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Ceraclea OF THE PEOPLE'S REPUBLIC OF CHINA (TRICHOPTERA: LEPTOCERIDAE)

By Yang Lian-fang and John C. Morse

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Ceraclea of The People's Republic of China

(Trichoptera: Leptoceridae)[1]

By

Yang Lian-fang[2] and John C. Morse[3]

ABSTRACT

The species of the long-horned caddisfly genus Ceraclea for The People's Republic of China are reviewed for the first time since 1975. Twenty-nine species of Ceraclea are known from China and are described or redescribed in the subgenera Ceraclea and Athripsodina, with 4 of them new to science. Ceraclea (C.) alboguttata (Hagen, of which Leptocerus biwaensis Tsuda & Kuwayama is a new synonym), previously known from Europe, Japan, and Korea, is reported for the Chinese fauna. Ceraclea (Athripsodina) riparia (Albarda), previously known only from central Europe, C. (A.) excisa (Morton), previously known from the northern Palearctic Region and northwestern North America, and C. (A.) lobulata (Martynov), previously known only from the Amur Region of Siberia, are reported for the Chinese fauna. Leptocerus kashingensis Tsuda is a new synonym of C. (A.) ensifera (Martynov) and Athripsodes bicalcarata Schmid is a new synonym of C. (A.) shuotsuensis (Tsuda). Ceraclea (C.) sinensis (Forsslund) and C. (A.) huangi (Tian) are new combinations, both of which were originally described in the genus Leptocerus. A key is provided to distinguish the males of all 29 species and the females of 16 species. Diagnoses are given for males and females and (where available) larvae and pupae for each of ten species groups. The phylogenetic associations and biogeography of these species suggest ancient and modern relationships of the Chinese fauna with those of the Palearctic, Nearctic, and Oriental Biogeographic Regions.

KEY WORDS: Leptoceridae, Ceraclea, The People's Republic of China, historical biogeography, water quality indicator organisms.

INTRODUCTION

During the past seven years, interest in the aquatic insect fauna of The People's Republic of China has increased because of the necessity for equipping the people to monitor the quality of their surface fresh waters. Since water pollution is essentially a biological phenomenon (Hynes, 1966), providing more direct evidence of its effects biologically than chemically, it is appropriate that this emphasis has developed. Aquatic insects live sufficiently long in aquatic ecosystems that the populations of sensitive species may reflect reasonably accurately whether streams and lakes have experienced biologically significant pollution.

Identification of species is the essential beginning of any accurate assessment of water quality (Resh and Unzicker, 1975). However, knowledge of the aquatic

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insect fauna of China is lagging far behind that of much of the rest of the world. Most of the species of China are still unknown even in the adult stages. Even for the few species identifiable in the adult stages, larvae and pupae of most of them still have not been described, such that the possibility to identify the aquatic stages (mostly immature forms) of these species is even less than for the mature terrestrial adult forms. Eggs of most aquatic insects, including caddisflies, have not been studied in sufficient detail to permit diagnoses even to family.

Caddisflies, especially of the families Leptoceridae and Hydropsychidae, are found very commonly in Chinese lakes and streams. The different species of Leptoceridae, or long-horned caddisflies, occur in a wide variety of habitats and, at least in other parts of the world, many of them are particularly sensitive to pollution (Hilsenhoff, 1982). It is evident from the revision that follows that most of the Chinese species of Ceraclea, and probably most other groups of aquatic insects, are not yet known to science: eleven of the 29 species described here were not known before this year. Furthermore, at least for Ceraclea and probably for many other aquatic insect groups, the fauna apparently is very rich: the 29 species were captured at only 27 collection localities (Fig. 1) in a country as large as all of Europe (in which there are 14 spp. of Ceraclea according to Malicky, 1983) or of the continental United States (34 spp. according to Morse, 1975), regions which have been much more thoroughly collected.

The revision by Morse (1974, 1975) provided the first summary of Chinese species of Ceraclea. Previous publications concerned only descriptions of individual species. Twelve species of Ceraclea have been known previously from China, one now considered to belong in the subgenus Ceraclea, the others in the subgenus Athripsodina:

C. (C.) sinensis (Forsslund, 1935), NEW COMBINATION
C. (A.) dingwuschanella (Ulmer, 1932)
C. (A.) fooensis (Mosely, 1942)
C. (A.) forcipata (Forsslund, 1935)
C. (A.) huangi (Tian, 1981), NEW COMBINATION
C. (A.) indistincta (Forsslund, 1935)
C. (A.) kashingensis (Tsuda, 1943) (N. SYN. of C. (A.) ensifera)
C. (A.) kolthoffi (Ulmer, 1932)
C. (A.) major (Hwang, 1957)
C. (A.) nankingensis (Hwang, 1957)
C. (A.) signaticornis (Ulmer, 1926)
C. (A.) yangi (Mosely, 1942)

We have seen types or recent specimens of all of these species except C. (A.) signaticornis.

The nominotypical subgenus is reported here for the first time as occurring in China. Three previously described species of this subgenus in China are as follows: C. (C.) alboguttata (Hagen, 1860), formerly known only from Europe and (as Leptocerus biwaensis Tsuda and Kuwayama, 1950, NEW SYNONYM) from Japan and Korea; superba (Tsuda, 1942b), previously known only from Japan; and sinensis (Forsslund, 1935, as Leptocerus), NEW COMBINATION.

We are convinced that Leptocerus kashingensis Tsuda, 1943, is a NEW SYNONYM of C. (A.) ensifera (Martynov, 1935), previously known only from the Amur region of Siberia. In addition, C. (A.) shuotsuensis (Tsuda, 1942a) was reported from northern China by Yang and Tian (1988) (as C. [A.] bicalcarata [Schmid, 1970], NEW SYNONYM), which was previously known only from Mongolia and Korea. In this work, we have discovered specimens of C. (A.) riparia (Albarda, 1874; previously known only from Europe), excisa (Morton, 1904; previously known from the northern Palearctic Region and northwestern North America), and lobulata (Martynov, 1935; previously known only from the Amur Region of Siberia). Ceraclea (A.) huangi (Tian, 1981, as Leptocerus), NEW COMBINATION, is added to this genus in China.

