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SYSTENA CHEVROLAT (COLEOPTERA: CHRYSOMELIDAE: ALTICINAE): NOTES ON NOMENCLATURE, REDESCRIPTION OF THE GENUS, AND A PRELIMINARY DISCUSSION OF CHARACTERS AND PHYLOGENETIC RELATIONSHIPS

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Abstract.—A summary of the taxonomic history for *Systena* Chevrolat (Coleoptera: Chrysomelidae: Alticinae) is presented. Detailed discussion and illustration of morphological characters are presented based on stereo, compound, and scanning electron microscopy of dissected exemplar specimens for eight species of *Systena* from North, Central, and South America. A discussion of putative relationships of *Systena* to other alticine genera is presented.

Key Words: *Systena,* Alticinae, Chrysomelidae, adult, morphology, character, nomenclature, systematic, flea beetle, leaf beetle

To help provide a foundation for future generic-level phylogenetic studies in Alticinae, a nomenclatural discussion and detailed morphological redescription with preliminary phylogenetic discussion are provided for *Systena.* Although the genus *Systena* was proposed in 1836, the first discussion of morphological characters of the genus was presented by Clark (1865). However, as is typical of many early works, the characters he used were superficial and not extremely useful considering the paucity of knowledge of character distribution among Alticinae on a worldwide level. When characters are viewed in this context, as we aspire to do here, their value as diagnostic and evolutionary indicators is greatly enhanced.

TAXONOMIC HISTORY

Systena was proposed by Chevrolat (1836:390). Heikertinger and Csiki (1939) and Blackwelder (1946) incorrectly attribute authorship of *Systena* to Melsheimer (1847), who indicated Chevrolat as author of *Systena.* In Melsheimer (1847), one additional species, *Systena blanda,* was described, but no other species were listed. Chevrolat (1848) stated that *Systena* was proposed by "us" (meaning himself) and adopted by Dejean. In this work, *Systena s-littera* (Linnaeus) and *S. vittata* (Fabricius) were mentioned as additional members of the genus. Clark (1865) in his examination of South American Alticinae provided the first characterization of *Systena,* and probably for this reason, Gemminger

Table 1. Character state information for the eight *Systena* species used for the generic characterization. Character numbers refer to text. Symbol, "+" indicates that both states present or too difficult to interpret.

↘Taxa Characters→	5	10	15	20	23
Systena blanda (Melsheimer)	00101	00030	010+0	+0000	000
Systena carri Blake	00001	00020	01000	10??0	???
Systena championi Jacoby	00001	01020	01000	00010	000
Systena elongata Fabricius	00000	00020	01000	00010	000
Systena frontalis (Fabricius)	00001	00030	01000	00110	000
Systena marginallis (Illiger)	00001	00020	01000	00000	000
Systena oberthuri Baly	+0001	00030	01000	+0000	001
Systena s-littera (Linnaeus)	00001	00020	01000	+0000	000

and von Harold (1874), Hatch (1927), Horn (1889), and Leng (1920) considered him to be the author of the genus. However, the mere use of one or more available species-group names in combination or clearly included under a new genus-group name (as done by Chevrolat 1836), is sufficient for availability for names published before 1931 (ICZN [1985] Article 12 b-5; summarized in Barber and Bridwell 1940). Other authors who also correctly attribute to Chevrolat authorship of *Systena* include Chapuis (1875), Crotch (1873), Seeno and Wilcox (1982), and Poole and Gentili (1996). *Systena frontalis* (Fabricius) was designated as the type species by Monrós and Bechyné (1956).

METHODS

The discussion of the adult characters and terminology follows that of Konstantinov and Lopatin (1987), Konstantinov (1994) and Konstantinov and Vandenberg (1996). Hind wing terminology follows Kukalová-Peck and Lawrence (1993, Fig. 36) since they provided the most explicit hypotheses of homology based on examination of all beetle families. Metafemoral spring terminology follows Furth (1982). Many characters are described here for the first time. Morphological characters are based on at least two examples of dissected, disarticulated specimens of *Systena blanda* (Melsheimer), *S. carri* Blake, *S. championi* Jacoby, *S. elongata* Fabricius, *S. frontalis* (Fabricius), *S. marginallis* (Illiger), *S. oberthuri* Baly, and *S. s-littera* (Linnaeus). These taxa which occur in North, Central, and South America are suggested to represent the spectrum of morphological diversity for *Systena*. Characters, many of which are described for the first time in Chrysomelidae, are discussed in detail below. A subset of the characters and states is coded in Table 1 to explicitly indicate variability or constancy within *Systena*. The appendix provides a brief description of the characters and states used in Table 1.

Characters of adult exemplars were examined using a Leica MZ-APO stereoscope, Leitz Diaplan compound microscope fitted with transmitted light interference contrast apparati (ICT), and an AMRAY 1810 scanning electron microscope. To ease examination of sclerotized features, adult specimens were partially disarticulated and placed in hot KOH for several seconds. Stereo and compound microscopic illustrations were made using camera lucidas. Images were scanned at 600 dpi using a Nikon Scantouch scanner and enhanced using Adobe Photoshop 3.0 and labeled using Macromedia Freehand 5.5 on a Power Macintosh 8500/132 with 50 megabytes RAM.

REDESCRIPTION OF *SYSTENA* CHEVROLAT

Body (Fig. 1): Moderately elongate, flat in lateral view. Body length/width ratio as measured by length of elytra divided by greatest width, ranging from 1.42 (*S. s-littera*)–1.91 (*S. oberthuri*). Elytron without apical declivity.

