Female copulatory tubes and the subdivision of the genus *Anthocoris* (Heteroptera: Anthocoridae: Anthocorini)

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**Key words.** Heteroptera, Anthocoridae, *Anthocoris*, copulatory tube, species group

**Abstract.** We report a systematic study of the female copulatory tubes of forty species in the genus *Anthocoris*, most of which are from the Northern Hemisphere. Our results indicate that female copulatory tubes can be used as a reliable character to identify females and analyze phylogenetic relationships in this genus. We propose thirteen species groups based on the copulatory tubes of females, other morphological characters of both sexes, and the previous species groups adopted in the continental faunas.

**INTRODUCTION**

The genus *Anthocoris* Fallén is the second largest genus in the family Anthocoridae of the suborder Heteroptera, which includes about seventy species (Gross, 1954; Henry & Froschener, 1988; Péricart, 1996; Carayon, 2002). As the taxonomy of *Anthocoris* is mostly based on the males, it is hard to identify female specimens to species in some cases, especially in closely related species, due to their similarity in the appearance.

The female copulatory tube in the family Anthocoridae is a secondary copulatory structure that exists in the tribes Anthocorini, Blaptostethini, Oriini and Scolopini. The entrance of this specialized structure is on the surface of the abdominal intersegmental membrane between sterna VII and VIII, very close to the valvulae (Carayon, 1957).

Carayon (1953) studied the copulatory tube of Anthocoridae first and suggested that this special structure might play a role in the temporary storage of sperm. Since then, a number of studies have demonstrated the differences in number, position, and structure of the copulatory tubes in several genera and some species in the family Anthocoridae (Carayon, 1956, 1957, 1961, 1972; Péricart, 1972; Muraleedharan & Ananthakrishnan, 1978; Yasunaga, 1997, 2000; Hernández & Stonedahl, 1999; Bu & Zheng, 2001; Postle et al., 2001; Ke & Bu, 2005).

Recently, the copulatory tube was reported to be stable within species, suggesting the feasibility of using this structure as an important character for identifying females in some genera, such as *Orius* Wolff, *Acompocoris* Reuter and *Tetraphleps* Fieber, and to infer the phylogenetic relationship of the Anthocoridae.

The present study, presents detailed examination of the copulatory tubes of forty species in the genus *Anthocoris*.

**MATERIAL AND METHODS**

**Material**

Some of the specimens examined are deposited in the Institute of Entomology, Nankai University (NKUM); others were on loan from four institutions, whose names are listed in acknowledgements.

**Method for preparing copulatory tubes**

Relax the specimen with a relaxing reagent (Ethanol 100 ml, distilled water 75 ml, Benzene 10 ml, Ethyl acetate 10 ml) for 3–5 min. Separate the abdomen from the thorax with a dissecting needle, place the abdomen into 1% KOH and heat it with boiling water for 20–30 min (the duration of heating may be adjusted according to the freshness of specimens, the hardness of the body wall etc.) to dissolve muscles and other tissues in the abdomen. Dye the abdomen with a solution of Chlorazol black for a few minutes; rinse with clean water once or twice; tear terga I to VII along the suture between terga and sterna with forceps and a dissecting needle; remove sterna II to VII leaving the intersegmental membrane between sterna VII and VIII.

Keep the intersegmental membrane connected to sternum VIII with boiling water for 20–30 min (the duration of heating may be adjusted according to the freshness of specimens, the hardness of the body wall etc.) to dissolve muscles and other tissues in the abdomen. Dye the abdomen with a solution of Chlorazol black for a few minutes; rinse with clean water once or twice; tear terga I to VII along the suture between terga and sterna with forceps and a dissecting needle; remove sterna II to VII leaving the intersegmental membrane between sterna VII and VIII. Keep the intersegmental membrane connected to sternum VIII to obtain a complete copulatory tube along with the genital segment. After drawing, the genital segment with the copulatory tube and other parts of the body should be preserved in a vial containing glycerin and the original label attached.

**RESULTS**

The copulatory tube of *Anthocoris* can be divided into two parts, a basal duct and an apical sac (Fig. 1). The duct is usually tubular and attached to the upper or lower surface, or the folded edge of abdominal intersegmental membrane (Fig. 2) between sterna VII and VIII, extending forwards to abdominal segment IV or III. The sac usually resembles a sphere or an ellipsoid and connects to the apical part of the duct.

