbok	29°47'S 17°50'E	this paper
	Northern Cape	Namaqualand, Mesklip	29°49'S 17°52'E	this paper
<i>Thaumastella</i> sp. (undescribed)				
South Africa	Western Cape	Farm Kantkraal, nr. Beaufort West	32°45'38"S 22°46'02"E	this paper

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References

- Adler, P.H. & Wheeler, A.G. Jr. (1984) Extra-phytophagous food sources of Hemiptera Heteroptera: Bird droppings, dung, and carrion. *Journal of the Kansas Entomological Society*, 57, 21–27.
- Afzal, M. & Sahibzada, S.S. (1988) Comparative studies of pterothoracic sclerites of some pentatomid bugs of Pakistan

- (Hemiptera: Heteroptera). *Biologia*, Lahore, 34, 249–256.
- Aukema, B., Rieger, C. & Rabitsch, W. (2013) *Catalogue of the Heteroptera of the Palaearctic Region. Vol. 6. Supplement*. The Netherlands Entomological Society, Amsterdam, xxiv + 629 pp.
- Baz, A., Cifrián, B., Martín-Vega, D. & Baena, M. (2010) Phytophagous insects captured in carrion baited traps in central Spain. *Bulletin of Insectology*, 63, 21–30.
- Berger, K., Haensler, A. & Luther-Mosebach, J. (2010) Gellap Ost, Climate. In: Jürgens, N., Haarmeyer, D.H., Luther-Mosebach, J., Dengler, J., Finckh, M. & Schmiedel, U. (Eds.), *Biodiversity in southern Africa 1: Patterns at local scale—the BIOTA Observatories*. Klaus Hess Publishers, Göttingen & Windhoek, pp. 400. [Complete pagination: xx + 801 pp.]
- Bianchi, F.M., Barão, K.R., Grassi, A. & Ferrari, A. (2021) A milestone for Pentatomoidea: *Grazia et al.* 2008 What do we know and where can we go? *Zootaxa*, 4958 (1), 406–429.
<https://doi.org/10.11646/zootaxa.4958.1.26>
- Bianchi, F.M. & Gonçalves, L.T. (2021) Borrowing the Pentatomomorpha tome from the DNA barcode library: Scanning the overall performance of *cox1* as a tool. *Journal of Zoological Systematics and Evolutionary Research*, 59, 992–1012.
<https://doi.org/10.1111/jzs.12476>
- Booth, C.L. (1990) Biology of *Largus californicus* (Hemiptera: Largidae). *Southwestern Naturalist*, 35, 15–22.
<https://doi.org/10.2307/3671980>
- Cassis, G. & Gross, G.F. (2002) Hemiptera-Heteroptera (Pentatomomorpha). In: Houston W.W.K. & Wells A. (Eds.), *Zoological Catalog of Australia. Vol. 27.3B*. CSIRO Publishing, Melbourne, pp. i–xiv + 1–737.
- Chérot, F., Pauwels, O.S.G., Eger, J.E. & Chimsunchart, C. (1998) Unusual feeding behavior in a Scutellerid: A case of scavenging on snake. *Natural History Bulletin of the Siam Society*, 46, 207–208.
- Cobben, R.H. (1968) Evolutionary trends in Heteroptera. Part I. Eggs, architecture of the shell, gross embryology and eclosion. *Mededelingen Landbouwhogeschool, Wageningen*, 151, 1–475.
- Davranoglou, L.-R., Taylor, G.K. & Mortimer, B. (2023) Sexual selection and predation drive the repeated evolution of stridulation in Heteroptera and other arthropods. *Biological Reviews*, 98, 942–981.
<https://doi.org/10.1111/brv.12938>
- Derjanschi, V.V. & Péricart, J. (2005) *Hémiptères Pentatomoidea euro-méditerranéens 1. Généralités. Systématique: Première Partie. Faune de France. Vol. 90*. Fédération Française des Sociétés de Sciences Naturelles, Paris, 494 pp.
- Dolling, W.R. (1981) A rationalized classification of the burrower bugs (Cydnidae). *Systematic Entomology*, 6, 61–76.