Four newly discovered species of the subgenus Athripsodina are being described elsewhere by Yang and Tian (1988). For the sake of completeness, the names of these species are provided herein. However, they are provided here only "conditionally" in the sense of Article 15 of the International Code of Zoological Nomenclature (Anonymous, 1985). The names will become "available" upon publication of the paper in press by Yang and Tian (1988) with their appropriate authorship and date of publication.

Four species are described herein as new to science, one in the nominotypical subgenus and three in subgenus Athripsodina, bringing the total of known Chinese Ceraclea species to 29. Eight species of Ceraclea are known from other parts of eastern Asia and six from the Oriental Region which have not been collected in China, but which may be discovered there in the future.

CHECKLIST OF SPECIES

The 29 Chinese species of Ceraclea presently known are as follows:

Ceraclea (Ceraclea) species
- Fulva Group
  - C. (C.) spinulicolis, n. sp., Figs. 2, 31.
  - C. (C.) alboguttata (Hagen, 1860), Figs. 3, 32, 47.
- Nigronervosa Group
  - C. (C.) superba (Tsuda, 1942b), Fig. 4.
  - C. (C.) sinensis (Forsslund, 1935), N. COMB., Figs. 5, 33.

Ceraclea (Athripsodina) species
- Tarsipunctata Group
  - C. (A.) major (Hwang, 1957), Fig. 6.
- Dissimilis Group
  - C. (A.) indistincta (Forsslund, 1935), Fig. 7.
  - C. (A.) lobulata (Martynov, 1935), Figs. 8, 34.
- Annulicornis Group
  - C. (A.) excisa (Morton, 1904), Figs. 9, 35, 48.
  - C. (A.) shuotsuensis (Tsuda, 1942a), Figs. 10, 36.
  - C. (A.) globosa, n. sp., Fig. 11.
- Riparia Group
  - C. (A.) polyacantha Yang & Tian, 1987, Fig. 12.
  - C. (A.) interispina Yang & Tian, 1987, Figs. 13, 37.
  - C. (A.) riparia (Albarda, 1874), Figs. 14, 38.
  - C. (A.) yangi (Mosely, 1942), Figs. 15, 39.
  - C. (A.) nankingensis (Hwang, 1957), Figs. 16, 40.
  - C. (A.) brachyacantha Yang & Tian, 1987, Fig. 17.
  - C. (A.) trifurca, n. sp., Fig. 18.
  - C. (A.) huangi (Tian, 1981), N. COMB., Figs. 19, 41.
  - C. (A.) forcipata (Forsslund, 1935), Figs. 20, 42.
- Marginata Group
  - C. (A.) lirata, n. sp., Fig. 21.
  - C. (A.) fooensis (Mosely, 1942), Figs. 22, 43.
- Kolthoffi Group, C. (A.) Incertae Sedis
  - C. (A.) ensifera (Martynov, 1935), Figs. 23, 44.
  - C. (A.) kolthoffi (Ulmer, 1932), Figs. 24, 45.
- Dingwuschanella Group, C. (A.) Incertae Sedis
  - C. (A.) brachycera Yang & Tian, 1988, Fig. 25.
  - C. (A.) curva Yang & Tian, 1988, Fig. 26.
  - C. (A.) dingwuschanella (Ulmer, 1932), Figs. 27, 46.
  - C. (A.) acutipennis Yang & Tian, 1988, Fig. 28.
- Ungulifera Group, C. (A.) Incertae Sedis
  - C. (A.) omeiensis Yang & Tian, 1988, Fig. 29.
- Ceraclea (Athripsodina) Incertae Sedis
  - C. (A.) signaticornis (Ulmer, 1926), Fig. 30.

SPECIMENS EXAMINED

Specimens used in this research were collected by the senior author with the help of Mr. Li Yu-wen, Mr. Xue Ying-gen and Mr. Sun Chang-hai or were obtained from the following institutions:

Bei-jing Agricultural University (BAU)
Northwest Agricultural University (NWAU)
Nan-kai University (NU)
Shang-hai Academy of Entomological Science (Academy of Science of China; SAES)
An-hui Agricultural College (AGC)

Localities of specimens studied are indicated with arabic numbers beside them in Figure 1. The localities are as follows:

1. An-kang, Shaan-xi Province
2. Zi-yang, Shaan-xi Province
3. Emei, Si-chuan Province
4. Hua-xi, Gui-zhou Province
5. Meng-xing, Yun-nan Province
6. Wu-da-lian-chi, Hei-long-jiang Province
7. Lang-xiang, Hei-long-jiang Province
8. Tian-jing
9. Xing-hua, Jiang-su Province
10. Nan-jing, Jiang-su Province
11. Wu-hu, An-hui Province
12. Tian-mu-shan, Zhe-jiang Province
13. Wang-jiang, An-hui Province
14. Guang-zhou, Guang-dong Province
15. Wu-yuan, Jiang-xi Province
16. Shao-wu, Fu-jian Province
17. Wu-yi, Fu-jian Province
18. Pu-tian, Fu-jian Province
19. Shang-hai
20. Fu-zhou, Fu-jian Province
21. Wen-zhou, Zhe-jiang Province
22. Big-yiao-shan, Guang-xi Province
23. Jia-xing, Zhe-jiang Province
24. Jin-hu, Jiang-su Province
25. Hong-ze, Jiang-su Province
26. I-chi-chang, Si-chuan Province
27. Chin-chin-kai, Si-chuan Province

Types of new species described herein are deposited in the collections of The Department of Plant Protection, Nan-jing Agricultural University (NAU) unless indicated otherwise.

SYSTEMATIC TREATMENT

Complete bibliographies, including synonyms, of each species described before 1961 can be found in Fischer's Trichopterorum Catalogus (1965, 1972). No attempt will be made here to complete these bibliographies to the present. However, all species described since 1960, as well as new synonyms and significant redescriptions, are included. Synonyms listed by Fischer are not repeated here unless a new opinion has been reported. The sex, repository collection, and type locality of each holotype is indicated, respectively, following the original description citation for each species.