Careful examination of forty species of *Anthocoris*, revealed distinct differences between the copulatory tubes of different species of *Anthocoris* in the following characters: the site where the duct joins the bulb, the length, texture and diameter of different parts, the number and degree of twist, and other special structures near the place where the duct and the sac are connected. The size and shape of the sac is not constant, even in same species, and can be altered during the preparation process. This reduces the taxonomical importance of the sac, so this...
character is not described in the following text. Based on the examination of forty species, we divide the copulatory tubes into ten types, described below.

**A. albiger type**

Duct very long, coiled; attached to extreme right of lower surface of intersegmental membrane between sterna VII and VIII; diameter of basal 3/4 slightly variable; a short section apparently thickened at apical 1/4, then thinned abruptly, sclerotized and reaching the sac; a relatively long apical section enters into the sac.

1. **A. albiger** (Fig. 3)

Duct length 1.9 mm; the thickening at apical 1/4 very short, twice as wide as basal 3/4; apical 1/8 of the whole duct entered into the sac, forms a U-turn and thickens gradually to sub-apex, then thinned abruptly at apex.

2. **A. whitei** (Fig. 4)

Duct length 2.5 mm; thickened section at apical 1/4 longer than that of *A. albiger*, more than twice diameter of basal 3/4; apical 1/12 enters into the sac, forms an arch, diameter of apical 1/12 hardly varies.

**A. alpinus type**

Duct usually with a few twists with many transverse rugosities on the wall; attached to extreme left of intersegmental membrane between sterna VII and VIII; basal section never dilated; apical section sclerotized and enters into the sac.

3. **A. alpinus** (Fig. 5)

Duct length 0.5 mm; attached to lower surface of intersegmental membrane; rugosities fine and dense; the whole duct thins gradually from base to apex.

4. **A. kerzhneri** (Fig. 6)

Duct thick; length 0.9 mm; attached to lower surface of intersegmental membrane; diameter of the whole duct nearly constant; wall of basal half slightly thin, with fine rugosities; wall of following 1/3 thickened, without rugosity; apical 1/6 sclerotized, nearly half of the sclerotized part enters into the sac.
5. *A. qinlingensis* (Fig. 7)

Intersegmental membrane between sterna VII and VIII with a thick apophysis on the left edge. Duct thick; length 0.7 mm; attached to upper surface of intersegmental membrane, left to the apophysis; the whole duct thins gradually from base to apex, rugosities fine; apical 1/8 sclerotized, most of the sclerotized section enters into the sac.

6. *A. zoui* (Fig. 8)

Duct length 1.1 mm; attached to lower surface of intersegmental membrane; basal 3/5 very thick with rough rugosities; apical 2/5 thinned, smooth without rugosity; subapical section connected with the sac sclerotized, thinnest; apical 1/10 enters into the sac.

**A. chibi type**

Duct short, attached to the left upper surface of intersegmental membrane between sterna VII and VIII; apical part sclerotized slightly. Sac with strongly sclerotized annular structure encircling the junction of duct and sac; the wall of sac within the annular structure thickened.

7. *A. chibi* (Fig. 9)

Duct length 0.4 mm; base to subapex thins gradually; apical ending thickened slightly.

8. *A. notatotibialis* (Fig. 10)

Duct length 0.6 mm; with a few twists; basal 1/4 much thicker than the rest; sub-basal to subapical part thins gradually; apex thickened.

The copulatory tubes are very similar between these two species, but they are different in the degree of twists, the variation in diameter and the length of the duct.

9. *A. fulvipennis type*

Duct attached to the right or extreme right of lower surface of intersegmental membrane between sterna VII and VIII. Duct divided clearly into two segments, basal half and apical half. Basal half thick and compressed, more or less transformed into a spoon-like structure, the wall of spoon handle thin and the wall of spoon bowl thick; apical half extended from the middle of the spoon bowl, tubular, with thick wall, usually thinner than basal half.

10. *A. nigripes* (Fig. 12)

Duct length 0.7 mm; attached to right lower surface of intersegmental membrane; basal half of spoon handle thick, narrowing near spoon bowl, spoon bowl relatively long and strongly curved; apical half thins gradually towards the subapical section, apical 1/4 thickened slightly and sclerotized.

11. *A. rufotinctus* (Fig. 13)

Duct length 0.6 mm; attached to extreme right lower surface of intersegmental membrane; basal half of spoon handle thins gradually towards the subapical section, apical part thickened and sclerotized. The wall of sac thickened around the junction with the duct.