<https://doi.org/10.1111/j.1365-3113.1981.tb00016.x>
- Eger, J.E., Brailovsky, H. & Henry, T.J. (2015) Heteroptera attracted to butterfly traps baited with fish or shrimp carrion. *Florida Entomologist*, 98 (4), 1030–1035.
<https://doi.org/10.1653/024.098.0404>
- Ekanem, M.S. & Dike, M.C. (2010) Arthropod succession on pig carcasses in Southeastern Nigeria. *Papeis Avulsos de Zoologia*, 50 (35), 561–570.
<https://doi.org/10.1590/S0031-10492010003500001>
- Gapud, V.P. (1991) A generic revision of the subfamily Asopinae, with consideration of its phylogenetic position in the family Pentatomidae and superfamily Pentatomoidea (Hemiptera—Heteroptera). Parts I and II. *Philippine Entomologist*, 8, 865–961.
- Ghahari, H., Moulet, P. & Rider, D.A. (2014) An annotated catalog of the Iranian Pentatomoidea (Hemiptera: Heteroptera: Pentatomomorpha). *Zootaxa*, 3837 (1), 1–95.
<https://doi.org/10.11646/zootaxa.3837.1.1>
- Gogala, M. (2006) Vibratory signals produced by Heteroptera—Pentatomomorpha and Cimicomomorpha. In: Drosopoulos, S. & Claridge, M.F. (Eds.), *Insect sounds and communication. Physiology, behaviour, ecology and evolution*. CRC Press, Boca Raton, Florida, pp. 275–295. [Complete pagination: xvii + 500 pp.]
<https://doi.org/10.1201/9781420039337.pt2>
- Grazia, J., Schuh, R.T. & Wheeler, W.C. (2008) Phylogenetic relationships of family groups in Pentatomoidea based on morphology and DNA sequences (Insecta: Heteroptera). *Cladistics*, 24, 1–45.
<https://doi.org/10.1111/j.1096-0031.2008.00224.x>
- Harten, A. van. (2008) Collecting methods and localities. In: Harten, A. van (Ed.), *Arthropod fauna of the UAE. Vol. 1. Dar Al Ummah Publishing, Abu Dhabi*, pp. 14–32. [Complete pagination: 754 pp.]
- Hemala, V., Kment, P., Tihlaříková, E., Neděla, V. & Malenovský, I. (2021) External structures of the metathoracic scent gland efferent system in the true bug superfamily Pyrrhocoroidea (Hemiptera: Heteroptera: Pentatomomorpha). *Arthropod Structure and Development*, 63 (101058), 1–25.
<https://doi.org/10.1016/j.asd.2021.101058>
- Henry, T.J. (1997) Phylogenetic analysis of family groups within the infraorder Pentatomomorpha (Hemiptera: Heteroptera), with emphasis on the Lygaeoidea. *Annals of the Entomological Society of America*, 90, 275–301.
<https://doi.org/10.1093/aesa/90.3.275>
- Henry, T.J. (2009) Biodiversity of Heteroptera. In: Footit, R.G. & Adler, P.H. (Eds.), *Insect Biodiversity: Science and Society*. Wiley-Blackwell, Chichester & Hoboken, pp. 223–263. [Complete pagination: xxi + 632 pp.]
<https://doi.org/10.1002/9781444308211.ch10>
- Henry, T.J. (2017) Biodiversity of Heteroptera. In: Footit, R.G. & Adler, P.H. (Eds.), *Insect Biodiversity: Science and Society*.

- Vol. I. Second Edition. John Wiley & Sons Ltd., Chichester, West Sussex, pp. 279–335. [Complete pagination: 912 pp.]
<https://doi.org/10.1002/9781118945568.ch10>
- Henry, T.J. & Froeschner, R.C. (Eds.) (1988) *Catalog of the Heteroptera, or true bugs, of Canada and the continental United States*. E. J. Brill, Leiden, New York, København, Köln, xix + 958 pp.
- Hoberlandt, L. (1981) Results of the Czechoslovak-Iranian entomological expeditions to Iran. Introduction to the Second expedition 1973. *Acta Entomologica Musei Nationalis Pragae*, 40, 5–32, 14 pls.
