Phylogenetic analysis of the *Systropha* Illiger 1806 (Hymenoptera: Apoidea: Halictidae) and description of a new subgenus

Sébastien Patiny[1] & Denis Michez[2]

[1] Faculté universitaire des Sciences agronomiques de Gembloux, Entomologie fonctionnelle et évolutive, Passage des Déportés 2, B-5030 Gembloux, Belgium

[2] Université de Mons-Hainaut, Laboratoire de Zoologie, Avenue Maistriau 19, B-7000 Mons, Belgium

Abstract. The family Halictidae includes four subfamilies, Halictinae, Nomioidinae, Nomiinae and Rophitinae, apparently monophyletic. *Systropha* Illiger is the most diverse genus in Rophitinae (the Holarctic genus *Dufourea* excluded). Several unique morphological, biogeographical and ecological features characterise the species within this taxon raising its interest for evolutionary studies. Now, to date there has been no extensive revision of the genus. The present work aims to alleviate this lack. In the first part, the authors propose an exhaustive catalogue, including the synonymy of the 26 described species. The last described species, *Systropha heinzi* Dubitzky 2004 **syn. nov.** is proposed as a junior synonym of *S. kazakhstaniensis* Patiny 2004, described one day earlier. The next parts of the study include a comprehensive key for the World species and the analysis of the species phylogeny based on 34 morphological characters. Converging with the conclusions of several former studies, this analysis points out the existence of 3 clades within the genus. These latter are described as 3 subgenera: *S.* (*Systropha*) Illiger 1806, *S.* (*Systrophidia*) Cockerell 1936 and *S.* (*Austrosystropha*) **n. sg.** Lastly, distribution and floral choices of taxa are specified.

Résumé. Analyse phylogénétique des *Systropha* Illiger 1806 (Hymenoptera : Apoidea : Halictidae) et description d'un nouveau-sous-genre. La famille des Halictidae comprend 4 sous-familles, les Halictinae, les Nomioidinae, les Nomiinae et les Rophitinae, toutes probablement monophylétiques. *Systropha* Illiger est le genre le plus diversifié au sein des Rophitinae (hormis le genre holarctique *Dufourea*). Plusieurs caractéristiques biogéographiques, morphologiques et écologiques font de ce genre un taxon très particulier et de grand intérêt. A ce jour, il n'existe aucune révision exhaustive de ce genre. Le présent article pallie à ce manque. D'une part, les auteurs proposent un catalogue complet des 26 espèces connues incluant leurs synonymes. La dernière espèce décrite, *Systropha heinzi* Dubitzky 2004 syn. nov. y est proposée comme synonyme de *S. kazakhstaniensis* Patiny 2004, décrite un jour plus tôt. D'autre part, les auteurs présentent une clé de détermination complète ainsi qu'une analyse de la phylogénie basée sur 34 caractères morphologiques. Cette dernière analyse met en évidence 3 clades au sein du genre. Ces derniers sont proposés comme 3 sous-genres : *S.* (*Systropha*) Illiger 1806, *S.* (*Systrophidia*) Cockerell 1936 et *S.* (*Austrosystropha*) n. sg. Enfin, nous précisons la distribution et les choix floraux des taxons.

Keywords: Apoidea, *Systropha*, phylogeny, new sub-genus, floral choice.

The family Halictidae includes four subfamilies, Halictinae, Nomioidinae, Nomiinae and Rophitinae (Michener 2000), of which monophyly was recently demonstrated (Alexander & Michener 1995; Pesenko 2000; Danforth 2002; Danforth *et al.* 2004). The Rophitinae (earlier named Dufoureinae) have a Worldwide distribution (except in Australia) and includes 13 genera, of which four are restricted to the Old-World: *Morawitzia* Friese 1902, *Morawitzella* Popov 1957, *Rophites* Spinola 1808 and *Systropha* Illiger 1806. This fourth genus is particularly interesting due to several characteristics: 1. Its specific diversity (the highest of the four genera); 2. Its

biogeographical features; 3. The floral choices of the included species, strongly directed toward *Convolvulus* L. (Convolvulaceae; morning glory); 4. The pollen collecting behavior of the females on the metasoma lateral parts; 5. The male's typical morphology, notably characterised by the strong transformations of the antenna flagella apex and of the sternal margins.

Two previous authors reviewed partly the described species. On one hand, Ebmer (1994) described *Systropha inexspectata* and proposed an annotated checklist of the tropical species (mainly African). On the other hand, Baker (1996) described *Systropha androsthenes* and *Systropha diacantha* in the frame of a more general work including a catalogue and a key to the males of the Palaearctic species. These two works constitute the only syntheses of numerous previous descriptive and taxonomical notes (Linné 1758;

Scopoli 1770; Pallas 1776; Olivier 1789; Spinola 1839; Eversmann 1852; Giraud 1861; Illiger 1879; Smith 1879; Morawitz 1880; Perez 1895, 1905; Cockerell 1911, 1931, 1936; Friese 1911, 1914, 1922; Strand 1911; Brauns 1926; Ponomareva 1967; Popov 1967; Warncke 1977, 1980, 1992; Ebmer 1978; Batra & Michener 1986). Incidentally, in the frame of these latter works, several authors underlined the intrinsic heterogeneity of the genus and the relevance of its subdivision into subgenera (Cockerell 1936; Batra & Michener 1986) or species groups (Ponomareva 1967). However, no previous study has attempted to develop the phylogenetic analyses supporting these proposals.

In the present work, the authors propose the first comprehensive catalogue of the World species as well as a key to males and females. Moreover, the central part of the study consists of an analysis of the species phylogeny. The results of this latter support notably the description of several subgenera: *Systropha* s.str., *Systrophidia* Cockerell 1936 and *Austrosystropha* **n. sg.**

Material and methods

Studied material

The genus *Systropha* includes 26 species (Patiny 2004; see the following catalogue) widely distributed in Palaearctic, India and sub-Saharan Africa. This distribution of the studied genus define implicitly the geographical limits of the present study. Within this geographical context, the type material of most species was reviewed. However, as precised here below, exceptions were made in the cases of some common and particularly well-known species: *S. curvicornis*, *S. pici* and *S. planidens.*

The material studied in the present work was borrowed to varied people and institutions: M. Schwarz (Ansfelden, Austria); the American Museum of Natural History (New-York, USA); the Conservatoire entomologique de Gembloux (Gembloux, Belgium); the Musée Royal de l'Afrique Centrale (Tervuren, Belgium); the National Museum of Natural History (London, UK); the OberOsterreich LandesMuseum (Linz, Austria); the Zoologische Museum Humboldt Universität (Berlin, Germany).

Catalogue

In the following catalogue, the species are listed in the alphabetical order. The synonyms, when relevant, are quoted under the prior species name, following the chronological order of their description. For each species, the subgeneric classification has been precised according to the results of the following cladistic analysis. Moreover, we gave the *locus typicus* (when not originally precised, the country of the locus typicus follows the original quotation into brackets) and holotype depository of each species name. Abbreviations of the institutions names as quoted in text:

AMNH: American Museum of Natural History, New-York, USA

CEGx-FuSaGx: Conservatoire entomologique de Gembloux-Faculté universitaire des Sciences agronomiques de Gembloux, Gembloux, Belgium

EBM: A.W.Ebmer's collection, Puchenau, Austria

MRAC: Musée Royal de l'Afrique Centrale, Tervuren, Belgium

MRNS: Museo Regionale di Storia Naturale, Torino, Italy

MNHN: Musée National Histoire Naturelle, Paris, France

NHM: Natural History Museum, London, UK

OOLL: OberÖsterreich LandesMuseum, Linz, Austria

OUM: Oxford University Museum, Oxford, UK

SEMK: Snow Entomological Museum Kansas, Lawrence, USA

ZISP: Zoology Institute, Saint Petersburg, Russia

ZMHB: Zoologische Museum Humboldt University, Berlin, Germany

Cladistic analysis

Taxa

Eighteen species representing most of the known morphological forms in *Systropha* were retained for the cladistic analysis (appendix 2). *S. inexspectata*, *S. iranica*, *S. krigei*, *S. macronasuta*, *S. rhodesiensis*, *S. ruficornis*, *S. tadjika* and *S. villosa* were rejected because the available specimens series do not allow the observation of varied important characters. Even if methodologically possible, the inclusion of these taxa in the studied data set would have introduced many cases of undetermined characters codings, without significative gain of relevance in the results.

The characters coded in the data set were checked on several specimens and when possible by either the holotypes or the paratypes. Exceptions were made in the cases of some common and particularly well-known species: *S. curvicornis*, *S. pici* and *S. planidens*.

Analysis

The cladistic analysis was carried out using PAUP version 4.0b10 (Swofford 2001). The tree search was heuristic using the parsimony optimality criterion. All multistate characters were primarily considered unordered and of equal weight. Further complementary trees searches were made considering the characters ordered or of "dollo.up" type. The starting tree was obtained via stepwise addition. The addition sequence was random (10,000 replicates) with tree-bisection-reconnection used as branch-swapping algorithm. A strict consensus of the obtained trees was computed after each tree search.

The weighting of the characters was made using the successive weighting method (Farris 1969; Carpenter 1994; Allard & Carpenter 1996). The characters were then weighted following their RC (rescaled consistency index) in the previous trees search.

The trees were rooted using *Morawitzia* Friese 1902 and *Rophites* Spinola 1808 as outgroups. The cladogramms presented (figs 24-28) illustrate the four main topologies encountered in the analysis results when considering the multistate characters unordered. The sixth displayed tree (fig. 29) is the strict consensus of the most parsimonious ones.

Characters

List of the abbreviations used to designate the described morphological areas:

A, antennal segment (with a number designating the segment position, A1 is scape);

Bt, basitarsus (with a number designating the leg concerned proceeding anterior to posterior);

Cx, coxa (with a number designating the leg concerned proceeding anterior to posterior);

F, femur (with a number designating the leg concerned proceeding anterior to posterior);

PLb, labial palpus;

PMx, maxillary palpus;

S, metasomal sternum (with a number designating the segment proceeding anterior to posterior);

T, metasomal tergum (with a number designating the segment proceeding anterior to posterior);

Tb, tibia (with a number designating the segment proceeding anterior to posterior).

Thirty-four morphological characters were identified for the analysis. Most are typical of the males (appendix 1). The *Systropha* females are morphologically very similar and display few morphological characters relevant for the phylogeny inference, as argued by Baker (1994). A global description of the considered morphological characters is given below. The characters codings and the data set are provided in appendix 2.