In the descriptions, the terminology for wing venation follows that of Hamilton (1972) and the terminology for genitalic structures generally follows that of Morse (1975) and Nielsen (1957) for males and of Nielsen (1980) for females. Abbreviations are indicated with the text and illustrations to designate the following structures:

Males -	ba.pl	= basal plate of the inferior appendages
	bv	= baso-ventral lobe of an inferior appendage
	do.par	= dorsal paramere
	har	= harpago of an inferior appendage
	inf.app	= inferior appendage
	IX	= abdominal segment IX
	lat.par	= lateral paramere
	me.rdg	= mesal ridge of an inferior appendage
	m.b.inf.app	= main body of an inferior appendage
	phb	= phallobase
	phc	= phalicata
	ph.gd	= phallic guide of an inferior appendage
	ph.sc	= phallotremal sclerite
	ph.sh	= phallic shield
	sap.do	= subapico-dorsal lobe of an inferior appendage
	sub.pl	= subanal plate
	sup.app	= superior appendage
	X	= abdominal segment X
Females -	go.pl	= gonopod plate of sterna VIII and IX
	lam	= lamella (= "IXd" of Nielsen, 1980)
	pr.sp.sc	= process of the spermathecal sclerite
	sp.sc	= spermathecal sclerite
	sup.app	= superior appendage (= "IXc" of Nielsen, 1980)

The basic phylogenetic relationships discussed herein were first inferred by Morse (1974, 1975). We have modified them somewhat to accomodate new characters and new species. Our phylogenetic philosophy and method were summarized by Morse and Holzenthal (1987). Our objective in this work is to infer monophyletic groups by their possession of one or more homologues (synapomorphies or uniquely shared characters) and to give formal names only to groups which evidently are monophyletic. Our phylogeny of Chinese Ceraclea species and their closest relatives is depicted in Fig. 49 along with their classification and distribution.

We sincerely appreciate the encouragement of Dr. Tian Li-xin for undertaking this research. The work was accomplished while the senior author was a Visiting Scholar at Clemson University.

Ceraclea Stephens, 1829

Type species: Phryganea nervosa Fourcroy, 1785, monobasic (a synonym of Ceraclea nigronervosa [Retzius, 1783]).

Morse and Wallace (1976) separated Ceraclea from Athripsodes; providing a brief history of the use of these generic names; supplying characters for distinguishing known larvae, pupae, and adults of their species; and establishing the tribe Athripsodini to indicate their close phylogenetic relationship. Morse (1974, 1975) revised the world fauna of Ceraclea subgenera Ceraclea and Athripsodina based on his study of adults. (Species of the only other known subgenus of Ceraclea, the subgenus Pseudoleptocerus, are recorded only from the Ethiopian Biogeographic Region [Morse, 1978]). Ross (1944, as "Athripsodes") and Resh (1976) published keys and descriptions for larvae of North American Ceraclea species, Lepneva (1966, as "Athripsodes" in part) presented keys and descriptions for larvae and pupae of Ceraclea species in the U.S.S.R., and Hickin (1967, as

"Athripsodes" in part) and Wallace (1981) provided keys to larvae of species in Great Britain and Ireland. Species groups recognized below are those proposed by Morse (1974, 1975) based on his inferences of monophyly within the genus.

Diagnosis: Adults of Athripsodini may be distinguished from those of other tribes of Leptocerinae by the following combination of characters (Mosely, 1939, as "Leptocerus"; Morse and Wallace, 1976): (1) Tibial spurs arranged 1, 2, 2 or 2, 2, 2 on the three legs of one side from anterior leg to posterior leg, respectively; (2) median vein of forewings branched beyond sectoro-medial and medio-cubital crossveins; (3) females usually with three branches of apparent median vein, males with 2 branches; and (4) anal region of hindwing usually broader than in other tribes. Adults of Ceraclea may be distinguished from those of other genera of Athripsodini by the following combination of characters (Mosely, 1939, first division of "Leptocerus"; Morse and Wallace, 1976): (1) Midcranial sulcus absent; (2) fourth segment of maxillary palps flexible due to mottled loss of sclerotization; and (3) male tergum X with an odd number of projections (due to fusion of the two median or main portions, Fig. 6B, X).

Larvae of Athripsodini may be distinguished from those of other tribes of Leptocerinae by the following combination of characters (Morse and Wallace, 1976): (1) Longitudinal or oblique mesonotal bars present on weakly sclerotized plates; (2) abdomen unusually thick anteriorly, tapering posteriorly; and (3) gills usually in clusters. Larvae of Ceraclea may be distinguished from other genera of Athripsodini by the following combination of characters (Lepneva, 1966, first division of "Athripsodes"; Morse and Wallace, 1976): (1) Mesonotal bars long and curved or angled about midlength, not straight as in Athripsodes; (2) head rather broad relative to its length and usually with parafrontal regions; (3) submental apotome of last instar short and broad, trapezoid or barrel-shaped; (4) lateral reinforcing sclerites of abdominal segment I straight or slightly curved near the anterior end; (5) gills present at least on abdominal segments II-VI, sometimes also I and VII and VIII; (6) pair of gill-like, filamentous, posterolateral projections present on tergum IX and this tergum without a distinct tergite, although sometimes weakly pigmented; (7) either one or two small accessory claws above each anal claw; (8) second instars with fringe of long swimming setae on hind legs; and (9) case with dorsal margin definitely overhanging ventral margin.

Pupae of Athripsodini may be distinguished from those of other tribes of Leptocerinae by the usually multifilamented condition of the gills (Lepneva, 1966, as "Athripsodes"). Pupae of Ceraclea differ from those of other genera of Athripsodini by the following combination of characters (Lepneva, 1966, first division of "Athripsodes"; Morse and Wallace, 1976): (1) Triangular process or bulge absent from anterior edge of labrum; (2) gills arranged generally as for larvae on abdominal segments II - VI and sometimes I and VII and VIII; (3) apex of each anal rod tapered, usually from about middle; and (4) closing membranes of case each with horizontal opening.

