

## The *Tachyusa coarctata* species group revisited: Phylogenetic relationships and a new species (Coleoptera: Staphylinidae: Aleocharinae)

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**Key words.** Coleoptera, Staphylinidae, Aleocharinae, *Tachyusa*, *coarctata*-group, new species, taxonomy, phylogeny

**Abstract.** The *Tachyusa coarctata* species group is revised. The species group is defined on the basis of the distinctly asperate punctation on elytra, the dense punctation on tergites III–V with interstices between punctures 1.5–2.0 times their diameter, and the dense, subrecumbent pubescence on the abdomen. The *T. coarctata* species group is composed of twenty three species restricted in occurrence to the Holarctic and Africa, including one new species described from Iran: *Tachyusa frischi* sp.n. A revised key to the species in this group is provided. An analysis of the phylogeny of the *Tachyusa coarctata* species group based on cladistic methods is presented and the phylogenetic relationships among species are discussed.

### INTRODUCTION

The genus *Tachyusa* Erichson, 1837 belongs to the staphylinid subfamily Aleocharinae, has a world-wide distribution and is most speciose in temperate regions but also occurs in the tropics.

A phylogenetic analysis of the world species of the genus *Tachyusa* (Paśnik, 2006) divided the genus into five groups of species on the basis of a variety of morphological characters: *coarctata*, *impressa*, *gemma*, *cordicollis* and *constricta* groups. The *Tachyusa coarctata* species group was erected for twenty two closely related species from the Nearctic, Palaearctic and Africa.

Within the *coarctata* group, species-level relationships were unresolved because of the extremely similar shape, punctation and microreticulation on the body, the range of variation in the colour pattern on the body and in the shape of terminal abdominal sclerites.

Material kindly provided for examination by Johannes Frisch (Berlin) included one new species of the *coarctata* group from Iran. The *T. coarctata* species group now includes twenty three species.

The purpose of this paper is to examine the phylogenetic relationships among the species of the *coarctata* group, provide a description of the new species and a new key to species.

### MATERIAL AND METHODS

The type material is deposited in the Museum für Naturkunde der Humboldt-Universität, Berlin, Germany (ZMHB).

Specimens were examined under a Leica MZ16 stereomicroscope. The male and female genitalia and terminalia were dissected using the technique described by Uhlig & Watanabe (1992). Strongly sclerotised body parts were bleached in a few drops of lactic acid, rinsed in distilled water and dehydrated in propyl alcohol until all the air bubbles disappeared. Dissected parts were mounted on small plastic slides using Marc Andre No 2 medium (Massoud, 1967) and pinned together with the specimen.

Illustrations were made using a drawing tube fitted to a Leica MZ16 stereomicroscope. Illustrations were digitalised as bitmap images and subsequently modified. Photographs were taken via a Leica DFC420 digital camera attached to the microscope.

The cladistic analysis was performed using maximum parsimony in PAUP\* version 4.0b10 (Swofford, 2001). Maximum parsimony searches were conducted using heuristic search methods with stepwise addition of taxa using the TBR branch-swapping algorithm and 100 replicates of random addition of taxa, using the “multiple trees” option in effect, “steepest descent” options not in effect, and branches collapsed if maximum branch length is zero.

Clade confidence values were measured using Bremer support (Bremer, 1988, 1994) and calculated in PAUP\* using a batch file generated by TreeRot (Sorenson & Franzosa, 2007).

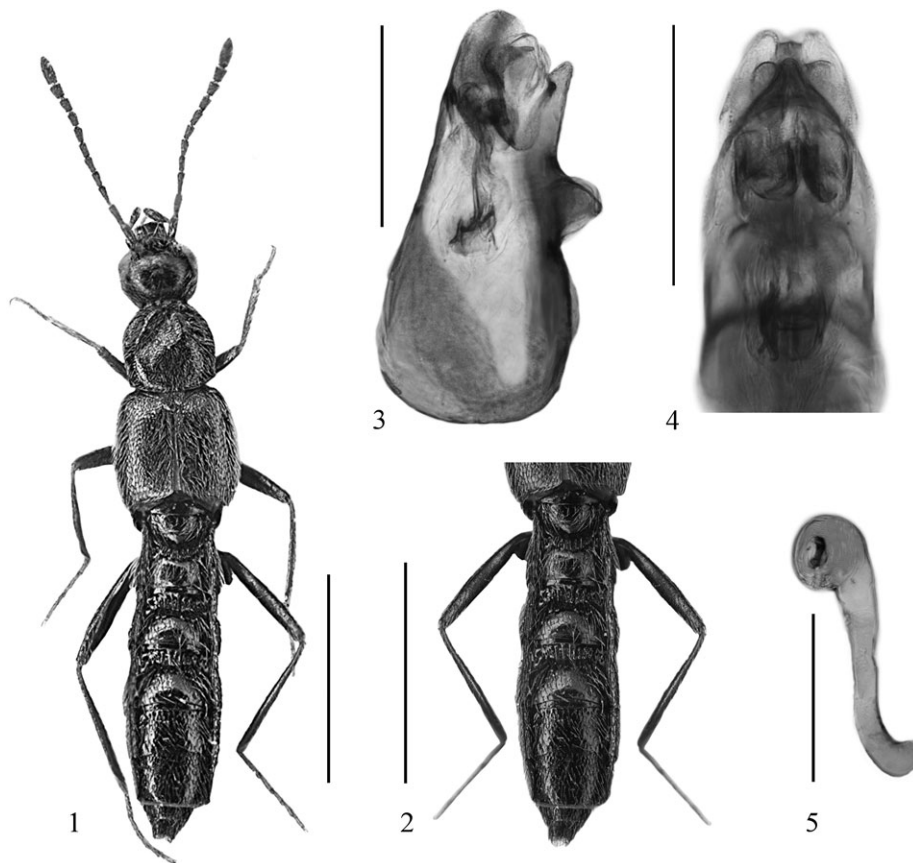
### SYSTEMATICS

#### The *Tachyusa coarctata* species group

**Diagnosis.** The *Tachyusa coarctata* species group includes twenty three species restricted in their occurrence to the Holarctic and Africa. This group is characterized by the following combination of characters: the punctation on abdominal tergites III–V moderately dense, interstices between punctures 1.5–2.0 times their diameter, the punctures small but well visible, the punctation on tergites VI–VII slightly denser than that on tergites III–V, the elytral punctation dense, interstices between punctures equal their diameter, the elytral punctation distinctly asperate, the abdominal pubescence short, dense and subrecumbent and the abdomen moderately glossy.