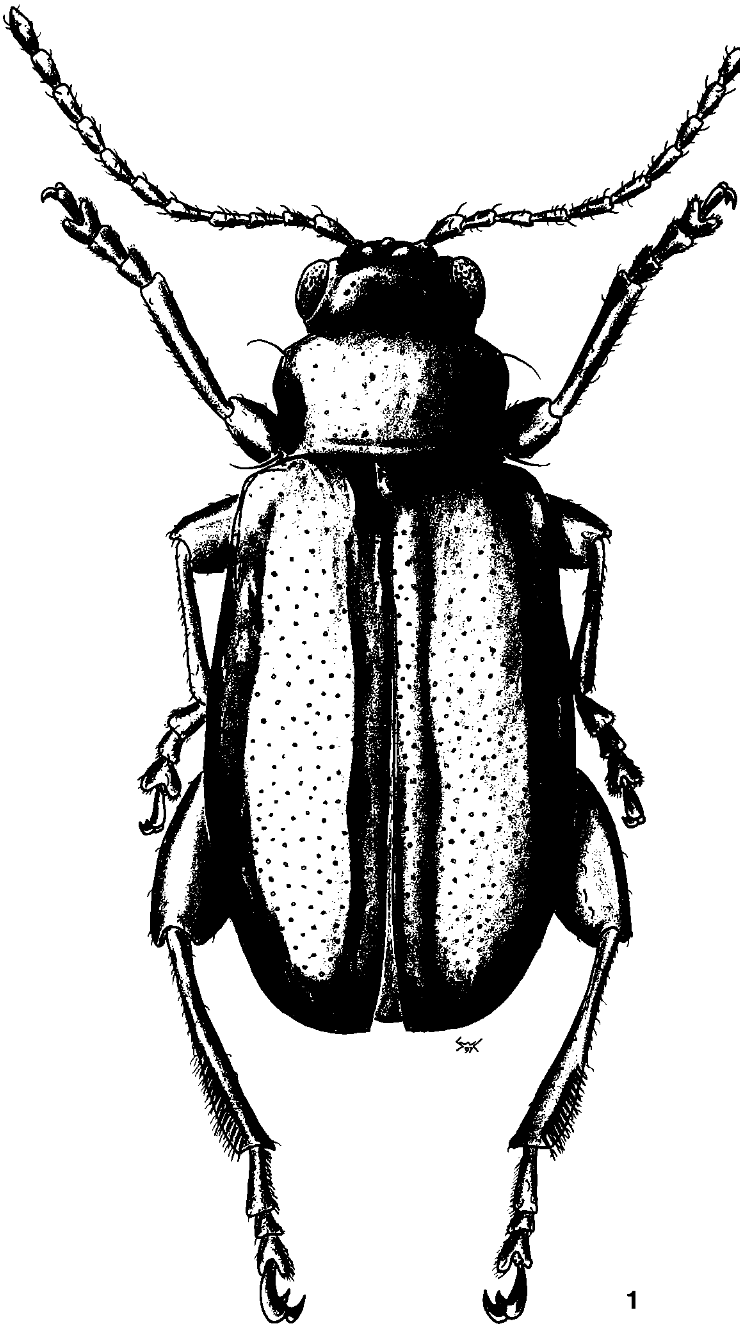


Fig. 1. *Systena blanda,* male, dorsal view.

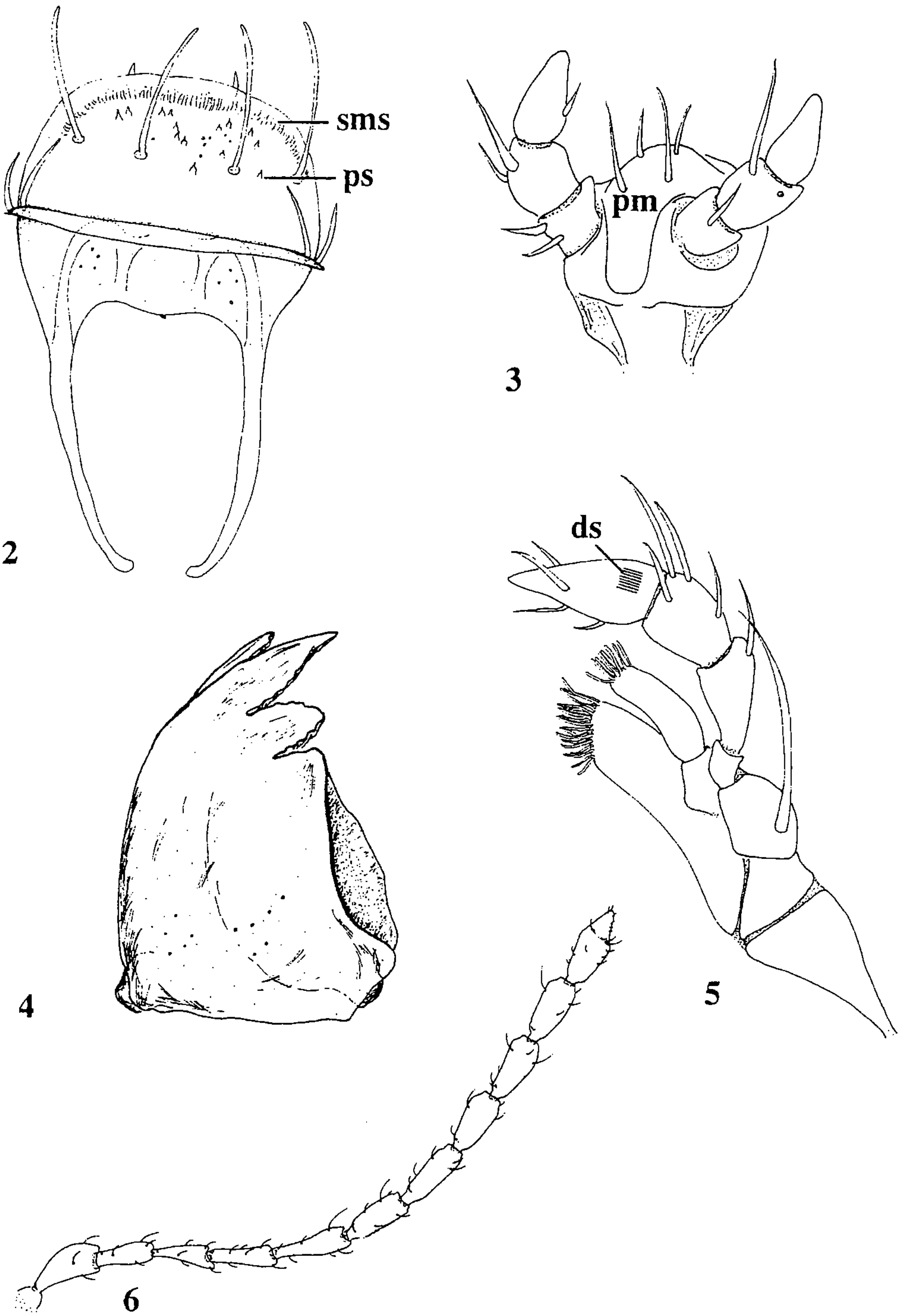
Head (Figs. 1, 7, 8): Antennal calli present, well developed, each as large as antennal socket, longer than wide, extending to antennal sockets. Supra-antennal sulcus distinct on anterior margin of antennal calli but otherwise shallow and not differentiated from surrounding area; not continuing beyond antennal socket. Supraorbital sulcus shallow, not well-differentiated from surrounding area. Supracallinal sulcus varies from well developed in *S. frontalis* to poorly developed in *S. blanda.* Anterofrontal ridge with distinct, narrow crest, lower than frontal ridge, contacting frontal ridge anteapically (before anterior end). Orbital sulcus absent (when present in other genera, extends from dorsal end of the supraorbital sulcus to dorsal margin of eye); dorsal margin of eye not demarcated from adjacent vertex. Frontal ridge well developed, extending between antennal calli to clypeus (declivous between antennal calli), not higher than rim of antennal socket when viewed from antero-ventral perspective along plane of labrum. Frontal-lateral sulcus poorly developed; region between frontal ridge and antennal socket not well differentiated. Subantennal sulcus absent. Subgenal suture well-developed. Tentorium incomplete, with only posterior arms extending dorsally less than one-fifth of distance from floor of the head to the vertex. Occipital opening nearly evenly oval, not subquadrate.

Mouthparts (Figs. 2–5): Labrum (Fig. 2) with submarginal row of fine sensilla on inner (ventral) surface; four long sensilla on outer (dorsal) surface; two short setae on mid-apical margin on inner (ventral) surface; and with erratic pattern of short, pitcher-shaped sensilla on inner (ventral) surface. Prementum (Fig. 3) with four setae (the posterior pair approximately the length of basal two labial palpomeres); base between labial palpi evenly rounded, not mildly acute. Apex of penultimate labial palpomeres with two long setae, the longest of which extends at least to apex of the apical palpomere. Apical maxillary palpomere (Fig. 5) about 1.5 times as long as penultimate palpomere, with small, basal, quadrate digitiform sensilla patch. Mandible (Fig. 4) with five teeth evenly distributed along inner (ventral) and outer (dorsal) surface. Mandibular teeth unevenly dull-serrate.