Distribution: Species of the genus Ceraclea are known from the Nearctic, Oriental, and Palearctic Biogeographic Regions.

Phylogenetic relationships (Fig. 49): According to Morse (1974, 1975, 1978, 1984), Morse and Wallace (1976), and Resh et al (1976), Ceraclea and Athripsodes probably are monophyletic sister lineages within the tribe Athripsodini. Homologues by which the monophyly of Ceraclea was inferred include the following: (1) the absence of a midcranial sulcus in the adults of both sexes; (2) mottled absence of sclerotization (resulting in flexibility) on the fourth segment of each maxillary palp of adults of both sexes; (3) the fusion of the two halves of tergum X of the adult male; (4) the relatively broad head of the larva; (5) the presence of parafrontal lines on the larval head; (6) the trapezoidal submental apotome of the larval head; (7) capacity of the larva to ingest whole particles of freshwater sponge. Homologues by which the monophyly of Athripsodes was inferred include the following: (1) the subapico-dorsal lobe of each inferior appendage of the male is smaller and more heavily sclerotized and (2) larvae and pupae lack filamentous gills on abdominal segments IV - VIII.

Ceraclea (Ceraclea) Stephens, 1829
Type species: Phryganea nervosa Fourcroy, 1785, as for the genus.

Diagnosis: Adults of the nominate subgenus may be differentiated from those of the rest of the genus by the following combination of characters (Morse, 1975): (1) Phallobase of male entire apico-ventrally and usually very long (Fig. 5D); (2) male with only one pair of lateral phallic parameres (Fig. 2D, lat.par); (3) male subanal plate usually present (Fig. 4A, sub.pl); and (4) species generally darker than those of subgenus Athripsodina and generally larger than those of both subgenera Athripsodina and Pseudoleptocerus. Reared larvae and pupae of Ceraclea species from around the world have been studied insufficiently to permit diagnosis of those life history stages for the subgenera of this genus.

Distribution: Species of this subgenus occur in the Nearctic, Palearctic, and Oriental Biogeographic Regions, but none have been reported previously from China.

Phylogenetic relationships (Fig. 49): Morse (1975) considered this subgenus to be the sister group of the subgenus Pseudoleptocerus based on the following shared homologues (synapomorphies): (1) the ventral apex of the phallobase is very long, serving as an accessory phallic guide for the cylindrical phalicata and (2) a subanal plate is present in the external membranes beneath the anus under tergum X. The evidence for the monophyly of Pseudoleptocerus species includes the following homologues (Morse, 1978): (1) the harpago is absent or fused with the main body of the male inferior appendage and (2) forewings of both sexes have yellowish-brown scales and clear patches on various portions of the wing membrane and large, white scales regularly spaced along the longitudinal veins.

Fulva Group

Diagnosis: According to Morse (1975), "The forewings of species in this group are various shades of brown, usually with a light patch at the arculus." Males of members of this species group may be distinguished by the following combination of characters (Morse, 1975): (1) Ventral apex of phallobase short (Fig. 2D, phb; except C. [C.] cama [Flint, 1965]); (2) phalicata (Fig. 2D, phc) with lateral grooves where parameres lie when phalicata and parameres retracted; (3) subapico-dorsal lobe of each inferior appendage (Fig. 2A, sap.do) usually bent caudad near its base (Fig. 3A); (4) harpago (Fig. 2C, har) with subapical triangular projection; and (5) tergite X divided apically into pair of large lateral lobes and smaller median finger-like lobe (which is itself divided in some specimens).

The genitalia of the females of C. (C.) resurgens (Walker, 1852; Ross, 1944), transversa (Hagen, 1861; Ross, 1944, as "Athripsodes angustus"), fulva (Rambur, 1842; Kimmins, 1964), albimacula (Rambur, 1842; Kimmins, 1964, as "Athripsodes alboguttatus"), and alboguttata (Hagen, 1860; Malicky, 1983, illustrations only) have been described for this group. They share the following distinctive characteristics: (1) Pair of gonopod plates ventrally on sternum IX (Fig. 30C, go.pl) with apico-lateral corners marked by parallel longitudinal grooves and ridges or striae; (2) spermathecal sclerite (Fig. 30D, sp.sc) with wide lateral expansions.

The larva of C. (C.) fulva has been described by Lepneva (1966) and Wallace (1981); that of albimacula by Lepneva (1966, as "Athripsodes alboguttatus") and Wallace (1981); that of alboguttata by Tsuda (1954, as "Leptocerus biwaensis", Fig. 47); that of transversa (Hagen, 1861) by Ross (1944, as "Athripsodes species a") and Resh (1976), and those of alces (Ross, 1941) and resurgens (Walker, 1852) by Resh (1976). All the known larvae of species in this group feed on freshwater sponge, apparently as a necessary part of their life cycle (Resh et al, 1976). Other characters for distinguishing larvae of the Fulva Group include the following: (1) Lines demarking parafrontal regions obscure posteriorly; (2) antennae only two times as long as broad in last instar; and (3) case made up almost entirely of salivary secretions (Lepneva, 1966), often with pieces of living sponge or sponge spicules or sand attached or incorporated (Resh et al, 1975; Resh, 1976).

Lepneva (1966) described the pupae of C. (C.) fulva and albimacula (the latter as "Athripsodes alboguttatus"); Resh (1976), those of alces, resurgens, and transversa. The anterior projection of the labrum, otherwise characteristic for the genus, is small or absent in these species. Each of the posterior hookplates of abdominal tergum V has 8-18 anteriorly directed hooks. Anal rods are variously shaped, with one or two mesal processes more or less strongly developed at the abrupt transition between the basal and apical portions.

Distribution: Species of the Fulva Group are known from the Nearctic and Palearctic Biogeographic Regions.