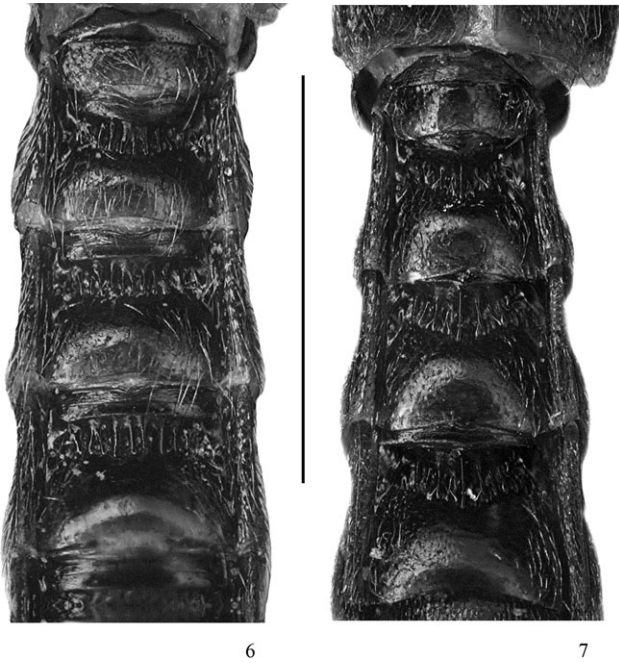
#### Key to species of the *Tachyusa coarctata* group

- 1 Basal transverse impressions of abdominal tergites distinctly V-shaped, with longitudinal ridges that strongly decrease in length laterally, majority of ridges divide posteriorly in two (Fig. 7). . . . . 2
- Basal transverse impressions of abdominal tergites slightly arcuate, C-shaped, with longitudinal ridges that slightly decrease in length laterally, majority of ridges do not fork posteriorly (Figs 2 and 6). . . . . 8



Figs 1–5. *Tachyusa frischi* sp.n.: 1 – habitus; 2 – abdomen; 3 – lateral view of aedeagus; 4 – ventral view of aedeagus; 5 – spermatheca. Scale bars: 1, 2 – 1 mm; 3–5 – 0.2 mm.

- 2 Eyes small, their length shorter than postocular region in dorsal view; pronotal sides strongly converging posteriorly; aedeagal median lobe concave in lateral view, its apex triangular in shape (Figs 52 and 55). . . . . 3
- Eyes large, their length subequal to postocular region in dorsal view; pronotal sides slightly to moderately converging posteriorly; aedeagal median lobe straight in lateral view, its apex rounded (Figs 58, 61, 64). . . . . 4
- 3 Antennomere 3 shorter than 2; elytra short with length at suture shorter than pronotal length at midline; aedeagal median lobe distinctly hooked apically (Fig. 52); aedeagus as in Figs 52–53, spermatheca as in Fig. 54. Distribution: North America. . . . . *T. americana* Casey
- Antennomeres 2 and 3 subequal in length; elytra long with length at suture equal to pronotal length at midline; aedeagal median lobe approximately straight apically (Fig. 55); aedeagus as in Figs 55–56, spermatheca as in Fig. 57. Distribution: North America. . . . . *T. americanoides* Pašnik
- 4 Head flattened dorsally; temples parallel-sided. . . . . 5
- Head convex dorsally; temples broadly rounded. . . . . 6
- 5 Body on average larger, length 2.7–3.0 mm; pronotum brownish red; pronotal surface moderately convex and very deeply impressed medially in male and without impression in female; aedeagus as in Figs 61–62, spermatheca as in Fig. 63. Distribution: North America. . . . . *T. cavicollis* LeConte
- Body on average smaller, length 2.5–2.8 mm; pronotum brown; pronotal surface weakly convex, moderately deeply impressed medially in male and without impression in female; aedeagus as in Figs 64–65, spermatheca as in Fig. 66. Distribution: North America. . . . . *T. obsoleta* Casey
- 6 Pronotum and elytra testaceous; surface of head and pronotum with distinct microsculpture; aedeagus as in Figs 58–59, spermatheca as in Fig. 60. Distribution: United States. . . . . *T. arida* Casey
- Pronotum and elytra brown to black; surface of head and pronotum without or with obsolete microsculpture; genitalia different. . . . . 7
- 7 Antennomeres 2 and 3 subequal in length; elytra brown to pitch brown; aedeagus as in Figs 67–68, spermatheca as in Fig. 69. Distribution: Canada, United States and Mexico. . . . . *T. faceta* Casey
- Antennomere 3 shorter than 2; elytra brown with posterior margin and shoulders yellow; aedeagus as in Figs 70–71, spermatheca as in Fig. 72. Distribution: North America. . . . . *T. smetanai* Pašnik
- 8 Tergites 3–6 deeply transversely impressed at base; tergite 5 more transverse, 1.6–1.8 times wider than long. . . . . 9
- Tergites 3–5 deeply transversely impressed at base; tergite 5 less transverse, 1.25–1.55 times wider than long. . . . . 10
- 9 Eyes large, length of each seen from above subequal to that of postocular region; antennomeres 2 and 3 subequal in length; elytral punctation similar to that on pronotum; aedeagus as in Figs 48–49, spermatheca as in Fig. 50. Distribution: Russian Far East. . . . . *T. sulciventris* Eppelsheim
- Eyes small, length of each seen from above shorter than postocular region; antennomere 3 shorter than 2; elytral punctation finer than that on pronotum; spermatheca as in Fig. 51. Distribution: Russian Far East. . . . . *T. pseudosulciventris* Pašnik
- 10 Elytral length at suture shorter than pronotal length at midline. . . . . 11



Figs 6–7. Abdomens of two species of *Tachyusa* Erichson: 6 – *T. objecta*; 7 – *T. americana*. Scale bar: 0.5 mm.