- Hoberlandt, L. (1983) Results of the Czechoslovak-Iranian entomological expeditions to Iran. Introduction to the Third expedition 1977. *Acta Entomologica Musei Nationalis Pragae*, 41, 5–24, 16 pls.
- Hoberlandt, L. (1997) Results of the Czechoslovak-Iranian entomological expeditions to Iran 1970, 1973 and 1977. Heteroptera: Acanthosomatidae, Cydnidae, Scutelleridae, Pentatomidae. *Acta Entomologica Musei Nationalis Pragae*, 44, 181–293. [1995]
- Horváth, G. (1896) Hemiptera nova palaeartica. *Természetrájsi Füzetek*, 19, 322–329.
- Jacobs, D.H. (1986) Order Hemiptera (bugs, leafhoppers, cicadas, aphids, scale-insects, etc.). In: Scholtz, C.H. & Holm, E. (Eds.), *Insects of Southern Africa*. Butterworth, Durban, pp. 112–152. [Complete pagination: 502 pp.]
- Jacobs, D.H. (1989) A new species of *Thaumastella* with notes on the morphology, biology and distribution of the two southern African species (Heteroptera: Thaumastellidae). *Journal of the Entomological Society of South Africa*, 52, 301–316.
- Jacobs, D.H. (2008) Heteroptera [excl. Hydrocorisae and Amphibiocoridae]. In: Scholtz, C.H. & Holm, E. (Eds.), *Insects of Southern Africa*. Second edition. Protea Book House, Pretoria, pp. 117–148, pl. II. [Complete pagination: 502 pp.]
- Jacobs, D.H., Apps, P.J. & Viljoen, H.W. (1989) The composition of the defensive secretions of *Thaumastella namaquensis* and *T. elizabethae* with notes on the higher classification of the Thaumastellidae (Insecta: Heteroptera). *Comparative Biochemistry and Physiology*, Series B, 93, 459–463.
[https://doi.org/10.1016/0305-0491\(89\)90107-7](https://doi.org/10.1016/0305-0491(89)90107-7)
- Kerzhner, I.M., Kuznetsova, V.G. & Rider, D.A. (2004) Karyotypes of Pentatomoidea additional to those published by Ueshima, 1979 (Heteroptera). *Zoosystematica Rossica*, 13 (1), 17–21.
<https://doi.org/10.31610/zsr/2004.13.1.17>
- Kment, P. & Vilímová, J. (2010a) Thoracic scent efferent system of the Tessaratomidae sensu lato (Hemiptera: Heteroptera: Pentatomoidea) with implication to the phylogeny of the family. *Zootaxa*, 2363 (1), 1–59.
<https://doi.org/10.11646/zootaxa.2363.1.1>
- Kment, P. & Vilímová, J. (2010b) Thoracic scent efferent system of Pentatomoidea (Hemiptera: Heteroptera): a review of terminology. *Zootaxa*, 2706 (1), 1–77.
<https://doi.org/10.11646/zootaxa.2706.1.1>
- Linnavuori, R.E. (1977) Hemiptera of the Sudan, with remarks on some species of the adjacent countries 5. Tingidae, Piesmididae, Cydnidae, Thaumastellidae and Plataspididae. *Acta Zoologica Fennica*, 147, 1–81.
- Linnavuori, R.E. (1989) Heteroptera of Yemen and South Yemen. *Acta Entomologica Fennica*, 54, 1–40.
<https://doi.org/10.33338/ef.83358>
- Linnavuori, R.E. (1993a) Cydnidae of West, Central and North-East Africa (Heteroptera). *Acta Zoologica Fennica*, 192, 1–148.
- Linnavuori, R.E. (1993b) Hemiptera of Iraq. II. Cydnidae, Thaumastellidae, Pentatomidae, Stenocephalidae, Coreidae, Alydidae, Rhopalidae, and Pyrrhocoridae. *Entomologica Fennica*, 4, 37–56.
<https://doi.org/10.33338/ef.83749>
- Linnavuori, R.E. & van Harten, A. (2002) Additional notes on the Heteroptera (Insecta: Hemiptera) of Yemen II. *Esperiana, Buchreihe zur Entomologie*, 9, 157–188.