Phylogenetic Relationships (Fig. 49): Monophyly for the Fulva Group was inferred from the following homologues (Morse, 1975; Resh et al, 1976): (1) the apex of male tergum X is three-pronged, with a pair of large lobes with lateral sensillae and between them a smaller, finger-like lobe; (2) the mesal ridge of each male inferior appendage is particularly wide; and (3) the apex of the male harpago is expanded with a subapical triangular projection; (4) the female spermathecal sclerite has semimembranous lateral expansions; (5) larval parafrontal lines are absent; (6) larval mesonotal bars are dichromatic; (7) tergum IX has only two long setae; (8) larval case constructed almost entirely with silk; and (9) antennae of last larval instar are short. According to Morse (1975), the remaining species of this nominotypical subgenus are the monophyletic sister group of the Fulva Group. Monophyly for the remaining species of the subgenus Ceraclea was evidenced by the following homologues (Morse, 1975): (1) scattered white scales are present on the forewings of both sexes (not present in some species) and (2) the female genitalia have a pair of longitudinal grooves dorsad of the lateral margins of the gonopod plates.

Ceraclea (C.) spinulicolis sp. n.

Description: Head and body of male reddish fuscous with brown and white hairs intermixed; forewings golden brown, covered densely with dark brown setae from anastomosis to apex.

Male genitalia (Fig. 2): Superior appendages (sup.app) broad and truncate in dorsal view. Tergum X (X) divided into two broad lobes apically with pair of short, broad median protuberances between lobes in ventral view (Fig. 2E). Dorsal and ventral edges of tergum X in lateral view subparallel, upturned from middle, rounded apically, not constricted subapically. Inferior appendages (inf.app) without ventral lobes; mesal ridge (me.rdg) broad basally to about midlength, with numerous short spines; subapico-dorsal lobe (sap.do) moderately developed, bent slightly caudad from near base, with long hairs; harpago (har) with acute subapico-mesal process. Phallobase (phb) with short ventral apex; parameres (lat.par) short, bent ventrad in even curve; phallotremal sclerite (ph.sc) with slender tube or spine protruding from beneath it, often with additional seta-like spines apparently in membranes around phallotremal sclerite, especially dorsally.

Female genitalia (Fig. 31): Superior appendages (sup.app) very short, each visible only as ridge in lateral view. Apical margin of lamella (lam) semicircular, with distinct membranous center in lateral view. Gonopod plates (go.pl) with evident longitudinal striae laterally. Spermathecal sclerite (sp.sc) about 1.25 times as long as broad.

Length of forewing: male - 10 mm, female - 9 mm.

Immature stages unknown.

Type material: Holotype MALE, Wu-hu, An-hui Province (N31.23, E118.25; Fig. 1, site #11), 9 Aug 1987, Li You-wen. Paratypes 4 males, 1 female, collected with holotype.

Etymology: Latin, "little spine penis", with reference to the slender structure beneath the male phallotremal sclerite.

Diagnosis: The apico-lateral lobes of male tergum X, like those of C. (C.) cama (Morse, 1975, fig. 33), are not constricted subapically; also, the mesal ridge of each inferior appendage is broad only basally and does not have a single conspicuous spine; but unlike that species the ventral apex of the phallobase is short. Unlike most species of the group, the male inferior appendages of this

species each lack a ventral lobe and the mesal lobe of male tergum X is very short, to be seen only as a pair of small protuberances in caudal view. Insofar as is known, the slender tube or spine in the membranes beneath the male phallotremal sclerite of this species is unique for the Fulva Group. Among known females of species of the Fulva Group, the spermathecal sclerite is narrower for this species than for the others.

Distribution: Known only from the type series from eastern China.

Phylogenetic relationships (Fig. 49): Ceraclea (C.) cama is the sister lineage for all remaining species of the Fulva Group. Those remaining ten species constitute a monophyletic group based on the following homologue (Morse, 1974): (1) apico-ventral lobe of phallobase short. Ceraclea (C.) spinulicolis is the sister lineage for the remaining nine species of the Fulva Group. Those species are a monophyletic group as evidenced by the following homologue (Morse, 1974): (1) lateral apical lobes of male tergum X constricted subapically, such that each lobe appears rather hatchet-shaped in lateral view.

Ceraclea (C.) alboguttata (Hagen)

Leptocerus alboguttatus Hagen, 1860, p. 70; lectotype = male; type repository = Harvard University Museum of Comparative Zoology, Cambridge, Massachusetts, United States of America; type locality = London.

Leptocerus spinosus Tsuda, 1942b, pp. 293-294, figs. 44-45; holotype not selected, syntype repository presumably = Nara Women's University, Japan; syntype localities = Keage, Kyoto, and Ōtsu, Shiga, Japan; name preoccupied by Navás, 1930; NEW SYNONYM.

Leptocerus biwaensis Tsuda and Kuwayama, 1950, p. 420, new name for L. spinosus; Tsuda, 1954, pp. 12-13, illustrations of larva and discussion of its association with freshwater sponge; NEW SYNONYM.

Athripsodes biwaensis (Tsuda and Kuwayama); Botosaneanu, 1970, p. 308, reported from Korea.

Ceraclea (C.) alboguttata (Hagen); Morse, 1975, pp. 27-28, fig. 38, lectotype designation and description of male; Malicky, 1983, pp. 275 and 279, illustrations of male and female.

Description: Body dark brown. Center of face with white setae. Sides of vertex with white and brown intermixed. Forewings concolorous brown with dark brown setae.

Male genitalia (Fig. 3): Superior appendages short, truncate to triangular in dorsal view. Tergum X divided into two long caudal lobes constricted subapically and truncate apically in lateral view; setose median lobe situated between them rounded in lateral view and triangular in dorsal and caudal views, sometimes with mesal notch; pair of high ear-like ridges laterally about midlength. Inferior appendages each with baso-ventral lobe varying from about 1/5 to 1/4 length of remainder of appendage, tapered or blunt apically, with one to five golden apical or subapical spines; mesal ridge with moderately strong spine on caudal face; harpago shape typical for Fulva Group, with eight to twelve stout spines apically. Phallic apparatus having phallobase with short ventral apex; parameres gradually curved, 1/2 to 3/4 as long as phalicata; phalicata with pair of ear-like projections basally below paramere grooves and with two pairs of semi-membranous lobes above these grooves apically.