- Elytral length at suture at least as long as pronotal length at midline. . . . . 12
- 11 Eyes small, length of each seen from above shorter than postocular region; pronotum moderately convex and depressed medially; pronotal hind angles rounded; legs yellow; aedeagus as in Figs 46–47. Distribution: China. . . . . *T. hammondi* Pašnik
- Eyes large, length of each seen from above subequal to that of postocular region; pronotum strongly convex and not depressed medially; pronotal hind angles obtuse; legs reddish brown; aedeagus as in Figs 43–44, spermatheca as in Fig. 45. Distribution: North America. . . . . *T. harfordi* Casey
- 12 Median lobe of aedeagus in lateral view short, subequal to length of apical margin of distal crest (Figs 16, 19). . . . . 13
- Median lobe of aedeagus in lateral view long, distinctly longer than length of apical margin of distal crest (Figs 10, 22, 28). . . . . 15
- 13 Antennomeres 2 and 3 subequal in length; surface of head and pronotum without microsculpture; apex of median lobe of aedeagus in lateral view triangular; aedeagus as in Figs 3–4, spermatheca as in Fig. 5. Distribution: Iran. . . . . *T. frischi* sp. n.
- Antennomere 3 shorter than 2; surface of head and pronotum with obsolete microsculpture; apex of median lobe of aedeagus in lateral view rounded; genitalia different. . . . . 14
- 14 Tergal basal transverse impressions with median carina; pronotum with a lead metallic reflection; tergite 8 lacking isodiametric mesh microsculpture; aedeagus as in Figs 16–17, spermatheca as in Fig. 18. Distribution: western Palaearctic. . . . . *T. concinna* Heer
- Tergal basal transverse impressions without median carina; pronotum without leaden reflection; tergite 8 with isodiametric mesh microsculpture; aedeagus as in Figs 19–20, spermatheca as in Fig. 21. Distribution: China and Russian Far East. . . . . *T. harbinica* Pašnik
- 15 Eyes large, seen from above longer than postocular region; temples strongly narrowed to neck; antennomeres 2 and 3 subequal in length; surface of head and pronotum with

- microsculpture; aedeagus as in Figs 40–41, spermatheca as in Fig. 42. Distribution: Democratic Republic of the Congo. . . . . *T. bertiae* Pašnik
- Eyes small, seen from above subequal in length to postocular region; temples broadly rounded to neck; antennomere 3 shorter than 2; surface of head and pronotum without microsculpture; genitalia different. . . . . 16
- 16 Pronotal punctation very fine and very weakly asperate. . . . . 17
- Pronotal punctation moderately fine and distinctly asperate. . . . . 18
- 17 Pronotum wider than long, moderately convex; elytra as long as wide; aedeagus as in Figs 25–26, spermatheca as in Fig. 27. Distribution: Palaearctic. . . . . *T. objecta* Mulsant & Rey
- Pronotum as long as wide, distinctly convex; elytra longer than wide; aedeagus as in Figs 22–23, spermatheca as in Fig. 24. Distribution: south-west Europe and North Africa. . . . . *T. nitidula* Mulsant & Rey
- 18 Apex of median lobe of aedeagus triangular in lateral view (Figs 10, 13, 28). . . . . 19
- Apex of median lobe of aedeagus rounded in lateral view (Figs 31, 34, 37). . . . . 21
- 19 Pronotum wider than long; median lobe of aedeagus very long, about 3 times longer than apical margin of distal crest and with a bulge at middle in lateral view (Fig. 28); aedeagus as in Figs 28–29, spermatheca as in Fig. 30. Distribution: Caucasus. . . . . *T. flavolimbata* Eppelsheim
- Pronotum as wide as long; median lobe of aedeagus relatively short, about 1.5 times longer than apical margin of distal crest and straight in lateral view (Figs 10, 13); genitalia different. . . . . 20
- 20 Pronotum glossy but without metallic lustre; male and female tergite VIII straight; apex of median lobe of aedeagus not hooked in lateral view (Fig. 10); aedeagus as in Figs 10–11, spermatheca as in Fig. 12. Distribution: Palaearctic. . . . . *T. coarctata* Erichson
- Pronotum with metallic lustre; male and female tergite VIII sinuate apically; apex of median lobe of aedeagus distinctly hooked in lateral view (Fig. 13); aedeagus as in Figs 13–14, spermatheca as in Fig. 15. Distribution: Austria, Bulgaria, Bosnia and Herzegovina, France and Germany. . . . . *T. coarctatoides* Pašnik
- 21 Pronotum wider than long; aedeagus as in Figs 34–35, spermatheca as in Fig. 36. Distribution: China, Japan, North and South Korea. . . . . *T. orientis* Bernhauer
- Pronotum as wide as long; genitalia different. . . . . 22
- 22 Body relatively broad; legs brown; aedeagus as in Figs 31–32, spermatheca as in Fig. 33. Distribution: China. . . . . *T. gilvipes* (Pace)
- Body relatively slender; legs testaceous; aedeagus as in Figs 37–38, spermatheca as in Fig. 39. Distribution: China, Japan and North Korea. . . . . *T. wei* Pace

***Tachyusa frischi* sp. n.**

(Figs 1–5)

**Description**

Body. Length 2.7–3.0 mm, convex, parallel-sided, glossy (Fig. 1); ground colour black; legs brown with reddish tarsi, antennae brown.