Head (characters, 01-07). The most notable cephalic characters consist of the typical male transformations of the flagellum and flagellar segment shapes (figs 1-3; 17-18). The males *Systropha* are characterised by the spiral arrangement of the five apical flagellum segments (A9-13). One used here as descriptors, the elongation of the A3 (character 02), the elongation of the following flagellum segments and the relative size of the spiral apex (some species display less than 13 flagellum segments, which is unusual among Apoidea; character 04). Mouthparts are very often used in bees phylogenetic studies. However, only two of our characters are based on these structures (characters 05, 06). By using mainly type material to construct the data set, numerous structures were not observed in all included species. Moreover, it can also be demonstrated that mouthparts display very often morphological convergences (Patiny 2001) making them few relevant characters for the phylogeny inference within the genus rank.

Wings (characters 08-11). We studied several structures of the forewing venation. The size and shape of the first and second submarginal cells were retained as descriptors in the following data set (characters 09, 10). The first submarginal cell (1st-R1) is either long or short, following the considered species; when long, the posterior margin (Rs+M) is gently curved in its distal part (character 10). The second submarginal (1st-Rs) displays also a trend to reduction. Moreover, in this latter case, the position of the junction between Rs+M and the first recurrent vein (1m-cu) modify strongly the shape of the cell, what was also used as a character (character 11).

Legs (characters 12-19). Numerous species display differentiation of certain parts of the legs especially in males. Enlargement of various legs segments is common across the species of *Systropha*. F1 and F2 are enlarged in several species. The F1 enlargement displays two distinct forms, on the one hand, a dorso-ventral enlargement (as observed on F2), on the other hand, a lateral enlargement, which makes the femur appear inflated (character 12). The F2 is dorso-ventrally enlarged by some species (*S. maroccana*, *S. tropicalis*) and can display a longitudinal ventral carina (characters 13, 14). Tb2 is enlarged in its proximal part by a small group of African

species (*S. bispinosa*, *S. norae* and *S. ugandensis*) (character 15). In the same species the Cx3 is flattened and strongly enlarged, particularly in the distal half (character 16). The development of the female's Tb3 inner spur seems to be also interesting. However, this character is parsimony uninformative, within the present data set due to the current lacks in the genus knowledge (numerous species known by one or else sex). For that reason, the character 19 describes the males' Tb3 inner spur shape. This latter character is weaker by males than by females but it can be assessed for a larger number of species. Bt3 is strongly elongated by a series of species, with notable excess in species like *S. androsthenes* and *S. maroccana* (character 18).

Mesosoma (characters 20-21). Only two mesosoma's characters were retained for the analysis: the depression of the propodeal area (character 20) and the development of typical tubercles (character 21) on the mesopleura ventral surface by some African species.

Metasoma (characters 22-34). These characters consist of varied typical accessory structures of the male's terga and sterna. The first tergum margin is notably convex and enlarged by several species. In *S. aethiopica* and *S. arnoldi*, the graduli (T1-4) are spiny (character 22). Likely by several other species one observes the development of lateral teeth on T6 and T7 (characters 23, 24) (figs 4; 16). The sterna are characterised in most species by the development of processes on S1-6 margins (following the concerned taxa) (characters 25-29) (figs 5-12; 19-20). Like often observed by Apoidea, the development of S7 and S8 is also typical and constitute interesting phylogenetic characters (characters 30-34) (figs 13-14).

It must be underlined that no characters were retained on the males genitalia while these structures are usually used for the Apoidea phylogeny inference (Patiny 2001). Considering the available literature (Ponomareva 1967; Warncke 1976, 1980, 1992; Ebmer 1994; Baker 1996), these structures appear unusually less differentiated by *Systropha* (figs 21-23). Moreover, due to the availability of few dissected material and because numerous species are only known by old typical material, these characters were particularly hard to review exhaustively.

Results

Catalogue of the *Systropha* Illiger 1806

Genus *Systropha* Illiger 1806: 28-175

Systropha (*Systrophidia*) **Cockerell 1936: 477-483**

Eucera **Scopoli 1770: 9**

Tenthredo **L. 1758: 731**

Andrena **Fabricius 1775 in Olivier 1789: 135, Eversmann 1852: 10, 22**

Type species: *Systropha curvicornis* (**Scopoli 1770**); by monotypy

01. ***Systropha (Austrosystropha) aethiopica* Friese 1911**
     Systropha (*Austrosystropha*) *aethiopica* **Friese 1911: 654**, «*Brit. Öst.Africa, Mulango*»; **holotype** ♂ (**labelled TYPE**); **ZMHB**
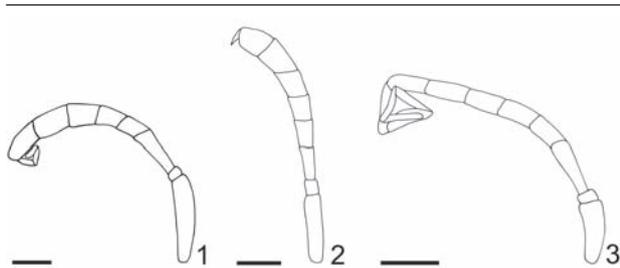
02. ***Systropha (Systropha) androsthenes* Baker 1996**
     Systropha (*Systropha*) *androsthenes* **Baker 1996: 1539**, «*Unites Arabian Emirates, Al Ain*»; **holotype** ♂; **OUM**

03. ***Systropha* (*Austrosystropha*) *arnoldi* Friese 1922**

Systropha (*Austrosystropha*) *arnoldi* **Friese 1922: 2**, «*Rhodesia, Bulawayo*» (**Zimbabwe**); holotype ♂ (labelled TYPE); ZMHB

04. ***Systropha* (*Austrosystropha*) *bispinosa* Friese 1914**

Systropha (*Austrosystropha*) *bispinosa* **Friese 1914** *in* **Schulthess: 296**, «*Kamerun, Dchang*» (**Cameroon**); holotype ♂ (labelled TYPE); ZMHB

05. ***Systropha* (*Systropha*) *curvicornis* (Scopoli 1770)**

Eucera curvicornis **Scopoli 1770: 9**, «*Circa Cremnizium in Hungary*» (**Slovakia, Kremnica**); holotype ♂; lost (see Baker 1996)

Tenthredo convolvuli **Pallas 1773: 731**, «*Russia*»; syntypes ♂; ?lost

Andrena spiralis **Olivier 1789: 135**, «*France, Provence*»; syntypes ♂; lost

Andrena labrosa **Eversmann 1852: 22**, «*Orenburgensi, in promotoris Uralensibus*»; syntypes ♀; ZISP

06. ***Systropha* (*Systropha*) *diacantha* Baker 1996**

Systropha (*Systropha*) *diacantha* **Baker 1996: 1542**, «*Oman, Wadi Khabb*»; holotype ♂; OUM

07. ***Systropha* (*Systropha*) *difformis* Smith 1879**

Systropha (*Systropha*) *difformis* **Smith 1879: 60**, «*Burmah*» (**Myanmar**); syntype ♂; NHM

08. ***Systropha* (*Systrophidia*) *glabriventris* Friese 1922**

Systropha (*Systrophidia*) *glabriventris* **Friese 1922: 2**, «*Rhodesia, Bulawayo*» (**Zimbabwe**); holotype ♂; ?lost

Systropha (*Systrophidia*) *ogilivei* **Cockerell 1936: 477-483**, «*S.W. Africa, Okahandja*» (**Namibia**); holotype ♀; NHM

09. ***Systropha* (*Systropha*) *hirsuta* Spinola 1839**

Systropha (*Systropha*) *hirsuta* **Spinola 1839: 516**, «*Egypt*»; lectotype ♂; MRNS

Systropha christae **Warncke 1992: 742**, «*Israel, Yeroham*»; holotype ♂; OOLL

10. ***Systropha* (*Systropha*) *inexspectata* Ebmer 1994**

Systropha (*Systropha*) *inexspectata* **Ebmer 1994: 808**, «*Siam, Nan*» (**Thaïland**); holotype ♂; NHM

11. ***Systropha* (*Systropha*) *iranica* Popov 1967**

Systropha (*Systropha*) *iranica* **Popov 1967: 193**, «*Iran, Kerman*»; holotype ♂; ZISP

12. ***Systropha* (*Systropha*) *kazakhstaniensis* Patiny 2004**

Systropha (*Systropha*) *kazakhstaniensis* **Patiny 2004: 909**, «*Kazakhstan, W. Mangistau Mts, Tunschibet*»; holotype ♂; OOLL

Systropha heinzi **Dubitzky 2004: 70 syn. nov.**, «*Kazakhstan, Turkestan*»; holotype ♂; ZSM

13. ***Systropha* (*Austrosystropha*) *krigei* Brauns 1926**

Systropha (*Austrosystropha*) *krigei* **Brauns 1926: 192**, «*Südafrika, Transvaal, Pretoria*» (**South-Africa**); syntypes ?lost

14. ***Systropha* (*Austrosystropha*) *macronasuta* Strand 1911**

Systropha (*Austrosystropha*) *macronasuta* **Strand 1911: 110**, «*Zanzibar*» (**Tanzania**); holotype ♀; ZMHB

15. ***Systropha* (*Systropha*) *maroccana* Warncke 1977**

Systropha (*Systropha*) *maroccana* **Warncke 1977: 97**, «*Süd-Marokko, km6 Sidi-Ifni-Goulimine Road*» (**Morocco**); holotype ♂; NHM

16. ***Systropha* (*Austrosystropha*) *norae* Patiny 2004**

Systropha (*Austrosystropha*) *norae* **Patiny 2004: 907**, «*Nigeria, Ile-Ife*»; holotype ♂; SEMK

17. ***Systropha* (*Systropha*) *pici* Pérez 1895**

Systropha (*Systropha*) *pici* **Pérez 1895: 177**, «*Ain Sefra*» (**Algeria**); lectotype ♀; MNHN

Systropha hirsuta **Spinola 1839. Ponomareva (1967)**, misidentification

Systropha hirsuta **Spinola 1839. Warncke (1977)**, misidentification

18. ***Systropha* (*Systropha*) *planidens* Giraud 1861**

Systropha (*Systropha*) *planidens* **Giraud 1861: 451**, «*Asia minor, Amasia*» (**Turkey**); syntypes : Spain, France, Austria (lost, see Baker 1996); NMW

Systropha chrysura **Pérez 1905: 85**, «*Cataloña, Tarragone*» (**Spain**); lectotype ♀; MNHN