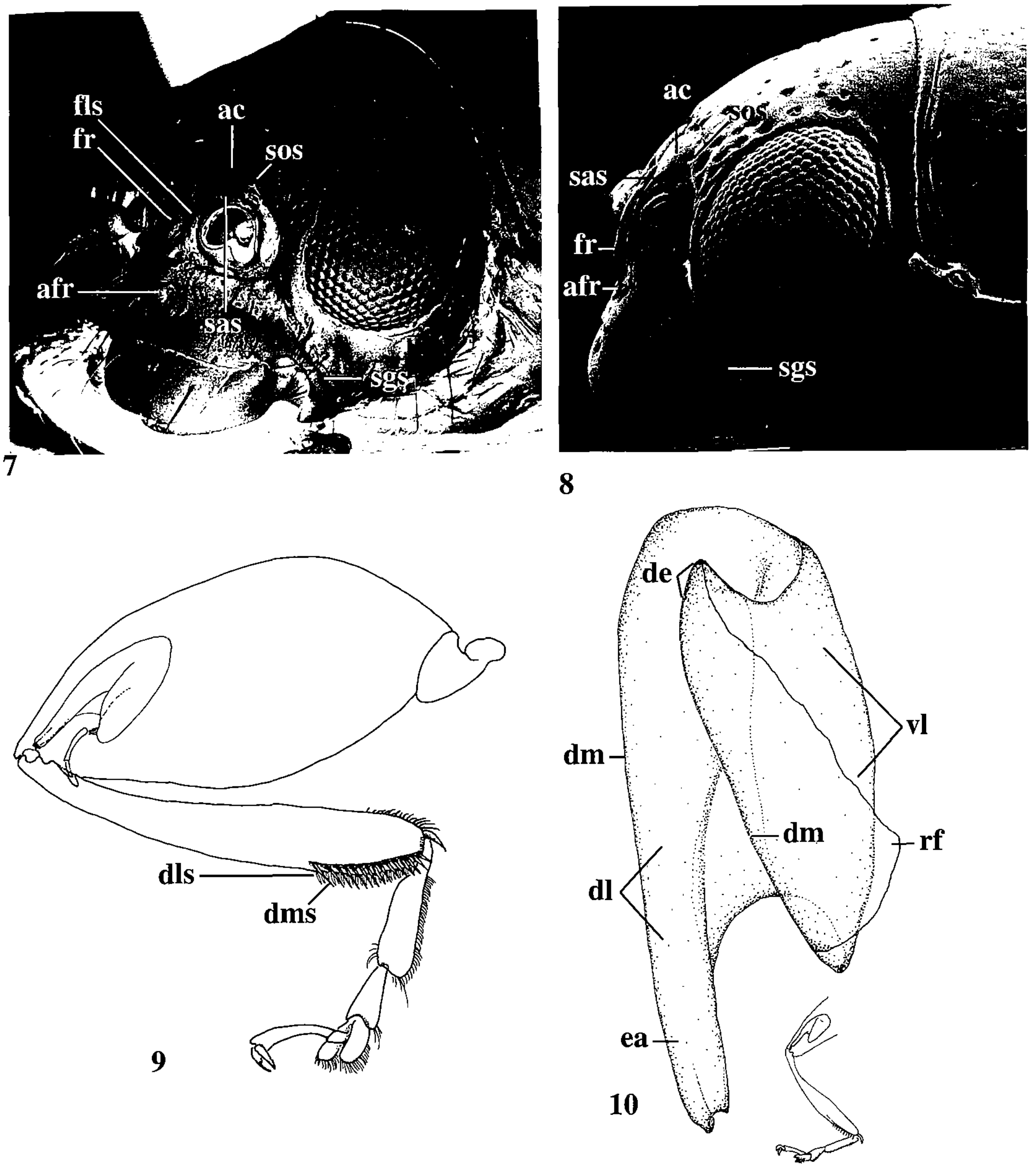
Antenna (Fig. 6): Apical antennomere constricted at apical two-thirds, becoming cone-shaped apically. Second antennomere shorter than third, longer than fourth. Fifth antennomere longer than fourth and sixth. Mesal margins of antennal sockets farther apart than diameter of antennal socket (Fig. 7).

Thorax: Pronotum (Fig. 1) without posterior (prebasal) transverse impression and without postero-lateral longitudinal impressions. Anterolateral and posterolateral corners of pronotum each bearing one long seta. Procoxal cavities closed (apex of intercoxal prosternal process contacting hypomeral projection). Intercoxal prosternal process strongly expanded apically (at least 2.0 times as wide at apex as narrowest region between procoxae). Mesocoxa (Fig. 32) broadly open laterally to mesepimeron (mesosternum and metasternum not contacting one another on the outer lateral margin of the mesocoxa). Intercoxal mesosternal process (Fig. 32) bilobed. Mesonotum (Fig. 34) strongly sclerotized and lacking stridulatory ridges. Mesoprescutum (scutellum, Fig. 34) is generally triangular, but more truncate posteriorly in *S. blanda* and *S. s-littera.* Metendosternite (Figs. 37, 38) with apex of anterior arms deflexed and tapering to a point; with long, narrow, dorsal ridge from anterior midpoint to posterior midpoint (Fig. 37); with poorly developed tendons of metafurcal-mesofurcal muscles; with poorly developed ventral process (Fig. 38) without visible contact to ventral projection; with poorly developed transverse connection from anterior arm into middle region. Metanotum (Fig. 33) less than 1.5 times as wide as long. Metanotal ridge e and c_2 fused, forming ridge c, thus appearing thickened at region where both converge with b_1 (terminology following Konstantinov, *in press*). Metanotal ridge d intersecting c at point one-third of c's length before posterior end, distinctly posterior to midpoint on c (in *S. blanda,* d intersects c at its midpoint). Metanotal ridge b_1 intersecting a below the median groove.

Wings and legs: Elytral punctation irreg-



Figs. 2–6. Adult anatomy of *Systena blanda*. 2, Labrum, dorsal (outer) view. 3, Labium, posterolateral view. 4, Right mandible, ventral (inner) view. 5, Right maxilla, dorsal (outer) view. 6, Antenna. Abbreviations: ds = digitiform sensillum; pm = prementum; ps = pitcher sensilla; sms = submarginal sensilla.