Head circular in outline, moderately convex, eyes large, moderately protruding from lateral contours of head, length of each seen from above subequal to that of postocular region; surface of head without microsculpture; punctation fine and dense. Antennae relatively long,

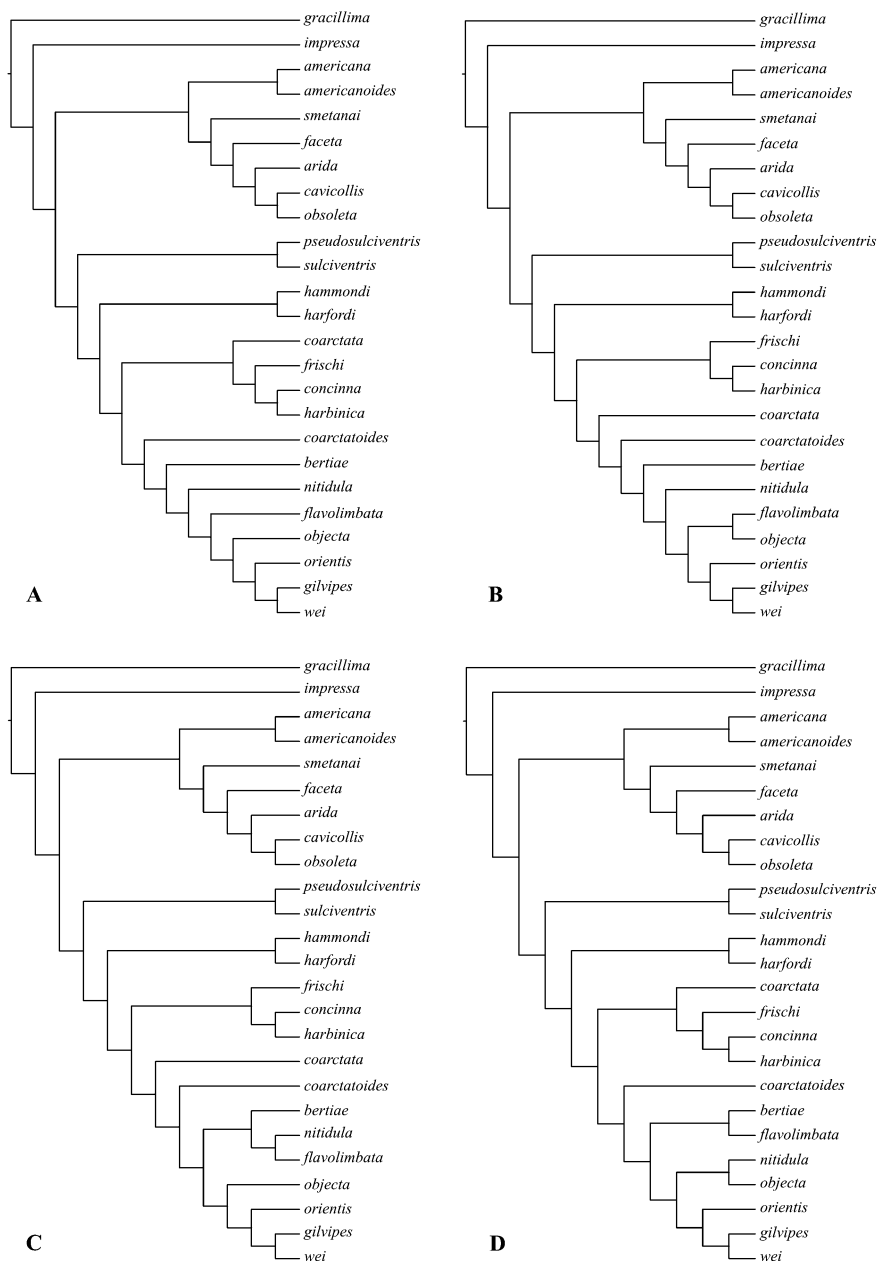


Fig. 8. Four most parsimonious trees resulting from parsimony analyses of the *Tachyusa coarctata* group of species.

extending to base of pronotum, weakly increasing in width apically, antennomeres 2 and 3 subequal in length, antennomeres 4–10 longer than wide, antennomere 11 nearly conical.

Pronotum quadrate, sides straight and gradually converging toward obtuse hind angles; before base with small and shallow transverse impression; surface without microsculpture; punctuation fine, dense and asperate; pubescence at midline directed posteriorly.

Elytra subquadrate, at suture as long as pronotal length at midline; surface lacking microsculpture; punctuation fine, dense and asperate.

Abdomen (Fig. 2) parallel-sided, bases of tergites III–V each with deep transverse impression, impressions with 7–8 longitudinal ridges, tergal punctuation fine and moderately dense, punctures moderately small and well visible, surface without microsculpture.

Male. Aedeagus as in Figs 3–4. Female. Spermatheca as in Fig. 5

**Remarks.** Externally, *Tachyusa frischi* sp. n. is similar to *T. coarctata* Erichson, 1837, but can be distinguished from that species as the antennomeres 2 and 3 are subequal in length (antennomere 3 shorter than 2 in *T. coarctata*) and by the shape of aedeagus: median lobe of aedeagus in lateral view very short, subequal in length to apical margin of distal crest (Fig. 3). In the shape of genitalia, the new species is closely related to *T. concinna* Heer, 1839, but may be separated from that species as the head and pronotum lacks microsculpture, the abdominal basal transverse impressions lack a median carina and the apex of median lobe of the aedeagus in lateral view is triangular (rounded in *T. concinna*, Fig. 16).