S. planidens planidens **Giraud 1861**

S. planidens anatolica **Warncke 1977**

S. planidens anatolica **Warncke 1977: 96**, «*Türkei, Tunceli*» (**Turkey**); holotype ♂; OOLL

S. planidens grandimargo **Pérez 1905**

S. planidens grandimargo **Pérez 1905: 84**, «*Cataloña, Antiga*» (**Spain**); lectotype ♂; MNHN

19. ***Systropha* (*Systropha*) *popovi* Ponomareva 1967**

Systropha (*Systropha*) *popovi* **Ponomareva 1967: 253**, «*Turkmenia, Kirzheli, 100km Kizyl-Arvat*»; holotype ♂; ZISP

Systropha ruficornis **Morawitz 1880. Popov 1960**, misidentification

20. ***Systropha* (*Systropha*) *punjabensis* Batra & Michener 1966**

Systropha (*Systropha*) *punjabensis* **Batra & Michener 1966: 651**, «*India, Ludhiana*»; holotype ♂; SEMK

21. ***Systropha* (*Austrosystropha*) *rhodesiensis* Friese 1922**

Systropha (*Austrosystropha*) *rhodesiensis* **Friese 1922: 3**, «*Rhodesia, Bulawayo*» (**Zimbabwe**); syntypes ♀ (labelled TYPE); ZMHB

22. ***Systropha* (*Systropha*) *ruficornis* Morawitz 1880**

Systropha (*Systropha*) *ruficornis* **Morawitz 1880: 356**, «*Turkmenistan; Krasnowodsk*»; syntype ♂; ZISP

Systropha rufiventris **Morawitz 1880. Friese 1901**, *lapsus calami*

23. ***Systropha* (*Systropha*) *tadjika* Warncke 1992**

Systropha (*Systropha*) *tadjika* **Warncke 1992: 743**, «*Tadjikistan, 3km W.Dusti, 130km S. Duschanbe*»; holotype ♂; OOLL

24. ***Systropha* (*Systropha*) *tropicalis* Cockerell 1911**

Systropha (*Systropha*) *tropicalis* **Cockerell 1911: 227**, «*Ceylon, Kandy*» (**Sri Lanka**); holotype ♂; NHM

Systropha butteli **Friese 1913: 87**, «*Ceylon, Seenigoda*» (**Sri Lanka**); lectotype ♂; ZMHB

25. ***Systropha* (*Austrosystropha*) *ugandensis* Cockerell 1931**

Systropha (*Austrosystropha*) *ugandensis* **Cockerell 1931: 400**, «*Uganda, Kampala*»; holotype ♂; NHM

26. ***Systropha* (*Systropha*) *villosa* Ebmer 1978**

Systropha (*Systropha*) *villosa* **Ebmer 1978: 86**, «*Iran, 150km E. Bandar Abbas*»; holotype ♂; EBM

Key to the species of *Systropha*

Males

1. Antennae with less than 13 well-differentiated segments (figs 1-2, 17). Apical segment minute. Southern Africa, Middle-East or India. **2**
– Antennae normal, with 13 well-differentiated segments (figs 3, 18). Apical segment of normal lenght. Old-World.. **4**

Figures 1-3
Flagellum apex ♂. 1, *Systropha androsthenes* (scale = 0,4 mm). 2, *S. glabriventris* (scale = 0,7 mm). 3, *S. maroccana* (scale = 0,7 mm).

2. Antennae with 9 well-differentiated segments, apex reduced to a minute apical hook (fig. 2). T6-7 laterally toothed (fig. 4). Sterna without tubercles. S8 apex large, elliptic, subperpendicular to the proximal part. Southern Africa (Namibia, Zimbabwe) .... **S. glabriventris Friese**
   – Antennae with 11 or 12 well-differentied segments, the apical forming a spiral (fig. 1). T6-7 untoothed. S2 with at least rounded tubercles (notably close one to each other). S8 different. United Arab Emirates or India **3**

3. Antennae with 11 well-differentiated segments (figs 1, 17). S2 with small but well developed, compressed tubercles (figs 5, 19). S8 apex sub-circular. United Arab Emirates .... **S. androsthenes Baker**
   – Antennae with 12 well-differentiated segments. S2 with short rounded tubercles (fig. 6). S8 apex sub-elliptic. India (Punjab). .... **S. punjabensis Batra & Michener**

4. S1 with a large and bifid process (fig. 12). S2 with 2 short acute tubercles. Near-East. .... **S. hirsuta Spinola**
   – S1 without such developed process. S2 without tubercle in some species, in most other taxa, this sternum bearing one or two well developed processes **5**

5. S2 with a single or T shaped process (figs 7, 8) **6**
   – S2 diferent: without process, with a large foliote process or with paired processes **8**

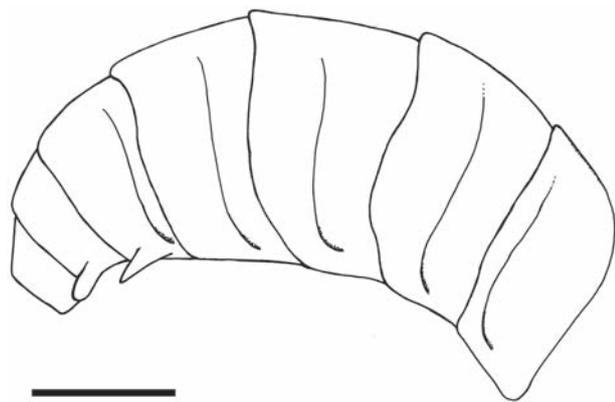6. T2-3 margins not differentiated. S2 with a median

Figure 4
*Systropha glabriventris.* Abdomen profil view (scale = 2 mm).

horseshoe-shaped ridge (fig. 7). S8 apex with 2 apico-longitudinal short rounded teeth (fig. 13). Oman, United Arab Emirates. .... **S. diacantha Baker**
   – T2-3 margins blade-shaped (fig. 15). S2 process differently conformed. S8 displaying not such paired teeth **7**

7. S2 with a large T-shaped (in ventral view) median process (fig. 8); process apex in one plan. S8 apex not enlarged; ended in a short rounded tooth. Burma. .... **S. difformis Smith**
   – S2 with a large T-shaped process with irregular apex (higher proximally than distally; illustrations see Baker 1996 and Ebmer 1994). S8 thicker, with successive opposed keels on dorsal and ventral surfaces. Nan (Thailand). .... **S. inexspectata Ebmer**

8. T6 and/or T7 laterally toothed. Sterna with or without processes. **9**
   – Terga untoothed. At least one sternum with well developed processes. **15**

9. S2 with 2 small processes. S3 with rounded elevations. T6 toothed. T7 untoothed. S8 apex elliptically enlarged, ended in a terminal tooth (fig. 14). Morocco. .... **S. maroccana Warncke**
   – Tubercles different, placed on other sterna or absent. T6-7 both toothed or T7 only toothed. S8 conformed differently **10**

10. A9-13 enlarged medially. S8 apex almond-like enlarged **11**
   – A9-13 not enlarged medially. S8 apex narrow with a longitudinal groove **13**

11. T1-5 untoothed. South-Africa .... **S. krigei Brauns**
   – T1-5 with small lateral spines or blades. **12**

12. T2-4 with lateral small acute spines (fig. 16). Kenya. .... **S. aethiopica Friese**
   – T2-4 with flattened blade-shaped spines. Zimbabwe .... **S. arnoldi Friese**

13. Mesopleura with well individualised ventral tubercles. S2-3 with blade-like convexities. Large species (ca. 10mm). Nigeria .... **S. norae Patiny**
   – Mesopleura ventrally spiny. S2-3 with more rounded convexities. Smaller species (<10mm). Eastern Africa . **14**

14. Medium sized species (9.5mm). S8 apex subrectangular. Pilosity greyish blonde. S2-3 with low rounded ridge medially interrupted. Uganda .... **S. ugandensis Cockerell**
   – Larger species (ca. 12mm). S8 apex nearly as long as wide. Pilosity blonde. S2-3 with more angular convexities. Cameroon .... **S. bispinosa Friese**

15. S2-3 with 2 acute processes (figs 9, 20). Palaearctic... .... **S. curvicornis (Scopoli)**
   – S2-3 with compressed tubercles, forming an apical lamella (fig. 10) **16**

16. S6 with a median short apical tooth. **17**
   – S6 untoothed (except *S. tropicalis* with a very short median tooth). **20**

17. Vertex short, not expanded beyond the posterior ocelli. S6 double toothed (a medio-proximal and a medio-terminalventral tooth). North-Africa. **S.pici Pérez**
   – Vertex usually wider expanded beyond the posterior ocelli. S6 mostly simply toothed **18**
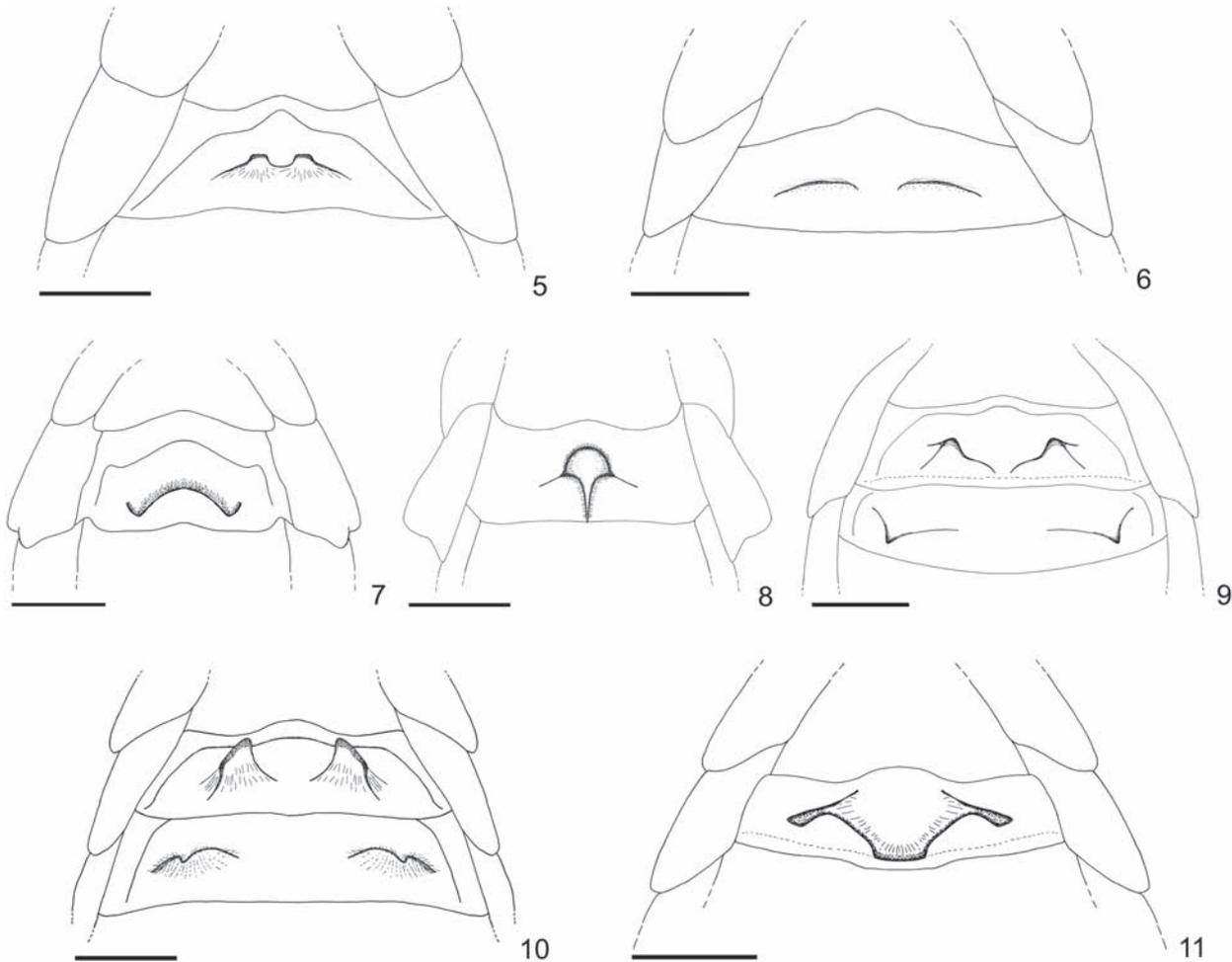
Figures 5-11