- Linnavuori, R.E. & van Harten, A. (2006) Additional notes on the Heteroptera (Insecta: Hemiptera) of Yemen IV. Pentatomomorpha. *Acta Universitatis Carolinae Biologica*, 49, 161–174.
- Lis, J.A. (1994) *A revision of Oriental burrower bugs (Heteroptera: Cydnidae)*. Upper Silesian Museum, Bytom, 349 pp.
- Lis, J.A. (2006) Family Thaumastellidae Seidenstücker, 1960. In: Aukema, B. & Rieger, Ch. (Eds.), *Catalogue of the Heteroptera of the Palaearctic Region. Vol. 5. Pentatomomorpha II*. The Netherlands Entomological Society, Amsterdam, pp. 117. [Complete pagination: xiii + 550 pp.]
- Lis, J.A. (2010) Coxal combs in the Cydnidae sensu lato and three other related “cydnoid” families—Parastrachiidae, Thaumastellidae, Thyreocoridae (Hemiptera: Heteroptera): functional, taxonomic, and phylogenetic significance. *Zootaxa*, 2476 (1), 53–64.
<https://doi.org/10.11646/zootaxa.2476.1.6>
- Lis, J.A. (2023) Molecular apomorphies in the secondary and tertiary structures of length-variable regions (LVRs) of 18S rRNA shed light on the systematic position of the family Thaumastellidae (Hemiptera: Heteroptera: Pentatomoidea). *International Journal of Molecular Sciences*, 24 (7758), 1–22.
<https://doi.org/10.3390/ijms24097758>
- Lis, J.A. & Domagała, P.J. (2024) Inconsistencies in the classification of the family Cydnidae (Hemiptera: Heteroptera: Pentatomoidea) revealed by molecular apomorphies in the secondary and tertiary structures of 18S rRNA Length-Variable Region L (LVR L). *International Journal of Molecular Sciences*, 25 (939), 1–27.
<https://doi.org/10.3390/ijms25020939>
- Lis, J.A., Domagała, P.J. & Lis, B. (2024) New molecular phylogenetic evidence confirms independent origin of coxal combs in

- the families of the ‘cydnoid’ complex (Hemiptera: Heteroptera: Pentatomoidea). *Insects*, 15 (792), 1–15.
<https://doi.org/10.3390/insects15100792>
- Lis, J.A., Ziaja, D.J., Lis, B. & Gradowska, P. (2017) Non-monophyly of the “cydnoid” complex within Pentatomoidea (Hemiptera: Heteroptera) revealed by Bayesian phylogenetic analysis of nuclear rDNA sequences. *Arthropod Systematics and Phylogeny*, 75, 481–496.
<https://doi.org/10.3897/asp.75.e31918>
- López, C.N., Portorreal, Y.C. & Martínez, Y.M. (2009) Artrópodos presentes en la putrefacción de cadáveres de cerdos (*Sus scrofa*) en Santiago de Cuba, Cuba. *Boletín de la Sociedad Entomológica Aragonesa*, 44, 441–447.
- Mucina, L. & Rutherford, M.C. (Eds.) (2006) *The vegetation of South Africa, Lesotho and Swaziland. Strelitzia 19*. South African National Biodiversity Institute, Pretoria, 808 pp.
- Oshanin, B. (1906) Verzeichnis des Palaarktischen Hemipteren mit besonderer Berücksichtigung ihrer Verteilung im Russischen Reiche. I. Band. Heteroptera. I. Lieferung. Pentatomidae-Lygaeidae. *Ezhegodnik Zoologicheskogo Muzeja Imperatorskoy Akademii Nauk*, 11 (Prilozhenie), i–lxxiv + 1–393.
<https://doi.org/10.5962/bhl.title.12423>
- Oshanin, B. (1912) *Katalog der paläarktischen Hemipteren (Heteroptera, Homoptera—Auchenorrhyncha und Psylloidea)*. R. Friedländer & Sohn, Berlin, 187 pp.
<https://doi.org/10.5962/bhl.title.13940>
- Payne, J.A., Mead, F.W. & King, E.W. (1968) Hemiptera associated with pig carrion. *Annals of the Entomological Society of America*, 61, 565–567.