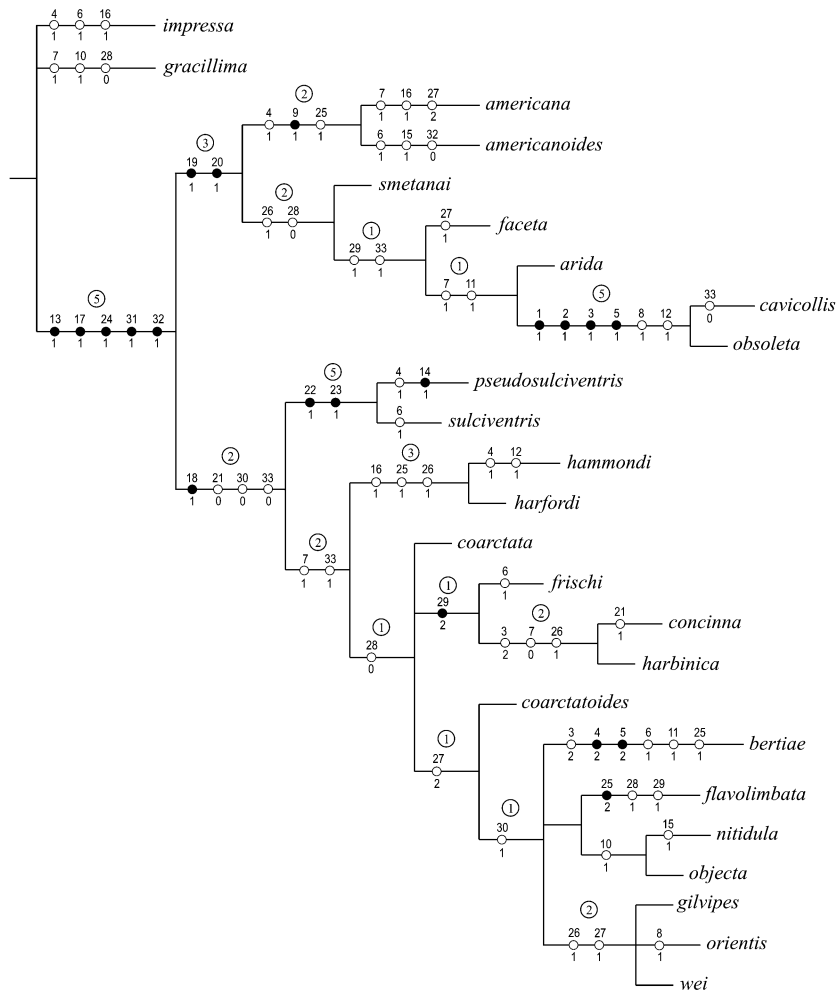


Fig. 9. The strict consensus cladogram of the four most parsimonious trees resulting from the maximum parsimony analysis ( $L = 81$ ;  $CI = 0.48$ ;  $RI = 0.67$ ). Unambiguously placed character changes are mapped on the cladogram. Unique and homoplasious changes are indicated by black and white dots, respectively. The numbers in circles are Bremer support values.

**Etymology.** The species is dedicated to Johannes Frisch (Berlin), specialist of Staphylinidae, who collected this new species and made it available for study.

**Type material.** Holotype: ♂ Iran, Azarbayjan-e Sharqi, Aras Valley at Qara Dagh: Marzaband, 400 m, 10.v.2005, leg. Frisch & Serri (ZMHB); Paratype: 2 ♀ same data as holotype (ZMHB).

#### PHYLOGENY

The twenty three species of *Tachyusa coarctata* species group were included as terminals in the analysis. Representative species of the *Tachyusa impressa* species group (*T. impressa* Eppelsheim, 1877) and *T. constricta* species groups (*T. gracillima* LeConte, 1863) were chosen as outgroups. The tree is rooted with *T. impressa* at its base, a member of the *T. impressa* species group which Pašnik (2006) hypothesized is closely related to the *T. coarctata* species group primarily because they share similar tergal punctation.

All characters were considered as unordered to avoid a priori decision of character state evolution. Unobserved character states are coded with “?” in the matrix. In describing character states no hypothesis is formulated about their transformation, in particular, whether a state is

derived or ancestral. All characters were considered unordered with forward and backward changes equally likely.

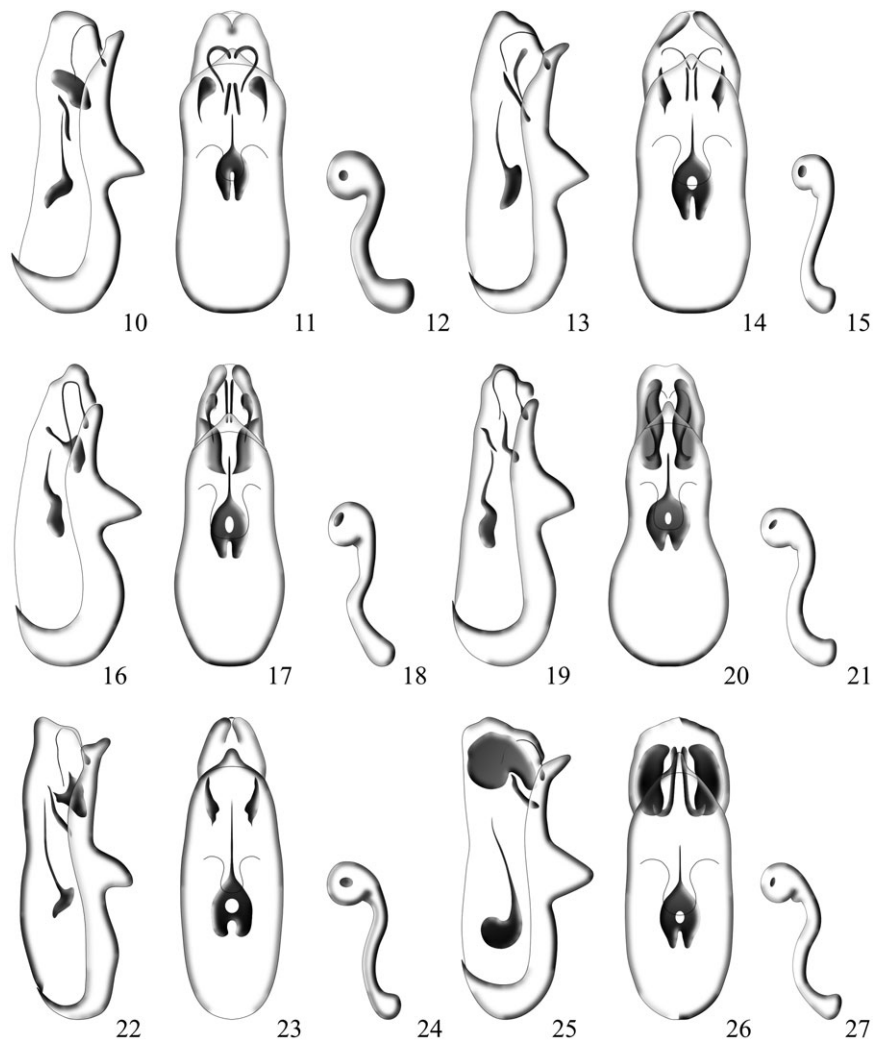
Characters used in the cladistic analyses are listed below. The character matrix is presented in Table 1.