Figs. 7–10. Adult anatomy of *Systena blanda*. 7, Head, anterolateral view. 8, Head, lateral view. 9, Left metafemur, posterior view. 10, Metafemoral spring, posterior view, dorsal side oriented to left. Abbreviations: ac = antennal callus; afr = anterofrontal ridge; de = declivous margin; dl = dorsal lobe; dls = dorsolateral apical spines; dm = dorsal margin; dms = dorsomesal apical spines; ea = extended arm; fls = frontolateral sulcus; fr = frontal ridge; rf = recurved flange; sas = supraantennal sulcus; sgs = subgenal suture; sos = supraorbital sulcus; vl = ventral lobe.

ular, confused arrangement (Figs. 1, 35). Ventrally elytra with two small, separate binding patches not extending beyond basal half of elytron (Fig. 35). Elytral apices rounded (Fig. 1, 35). Elytral epipleuron subvertical, continuous nearly to apex. Hind wing CuA_2 not attached to CuA in most species. In others such as *S. blanda, S. car-*

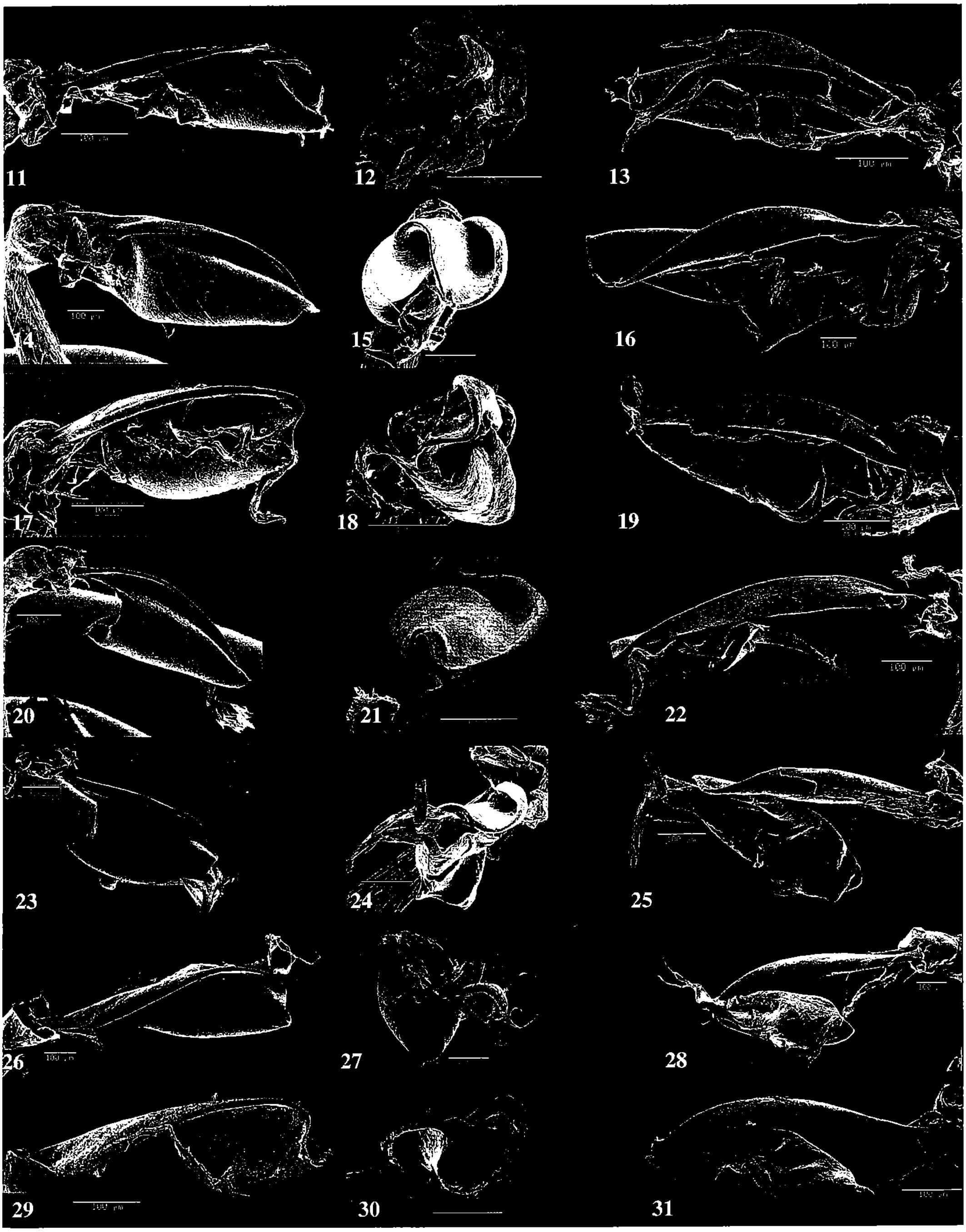
ri, S. oberthuri, and *S. s-littera,* a dark pigmentation appears to connect the CuA_2 to the CuA, this indicated by a "+" in Table 1. Hind wing AA unbranched and connected to CuA_{3+4} at about half the distance from the origin of CuA. Hind wing RP-MP_2 not reaching R_4. Hind wing venation not developed beyond basal ⅔ of wing. Dorsolateral apex of metatibiae with row of 22–30 small spines (Figs. 1, 9). Dorsomesal apex of metatibiae with row of 15–25 long, thick spines (Fig. 9). Dorsal surface of metatibiae convex at basal ¾. Apical ¼ nearly flat with small convexity near middle. Metafemur (Fig. 9) moderately broad (1.8—2.2 times longer than wide). First metatarsus moderately long, approximately ⅓ length of metatibia (Fig. 9). Tarsal claws appendiculate. Third metatarsomere bilobed. Metafemoral spring (Figs. 11–31) with variably developed recurved flange; elongated arm portion of dorsal lobe ranging from 0.25 to 0.35 length of metafemoral spring; dorsal margin of dorsal lobe variable in curvature; dorsal margin of the ventral lobe varies in the angle to the dorsal-ventral axis of the metafemoral spring; tightness of the coiling of the dorsal and ventral lobes variable.

Abdomen and genitalia: Apex of sternite VII of males with median truncate extension bordered by two apico-marginal impressions. Aedeagus from lateral view (Fig. 45) with only slight concavity along ventral profile; slight convexity along dorsal profile. Aedeagus apex arrow-shaped with fine striae at extreme apex (Fig. 46). Aedeagus apex dorsally with broad, flat, raised area extending anteriorly to narrow, raised ridge (Fig. 44). Central part of median lobe dorsally with broad ridge, narrowing anteriorly, and margined on either side by long narrow ridge (Fig. 44). Aedeagus from ventral view with basal opening slightly constricted posteriorly; posterior opening narrower than at anterior end (Fig. 46).

Female abdomen with seven visible tergites and seven pairs of spiracles. The last tergite, tergite VII, may be homologous with tergite VIII of other beetles, but more study on developmental segmentation needs to be done. [Cox (1996) showed variability in numbers of tergites on pupae within Alticinae but this variability was not discussed.] Tergite VII (Fig. 39) base of female with dense, microtrichia of two types: (a) compound (with 3–6 parallel spicules of differing lengths) and (b) spiniform (regular, ordered distribution, with short spicule originating from apex of triangular cuticular plate. Tergite VII apex of female with numerous long, tapering setae, evenly distributed. Apex with about 10–15 longer, apically-curved setae (Fig. 39). Sternite VII (fifth visible sternite) (Fig. 40) of female with about 12–16 long, apically-curved setae along apical margin. Otherwise with regularly distributed normal setae. Spermatheca (Fig. 43) with short, abruptly curved pump (apical region). Spermathecal duct (basal, sclerotized region, fig. 43) complex in shape, twisted. Spermathecal gland base extending nearly one-half length of sclerotized portion of spermathecal duct (basal region). Spermathecal gland surface micro-convoluted and irregular; nearly length of spermatheca. Vaginal palpus (Fig. 42) with 6–8 fleshy setae. Vaginal palpi slightly divergent at base, nearly contiguous at apex. Ventral, anterior sclerotization of vaginal palpi slender, longer than posterior sclerotization, nearly as long as posterior part of palpi behind point of their connection. Tignum apex (Fig. 41) (sternite VIII) unmodified, with apical margin of short setae. Tergite VIII (Fig. 41) of female with darkly pigmented lateral margins and an apical margin with row of short setae. In *A. frontalis,* this tergite is moderately and evenly sclerotized and spoon shaped.