Figs 12–18: Copulatory tubes of *Anthocoris* spp. 12 – *A. nigripes*; 13 – *A. rufotinctus*; 14 – *A. variipes*; 15 – *A. bakeri*; 16 – *A. confusus*; 17 – *A. gylla*; 18 – *A. japonicus*. Scale = 0.1 mm.
12. *A. variipes* (Fig. 14)

Duct length 0.8 mm; attached to right lower surface of intersegmental membrane; spoon handle of basal half thinned gradually to spoon bowl, spoon bowl long and strongly curved; diameter of apical half nearly same, apical part thickened slightly and sclerotized.

*A. gallarumulmi* type

Intersegmental membrane between sternae VII and VIII often with some thick apophyses. Duct usually long, with a lot of twists, attached near the middle edge of intersegmental membrane; diameter of the whole duct varied little in most species; apical part sclerotized, often slightly entering the sac. Two, four or six wire-like short tubules with rough outer surfaces often on the sac, very close to the apex of the duct; their apices opening into the abdominal cavity; function uncertain.

13. *A. bakeri* (Fig. 15)

Lower surface of intersegmental membrane expanded extensively, forming a flat apophysis. Duct thin, length 1.2 mm; attached to the place near the middle edge of the apophysis; basal section slightly sclerotized, turned to the right, then bent to the left. Sac with two tubules near the junction of duct and sac.

14. *A. confusus* (Fig. 16)

Intersegmental membrane with an apophysis at each side. Duct thin; length 1.5 mm; attached to the middle of intersegmental membrane.

15. *A. gallarumulmi* (Fig. 17)

Intersegmental membrane with an arched apophysis at each side. Duct length 0.9 mm; attached to left edge of intersegmental membrane, then turned to the right; thickened at basal 1/7, two times as thick as the rest of duct. Sac with an elliptical vesicle within enclosing apical section of duct; four tubules surrounding subapical section of duct symmetrically.

16. *A. japonicus* (Fig. 18)

Duct thin; length 1.4 mm; attached to left edge of intersegmental membrane; basal part turned to the right, then bent left; apical section slightly thickened.

17. *A. minki* (Fig. 19)

Apophysis at each side of intersegmental membrane with a rough edge. Duct length 0.9 mm; attached to the middle of intersegmental membrane; basal part bent to the right horizontally, then turned to the left; the whole duct except apical part narrows gradually to apex; apical part thickened slightly. Sac with two tubules near the junction of duct and sac.

18. *A. sarothamni* (Fig. 20)

Intersegmental membrane with arched apophysis on extreme right margin. Duct length 1.2 mm; attached near the middle edge of intersegmental membrane; basal 1/7 thick, with some transverse rugosities; rest relatively thin, without rugosity. Sac with two tubules near the junction of duct and sac.

19. *A. simulans* (Fig. 21)

Apophysis at each side of intersegmental membrane with a rough edge. Duct length 0.9 mm; attached to the middle of intersegmental membrane, basal part thinner than the rest, slants towards the left, then bent to the right. Sac with two tubules near the junction of duct and sac.
The copulatory tubes are very similar in *A. minki* and *A. simulans*, but they are different in the diameter of basal section of the duct, and how they bend in the basal and sub-basal parts of the duct.

20. *A. takahashii* (Fig. 22)

Duct length 0.6 mm; attached to left of upper surface of intersegmental membrane, extended rightwards, then bends to the left; basal 1/3 much thicker than rest, rest very thin; apical part thickened slightly, connected with a gourd-shaped vesicle in the sac. Sac with two tubules near the junction of duct and sac.

21. *A. ussuriensis* (Fig. 23)

Intersegmental membrane with an apophysis at each side of lower surface. Duct length 1.2 mm; attached to the middle of intersegmental membrane, basal and apical parts slightly thicker than rest.

22. *A. visci* (Fig. 24)

Duct length 1.2 mm; attached to the middle of intersegmental membrane, thinned gradually to apex; basal part with many rough transverse rugosities; rest relatively smooth with a few fine rugosities. Sac with the wall around where it connects with the duct thickened and bulged; on the bulge, six tubules encircled the junction of duct and sac.

23. *A. miyamotoi* type

Duct attached to middle of intersegmental membrane between sterna VII and VIII; apical part of duct or the whole duct except basal part extremely thin, wire-like, smooth and sclerotized.