Sterna ♂. 5, *Systropha androsthenes* S2 (scale = 0.8 mm). 6, *S. punjabensis* S2 (scale = 0.6 mm). 7, *S. diacantha* S2 (scale = 1 mm). 8, *S. difformis* S2 (scale = 1.2 mm). 9, *S. curvicornis* S2-3 (scale = 0.6 mm). 10, *S. planidens* S2-3 (scale = 1.2 mm). 11, *S. aethiopica* (scale = 1 mm).

18. First terga margins angulous (like in *S. difformis* and *S. inexspectata*). S2 with long spiny and well distinct tubercles. S3 with lateral angulosities. S8 apex subrectangular, transverse, rounded. Pakistan .... **S. popovi Ponomareva**
– Terga margins not angulous. S2 tubercles usually flattened. Tubercles on S3 more rounded. S8 different, narrower or subelliptic **19**
19. Flagellum dark. A7 three times as long as wide; A8 5-6 times as long as wide. S1 medially short emarginated. S2-3 bearing low tubercles, conformed like in *S. planidens*. S8 terminal plate subelliptic, nearly as long as wide. Iran . ... **S. iranica Popov**
– Flagellum lower side reddish-yellow. A7-8 shorter. S2-3 with tubercles like in *S. planidens* but distinctly smaller. S8 terminal plate quadratic, nearly as long as wide. Iran .... **S. villosa Ebmer**
20. Tubercles mainly developed on S2 .... **21**
– Tubercles mainly developed on S3 or S4 .... **23**
21. S2 with large angular tubercles (fig. 10). S3 with

smaller but well developed tubercles. S8 with a very large, well developed and differentiated terminal plate. Southern West-Palaearctic .... **S. planidens Giraud**

S8 apex sub-quadratic. Turkey and surrounding areas : *S. planidens anatolica* Warncke

S8 apex asymmetric, subelliptic, the anterior part enlarged. Iberian Peninsula : *S. planidens grandimargo* Pérez

S8 apex subelliptic. Europe : *S. planidens planidens* Giraud

– S2-3 with generally smaller processes, even if likely shaped. S8 apex always subrectangular; distally notched by one species. Central-Asia **22**
22. S3 nearly flat, with smooth areas, slightly convex. S8 apex not notched apico-medially. Turkmenia .... **S. ruficornis Morawitz**
– S3 with well developed processes (like in *S. planidens*). S8 apex apico-medially notched. Kazakhstan .... **S. kazakhstaniensis Patiny**
23. Tubercles mainly developed on S4. S8 apex subrectangular, angulous. Tadjikistan ....**S. tadjika Warncke**
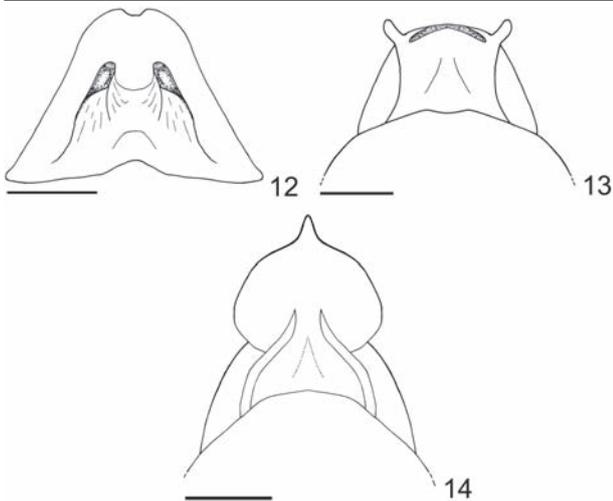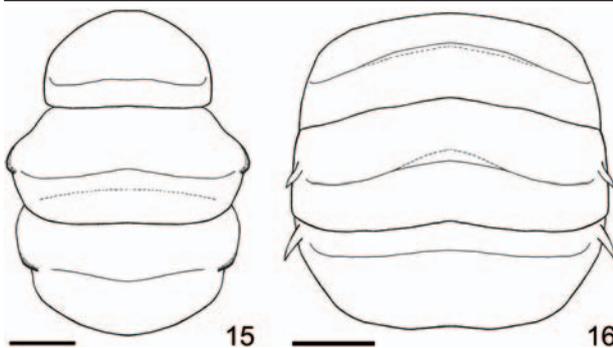
Figures 12-14
Sternum 1 ♂. 12, *Systropha hirsuta* (scale = 1 mm). Sternum 8 apex ♂. 13, *Systropha diacantha* (scale = 0.5 mm). 14, *S. maroccana* (scale = 0.5 mm).

– Rounded tubercles mainly developed on S3. S8 apex subelliptic acute (close to the *S. maroccana*, the apical tooth lesser differentiated). Sri Lanka ....
... ***S. tropicalis* Cockerell**

Females

1. Palaearctic and Indian species **2**
– Sub-Saharan species.. **11**
2. Indian species **3**
– West-Palaearctic species **4**

3. Mouthparts as long as head and mesosoma together. Second submarginal cell large, square shaped. Sri Lanka .... ***S. tropicalis* Cockerell**
– Mouthparts, shorter than head and mesosoma together. Second submarginal cell strongly reduced, subtrapezoidal. India ....
.... ***S. punjabensis* Batra & Michener**

Figures 15-16
Terga 1-3 ♂. 15, *Systropha difformis* (scale = 1.8 mm). 16, *S. aetiopica* (scale = 1 mm).

4. Small species (<7.5 mm) with the terga margins dark or larger with the terga margin yellowish, transparent. In smaller species, pilosity not abundant on the side of metasoma. Endemic in eastern Arabian Peninsula or middle-East **5**
– Larger taxa (>7.5 mm). Terga margin never likely yellowish. In the smaller taxa, the pilosity abundant on all body parts. Not endemic in these areas **6**

5. Head shorter than wide (L/W ca.1,3). Flagellum lower side orangish. Terga margin not notably discoloured. Pilosity whitish-grey, not particularly developed on terga apex. Pp not particularly developed. Oman, United Arab Emirates .... ***S. diacantha* Baker**
– Head rounded. Flagellum reddish on apex ventral surface. Terga margin discoloured, yellowish. Pilosity whitish-grey. Metasoma pilosity downy on ventral surface, applied of the terga margins. Pp long with typical narrowed apex. Pakistan, Turkmenistan .... ***S. popovi* Ponomareva**

6. Medium sized species (<10 mm). Flagellum lower side reddish brown. Pilosity whitish-grey, long and abundant, covering almost all body parts. Metasoma hairs abundant and strongly downy Morocco .... ***S. pici* Pérez**
– Species larger (>10 mm). Flagellum lower side paler (light reddish to yellowish) by several species. Pilosity whitish-brownish, generally sparser **7**

7. Cuticle with blue reflect **8**
– Cuticle without any blue reflect **9**

8. Medium sized species (ca. 9 mm). Head small, the vertex few extended dorsally. Metasoma with downy brownish pilosity; on the whole body, the hairs dark, the apex generally paler. Cuticle with a light blue reflect. Palaearctic .... ***S. curvicornis* (Scopoli)**
– Large species (ca. 10 mm). Head wider, the vertex strongly extended dorsally. Pilosity often paler, generally greyish. Cuticle with strong blue reflect. West-Palaearctic .... ***S. planidens* Giraud**

9. Very large species (ca. 12 mm). Terga with dense apical hairs fringes. Iranian .... ***S. villosa* Ebmer**
– Smaller species (ca. 10 mm). Terga without hairs fringes
.... **10**

10. Flagellum apex reddish. Metasoma pilosity yellowish-white, densely downy. T1-3 apical margin yellowish transparent. Anal fringe whitish-blonde. Near-East .... ***S. hirsuta* Spinola**
– Flagellum black. Metasoma pilosity downy; the hairs bicolour, paler apically (globally whitish-blonde on T1-3, darker from T4). T1-3 entirely dark without discoloured margin. Anal fringe dark brownish. Morocco .... ***S. maroccana* Warncke**

11. Tb3 inner spur smooth. Zimbabwe, Namibia ....
.... ***S. glabriventris* Friese**
– Tb3 inner spur with 2 strands of strong teeth along ventral edge **12**