Variation: Chinese specimens examined for this study lie well within the range of variations seen in European material. In European males, even in specimens at the same locality, we have seen variations especially in the following characters: (1) The shape of the apex of the superior appendages, ranges from subtruncate (lectotype [Morse, 1975, fig. 38B]) to subtriangular (similar to Fig. 3B), depending on the extent of development of the bump or protrusion in the middle

of the distal edge of each. (2) The shapes of the processes at the apex of tergum X are variable, especially the mesal process, which ranges from being poorly differentiated from the apico-lateral lobes and with a relatively wide mesal excision in dorsal view (as in the lectotype [Morse, 1975, fig. 38B]) to being well differentiated from those lobes, triangular in profile, and with or without a narrow mesal notch (Figs. 3B, 3'B, 3'B inset). (3) The length and shape of the ventral lobe of each inferior appendage and the number of apical and subapical spines vary as described above. (4) The mesal ridge of the inferior appendage may or may not project caudad, such that it may or may not be visible in lateral view (visible in C. [C.] "biwaensis" [Tsuda, 1942b, fig. 45a, and Morse, 1975, fig. 35A]; not visible in alboguttata lectotype [Morse, 1975, fig. 38A] or some Chinese specimens, Fig. 3A). (5) The phallic parameres range in length as described above from 1/2 the length of the phalicata (as in the lectotype [Morse, 1975, fig. 38D]) to 3/4 its length (as in Fig. 3D).

Female genitalia (Fig. 32): Superior appendages conspicuous, semicircular from above, triangular in lateral view. Apical margin of each lamella semicircular, striated ventrally. Gonopod plates with deep longitudinal striae laterally. Spermathecal sclerite about as broad as long.

Length of forewing: male - 13 mm (10-12 mm according to Malicky, 1983, for European specimens), female - 11 mm (10-11 mm, Malicky, 1983).

Larva (Fig. 47): Description and illustration provided by Tsuda (1954, as "Leptocerus biwaensis"). Structure typical for species group. Parafrontal sutures not apparent, but regions usually defined by such sutures and frons brown, genae brown, two pairs of dark spots posteriorly on either side of frons and epicranial sulcus, otherwise pair of yellow bands from eye regions to occipital foramen. Pronotum yellow with transverse row of dark spots near anterior margin, four spots on each side, each with seta from middle of spot. Case primarily of silk.

Other immature stages unknown.

Diagnosis: Among males of species of the Fulva Group, C. (C.) alboguttata resembles fulva and albimacula in possessing a short stout spine on the caudal face of the mesal ridge of each inferior appendage (transversa and latahensis [Smith, 1962] also have stout spines in this position, but the spines are much longer in these species). Ceraclea (C.) alboguttata differs from these species in the long baso-ventral lobe of each inferior appendage, at least twice as long as broad basally, with two or three long stout spines apically. Among females of known Chinese species of the Fulva Group, the spermathecal sclerite is broader for this species than for C. (C.) spinulicolis. Among larvae of this species group, C. (C.) alboguttata is distinctive in the brown frontal and "parafrontal" area and pair of dark spots posteriorly on the head and in the transverse row of dark spots near the anterior margin of the pronotum.

Distribution: Known previously from Europe and (as C. [C.] biwaensis) Japan and Korea, this species has now been collected in northern China: Wu-da-lian-chi, Hei-long-jiang Province (N48.45, E125.55; Fig. 1, #6), 8 August 1987. It is possible that the species will be found also in northcentral Asia, between these eastern and western ends of the Palearctic Region.

Phylogenetic relationships (Fig. 49): Within the Fulva Group, C. (C.) alboguttata is most closely related to four other species with the following homologue (Morse, 1974): (1) a stout spine is present on the caudal face of the median ridge of each male inferior appendage. Among these, C. (C.) transversa and latahensis share the homologously very long and sinuous shape of this spine. Evidence from other life history stages may reveal whether C. (C.) alboguttata, fulva, and albimacula are a monophyletic group within this complex.

Nigronervosa Group

Diagnosis: According to Morse (1975), members of this group are "generally large, dark species with wing veins particularly conspicuous (except mentiea, slossonae, and ophioderus). Species with white scales (erulla, erratica, and albosticta) have them scattered generally over the forewing except clusters at arculus and before stigma." Males of members of this group may be distinguished

from those of other groups by the following characters (Morse, 1975): (1) A pair of large, lateral, sclerotized, ear-like lobes are differentiated from the main body of tergum X, in many non-Chinese species each of these lobes has an additional process (e.g., Morse, 1975, fig. 53A); and (2) phallic paramere spines of all species except erulla have fine silky setae subapically.

The genitalia of the female of C. (C.) nigronervosa were described and illustrated by Kimmins (1964) and Malicky (1983) and those of the females of albosticta (Hagen, 1861; as "Athripsodes saccus"), erratica (Milne, 1936), erulla (Ross, 1938b), and mentiea (Walker, 1852) were described and illustrated by Ross (1944). In most of these species, a mesal sclerite is positioned between the gonopod plates ventrally as in the Senilis Group, but this sclerite is larger in the Nigronervosa Group.

The larva of C. (C.) nigronervosa was described by Resh (1976) and Wallace (1981) and those of mentiea and slossonae (Banks, 1938) by Resh (1976). All three species have broad, light-colored bands extending from around the eyes to the occipital foramen.

Distribution: Species of the Nigronervosa Group are known from the Palearctic and Nearctic Biogeographic Regions.

Phylogenetic relationships (Fig. 49): According to Morse (1975) the Nigronervosa Group is a monophyletic group whose monophyletic sister group is the Senilis Group based on the following homologue: (1) a mesal sclerite is present between the gonopod plates of the female. A homologue for the Nigronervosa Group is (1) the pair of ear-like lobes present on the lateral surfaces of male tergum X. A homologue for the Senilis Group is (1) the elongate baso-ventral lobe of each male inferior appendage.