24. *A. dividens* (Fig. 25)

Duct length 0.3 mm; attached to middle of upper surface of intersegmental membrane; with a few twists; basal 1/3 relatively thick; apical 2/3 wire-like.

24. *A. miyamotoi* (Fig. 26)

Duct length 0.7 mm; attached to middle of lower surface of intersegmental membrane; lot of twists; diameter of whole duct varied markedly; basal 1/5 thick; middle 3/5 thinned, about 2/5 as thick as basal part; apical 1/5 wire-like. Sac connected to wire-like section of duct.

Although we dissected as many specimens of *A. miyamotoi* as we could, no trace of the sac at the end of duct was seen. The sac probably broke off during the dissections.

*A. nemoralis* type

Intersegmental membrane between sterna VII and VIII with thick, rough-edged apophyses at both sides. Whole duct long; attached to left of lower surface of intersegmental membrane; lot of twists; basal part dilated, cystiform; rest thins gradually subapically; apical section sclerotized, partially entering into the sac.
25. *A. butleri* (Fig. 27)

Duct length 1.2 mm; basal part irregularly cystiform; wall of subapical 1/8 a little thinner, densely covered with rough transverse rugosities; apical part entering into the sac and connecting with its internal gourd-shaped vesicle.

26. *A. nemoralis* (Fig. 28)

Duct length 1.2 mm; basal part regularly cystiform, apical part that enters into the sac thickens abruptly, then thins gradually.

**A. nemorum** type

Duct attached to left or extreme left of intersegmental membrane between sterna VII and VIII; diameter of whole duct varies a little; usually with a few twists. Sac with wire-like tubules similar as those of *A. gallarumulmi* type near junction of duct and sac, except sac of *A. musculus* with four tubules congregated into two pairs, other four species with two tubules.

27. *A. antevolens* (Fig. 29)

Duct length 0.7 mm; attached to left of lower surface of intersegmental membrane.

28. *A. limbatus* (Fig. 30)

Interalsegmental membrane with an apophysis near middle of edge. Duct length 0.5 mm; attached to left lower surface of intersegmental membrane; apical 1/6 sclerotized, slightly enters into the sac.

29. *A. montanus* (Fig. 31)

Interalsegmental membrane with small apophysis in middle of edge. Duct length 0.7 mm; attached to extreme left of lower surface of intersegmental membrane; whole duct with fine transverse rugosities on the wall; apical 1/6 sclerotized, most of the sclerotized part enters into the sac.

30. *A. musculus* (Fig. 32)

Duct length 0.5 mm; attached to left of lower surface of intersegmental membrane; thins slightly and gradually to apex; basal 1/2 with fine transverse rugosities on wall; apical 1/2 without rugosity.

31. *A. nemorum* (Fig. 33)

Duct thin, length 0.6 mm; attached to left of upper surface of intersegmental membrane; whole duct with fine transverse rugosities on wall; apical 2/7 sclerotized; 2/3 of sclerotized part enters into the sac, bent slightly.

**A. sibiricus** type

Whole duct short; attached to left edge of intersegmental membrane between sterna VII and VIII; duct thin except basal and apical parts; basal part dilated; apical part widens gradually, campaniform or speaker-like. Sac with a strongly sclerotized annular structure encircling junction of duct and sac; wall of the sac within the annular structure thickened.

32. *A. pilosus* (Fig. 34)

Duct length 0.5 mm; basal 1/5 extends to the right horizontally, about 3 times as thick as middle 3/5, then duct narrows; apical 1/5 speaker-like.

33. *A. sibiricus* (Fig. 35)

Duct length 0.4 mm; basal 1/3 extends to the right horizontally; 4 times as thick as middle 1/2; apical 1/6 speaker-like.

The copulatory tubes are very similar in *A. sibiricus* and *A. pilosus*, but they are differing in the degree of dilation of basal part and proportion of dilated basal part compared to the whole length of the duct.

Péricart (1972) considered *A. pilosus* to be a junior synonym of *A. sibiricus*. Elov & Kerzhner (1977) retained their species levels. The differences in the copu-
latory tubes between these two species in our study also indicates that they are different species.

34. *A. tomentosus* (Fig. 36)

Duct length 0.4 mm; basal 1/10 dilated, about 2.5 times thickness of middle 4/5; apical 1/10 thickened, campaniform.