<https://doi.org/10.1093/aesa/61.3.565>
- Péricart, J. (1996) Désignation de lectotypes et paralectotypes pour des Lygaeidae paléarctiques et commentaires [Heteroptera]. 2. Les types de Geza Horváth. *Revue Française d'Entomologie, Nouvelle Série*, 18 (4), 153–157.
- Pluot-Sigwalt D. & Lis, J.A. (2008) Morphology of the spermatheca in the Cydnidae (Hemiptera: Heteroptera): Bearing of its diversity on classification and phylogeny. *European Journal of Entomology*, 105, 279–312.
<https://doi.org/10.14411/eje.2008.038>
- Popov, Yu.A. (1986) Peloridiina (=Coleorrhyncha) et Cimicina (=Heteroptera). In: *Nasekomye v rannemelovykh ekosistemakh Zapadnoy Mongolii. (Insects in early Cretaceous ecosystems of Western Mongolia)*. Nauka, Moscow, pp. 50–83. [in Russian]
- Popov, Yu.A. & Pinto, I.D. (2000) On some Mesozoic burrower bugs (Heteroptera: Cydnidae). *Paleontological Journal*, 34 (Supplement 3), 298–302.
- Puton, A. (1899) *Catalogue des Hémiptères (Hétéroptères, Cicadines et Psyllides) de la faune paléarctique. Quatrième Édition*. Bureau de la Société Française d'Entomologie, Caen, 121 pp.
<https://doi.org/10.5962/bhl.title.12421>
- Rider, D.A., Schwertner, C.F., Vilímová, J., Rédei, D., Kment, P. & Thomas, D.B. (2018) Higher systematics of Pentatomoidea. In: McPherson, J.E. (Ed.), *Invasive stink bugs and related species (Pentatomoidea): Biology, higher systematics, semiochemistry, and management*. CRC Press, Taylor & Francis Group, Boca Raton, London, New York, pp. 25–201. [Complete pagination: xix + 819 pp.]
<https://doi.org/10.1201/9781315371221-2>
- Roca-Cusachs, M., Schwertner, C.F., Kim, J.-G., Eger, J., Grazia, J. & Jung, S.-H. (2022) Opening Pandora’s box: molecular phylogeny of the stink bugs (Hemiptera: Heteroptera: Pentatomidae) reveals great incongruences in the current classification. *Systematic Entomology*, 47, 36–51.
<https://doi.org/10.1111/syen.12514>
- Schaefer, C.W. (1975) Heteropteran trichobothria (Hemiptera: Heteroptera). *International Journal of Insects Morphology and Embryology*, 4 (3), 193–264.
[https://doi.org/10.1016/0020-7322\(75\)90034-3](https://doi.org/10.1016/0020-7322(75)90034-3)
- Schaefer, C.W. (1981) The sound-producing structures of some primitive Pentatomoidea (Hemiptera: Heteroptera). *Journal of the New York Entomological Society*, 88, 230–235. [1980]
- Schaefer, C.W. (1988) The food plants of some “primitive” Pentatomoidea (Hemiptera: Heteroptera). *Phytophaga*, 2, 19–54.
- Schaefer, C.W. (1993) The Pentatomomorpha (Hemiptera: Heteroptera): an annotated outline of its systematic history. *European Journal of Entomology*, 90, 105–122.
- Schaefer, C.W. & Wilcox, D.B. (1971) A new species of Thaumastellidae (Hemiptera: Pentatomoidea) from southern Africa. *Journal of the Entomological Society of South Africa*, 34 (2), 207–214.
- Schuh, R.T. & Slater, J.A. (1995) *True bugs of the world (Hemiptera: Heteroptera). Classification and natural history*. Comstock Publishing Associates, Cornell University Press, Ithaca & London, xii + 336 pp.
- Schuh, R.T. & Weirauch, C. (2020) *True bugs of the World (Hemiptera: Heteroptera). Classification and Natural history. 2nd Edition. Monograph Series. Vol. 8*. Siri Scientific Press, Manchester, 767 pp., 32 pls.
- Seidenstücker, G. (1960) Heteropteren aus Iran 1956, III. *Thaumastella aradooides* Horv., eine Lygaeidae ohne Ovipositor. *Stuttgarter Beiträge zur Naturkunde*, 38, 1–4.