12. Rather small species (ca. 8 mm). Pilosity white on face, mesoscutum and first terga, reddish-orange on scutellum and metasoma apex (anal fringe and previous sclerites). Wings hyaline. South-Africa ....
.... ***S. krigei* Brauns**
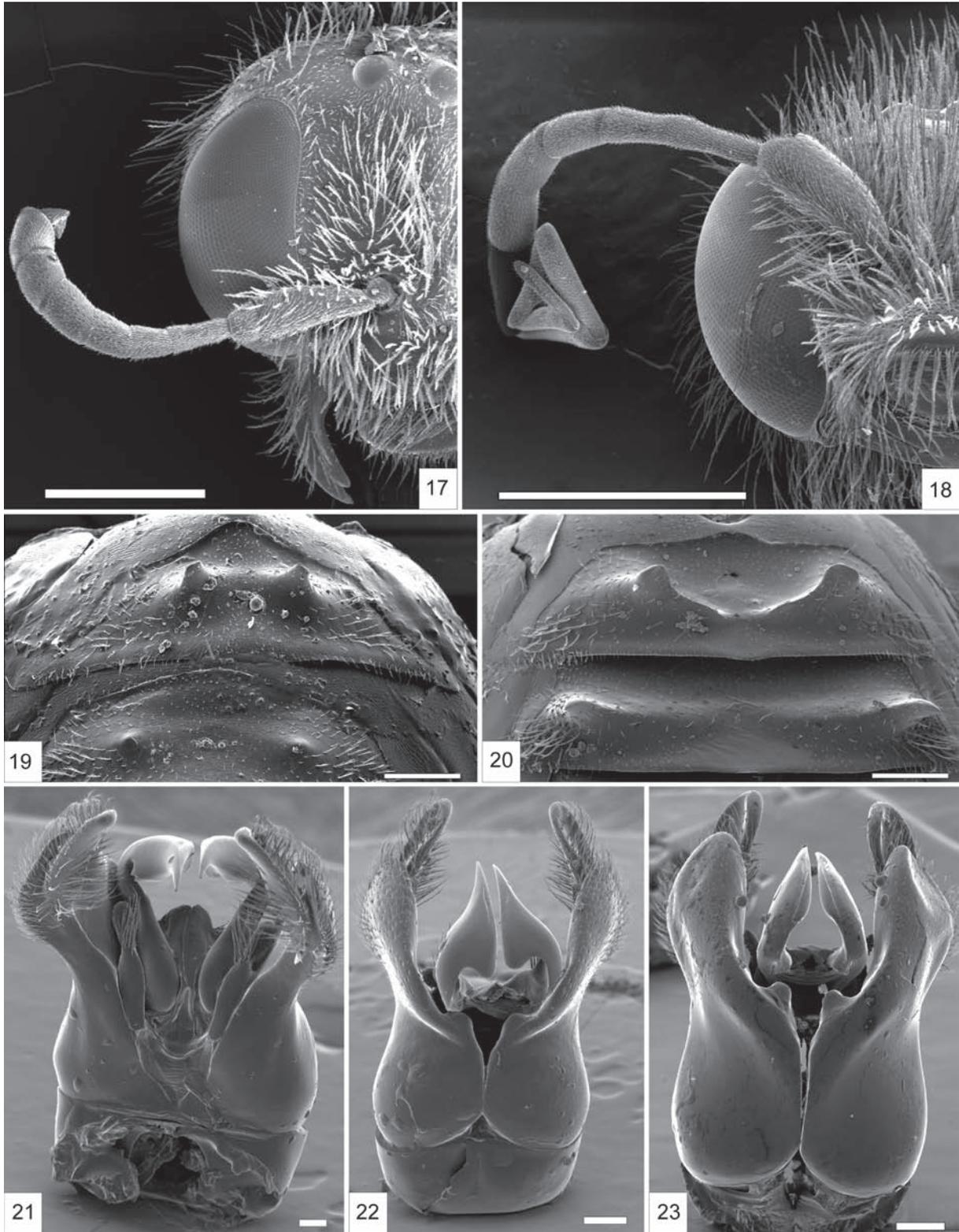
Figures 17-23
Systropha spp. ♂ SEM pictures. 17, head of *Systropha androstenes* (scale = 600 μm). 18, head of *S. curvicornis* (scale = 1 mm). 19, S2-3 of *S. androstenes* (scale = 300 μm). 20, S2 of *S. curvicornis* (scale = 0.5 mm). 21-22, *S. planidens* genitalia ventral and dorsal view (scale = 200 μm). 23, *S. curvicornis* genitalia dorsal view (scale = 200 μm).

Table 1. Yielded trees' characteristics in regard of the used analysis method and the characters weighting.

	Unweighted characters			Characters weighted		
	Length	CI	HI	Length	CI	HI
Ordered and unordered	79	0.5316	0.4684	31.5	0.7653	0.2347
Ordered	88	0.4773	0.5227	30.34363	0.7197	0.2803
Dollo.up	103	0.4078	0.5922	33.92398	0.6409	0.3591

– Pilosity differently coloured **13**

13. Mesoscutum and scutellum covered with rather sparse and short greyish pilosity. Metasoma with strong black hairs on terga and sterna. Legs hairs black. Medium sized species (ca 9 mm). Nigeria .... **S. norae** Patiny

– Pilosity variably dark, usually brownish on mesosoma, legs and metasoma. One of the species quite larger. Eastern-Africa **14**

14. Mesoscutum pilosity golden blonde. Terga with dark brownish hairs; paler on sterna. Second submarginal cell subtrapezoidal. Medium sized species (ca. 9 mm). Zimbabwe .... **S. rhodesiensis** Friese

– Mesoscutum pilosity greyish. Terga and sterna with dark brown hairs. Second submarginal cell pentagonal. Very large species (ca. 12 mm). Zanzibar .... **S. macronasuta** Strand

Results of the phylogenetic analysis

The heuristic search based on the study of the data set (appendix 2), considering the binary characters ordered, the multistates unordered and using ACCTRAN character-state optimization, yields 321 equally parsimonious trees displaying a handful of topologies (figs 24-28; tab. 1). These trees are of length
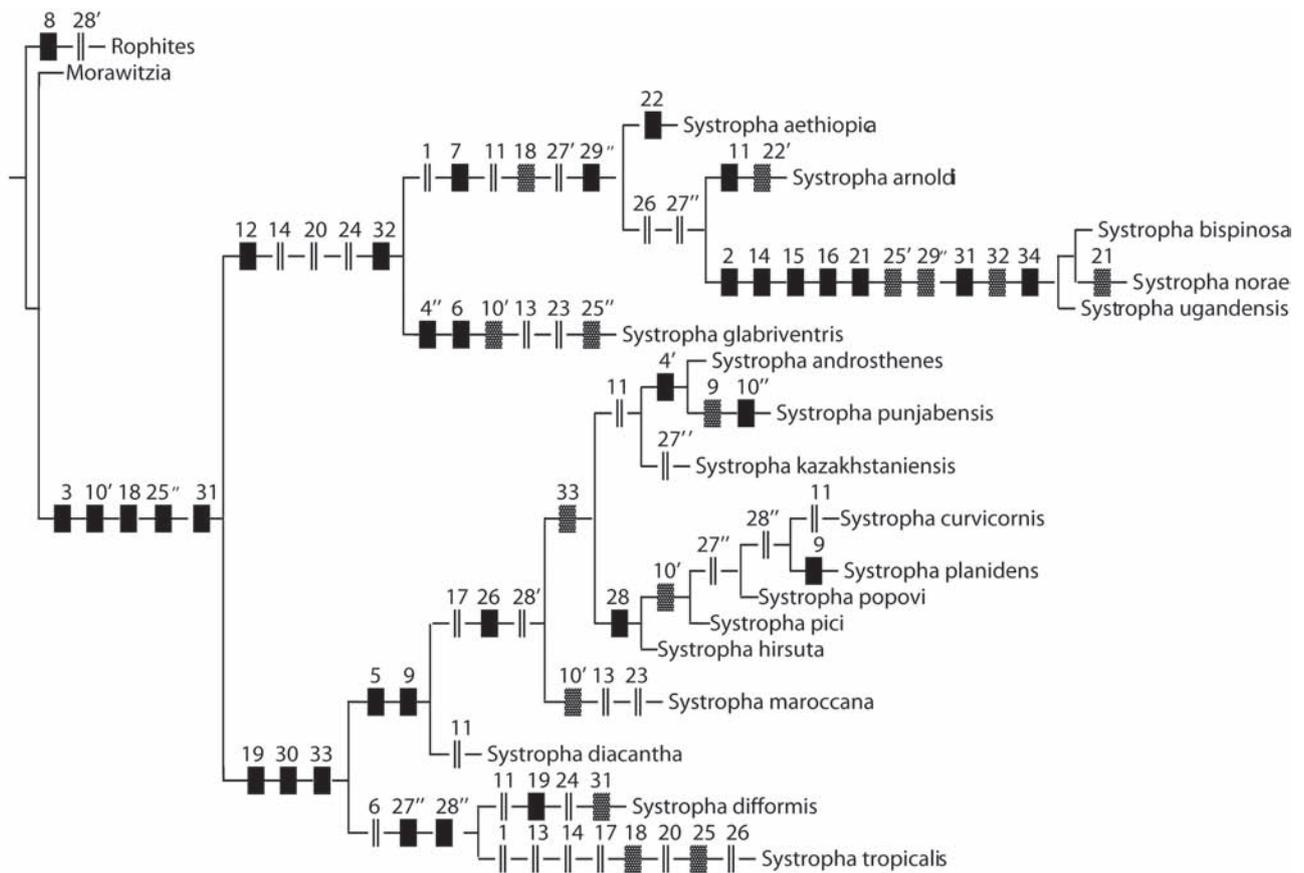
Figure 24
Selected phylogram between the most parsimonious trees (length = 79 ; CI = 0,5316 ; HI = 0,4684 ; RI = 0,7431). ■ = apomorphy ; ‖ = homoplasy ; ▦ = reversion. Different states are indicated with « ' ».
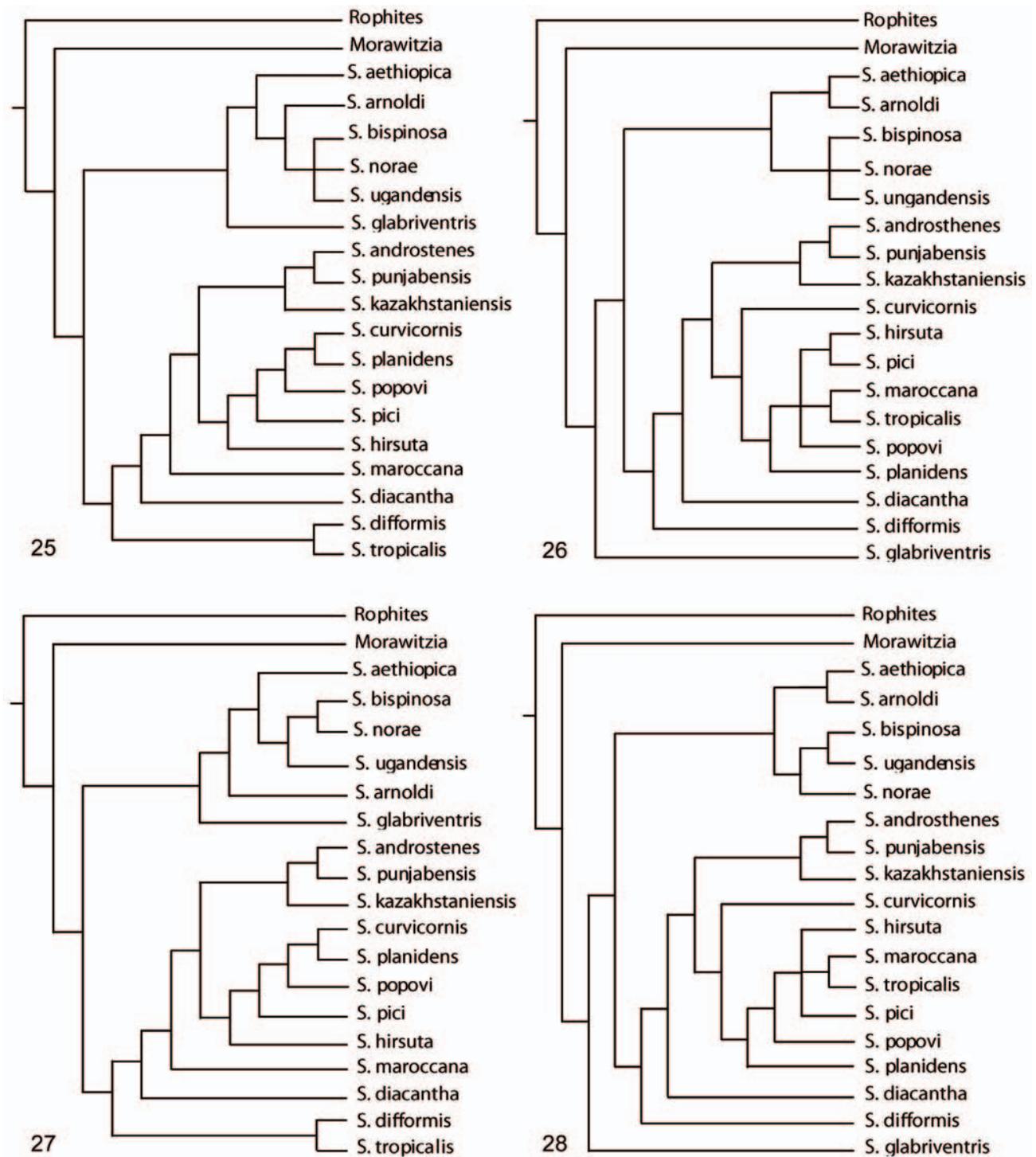
Figures 25-28
Selected topologies among the most parsimonious trees obtained in analysis of the data set when considering the characters unordered. Length = 79, CI = 0.5316, HI = 0.4684, RI = 0.7431, RC = 0.3950.
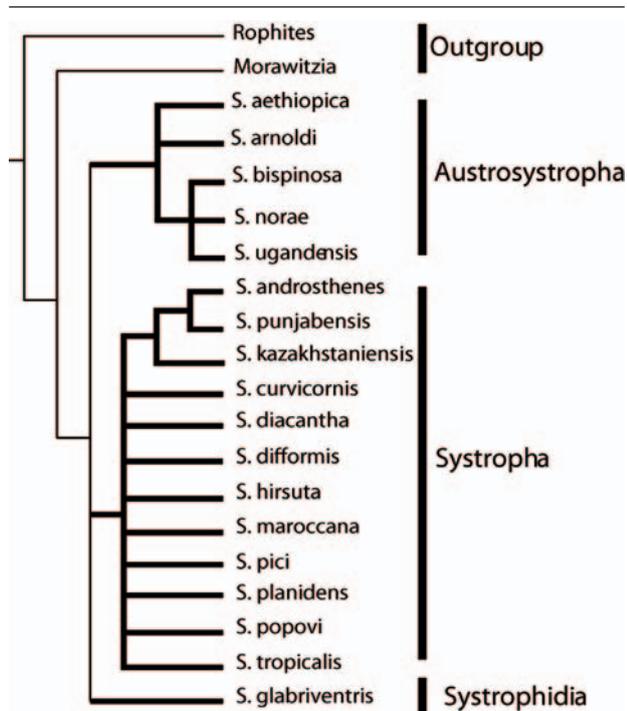
Figure 29
Strict consensus of the most parsimonious trees (multistate characters unordered and of equal weight). First clade = subgenus *Austrosystropha*, second clade = subgenus *Systropha*, third clade = subgenus *Systrophidia*.