*A. thibetanus* type

Whole duct short; attached to middle or middle edge of intersegmental membrane between sterna VII and VIII; basal part usually dilates into various shapes.

35. *A. armatus* (Fig. 37)

Duct length 0.3 mm; attached to the middle of lower surface of intersegmental membrane; basal part expanded extremely, forms a flat, approximately semi-circled structure; the rest thin; diameter of duct except basal part hardly varies. Sac with two tubules near the junction of duct and sac.

36. *A. atricornis* (Fig. 38)

Duct length 0.4 mm; attached to middle of lower surface of intersegmental membrane; basal part dilated apparently, forms a flat, shovel-like structure, about 4 times as wide as middle part; diameter of duct constant except for basal part.

37. *A. dimorphus* (Fig. 39)

Duct length 0.3 mm; attached to middle of lower surface of intersegmental membrane; basal half thicker than apical half, thins gradually from base to middle; apical half with same diameter, about 1/2 times as thick as base. We only saw a trace of the sac at the end of duct in a few specimens (including paratypes) examined. The sac probably broke off during the dissection.

38. *A. hirsutus* (Fig. 40)

Duct length 0.3 mm; attached to middle of lower surface of intersegmental membrane; basal part dilated apparently, forms an acute triangular, sheet-like structure; sub-basal to middle thins gradually, generally thicker than apical half, apical half thin with same diameter. We only saw a trace of sac at the end of duct in the specimens dissected. The sac probably broke off during the dissection.

39. *A. hsiaoii* (Fig. 41)

Duct length 0.5 mm; attached to middle edge of intersegmental membrane; basal part dilated apparently, forms an obtuse triangle; whole duct except basal part thin with same diameter.

40. *A. thibetanus* (Fig. 42)

Duct length 0.7 mm; attached to middle edge of intersegmental membrane; basal part greatly expanded, irregular, vesica-shaped with many rough rugosities, alternated between dark and pale stripes on wall; base of tubular part extended rightward from the middle of the vesica-shaped structure, then thins gradually to subapex; apical part thickened slightly, connected to the sac by a sclerotized annular structure.

**Analysis**

In the ten types of copulatory tubes of *Anthocoris*, *A. alpinus* type is probably the plesiomorphic form, but it is hard to determine how it had been transformed into the other types. The homologous characters of the ten types of copulatory tubes described above, however, show the following transformations.

**Duct**

I. Basal part: tubular, not dilated – 0; tubular, dilated – 1; cystiform – 2.
II. Middle part: tubular, neither thick or thin – 0; with abrupt dilation – 1; more or less spoon-like – 2.
III. Apical part: neither thick or thin – 0; widening slightly – 1; widening – 2; narrowing slightly – 3; wire-like – 4.
IV. Texture of the apical duct wall: not sclerotized – 0; sclerotized – 1.
V. Junction between duct and sac: connects directly – 0; enters into sac, apex open – 1; enters into the sac, apex connected with a vesicle – 2.

**Sac**

VI. Near the junction of duct and sac: without any particular structures – 0; membrane thickened – 1; with a sclerotized annular structure – 2; with pairs of short tubules – 3.

The distribution of the six characters in the ten types of copulatory tubes is summarized in Table 1.

**Table 1. Distribution of six characters in the ten types of copulatory tubes.**

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<th>Types characters</th>
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**Conclusions**

1. The structures of the female copulatory tubes of the genus *Anthocoris* vary between species, but are stable within a species, suggesting they may be of use in identifying females at species level.
2. The copulatory tubes of the forty species can be divided into ten types, and employed for subdivision of the genus *Anthocoris*.
3. The copulatory tubes are useful for the phylogenetic study of the genus.

**Subdivision of the genus *Anthocoris***

The subdivision of the genus *Anthocoris* is poorly studied on a worldwide scale. Hill (1957) divided the six
North American species into three groups according to body form, color and male genitalia. Péricart (1972) investigated Anthocoridae of the West Palaearctic region, and grouped fifteen species into six groups and one particular species based on characters of the fore wing, sternum II of the abdomen and male genitalia. Accepting Péricart (1972)’s groups and adding more species, Bu & Zheng (2001) grouped thirty-seven species from China into nine groups. The above three papers dealt with a total of fifty-two species.

Using body form, color pattern, luster and pubescence of fore wing, morphology of sternum II and III of abdomen, male genitalia, and the female copulatory tubes of forty species, of which thirty-six species had been considered previously, four species from North America, fifty-six species from the Holarctic region, northern parts of the Oriental and Neotropical regions were divided into thirteen groups.