Ceraclea (C.) superba (Tsuda)

Leptocerus superbus Tsuda, 1942b, pp. 292-293, fig. 43, holotype not selected; syntype repository presumably = Nara Women's University, Japan; syntype localities = Keage and Kitaôji-bashi, Kamogawa, Kyoto, Japan.

Ceraclea (C.) superba (Tsuda); Morse, 1975, p. 34, fig. 59, review of male genitalia.

Description: Head and body of male dark brown, forewings golden brown, darkened in apical quarter, with white streak along posterior vein of discal cell (S_{3+4}).

Male genitalia (Fig. 4): Superior appendages short, each with two to seven long apical setae about two-thirds as long as superior appendage. Tergum X shorter than superior appendages, with pair of well-defined ear-like lobes laterally, otherwise subquadrate in lateral view with blunt protrusion apically. Subanal sclerite projecting caudally well beyond tergum X. Inferior appendages each with subrectangular main body in lateral view, its baso-ventral region broadly rounded, and its ventro-caudal margin concave; large subapico-dorsal lobe as long as main body of appendage; mesal ridge broad, truncate, setose; each harpago huge, one and one-third as long as main body of inferior appendage, bent mesad in right angle arch about midway. Phallobase with ventral apex vestigial or not projecting; single pair of parameres asymmetrically sinuous, long, with fine setae clustered around darkened apex.

Female and immature stages unknown.

Length of forewing: male - 8.5 mm.

Diagnosis: Within the Nigronervosa Group, this species most closely resembles C. (C.) ramburi Morse, 1975, nigronervosa, and erratica in the broadly rounded baso-ventral lobe of each inferior appendage; like nigronervosa and erratica, tergum X is short, even shorter than in those two species; also like those two species, the apex of each phallic paramere is noticeably darkened; like nigronervosa, there is no pair of additional lateral projections on tergum X; like ramburi, the harpagones and the subanal plate are long, considerably longer even than in that species; and like erratica, the mesal ridge of the inferior appendage is large and spinose. This species differs from all other members of the

Nigronervosa Group, including these three species, by the very short tergum X, by the very long and curved harpagones, by the absence of a long ventral apex of the phallobase, and by the distinctively sinuous and dark-tipped phallic parameres.

Distribution: Kyoto, Japan, and now China: Wu-da-lian-chi, Hei-long-jiang Province (N48.45, E125.55; Fig. 1, #6), 8 August 1987.

Phylogenetic relationships (Fig. 49): This and the following species apparently are members of the Nigronervosa Group as evidenced by their possession of a few silky setae subapically on the male paramere spines, a character seen uniquely in most members of the group. These two are probably sister species according to the following homologues: (1) the mesal ridge of each inferior appendage is confined to the base of the appendage and bears many short, stout setae and (2) the ventral apex of the phallobase is short. Study of characters from other life history stages may reveal the relationships of these two species to others in the Nigronervosa Group.

Ceraclea (C.) sinensis (Forsslund, 1935)
NEW COMBINATION

Leptocerus sinensis Forsslund, 1935, pp. 8-9, fig. 8; holotype = male, abdomen missing; type deposition = National Museum of Natural History, Stockholm; type locality = I-chi-chang, Si-chuan Province (N30.50, E106.60; Fig. 1, #26).

Description: Head and body reddish-brown, vertex and frons mostly with white setae, sides with white and brown setae intermixed. Forewings light reddish-brown.

Male genitalia (Fig. 5): Superior appendages short, separate basally, obliquely truncate apically. Tergum X 2.2 times as long as superior appendages, broad, lightly sclerotized, pair of reinforcing carina internally at base near meson; its apical quarter with U-shaped cleft; lateral processes nearly as broad as central portion of tergum in lateral view, arising from surface of tergum and closely appressed to tergum, each with one apical and one subapical very stout spines. Inferior appendages broad, bent mesad in pair of semicircular arches in caudal view; each with thick subapico-dorsal lobe arising on dorsal edge of basal segment about middle, initially directed dorsad then abruptly angled caudad; mesal ridge confined to base of appendage, transverse to appendage, with small baso-ventral lobe at caudal end; harpago nearly half as long as rest of appendage, sinuous, blunt apically. Phallobase without long apico-ventral projection; phalicata tube-like, with wide dorsal longitudinal groove for reception of parameres; paramere spines fused basally, divergent apically, with few fine subapical setae.

Female genitalia (Fig. 33): Pleura of segment IX narrowed and concave anteriorly in pair of grooves, vertical along middle of anterior edge and longitudinal along ventral edge in lateral view. Superior appendage very short and broad, pair of setose transverse ridges in dorsal view, triangular in lateral view. Lamellae pentagonal in lateral view, parallel-sided basally with dorsal and ventral edges oblique from middle to blunt apex. Gonopod plates closely approximate on meson anteriorly, abruptly divergent posteriorly beyond middle, each plate with triangular transverse ridge near middle; broad membranous region posterior to plates. Spermathecal sclerite ovoid to pear-shaped in ventral view; anterior portion solid plate concave ventrally (except for mesal spermathecal process), posterior supporting band V-shaped; two pairs of dark, sclerotized spots in membranes dorsad of sclerite.

Length of forewing: male - 7 mm, female - 5.8 mm.

Immature stages unknown.

Diagnosis: The male of this species resembles C. (C.) superba in the shapes of its inferior appendages and phallus, but differs from it in the much longer tergum X with spinose lateral processes and from all other species of Ceraclea by the position of the subapico-dorsal lobe of each inferior appendage in the middle of the dorsal edge of the appendage. The female of this species differs from those known for other Nigronervosa Group species in the absence of a mesal sclerite between the gonopod plates and from those of other Ceraclea species in the

presence of deep vertical and longitudinal grooves on the pleura of segment IX, the presence of triangular transverse ridges on the gonopod plates, and the ovoid to pear-shaped spermathecal sclerite.