= 79, CI = 0.5316 and HI = 0.4684 (tab. 1). After application of the successive weighting method, 6 equally parsimonious trees are found, in which CI = 0.7653 and HI = 0.2347. The same analysis procedure considering the character ordered yields more trees (8836) of length = 88, CI = 0.4773 and HI = 0.5227. The successive weighting yields two trees with CI = 0.7197 and HI = 0.2803. Eventually, the "dolloup" method leads to 8 trees of which length = 103, CI = 0.4078 and HI = 0.5922. When weighted in this method, the data set yields two trees, in which CI = 0.6409 and HI = 0.3591.

In regard of the strong similarity of the topologies yielded following the various analysis methods tried, one chooses to present the cladograms issued from the first analysis method (considering the binary characters ordered, the multistates unordered, figs 24-28).

Three species groups can be described based on the presented cladograms (figs 24-28). One first includes *S. aethiopica*, *S. arnoldi*, *S. bispinosa*, *S. norae* and *S. ugandensis*, associated within most of the yielded trees, independently of the used method. This first clade is supported by a Jackknife value of 60 and described by the apomorphic states of characters 7 and 29. The five species included are notably well-characterised by the shape of the Tb3 spur. Within this first group, three species, *S. bispinosa*, *S. norae* and *S. ugandensis*, form a very stable clade also supported by high Jackknife value (99). The species included in this latter group are characterised by apomorphic states of the characters 2, 15, 16, 21 and 34. These three species share notably

Table 2. Compared morphology of the subgenera.

Characters	*Systropha* s.str.	*Systrophidia* Cock.	*Austrosystropha* subg.nov.
Males			
Flagellum apex	A9 and following well differentiated in spiral arrangement	A9 and following fused in a single short hook	A9 and following all long, well differentiated, in spiral arrangement
Legs parts differentiation	F2 dorso-ventrally enlarged by some species	Tr2, F2, Tr3 and F3 carinated. Cx3 with a typical inner bud	F1 usually enlarged dorso ventrally and laterally. F2 often enlarged as well as Tb2 proximal part. Cx3 distally enlarged by several species
Development of teeth on Terga	Terga untoothed, except T6 by *S. maroccana*, T7 by *S. difformis*	T7 laterally toothed	T7 always laterally toothed. T6 bearing often teeth. T1-5 with angular or spiny graduli by *S. aethiopica* and *S. arnoldi*
Sterna tubercles differentiation	Well developed tubercles on S2-4	Tubercles strongly reduced, first sterna with small smooth areas	Sterna margin variably transformed in wide expansions (*S. aethiopica*, *S. arnoldi*) or in low blade-like margins
S8 apical enlargement	S8 apex variably enlarged	S8 apex elliptically enlarged	S8 apex elliptically enlarged or not enlarged but with a well developed ventral groove
Females			
Tb3 inner spur	Straight and finely toothed	-	Curved and coarsely toothed following 2 ventral ranks
Sterna pilosity	Less developed, downy	-	Densely developed, lesser downy, coarse by several species.

Table 3. Literature reported data on the species floral choices. Except when otherwise precised, the quoted botanic genera belong to Convolvulaceae.

Systropha species	Visited plant species	References
Subgenus *Systropha*		
S. androsthenes Baker	*Convolvulus* sp. Low-growing species	Baker (1996)
S. curvicornis Scopoli	Asteraceae : *Cichorium intybus* L. used as shelter; Convolvulaceae : *Calystegia* R.Brown, *Convolvulus* sp.; *Convolvulus arvensis* L.; Fabaceae : *Melilotus albus* Medikus ; Linaceae : *Linum hirsutum* L.	Friese (1901); Stoeckhert (1933); Herbert (1982); Baker (1996)
S. inexspectata Ebmer	Convolvulaceae : *Convolvulus* sp. ; species with white flowers, interpreting Baker's reading of the Cockerell's labelling	Baker (1996); Ebmer (1994)
S. iranica Popov	Convolvulaceae : *Convolvulus leiocalycinus* Boissier, *Convolvulus spinosus* Burman; Punicaceae : *Punica granatum* L.	Popov (1967); Baker (1996); Warncke (1980)
S. maroccana Warncke	Convolvulaceae : *Convolvulus trabutianus* Schweinfurth & Muschler	Baker (1996)
S. pici Pérez	Convolvulaceae : *Convolvulus spinosus* Burman	Baker (1996)
S. popovi Ponomareva	Convolvulaceae : *Convolvulus* sp.	Ponomareva (1967)
S. planidens Giraud	Convolvulaceae : *Convolvulus arvensis* L.	Friese (1901); Ebmer (1978); Herbert (1982); Stoeckhert (1933)
S. punjabensis B.&M.	Convolvulaceae : *Convolvulus arvensis* L.	Batra & Michener (1966)
S. tropicalis Cockerell (*butteli* Friese)	Convolvulaceae : *Convolvulus* sp.	Friese (1913)
Subgenus *Systrophidia*		
S. glabriventris Friese	Convolvulaceae : *Merremia palmata* Hallier f.	original data (AMNH)
Subgenus *Austrosystropha*		
S. ugandensis Cockerell	Convolvulaceae : *Convolvulus* sp.	Cockerell (1931)

the synapomorphic development of tubercles on the mesopleura ventral surface. Within the yielded trees, *S. glabriventris* constitutes a single species clade, which is associated with the previous described species-set (figs 25, 27) or placed as the *Systropha* sister-species (figs 26, 28). The other species included in the analysis form a third notable clade including the species displaying strongly differentiated processes on the S1-6. However, the terminal groupings of the included species are rather variable and the clade is only supported by low Jackknife score (39). This latter group contains: *S. androsthenes*, *S. punjabensis*, *S. kazakhastaniensis*, *S. diacantha*, *S. maroccana*, *S. curvicornis*, *S. hirsuta*, *S. pici*, *S. popovi* and *S. planidens*, most of these previously included in the Ponomareva' species groups. These latter species are interestingly characterised by the untoothed tibial spur (character 19). Within this clade *S. androsthenes* and *S. punjabensis*, displaying a strong reduction of the last falgellum segments, constitute a notable group supported by a Jackknife of 48.