A comparison of the species grouping in the present paper and the former three papers is shown in the following table (Table 2). For clarity, previous groups are placed in the groups adopted here.

Compared with the former species groupings, we studied more species from more regions and used copulatory tubes to determine our species grouping. Here, seven groups are consistent with the previous groupings. Due to the lack of specimens of the alienus group of Péricart (1972), and unsuccessful dissection of specimens from the angustatus group of Bu & Zheng (2001), we retained these two groups. Combination and rearrangement of previous groups and addition of a new one resulted in the following subdivision of Anthocoris:

**A. albiger group**

Body slender. Pubescence on hemelytron relatively dense, decumbent or semi-erect. Clavus and inner portion of endocorium dull; outer portion of endocorium, exocorium and cuneus shiny. Sternum II or III of abdomen without membranous area. Paramere lamellate, without longitudinal groove. Copulatory tube of A. albiger type. Western and southwestern areas of North America; two species: *A. albiger* Reuter, 1884 and *A. whitei* Reuter, 1884.

**A. alienus group**

Body relatively narrow and elongate. Clavus more or less dull brown; corium and cuneus shiny. Sternum II of abdomen with a pair of membranous areas. Paramere lamellate, without longitudinal groove, with an obtuse dentation at inner margin. Copulatory tube has never been studied. Western Palaearctic region. Two species: *A. alienus* (White, 1880) and *A. salicis* Lindberg, 1953.

**A. angustatus group**


**A. chibi group**

Body relatively small, elongately oval. Pubescence on hemelytron mostly decumbent, with a few erect or semi-erect hairs, more or less curved. Clavus and endocorium dull, with silvery white pubescence; exocorium and cuneus strongly shiny, with golden brown pubescence. Sternum II of abdomen with a pair of kidney-shaped membranous areas. Paramere slender, most of outer margin reflexed, apical portion slightly curving inward. Copulatory tube of *A. chibi* type. The eastern part of Asia, two species: *A. chibi* Hiura, 1959 and *A. notatotibialis* Bu & Zheng, 2001.

**A. confusus group**

Body elongately oval. Pubescence on hemelytron semi-erect. Clavus, inner portion or the whole endocorium dull, sometimes inner portion of exocorium also dull. Sternum II of abdomen with a pair of membranous areas. Paramere

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<td><em>A. nemoralis</em> group</td>
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<td><em>A. nemorum</em> group</td>
<td>Group I</td>
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<tr>
<td><em>A. sibiricus</em> group</td>
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<td><em>A. thibetanus</em> group</td>
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<td>thibetanus group</td>
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**A. flavipes** group


**A. fulvipennis** group


**A. gallarumulmi** group


**A. miyamotoi** group

Body narrowly elongate. Callar area relatively extensive and strongly swollen, post-callar depression deep; posterior lobe of pronotum smooth, not rugulose. Hemelytron shiny, with long, sparse pubescence; outer part of median portion in clavus and endocorium, median portion of exocorium, areas around cuneal suture light in color and transparent; other areas of hemelytron shiny, blackish brown. Sternum III of abdomen with a pair of kidney-shaped membranous areas. Paramere lamellate or sinuate, without longitudinal groove. Copulatory tube of A. miyamotoi type. Eastern part of Asia; two species: A. dividenis Bu & Zheng, 2001 and A. miyamotoi Hiura, 1959.

**A. nemoralis** group


**A. nemorum** group


**A. sibiricus** group


**A. thibetanus** group


The new grouping proposed here includes about eighty percent of the species of Anthocoris. Due to the lack of specimens, 15 species were not studied: A. annulipes Poppius, 1909, A. excelsus Péricart, 1987 and A. indicus Poppius, 1909 (Oriental region); A. angularis Reuter, 1884, A. caucasicus Kolenati, 1857, A. kalopanacis Kerzhner, 1976, A. poissoni Kirishchenko, 1952 and A. similimus Poppius, 1909 (Palaearctic region); A. dimor-
phicus Anderson & Kelton, 1963 and A. tristis Van Duze, 1921 (Nearctic region); A. dentipes Champion, 1900 and A. varicicornis Champion, 1900 (Neotropical region); A. austropiceus Gross, 1954 and A. pacificus Kirkaldy, 1908 (Australian region); A. nitidulus Poppius, 1920 (Afrotropical region).

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