DIAGNOSTIC CHARACTERS

The following characters are apparently unique (autapomorphies) for *Systena:* spermathecal duct irregulary shaped with several widened and curved regions (Fig. 43); basal, sclerotized portion of spermathecal gland long and roughly parallel sided (Fig. 43); and metanotal ridge *d* intersecting *c* at



Figs. 11–31. Right metafemoral springs of *Systena* spp. Dorsal lobes are oriented to the top except in the proximal end views in which the dorsal lobe is generally oriented to the top right. White bar represents 100 micrometers. 11, *S. blanda,* dorsal (posterior) view. 12, *S. blanda,* proximal end view. 13, *S. blanda,* ventral (anterior) view. 14, *S. championi,* dorsal (posterior) view. 15, *S. championi,* proximal end view. 16, *S. championi,* ventral (anterior) view. 17, *S. elongata,* dorsal (posterior) view. 18, *S. elongata,* proximal end view. 19, *S. elongata,* ventral (anterior) view. 20, *S. frontalis,* dorsal (posterior) view. 21, *S. frontalis,* proximal end view. 22, *S. frontalis,* ventral (anterior) view. 23, *S. marginallis,* dorsal (posterior) view. 24, *S. marginallis,* proximal end view. 25, *S. marginallis,* ventral (anterior)

point one-third of *c*'s length before posterior end, distinctly posterior to midpoint on *c*.

Characters which occur in *Systena* and other hypothetically closely related genera (potential synapomorphies for Systenini, see discussion below) include: parallel sided body (Fig. 1); elytron without apical declivity; frontal and anterofrontal ridges (Figs. 7, 8) well developed but not high; anterofrontal ridge lower than frontal ridge; and labrum with four long sensilla on outer (dorsal) surface (Fig. 2); apex of tergite VII of female with about 10–15 longer, apically-curved setae and compound microtrichiae (Fig. 39).

PRELIMINARY DISCUSSION OF RELATIONSHIPS OF *SYSTENA*

We provide here a summary of most of the genera that have been implicitly or explicitly suggested to share a close relationship to *Systena.* We have examined exemplars of these taxa and in cases where these do not represent the type species of the genus, we consider them representative of the genus.

Clark (1865) in the first characterization of the genus believed that *Systena* is closely related to *Oxygona* Chevrolat (now *Platiprosopus* Chevrolat). The diagnostic characters he provided to distinguish the two genera include the shape of the body and pronotum. In *Systena,* the body is more parallel-sided and narrower than in *Platiprosopus,* and the pronotum is more quadrate and rectilinear with the posterior corners sharp and not rounded. Our examination of *Platiprosopus acutangula* (Chevrolat) has shown other differences and similarities. We observed that *Platiprosopus* has the elytron with an apical declivity, labrum with at least 8 long setae, and fifth antennal segment longer than sixth but shorter than fourth. Our observations reveal a great similarity in the female genitalia (including the spermathecae) of the two genera. The setation of the last abdominal tergite in females of *Systena* and *Platiprosopus* are the same except there are many more compound microtrichia (Fig. 39a) distributed along the basal margin of the tergite in *Platiprosopus.*

Heikertinger and Csiki (1939) arranged a worldwide catalog based on their ideas about relationships among flea beetle genera. They placed *Systena* between *Prasona* Baly and *Agasicles* Jacoby. These taxa were followed by *Tanygaster* Blatchley, *Heikertingeria* Csiki, and *Acanthonycha* Jacoby. In 1962 Scherer synonymized *Prasona* with *Systena,* although he did not explicitly indicate, "New Synonymy." Scherer mentioned that Jacoby previously had reservations about the validity of *Prasona* (no reference indicated, however), but Jacoby did not formally synonymize them.

Our examination reveals that *Prasona* (based on *P. viridis* Baly) shares several putative synapomorphies with *Systena:* spermatheca with short, abruptly curved pump (Fig. 43), spermathecal duct wide, and metanotal ridge *d* intersecting *c* at point one-third of *c*'s length before posterior end, distinctly posterior to midpoint on *c* (Fig. 33). They also share the bilobed intercoxal mesosternal process (Fig. 32), and dorsally flattened apical fourth of the metatibia. Differences among these taxa include the shape of the spermathecal receptacle, posterior part of the tignum, abdominal tergites VIII and IX, median lobe of aedeagus, and the width of the frontal ridge. From other studies it is known that these latter characters typically vary at the species level. Therefore, we support the synonymy of *Prasona* with *Systena.* Our investigation of