Subgenera descriptions and diagnoses

Systropha Illiger 1806 s.str.

Type species. *S. curvicornis* (**Scopoli 1770**); by monotypy

Previous descriptions. Ponomareva (1967), Batra & Michener (1986) and Baker (1996)

Diagnosis (see also tab. 2; figs 1, 5-10, 12-13, 15, 17-23). Medium sized species. Mouthparts of usual length (see figures in Ebmer 1994). ♀. Tb3 inner spur straight, finely toothed. Metasomal pilosity dense and downy. Flagellum short but not particularly

thick. ♂. Antennae with 13 well-developed segments; in some species less than 13 segments (*S. androsthenes*, *S. punjabensis*). These latter segments distinct, not fused in a single terminal hook. F1, Tb2, Cx3 weakly differentiated, not enlarged. Terga not toothed laterally (except T6 by *S. aroccana*; T7 by *S. difformis*). First sterna (S1 in one species; S2-S3 in most taxa) with well-developped typical processes. S8 apex strongly differentiated, variably shaped and bearing typical terminal appendages (by *S. diacantha*, *S. difformis*, *S. maroccana*, *S. tropicalis*).

Included species. *S. androsthenes*, *S. curvicornis*, *S. diacantha*, *S. difformis*, *S. hirsuta*, *S. inexspectata*, *S. iranica*, *S. kazakhstaniensis*, *S. maroccana*, *S. pici*, *S. planidens*, *S. popovi*, *S. punjabensis*, *S.ruficornis*, *S. tadjika*, *S. tropicalis*, *S. villosa*.

Floral choices. Tab. 3

Distribution. Palaearctic, see details in the key

Systropha (Systrophidia) Cockerell 1936

Type species. *S. glabriventris* **Friese 1922; by monotypy**

Previous descriptions. Cockerell (1936) and Batra & Michener (1986)

Diagnosis (see also tab. 2; figs 2, 4). Very large species. Mouthparts strongly elongated (as long as half of the body length). PMx unusually short. ♀. Tb3 inner spur smooth. Metasoma with short and not notably downy pilosity. Flagellum short and thick. ♂. Antennae with 8 normal segments; the flagellum apex forming a short hook. F1, Tb2, Cx3 weakly differentiated. F2 longitudinally carinate. T6-7 laterally toothed. First sterna without process. S8 apex almond-shaped.

Included species. *S. glabriventris*

Floral choices. Tab. 3

Distribution. Namibia, Zimbabwe

Systropha (Austrosystropha) n. subg.

Type species. *S. norae* Patiny 2004

Etymology. The group includes exclusively Sub-Saharan species distributed south of the Tropic of Cancer. The subgenus name refers to this characteristic Southern distribution.

Diagnosis (see also tab. 2; figs 11, 16). ♀. Tb3 inner spur thick, sigmoid, with two rows of coarse teeth along the ventral edge. Metasomal pilosity rather sparse and less downy than in *Systropha* s.str; more abundant on sterna. ♂. Antennae always 13-segmented; the last five segments of usual length, spiral, usually a little flattened. F1 inflated. Tb2 dorso-ventrally enlarged in several species. Cx3 enlarged, apex angulate (in a group of 3 species). At least the T7 laterally toothed. First sterna with low processes. S8 apex elliptical subperpendicular to the sternum base or not enlarged and displaying a typical ventral longitudinal groove.

♀. **Head.** Facial pilosity usually pale, well-developed. Mouthparts shorter than head and mesosoma together. Ocellar area convex. **Mesosoma.** Mesoscutum and scutellum with short continuous blonde or grey pilosity. Tb3 inner spur thick sigmoid with two ventral ranks of coarse teeth. **Metasoma.** Terga and sterna with usually strong hairs (less downy than by *Systropha* s.str.); pilosity abundant on sterna.

♂. **Head.** Facial pilosity forming long crests of hairs behind scape. Genae densely hairy; the ventral part with a beard-like pilosity. Ocellar area convex. A3 long. Flagellum last segments spiral, usually sensitively flattened; antennae 13-segmented. **Mesosoma.** Propodeal area depressed. Several species with the ventral portion of the mesopleura arched or bearing distinct tubercles. F1 inflated. Proximal part of Tb2 enlarged. Cx3 angular; apex enlarged. **Metasoma.** Terga graduli angular or forming a spine in some species. T7 laterally toothed in all species. First sterna processes appearing as a low blade-like modification of the S2(3) margin. These latter structures sometimes very large. Terminal appendages of S7 large. Apex of S8 almond-shaped or narrower with a typical ventral groove.

Included species. *S. aethiopica, S. arnoldi, S. bispinosa, S. krigei, S. macronasuta, S. norae, S. rhodesiensis, S. ugandensis*

Floral choices. Tab. 3

Distribution. Sub Saharan Africa, see details in the key

Discussion

Species taxonomy

Prior to the previous catalogue, the status of several species remained unclear in the available literature (Ebmer 1994; Baker 1996). The solutions proposed to these taxonomical problems in the present work are discussed hereafter.

Ebmer (1979, following the label's date) designated one female conserved in the NHM (London) collections as the *S. aethiopica* Friese allotype. Now, when comparing this latter specimen with the species holotype (ZMHB, Berlin), the Ebmer's designation seems not relevant in regard of the available evidences. The male holotype is unusually much bigger than the proposed allotype. Moreover, the two specimens differ strongly by the abundance and colour of the pilosity, whereas these features are generally very similar in males and females in the other species of the genus. One can even doubt that the designated female belongs to the subgenus *S. (Austrosystropha)* in which *S. aethiopica* is placed based on several strong male characters (observed on the holotype; see catalogue and cladistic analysis). None of the *S. (Austrosystropha)* diagnostic character, notably the typical coarsely toothed Tb3 inner spur by females, is displayed by the proposed allotype. From the biogeographical point of view, no more argument can be found supporting the two specimens association. The holotype locus typicus "Br. O. Afrika, Mulango", following the specimen's labelling, can in no way be evidently related to this of the proposed allotype "Dhofar, Wadi Sayq s.l.". These observations lead to conclude that no character supports the association of the male holotype and the female allotype. Consequently, *S. aethiopica* is considered here (see the key and the matrix in appendix) as known by the males only. Currently, one chooses to not describe the Ebmer's female, having only one specimens without any strong morphological features.

A second taxonomical problem consists in the status given to the taxa implied in the *S. hirsuta* complex: *S. christae, S. hirsuta, S. pici*, which includes in fact only two well-distinct species. On one hand, *S. pici* is a small species seemingly close to *S. planidens*. On the other hand, *S. hirsuta* is a typical taxon, of which males are uniquely characterised by the differentiation of a process on S1 (fig. 12). Baker (1996) pointed out that Ponomareva (1967) and Warncke (1977) introduced more and more confusion between *S. hirsuta* and *S. pici*, due to misidentifications of *S. pici* erroneously named *S. hirsuta*. One notes that this confusion was earlier already made by Friese. The Berlin museum series contain notably one specimen caught in Algeria in 1890, obviously belonging to *S. pici* and labelled "*Systropha hirsuta* Spin. det. Friese 1898". The third species included in the complex, *S. christae*, must be considered as a junior synonym of *S. hirsuta*. In the above catalogue, after the types revision, we followed the Baker's synonymy, considering *S. pici* and *S. hirsuta* as distinct species. *S. pici* is North-African, described on the basis of female from Ain Sefra (Algeria) and also present in Morocco. *S. hirsuta* is a species from Near-East. The male lectotype is from Egypt (Casolari & Casolari 1978; Baker 1996) and several specimens were caught in Israel (*S. christae*; Warncke 1972).

The NHM (London) series contain also two specimens from Uganda, labelled *S. antinorii* and belonging to *S. bispinosa* Friese. We cannot find any trace in literature and other collections of the name

antinorii. This latter was consequently not quoted in the previous catalogue. However, the concerned specimens have a high biogeographical interest because they constitute a first record of the species in Eastern Africa and a strong eastward expansion of the *S. bispinosa* distribution.

The present catalogue includes naturally also the more recently described species: *S. kazakhstaniensis* Patiny 2004 and *S. norae* Patiny 2004. The last described species, *S. heinzi* Dubitzky 2004 (description published on the 1st of December) is proposed as a new synonym of *S. kazakhstaniensis* (description published on the 30th of November).

Supraspecific level

At higher taxonomical level, several subgenera and species groups were formerly described in *Systropha* (Cockerell 1936; Ponomareva 1967; Batra & Michener 1966). Nowadays, no study of the concerned species phylogenetic relationships supports these groupings and taxonomical propositions. The trees presented in the frame of the present study (figs 24-29) are consequently the first evidences supporting the genus subdivision into subgenera. Three species groups are described as subgenera based on the results of the phylogeny analysis: *Systropha* s.str., *Austrosystropha* **n. subg.** and *Systrophidia* (tab. 2). The first includes the species contained in the two Ponomareva' species groups, the second consists in most sub-Saharan species (not considered by the previous authors) and the last keeps its original definition as given by Cockerell (1936), containing *S. glabriventris* only.

Among the three described subgenera, *Systropha* s.str. appears less consistent and more variable (only supported by low jackknife values). However, the observed variability consists mainly in the included species terminal groupings and not in the subgenus specific composition. Light changes in this latter are only observed when one considers the characters ordered or "dollo.up". Following these latter methods, *Systropha* s.str. include only *S. curvicornis, S. hirsuta, S. kazakhstaniensis, S. pici, S. planidens* and *S. popovi*, while *S. androsthenes-S. punjabensis* and *S. difformis-S. tropicalis* are excluded and form most often distinct groups.