#### Head

1. Convexity: (0) distinctly convex; (1) flattened dorsally.
2. Surface, medial impression: (0) absent; (1) present.
3. Microsculpture: (0) absent; (1) present in male only; (2) present in male and female.
4. Eye length in dorsal view: (0) as long as temples; (1) shorter than temples; (1) longer than temples.
5. Temples: (0) broadly rounded; (1) parallel-sided; (2) strongly converging towards neck.
6. Antennomere 3: (0) shorter than antennomere 2; (1) as long as antennomere 2.
7. Antennomere 10: (0) as long as wide; (1) wider than long.

#### Pronotum

8. Shape: (0) as long as wide; (1) wider than long.
9. Sides: (0) moderately converge towards hind angles; (1) strongly converge towards hind angles.

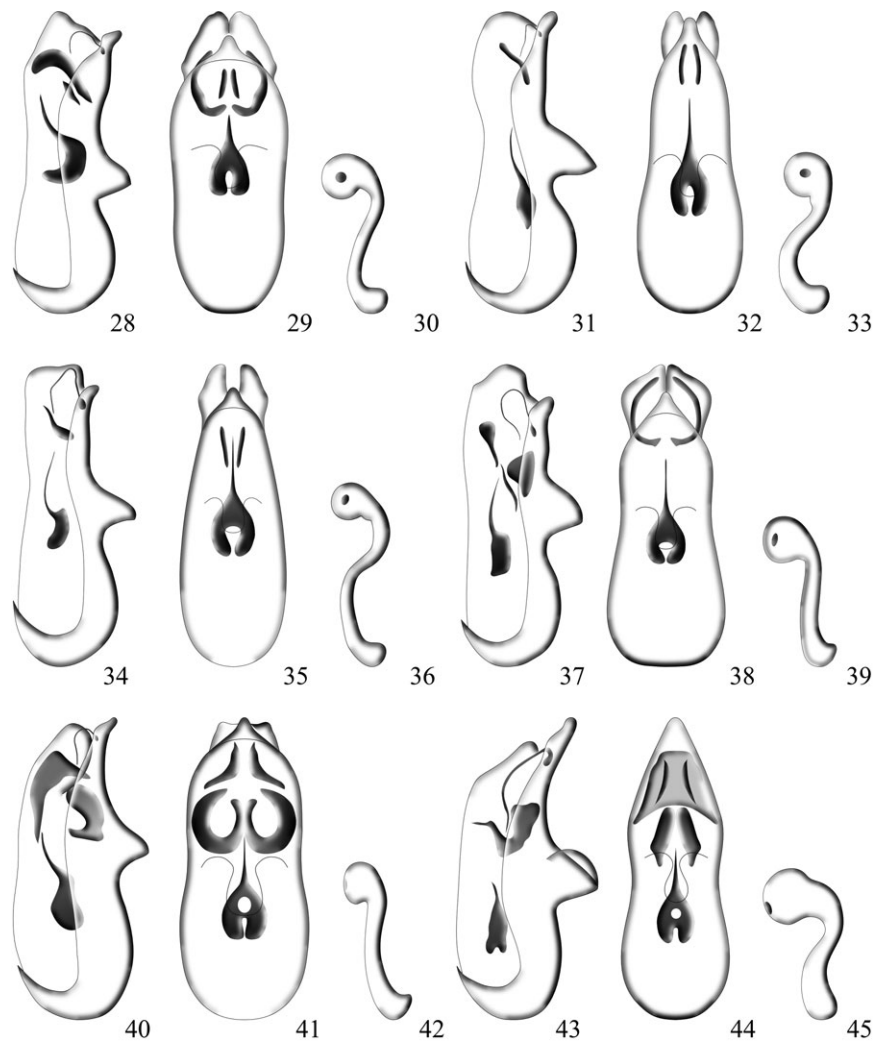


Figs 10–27. Genitalia of the *Tachyusa coarctata* group of species, lateral and ventral views of aedeagus and the spermatheca. 10–12 – *T. coarctata*; 13–15 – *T. coarctatoides*; 16–18 – *T. concinna*; 19–21 – *T. harbinica*; 22–24 – *T. nitidula*; 25–27 – *T. objecta*.

TABLE 1. Data matrix of thirty three characters for the twenty five species, included in the cladistic analysis of the *Tachyusa coarctata* group of species.