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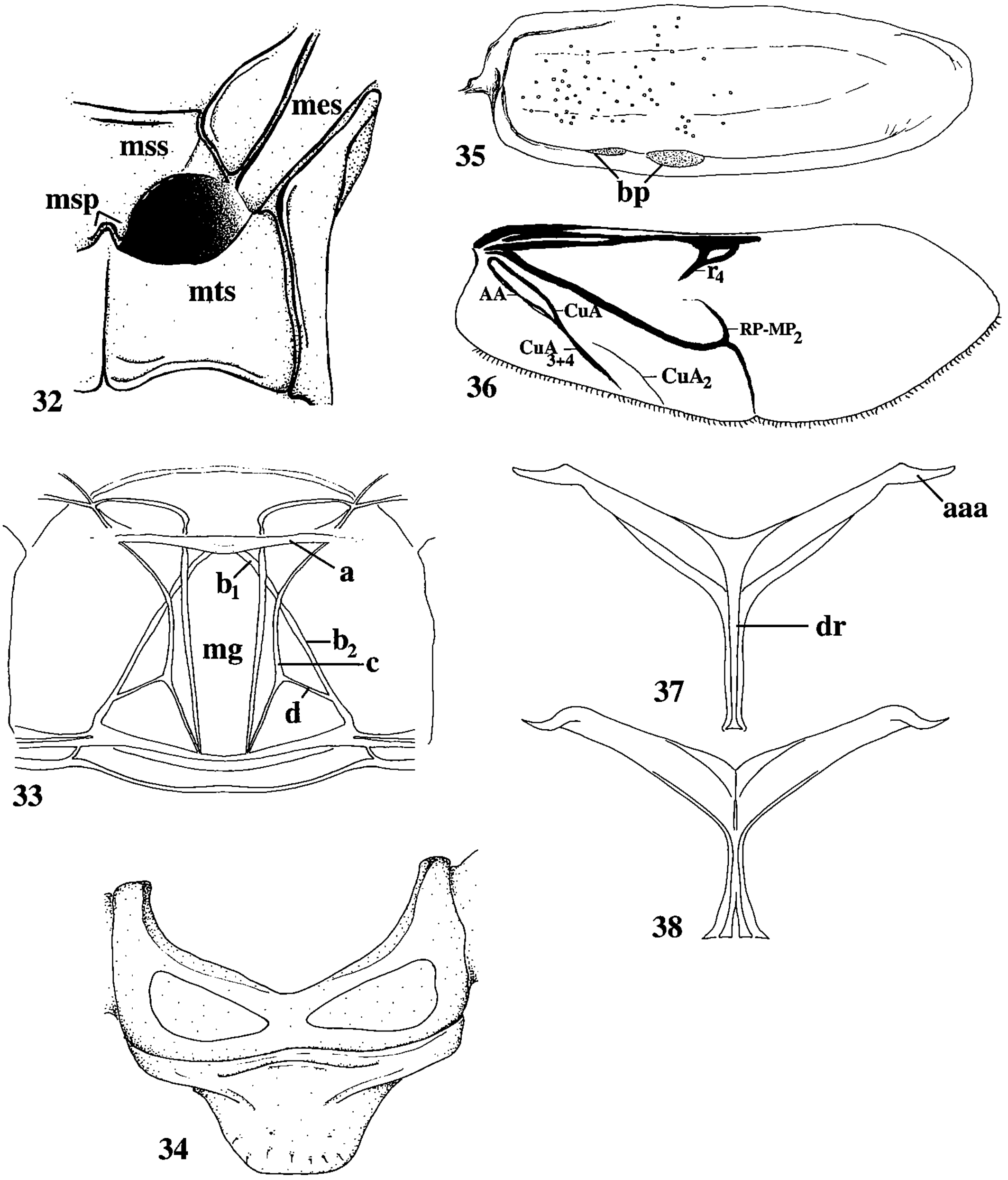
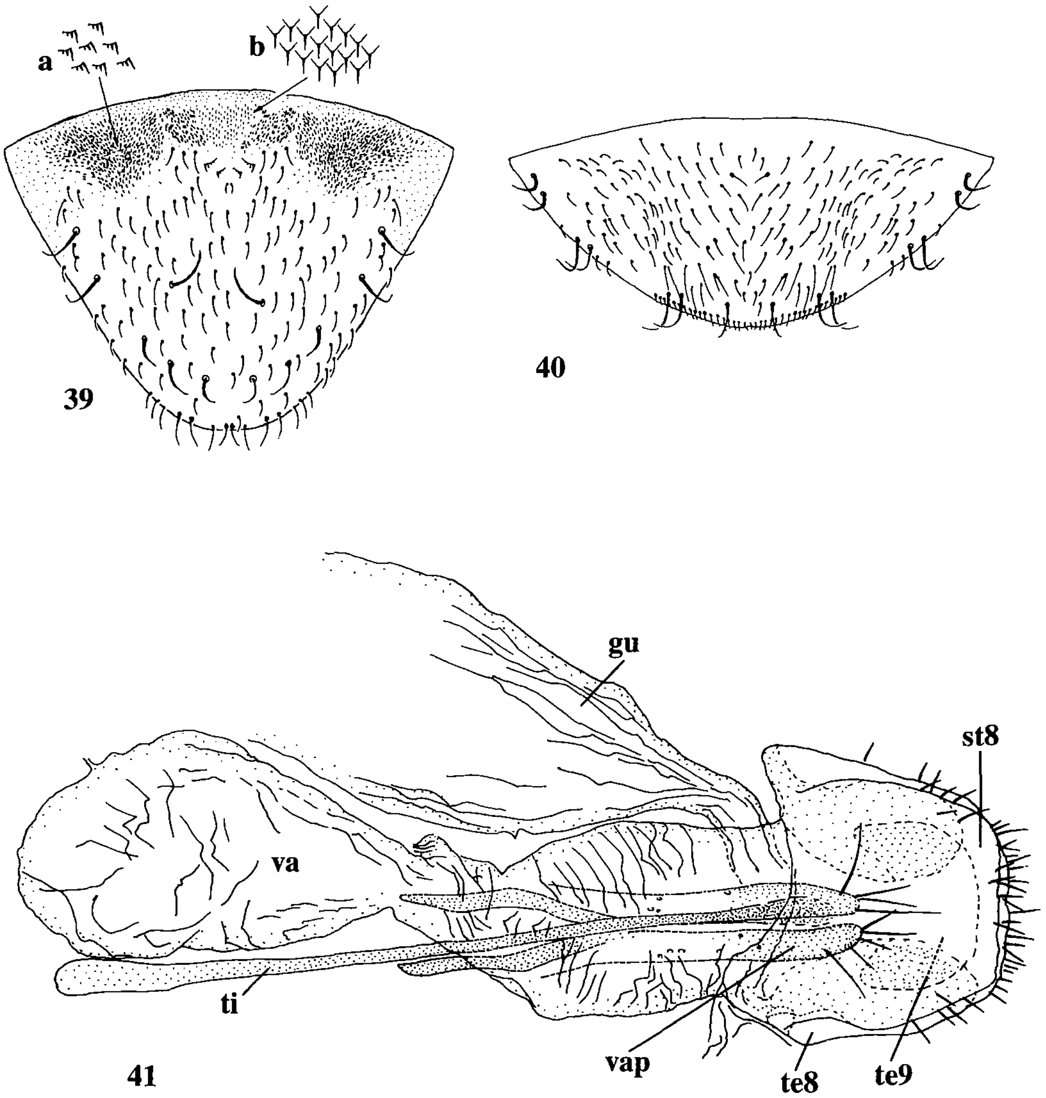
view. 26, *S. oberthuri,* dorsal (posterior) view. 27, *S. oberthuri,* proximal end view. 28, *S. oberthuri,* ventral (anterior) view. 29, *S. s-littera,* dorsal (posterior) view. 30, *S. s-littera,* proximal end view. 31, *S. s-littera,* ventral (anterior) view.



Figs. 32–38. Adult anatomy of *Systena blanda.* 32, Meso- and metasternum, left ventrolateral view. 33, Metanotum (abbreviations from Konstantinov, *in press*). 34, Mesonotum and scutellum. 35, Right elytron, ventral view. 36, Hind wing (terminology from Kukalová-Peck and Lawrence 1993). 37, Metendosternite, ventral view. 38, Metendosternite, dorsal view. Abbreviations: aaa = anterior arm apex; bp = binding patch; dr = dorsal ridge; mes = mesepimeron; mg = median groove; msp = mesosternal process; mss = mesosternum; mts = metasternum.



Figs. 39–41. Adult anatomy of *Systena blanda*. 39, Tergite VII, female (a) compound microtrichia, (b) spiniform microtrichia. 40, Sternite VII, female. 41, Female genitalia, oblique lateral view. Abbreviations: gu = digestive tract; st8 = sternite VIII; te8 = tergite VIII; ti = tignum; va = vaginal palpi.

Disonychodes exclamationis (Boheman) shows agreement in most characters with *Systena*.

Agasicles (based on *A. connexa* Boheman) has a well developed recurved flange of the metafemoral spring. The female genitalia are extremely unusual: tergite VII lacks the setal and microtrichial characters found in *Systena*; tergites VIII and IX of females are transformed into a strongly sclerotized plate with a very complicated shape; vaginal palpi are absent; the tignum is robust and strongly sclerotized; the spermathecal receptacle is wider than long; the basal part of the duct is horizontal; the basal part of the pump is long and extremely weakly sclerotized; and the horizontal part of the pump is short and sclerotized as strongly as the receptacle. On the metanotum, ridge *c* is extremely close to the median groove. The metendosternite has an extremely narrow stalk. The procoxal cavities are open behind. The dorsal side of the labrum has at least 6 setiferous pores. The anterofrontal ridge is extremely low, especially at the middle and has patches of setae laterally. The only character that is shared by *Agasicles* and *Systena* is the elongate, parallel sided body and elytron without an apical declivity. We therefore believe *Agasicles* is only distantly related to *Systena.*