On the contrary, *Austrosystropha* **n. subg.** is strongly supported in the computed topologies, scoring high jackknife values. From the morphological point of view, the subgenus can be described based on numerous characters, included or not in the analyzed dataset (tab. 2, subgenera descriptions). One of the more typical characters supporting the *Austrosystropha* monophyly is the coarse teeth of the female inner

hind tibial spur. *Systropha* females display in most species a straight and nearly smooth hind spur. On the contrary, the known females of African species have a typical strong, sigmoid and coarsely toothed spur. This character was not included in the studied dataset because in African species one usually lacks one of the two sexes. The inclusion of these characters would consequently lead to the introduction of numerous indeterminations cases. However, observations made on *S. norae* females and not previously studied samples of *S. bispinosa* (MRAC), confirm the interest of this character. In the studied data set, one inserts a character relative to the male spur morphology (character 19), also sensitively different in *Austrosystropha*. In males, the development of facial hairs crests (character 01) is another typical character for *Austrosystropha*. One notes that this character is also observed in *S. tropicalis*, which is grouped with the *Austrosystropha* when considering characters of the type dollo.up. The species included in *Austrosystropha* share several other characters, notably the previously discussed shape of the females Tb3 inner spur but also F1 differentiation, the Cx3 enlargement and the development of teeth on T7 (characters 16, 19, 24). Within *Austrosystropha*, another species group can be identified. This latter pools the taxa characterised by the development of tubercles on the mesopleural ventral surface (character 21). *S. bispinosa*, *S. norae* and *S. ugandensis* display such structures variably well individualised following species, while the other *Austrosystropha* have usual flat mesopleura. Despite this dichotomy, the *Austrosystropha* are considered, based on the previous topologies (figs 24-29) as forming a single group.

As stated in the results chapter, *S. glabriventris* is generally excluded of the previous species groups and seems to constitute a monobasic subgenus as earlier suggested by Cockerell (1936). This latter species is morphologically very well-distinct of the other *Systropha* and can be easily considered as the sister-species of the *Austrosystropha* or of all the other species (figs 24-29). This appears particularly interesting in regard of the species distribution. In varied bees groups (like Meganomiinae, *Rediviva, Mermiglossina* i.e.; Michener 1981; Patiny 2001; Ascher 2004), one find sister-group of other more diversified taxa isolated in Southern Africa (notably in Namibia). Considering *S. glabriventris* as the *Systropha* or *Austrosystropha* outgroup leads to the description of an similar biogeographical pattern.

Moreover, from the biogeographical point of view, the three described subgenera are well separated one of each other. *Systropha* s.str. are strictly Palaearctic, the most southern encountered species being

S. tropicalis (Sri Lanka) and *S. maroccana* (Morocco). *S.* (*Austrosystropha*) are strictly subsaharan, ranging mainly in southern and eastern Africa. Northern, they seem distributed in the northern savannas of Central Africa, reaching Cameroon and Nigeria to the west. Eventually, the early described subgenus *S.* (*Systrophidia*) is restricted, according to the current knowledge, to Namibia and Zimbabwe. The presence of this species in Botswana too cannot be excluded.

Floral choices

We did not use aspects of the species ecology as descriptors in the previous phylogenetic analysis. However, it is important to point out that the *Systropha* display a remarkable level of oligolecty (monolecty in some species). As it's shown by the floral records reported for 11 of the 26 described species (tab. 3). In most cases, specimens were caught on Convolvulaceae, mainly on *Convolvulus* L. Based on these data, one can hypothesize a strong (nearly exclusive) association of *Systropha* with *Convolvulus*. Only two species, *S. curvicornis* and *S. iranica*, were caught while visiting other host plants. In the case of *S. curvicornis*, it can reasonably be suggested that the large distribution of the species lead to more opportunities for unusual adaptative behaviours. Moreover, it seems that these exceptions to the general oligolecty of the species are anecdotic.

Among the *Convolvulus* species visited by the *Systropha*, several vegetative forms are represented. *C. spinosus* and *C. trabutianus* are bush species, typically growing in steppes. On the contrary, *C. arvensis*, visited by several species (tab. 3), is a low growing herbaceous plant. One can wonder if the studied bees are linked to the flower type or to the vegetative form. However, despite these morphological divergences in the host plants, the available data suggest an association between *Systropha* and species of *Convolvulus* with tricolporate pollen grains (Wodehouse 1965). The record on *Calystegia* sp. is the only one on a Convolvulaceae with another pollen morphology.

In *Systropha*, one notes the absence of variation in the floral choices of the three subgenera. Contrary to other groups of bees (*Dasypoda* Latreille 1802 e.g.), in which it seems exist an evolutionary relation between the choice of the food resources and the subgeneric divergence (Michez *et al.* 2004), it seems that the ecological preferences were here conserved during and despite the evolutionary radiation.

Conclusions

The present work fixes several taxonomical problems previously still remaining in the *Systropha* classification. One also gives the first exhaustive catalogue for the World species, including the most recently described ones.

In the supraspecific level, three subgenera are described or re-described. The previous position if species included in *Systropha* s.str. and *S.* (*Systrophidia*) is not modified. All the subsaharan species for which no precise subgeneric classification had been previously suggested, fall into the new subgenus *S.* (*Austrosystropha*). Parallel to this action in the group taxonomy, a first analysis of the species phylogenetic relationships is realised.

No particular study was directed to enhance the knowledge of the *Systropha* floral choices. However, having a particularly wide overview of the available literature, one sets the first synthesis of that knowledge. This part of the work underlines clearly the oligolecty of the genus species on the *Convolvulus* and Convoluvulaceae *Convolvulus*-like flowers.

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Appendix 1.

Characters used for the phylogeny relationships analysis.

01. Development of the males' facial pilosity
    0, undifferentiated; 1, forming typical crests behind scapes
02. A3 elongation
    0, A3 short; 1, A3 elongated
03. Differentiation of the males' antennae apex
    0, males' antennae apex straight; 1, males antennae apex spiral
04. Males' flagellum reduction
    0, flagellum with 13 well-differentiated segments; 1, less than 13 segments, the apical very short; 2, less than 13 segments; the apical forming a typical hook
05. PMx relative size
    0, PMx shorter than PLb; 1, PMx longer than PLb
06. Mouthparts elongation
    0, mouthparts shorter than half of the body length; 1, mouthparts as long as, or longer than, half of the body length
07. Ocellar area convexity
    0, ocellar area flat; 1, ocellar area notably convex
08. Reduction of the submarginal cell number
    0, Forewing with 3 submarginal cells; 1, Forewing with 2 submarginal cells
09. Size of the first submarginal cell
    0, first submarginal cell short and straight; 1, first submarginal cell longer and curved
10. Shape of the second submarginal cell (using the Rs/Rs+M ratio as estimator)
    0, second submarginal nearly as wide anteriorly as posteriorly; 1, second submarginal narrowed; 2, second submarginal cell unusually narrowed
11. Position of the 1m-cu vein junction on Rs+M of 2sd smarginal cell
    0, distal; 1, median
12. Enlargement of the males' F1
    0, F1 dorso-ventrally enlarged; 1, F1 dorso-ventrally and laterally enlarged, appearing inflated
13. Enlargement of the males' F2
    0, F2 not enlarged; 1, F2 dorso-ventrally enlarged
14. Males' F2 carinate
    0, not carinate; 1, carinate
15. Enlargement of the males' Tb2
    0, tibia proximal half not enlarged; 1, tibia proximal part nearly as large as the distal part
16. Enlargement of the males' Cx3 apex
    0, Cx3 apex not enlarged; 1, Cx3 flattened, distally enlarged
17. Hind tarsus median segments size
    0, segments 3&4 of the Hind tarsus short; 1, segments long
18. Males' Bt3 elongation
    0, Bt3 less than 0,6 time as long as Tb3; 1, Bt3 longer
19. Males Tb3 inner spur
    0, ventral edge of the Tb3 inner spur finely toothed along 2 ranks; 1, spur seemingly smooth
20. Propodeal area depression
    0, propodeal area not depressed, propodeum regularly convex; 1, propodeal area depressed
21. Development of tubercles on the males' mesopleurae ventral part
    0, males' mesopleurae flat; 1, males' mesopleurae with short spiny tubercles; 2, males' tubercles larger (*S.norae*)
22. Lateral differentiation of the males' terga graduli
    0, graduli undifferentiated laterally; 1, graduli forming lateral spines on first terga
23. Males' T6 laterally toothed
    0, T6 untoothed; 1, T6 toothed
24. Males T7 laterally toothed
    0, T7 untoothed; 1, T7 toothed
25. Differentiation of processes on the males' S2
    0, S2 without process; 1, S2 margin notably convex; 2, S2 margin well differentiated in process(es)
26. Males' S2 with paired processes
    0, S2 processes unpaired; 1, S2 processes paired
27. Differentiation of processes on the males' S3
    0, S3 without process; 1, S3 margin notably convex; 2, S3 margin with well differentiated process
28. Males' S6 with a longitudinal carina
    0, carina absent; 1, carina low; 2, carina well convex; 3 carina with well individualized proximal and distal teeth
29. Males' S6 with a terminal angular bud
    0, S6 apex undifferentiated; 1, S6 with one apical median tooth; 2, S6 with 2 successive teeth along its longitudinal axis
30. Males' S7 terminal processes tapered
    0, S7 terminal processes large; 1, S7 terminal processes apex tapered
31. Males' S8 apex enlarged
    0, S8 apex not enlarged; 1, S8 strongly enlarged and flattened
32. Males' S8 enlargement almond-shaped
    0, S8 apex other; S8 apex with a typical elliptic almond like shape
33. Males' S8 apex bearing small terminal process(es)
    0, S8 without terminal process; 1, S8 apex toothed
34. Males' S8 apex with a ventral groove
    0, no differentiated groove on the males' S8 apex; 1, S8 apex with a longitudinal ventral groove

Appendix 2.

Analysed data set. The 18 *Systropha* species are included in analysis ingroup. *Rophites* and *Morawitzia* are used as outgroups. 34 characters are used as taxa's descriptors.

| | 1111111111 2222222222 33333 |
| | 123456789 0123456789 0123456789 01234 |

Rophites	000000010 0000000000 0000000010 00000
Morawitzia	000000000 0000000000 0000000000 00000
S.aethiopica	101000100 1110100000 1020120102 01100
S.androsthenes	001110001 1100000111 0000021010 11000
S.arnoldi	101??0100 1010100000 1010121202 01100
S.bispinosa	111000100 1110011000 1100111201 00001
S.curvicornis	001010001 0100000111 0000021200 11000
S.diacantha	001010001 1100000011 0000020000 11010
S.difformis	001001000 1100000010 0000120220 10010
S.glabriventris	001201000 0011100010 1001100000 01100
S.hirsuta	001010001 1000000111 0000021020 11000
S.kazakhstaniensis	001010001 1100000111 0000021210 11000
S.maroccana	001010001 0001000111 0001021010 11010
S.norae	111000100 1110011000 1200111201 00001
S.pici	001010001 0000000111 0000021020 11000
S.planidens	001010000 0000000111 0000021200 11000
S.popovi	001010001 0000000111 0000021220 11000
S.punjabensis	001110000 2100000111 0000021010 11000
S.tropicalis	101001000 1001100101 1000011220 11010
S.ugandensis	1?10?0100 1110011000 1100111201 00001