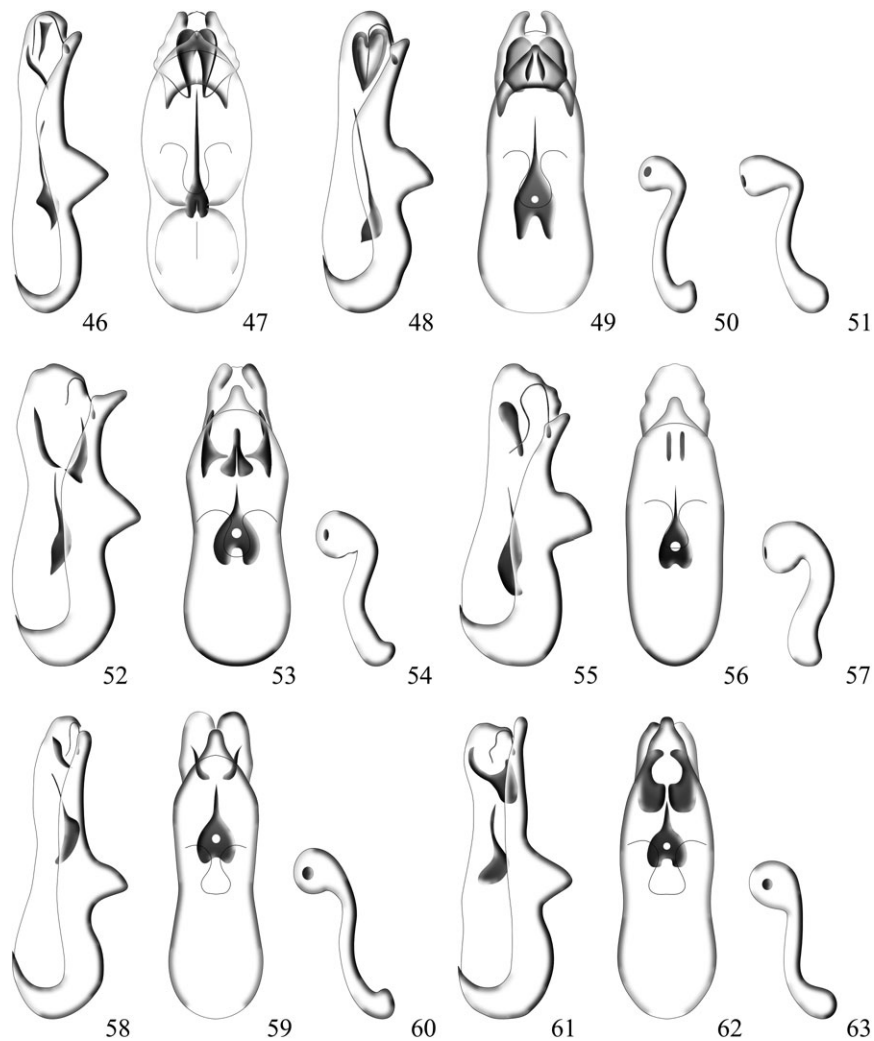
Taxon	Character No.																																		
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33		
<i>impressa</i>	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>gracillima</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>americana</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>americanoides</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>arida</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>bertiae</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>cavicollis</i>	1	1	1	0	1	0	1	1	1	0	0	1	1	1	0	1	0	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1
<i>coarctata</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>coarctatoides</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>concinna</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>faceta</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Flavolimbata</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Frischi</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>gilvipes</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>hammondi</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>harbinica</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>harfordi</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>nitidula</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>objecta</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>obsoleta</i>	1	1	1	0	1	1	1	0	0	1	1	1	1	0	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
<i>orientis</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>pseudosulciventris</i>	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	
<i>smetanai</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>sulciventris</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>wei</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	

- 10. Punctuation: (0) distinctly asperate; (1) not or weakly asperate.
  - 11. Microsculpture in male: (0) without or with obsolete microsculpture; (1) with isodiametric mesh microsculpture.
  - 12. Surface, medial impression: (0) absent; (1) present.
- Elytra
- 13. Punctuation, roughness: (0) not or weakly asperate; (1) distinctly asperate.
  - 14. Punctuation, size of punctures: (0) as on pronotum; (1) much smaller than on pronotum.
  - 15. Shape: (0) quadrate or weakly transverse (ratio width : length 1.0–1.2); (1) longer than wide (ratio width : length 0.9–0.95).
  - 16. Length at suture: (0) as long as pronotal length at midline; (1) shorter than pronotal length at midline.
- Abdomen
- 17. Punctuation on tergites III–V: (0) sparse, interstices between punctures 3.0–4.0 times their diameter; (1) dense, interstices between punctures 1.5–2.0 times their diameter.



Figs 28–45. Genitalia of the *Tachyusa coarctata* group of species, lateral and ventral views of aedeagus and the spermatheca. 28–30 – *T. flavolimbata*; 31–33 – *T. gilvipes*; 34–36 – *T. orientis*; 37–39 – *T. wei*; 40–42 – *T. betriae*; 43–45 – *T. harfordi*.

18. Tergal basal transverse impressions, arrangements of ridges: (0) V-shaped (Fig. 7); (1) straight or slightly arcuate (Figs 2 and 6).
19. Tergal basal transverse impressions, length of ridges: (0) ridges slightly decrease in length laterally (Fig. 6); (1) ridges strongly decrease in length laterally (Fig. 7).
20. Tergal basal transverse impressions, ending of ridges: (0) ridges straight posteriorly (Fig. 6); (1) ridges forked posteriorly.
21. Tergal basal transverse impressions, median carina: (0) absent; (1) present.
22. Tergite VI, basal transverse impression: (0) absent; (1) present.
23. Tergite V, width: (0) slightly transverse, 1.2–1.5 times wider than long; (1) strongly transverse, at least 2.0 times wider than long.
24. Pubescence: (0) sparse; (1) dense.
- Aedeagus**
25. Median lobe in lateral view: (0) straight (Figs 10, 16, 22); (1) concave (Figs 40, 43, 52); (2) bulge in middle (Fig. 28).
26. Median lobe in lateral view: (0) straight (Figs 19, 22, 61); (1) bent ventrally (Figs 48, 55)
27. Apex of median lobe in lateral view: (0) triangular in shape (Figs 13, 25, 52); (1) rounded in shape (Figs 16, 31, 46, 61).
28. Apex of median lobe in lateral view: (0) straight; (1) slightly bent ventrally (Figs 31, 34, 67); (2) distinctly hooked (Figs 13, 25, 52).
29. Median lobe, length in relation to length of apical margin of distal crest (lateral view): (0) 1.5–2.0 times longer than length of apical margin of distal crest (Figs 10, 22, 46); (1) more than 2.5 times longer than length of apical margin of distal crest (Figs 28, 61, 64); (2) subequal in length to apical margin of distal crest (Figs 16, 19).
30. Apex of median lobe in ventral view: (0) slightly pointed (Figs 11, 17, 49); (1) strongly pointed (Figs 29, 41, 56).
- Spermatheca**
31. Capsule: (0) elongate in outline; (1) circular in outline.