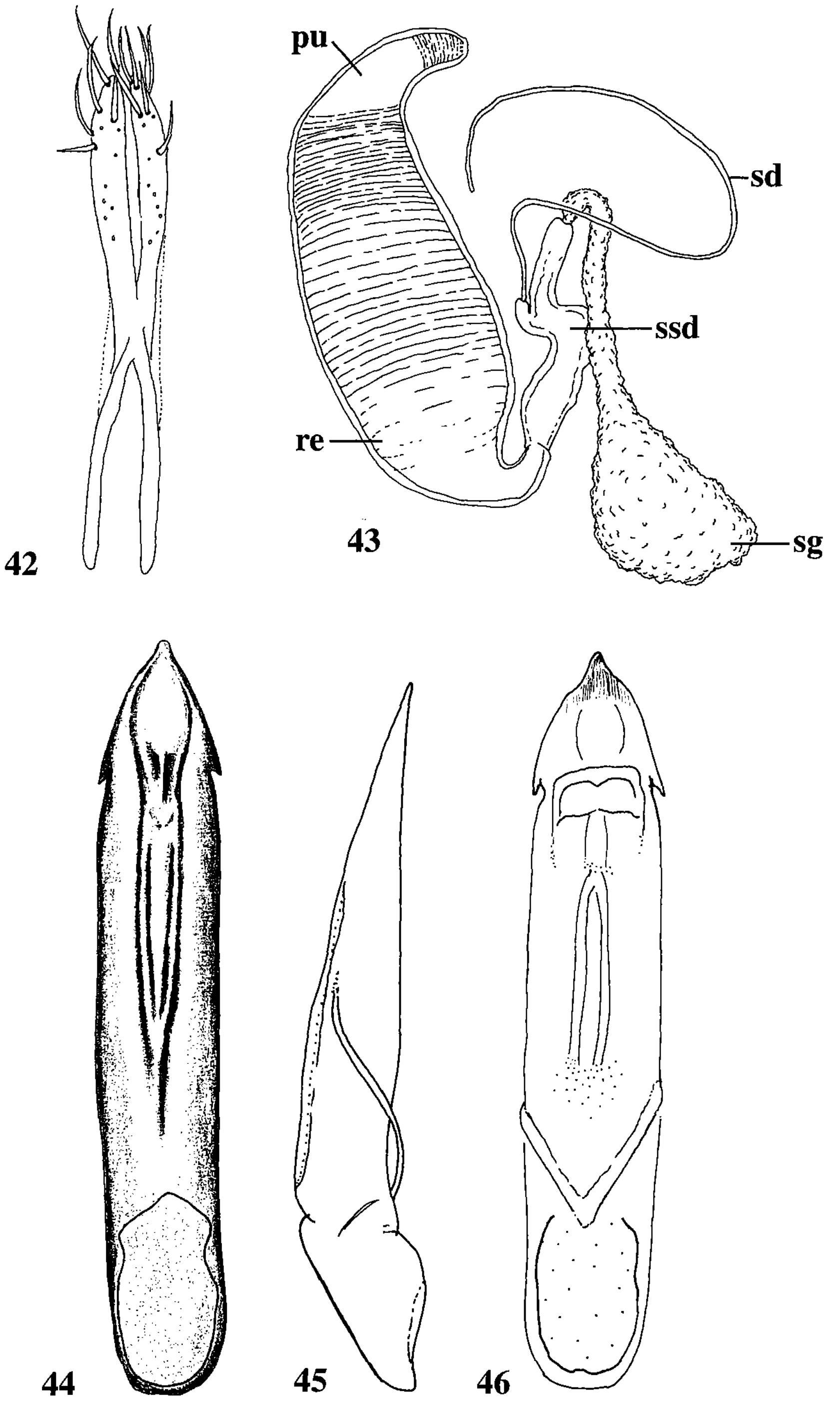
Our examination of specimens of *Heikertingeria* was limited since only males of an undetermined species were available for study. These specimens have an elytral apical declivity and a slightly convex dorsal surface of the metatibiae with an apically flat longitudinal ridge.

Like specimens of *Agasicles, Acanthonycha* females (*A. jacobyi* Bechyné) examined lacked the usually developed tergites VIII and IX and apparently also the vaginal palpi although there are 2 transverse sclerotized structures below tergite VII. The tignum in *Acanthonycha* is robust and more strongly sclerotized than in *Systena.* In *Acanthonycha,* the procoxal cavities are open behind, the intercoxal mesosternal process is narrow and not bilobed, the setation of tergite VII of females varies greatly from *Systena,* and the metendosternite has an extremely slender stalk.

Chapuis (1875) included *Systena, Prasona,* and *Chlamophora* Chevrolat (= *Clamophora* Jacoby) in the taxon called Crepidoderites (Crepiderini) based on the oblongo-oval or elongate shape of the body and the presence of the transverse impression on the pronotum. Horn (1889) also recognized the close relationship of *Chlamophora* with *Systena,* but believed it was a mistake to include them in the Crepidoderites and rather proposed a suprageneric taxon called Systenae. Specimens of *Chlamophora* (*C. meridionalis*) share similarities with *Systena* in the following character states: four long sensilla on the labrum; absence of supraorbital sulci; third metatarsomere bilobed; short, abruptly curved pump of spermatheca; curved setae on sternite VII of female; and well-developed supracallinal sulcus. Differences include the following: anterofrontal ridge with medial depression; antennal calli well-developed; pronotum with antebasal transverse and longitudinal impressions; strong elytral costae; metatibiae with long, well-defined ridge dorsally (at least ½ length of tibia); spermathecal duct coiled; and vaginal palpi robust, with long, strong sclerotization anteriorly. Some of these differences are shared with *Altica* Geoffroy, and the spermatheca in particular suggests that *Chlamophora* is more closely related to *Altica.*

Seeno and Wilcox (1982) recognized the tribe Systenini containing, besides the type genus, *Prasona, Egleraltica* Bechyné and Bechyné and *Pseudogona* Jacoby. The group of related genera separated from the tribe contains *Dysphenges* Horn, *Cyrsylus* Jacoby, *Trifiniocola* Bechyné and Bechyné, *Andiroba* Bechyné and Bechyné and *Agasicles.* No specimens of *Egleraltica, Dysphenges, Andiroba, Pseudogona, and Trifinocola* were available for examination, so Seeno and Wilcox's idea on their relationship to *Systena* cannot be addressed.

The last references to show a grouping of taxa with *Systena* are Furth (1985, 1989). It is unclear whether or not he intends the morphogroups to reflect potential phylogenetic affinity, although he has discussed patterns of congruence between metafemoral spring morphogroups to generic proximity in catalogues (Furth 1989: 499–503). Furth (1985) included *Systena* in morphogroup 3, containing *Dysphenges* Horn, *Phyllotreta* Chevrolat, *Pseudolampsis* Horn, *Pachyonychus* Chevrolat and *Lupraea* Jacoby. Our study of *Systena* metafemoral springs (Figs. 10–31) reveals extreme variation in the length of the dorsal lobe's extended arm, the curvature of the dorsal margin of the dorsal lobe, the angle of the dorsal margin of the ventral lobe to the dorso-ventral axis, the development of the recurve flange, and in the tightness of



Figs. 42–46. Adult anatomy of *Systena blanda*. 42, Vaginal palpi. 43, Spermatheca and gland. 44, Aedeagus, ventral sculpturing. 45, Aedeagus, lateral view. 46, Aedeagus, dorsal view. Abbreviations: pu = pump; re = receptacle; sd = spermathecal duct; sg = spermathecal gland; ssd = sclerotized spermathecal duct.

the coiling of the dorsal and ventral lobes. *Systena* approximates morphogroup 2 or 3, but we cannot unambiguously assign it because the differences between them are unclear. We extract their definitions here:

Morphogroup 2.—Furth (1980:267): "is distinctive but is apparently close to [morphogroup 1]"; Furth (1982:20): "very similar to morphogroup 1 with one major difference; the presence of the recurve flange as an extension of the ventral lobe. Sometimes the recurve flange is highly developed . . . yet in others . . . the recurve flange is only slightly developed."; Furth (1989: 508): "simple modification of morphogroup 1, possessing the addition of a well-developed recurve flange attached to the ventral lobe."