- Seidenstücker, G. (1964) Zur Systematik von *Bledionotus*, *Bethylimorphus* und *Thaumastella* Horvath (Heteroptera, Lygaeidae). *Reichenbachia*, 3, 269–279.
- Shorthouse, D.P. (2010) *SimpleMappr, an online tool to produce publication-quality point maps*. URL: <https://www.simplemappr>.

net (accessed 15 June 2024)

- Slater, J.A. (1964) *A catalogue of the Lygaeidae of the World. Vol. II.* University of Connecticut, Storrs, pp. 779–1668.
- Stichel, W. (1959) *Illustrierte Bestimmungstabellen der Wanzen. II. Europa (Hemiptera-Heteroptera Europae). Vol. 4. Fascicle 21.* Wolfgang Stichel, Berlin—Hermsdorf, pp. 321–336.
- Stichel, W. (1960) *Verzeichnis der Paläarktischen Hemiptera-Heteroptera. III. Cimicomorpha (Cimicoidea excl. Miridae—Reduvioidea—Saldoidea—Tingoidea), Pentatomomorpha (Aradoidea—Lygaeoidea—Pyrrhocoroidea).* Wolfgang Stichel, Berlin—Hermsdorf, pp. 94–186.
- Štys, P. (1964) Thaumastellidae—a new family of Pentatomoid Heteroptera. *Acta Entomologica Bohemoslovaca*, 61, 238–253.
- Valcárcel, J.P. & Goula, A.M. (2018) Necrophagous behaviour in *Melanocoryphus albomaculatus* (Goeze, 1778) (Heteroptera: Lygaeidae: Lygaeinae). *Arquivos Entomológicos*, 19, 133–134.
- Voigt, K. (2001) *Thyreocoris scarabaeoides* (L.) an Aas gefunden (Insecta, Heteroptera, Cydnidae). *Carolinea*, 59, 133–134.
- Weirauch, C., Schuh, R.T., Cassis, G. & Wheeler, W.C. (2019) Revisiting habitat and lifestyle transitions in Heteroptera (Insecta: Hemiptera): insights from a combined morphological and molecular phylogeny. *Cladistics*, 35, 67–105. <https://doi.org/10.1111/cla.12233>
- Wu, Y.-Zh., Yu, Sh.-Sh., Wang, Y.-H., Wu, H.-Y., Li, X.-R., Men, X.-Y., Zhang, Y.-W., Rédei, D., Xie, Q. & Bu, W.-J. (2016) The evolutionary position of Lestoniidae revealed by molecular autapomorphies in the secondary structure of rRNA besides phylogenetic reconstruction (Insecta: Hemiptera: Heteroptera). *Zoological Journal of the Linnean Society*, 177, 750–763. <https://doi.org/10.1111/zoj.12385>
- Yao, Y.-Z., Ren, D., Rider, D.A. & Cai, W.-Z. (2012) Phylogeny of the infraorder Pentatomomorpha based on fossil and extant morphology, with description of a new fossil family from China. *PLoS One*, 7 (5), e37289, 1–17. <https://doi.org/10.1371/journal.pone.0037289>
- Yao, Y.-Z., Cai, W.-Z., Rider, D.A. & Ren, D. (2013) Primipentatomidae fam. nov. (Hemiptera: Heteroptera: Pentatomomorpha), an extinct insect family from the Cretaceous of north-eastern China. *Journal of Systematic Palaeontology*, 11 (1), 63–82. <https://doi.org/10.1080/14772019.2011.639814>
- Ye, F., Kment, P., Rédei, D., Luo, J.-Y., Wang, Y.-H., Kuechler, S.M., Zhang, W.-W., Cheng, P.-P., Wu, H.-Y., Wu, Y.-Zh., Sun, X.-Y., Ding, L., Wang, Y.-R. & Xie, Q. (2022) Diversification of the phytophagous lineages of true bugs (Insecta: Hemiptera: Heteroptera) shortly after that of the flowering plants. *Cladistics*, 38, 403–428. <https://doi.org/10.1111/cla.12501>
- Zrzavý, J. (1990) Evolution of antennal sclerites in Heteroptera (Insecta). *Acta Universitatis Carolinae, Biologica*, 34, 189–227.