Figs 46–63. Genitalia of the *Tachyusa coarctata* group of species, lateral and ventral views of aedeagus and the spermatheca. 46–47 – *T. hammondi*; 48–50 – *T. sulciventris*; 51 – *T. pseudosulciventris*; 52–54 – *T. americana*; 55–57 – *T. americanoides*; 58–60 – *T. arida*; 61–63 – *T. cavicolis*.

32. Duct: (0) straight; (1) bent posteriorly.

33. Shape: (0) L-shaped (Figs 57, 72); (1) S-shaped.

## RESULTS

The analysis of the character state matrix (Table 1) produced four most parsimonious trees with a length = 81, consistency index (CI) = 0.48 and retention index (RI) = 0.67 (Fig. 8).

The trees differ slightly from each other only in the arrangement of terminal taxa (Fig. 8). The strict consensus of these trees, with Bremer support, is presented in Fig. 9, with areas of topological conflict shown as polytomies.

The monophyly of the *Tachyusa coarctata* species group is supported by the distinctly asperate punctation of elytra (character state 13:1); the dense punctation on tergites III–V, with interstices between punctures 1.5–2.0 times their diameter (character state 17:1); the dense pubescence on abdomen (character state 24:1); the spermatheca with circular capsule (character state 31:1) and duct bent posteriorly (character state 32:1). The last two

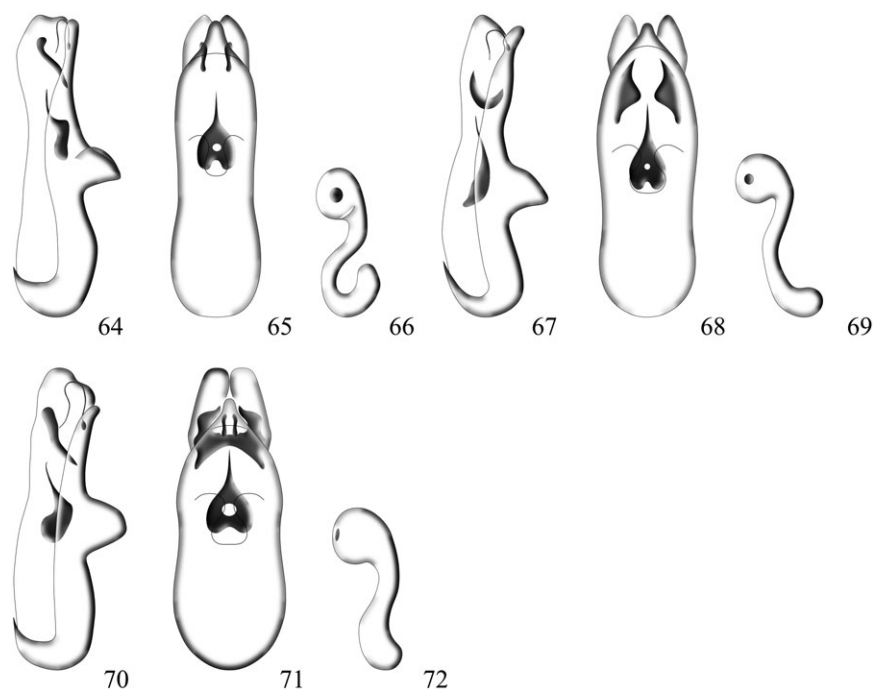
features also occur sporadically in some other species of *Tachyusa*.

The members of *Tachyusa coarctata* species group are subdivided into two main clades. The first clade, which includes *T. americana* through *T. obsoleta* (Fig. 9), is supported by the possession of tergal basal transverse impressions with longitudinal ridges which are forked posteriorly and strongly decrease in length laterally (Fig. 7). This clade includes seven species restricted in distribution to the Nearctic Region. The only Nearctic species that does not belong to this clade is *T. harfordi*, which is in the second clade. The relationships between the species of this clade are fully resolved.

The second clade, from *T. pseudosulciventris* through *T. wei*, includes 14 Palearctic species, one Nearctic species (*T. harfordi*) and one Afrotropical species (*T. bertiae*). This clade is supported by the possession of tergal basal transverse impressions with longitudinal ridges arranged in a straight or slightly arched line.

Within this clade, *T. pseudosulciventris* and *T. sulciventris* form a monophyletic group based on possession of two unique characters among *Tachyusa* species: (1) deep





Figs 64–72. Genitalia of the *Tachyusa coarctata* group of species – lateral and ventral views of aedeagus and the spermatheca. 64–66 – *T. obsoleta*; 67–69 – *T. faceta*; 70–72 – *T. smetanai*.

basal transverse impression on tergite VI and (2) strongly transverse tergite V (at least 1.8 times wider than long versus 1.2–1.5 times wider than long in remaining *Tachyusa* species).

The clade that includes *T. frischi*, *T. concinna* and *T. harbinica* is a group of closely related species well characterized by the shape of their aedeagus: the median lobe of aedeagus in lateral view is very short, subequal in length to apical margin of distal crest.

The clade including *T. coarctata* through *T. wei* is supported by the median lobe of aedeagus not bent ventrally in lateral view. It forms a monophyletic group of species that are very similar morphologically. The members of this clade are coincident in the shape, punctuation, microreticulation of the body and build of abdominal sclerites. The morphological differences between species are very small and often subjective. A reliable identification is not possible without examining the aedeagus. The relationships among these species remain largely unresolved and new characters are required (such as immature stages or molecular data) if the relationships are to be resolved.

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