Morphogroup 3.—Furth (1980:267): "also distinctive from [morphogroup 1 and morphogroup 5] but seems to have some similarities to both"; Furth (1982:22): "relatively short extended arm of dorsal lobe which is significantly depressed apically and out of line from horizontal axis of dorsal lobe. Also the ventral lobe is extended into recurve flange, though not well developed"; Furth (1989:508): "has a shorter dorsal lobe (but noticeably longer than ventral lobe), apically depressed, with a small recurve flange."

It is clear that both morphogroups are characterized by a recurve flange but it is unclear how the flange differs, if at all. Apparently morphogroup 3 differs from 2 in having a "relatively short extended arm" although it is unclear if it is shorter relative to morphogroup 1 or 2 or both, and it is impossible to know at what point the extended arm becomes long enough to merit placement into another morphogroup. The apical depression of the dorsal lobe, characteristic of morphogroup 3, is unclear and is not strikingly different in any of the illustrations of Furth (1985, 1988, 1989).

Scanning electron microscopy is the best procedure to accurately determine the characteristics of the metafemoral spring. The views from the proximal end are particularly revealing of differences in the coiling of the dorsal and ventral lobes and the extent of the recurve flange. Compound microscopy is hampered because of the difficulty to position the metafemoral spring in a standard position for comparison with other taxa. A slight rotation on one axis can alter the appearance of structures or hide others. Compound microscopy does not always reveal the complicated folding patters accurately and does not always reveal the recurve flange when it is in fact present. The characteristics of the metafemoral spring defining the morphogroups should be reassessed with discrete states, perhaps in a matrix format so they can aid in identifying generic groups and be used in phylogenetic investigations. Only with explicit character states can genera be assigned unambiguously (since morphogroups were proposed, [Furth 1980], about 10 genera have been reassigned [Furth 1982, 1989]).

Comments on potential relationships of the remaining taxa in morphogroup 3 (Furth 1985) are listed here based on comparison with many of the character states found in the examined *Systena* species. *Pseudolampsis* (*P. guttata* LeConte) and *Pachyonychus* share many features (apically swollen last metatarsomere; short, straight, dorsally flat metatibia with preapically inserted metatarsus; flat and moderately wide frons) with Monoplatini, a well supported lineage in Alticinae, and are only distantly related to *Systena. Phyllotreta* species (including *Tanygaster,* synonymized by Smith, 1979) share with *Systena* a moderately flat body shape and elytra without an apical declivity. *Phyllotreta* differs by its undeveloped or extremely poorly developed supracallinal, midfrontal and suprafrontal sulci, much longer dorsolateral row of small spines on the apex of the metatibiae, arcuate intercoxal mesosternal process, open procoxal cavities, metendosternite well developed, with fully developed ventral process contacting the ventral projection, and fully developed tendons of the metafurcal-mesofurcal muscles. These differences and the fact that they share no presumed synapomorphies of Systenini, strongly suggests they belong in different alticine lineages. *Lupraea* (*L. longicornis* Jacoby) shares no provisional synapomorphies of Systenini. Several character states place it in different groups of genera: the orbit is extremely narrow, the frontoclypeal suture is undeveloped, the labrum has more than 15 setae on the dorsal surface, the antero and posterolateral callosities of pronotum are undeveloped, the lateral margin of the pronotum is broadly explanate, the prosternal intercoxal process is narrow and short, and the procoxal cavities are open. *Lupraea* also exhibit sexual dimorphism in the size of the eyes. *Cyrsylus* Jacoby specimens (based on *C. recticollis* Jacoby) also do not possess any of the provisional synapomorphies of Systenini. The remaining genera in Furth's (1985) morphogroup 3, *Glenidion* Clark and *Phydanis* Horn, were unavailable for examination, so comments on their relationship to *Systena* cannot be made here.

Our study suggests that many of these genera which have previously been aligned with *Systena,* either in a catalog listing or morphological grouping share few of the uncommon characters (provisional synapomorphies) of the tribe Systenini, and therefore probably belong to different alticine lineages. *Platiprosopus* seems to be the only genus that shares with *Systena* some of these characters.

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APPENDIX

Characters and states for *Systena* species compared in Table 1. More thorough descriptions given in text.

1. Body proportions ratio measured as length of elytron divided by greatest width of elytra. (0) 1.40–1.80; (1) >1.80
2. Elytron apex. (0) without apical declivity; (1) with apical declivity
3. Antennal calli. (0) as large as antennal socket, longer than wide; (1) not as large as antennal socket, wider than long
4. Anterofrontal ridge. (0) lower than frontal ridge; (1) higher than frontal ridge
5. Supracallinal sulcus. (0) well developed; (1) poorly developed (indistinct)
6. Orbital sulcus. (0) absent; (1) present
7. Frontal ridge. (0) well developed; (1) poorly developed
8. Dorsal surface of labrum. (0) with 4 setae; (1) with more or less setae
9. Fifth antennomere length relative to fourth and sixth. (0) longer than 4&6; (1) shorter than 4&6; (2) 4=5>6; (3) 4>5=6
10. Procoxal cavities. (0) closed; (1) open
11. Prosternal intercoxal process. (0) strongly expanded at apex; (1) narrowly expanded at apex
12. Mesoprescutum. (0) truncate posteriorly; (1) triangular in shape
13. Metendosternite anterior arms. (0) deflexed anteapically; (1) not deflexed at ends
14. Metanotal ridge *d.* (0) intersecting *c* at point one-third of *c*'s length before posterior end, distinctly posterior to midpoint on *c* (1) not as in *0, d* intersecting *c* at point much anterior (at least anterior to midpoint of *d*).
15. Elytral punctation. (0) irregular, confused; (1) arranged more or less in striae
16. CuA_2. (0) not attached to CuA; (1) reaching CuA
17. Dorsolateral apex of metatibia. (0) with 22–30 small spines; (1) less than 20 spines present
18. Coiling of dorsal lobe. (0) coiled nearly completely along dorso-ventral axis;

(1) coiled only at extreme distal end (near attachment to tibia).

19. Extended arm of metafemoral spring. (0) between 0.35 and 0.25 length of spring; (1) less than 0.25 length of spring.
20. Aedeagus apex. (0) arrow shaped with fine striae at extremity; (1) not arrow shaped and without striae.
21. Tergite VII of female. (0) with compound and spiniform microtrichiae; (1) without both types
22. Spermathecal duct. (0) irregulary shaped with several widened and curved regions; (1) not as in 0
23. Spermathecal gland. (0) basal, sclerotized portion long and roughly parallel sided; (1) not as in 0