Distribution: Besides the type locality in southcentral China, this species now is known from southeastern China: Wu-yuan, Jiang-xi Province (N29.15, E117.53; Fig. 1, #15), 18 August 1985, and Shao-wu, Fu-jian Province (N27.21, E117.27; Fig. 1, #16), 2 August 1983.

Phylogenetic relationships (Fig. 49): As discussed above, this species is the sister species of C. (C.) superba. The absence of a sclerotized plate between the gonopod plates of the female of this species introduces an element of doubt about their relationships with the Nigronervosa Group or about the value of this character for indicating monophyly of the Senilis + Nigronervosa Groups.

Ceraclea (Athripsodina) Kimmins, 1963

Type species: Leptocerus marginatus Banks, 1911, original designation.

Diagnosis: Adults of this subgenus may be differentiated from those of the rest of the genus by the following combination of characters (Morse, 1975): (1) Male phallobase almost always cleft apico-ventrally. (2) Male tergum X in many species with a pair of rod-like lateral processes on the ventro-lateral edge of the tergite (not from the surface of the tergite as in many species of the Ceraclea (C.) Nigronervosa Group). (3) The semimembranous subapico-dorsal lobe and the harpago of each male inferior appendage is generally smaller than in the subgenus Ceraclea. (4) The male phalicata is never a conspicuous tubular structure as is usual in the rest of the genus. (5) Specimens are generally smaller than those in the subgenus Ceraclea and lighter colored than those in the rest of the genus.

Distribution: Ceraclea (Athripsodina) species are known from the Nearctic, Oriental, and Palearctic Biogeographic Regions.

Phylogenetic relationships (Fig. 49): The sister group of this subgenus is the pair of subgenera Ceraclea (C.) + C. (Pseudoleptocerus) according to Morse (1975). Evidence for the monophyly of the three subgenera of Ceraclea was cited in the discussion of the genus above. Evidence for the monophyly of Ceraclea (C.) + C. (Pseudoleptocerus) was cited in the discussion of the subgenus Ceraclea (C.) above.

Tarsipunctata Group

Diagnosis: According to Morse (1975), species of the Tarsipunctata Group are similar in general appearance to members of the Ceraclea (C.) Fulva Group in that the forewings are various shades of brown with light brown hairs in small patches, especially at the arculus. Distinguishing characters for the males include the following (Morse, 1975): (1) Lateral processes of tergum X usually very long, upturned, and always nearly or completely separate from main body of tergite; inferior appendages each with (2) acute baso-ventral lobe (except C. [A.] brevis [Etnier, 1968]), (3) rounded and setose mesal ridge, and (4) large harpago; (5) phallobase narrow near base and with pair of deep, rounded, longitudinal-oblique grooves; (6) sternum IX sclerotized strips and phallic shield sclerotized strips present but not touching; (7) phallic shield strips short, each with large, rounded, extrinsic posterior projection especially evident in C. (A.) nepha (Ross, 1944) and protonepha (Morse and Ross, in paper by Morse, 1975, fig. 70D); (8) both pairs of phallic parameres present, although dorsal pair usually reduced and easily confused with pair of reticulate, semimembranous dorsal lobes of phalicata; and (9) phalicata membranous dorsally, sclerotized ventrally, supporting endophallic membranes in manner of Mexican taco.

Females of C. (A.) tarsipunctata (Vorhies, 1909) and alagma (Ross, 1938a) were described by Ross (1944). Known females of species in the Tarsipunctata Group may be diagnosed by the following combination of characters: (1) Gonopod plates generally flat or convex; (2) pair of mesally curved processes projecting caudally from apices of the gonopod plates between lamellae; and (3) posterior ends of arms of spermathecal sclerite curve ventrad, conspicuous as semicircles in ventral view.

Larvae of C. (A.) tarsipunctata, alagma, and nepha were described by Resh

(1976). These species are recognizable by the following combination of characters: (1) Parafrontal areas present, each 1/2 as wide as frontoclypeal apotome; (2) antennae long, three to five times as long as thick; (3) mesonotal bars without contrasting colors; (4) mesonotum with only few setae along mid-dorsal sulcus; (5) head without longitudinal stripes; (6) only one dorsal seta on each trochantin; (7) tergite IX with two pairs of long setae; (8) anal legs with either plate-like support (tarsipunctata and nepha) or no sclerotization (alagma), but clearly no long and rod-like dorsolateral sclerite.

Distribution: Species of the Tarsipunctata Group were known previously only from central and eastern North America.

Phylogenetic relationships (Fig. 49): The sister group of the Tarsipunctata Group is the Spinosa Group, known only from central Africa (Morse 1975, 1978). Monophyly for the Tarsipunctata Group is evidenced by the following homologues: (1) an oblique constriction is present in the basal half of the male phallobase and (2) the phallic shield is produced laterally at the base of each sclerotized strip into a broadly rounded periphallic projection. A third homologue mentioned by Morse (1975) applies only to the Nearctic species of this group. Homologues implying monophyly for the Spinosa Group include the following: (1) the superior appendages are very long, (2) the ventral portion of the phallic shield is long and fused with the basal plate of the inferior appendages, (3) paramere spines are absent, and (4) phalicata sclerotization is greatly reduced. Evidence for the sister group relationship of these two species groups includes the following homologue: (1) the lateral processes of tergum X are very long and distinct from the tergite nearly to the base of the tergum.

Ceraclea (Athripsodina) major (Hwang)

Leptocerus major Hwang, 1957, pp. 390-391; holotype = male; type repository = Chinese Academy of Science, Bei-jing; type locality = Big-yiao-shan, Guang-xi Province, China (N24.00, E110.20; Fig. 1, #22), 19 April 1938.

Ceraclea (Athripsodina) major (Hwang); Morse, 1975, pp. 48-49, fig. 104, redescription of the male.

Description: Head and body of male dark reddish brown. Center of face and vertex with white and brown setae intermixed. Forewings concolorous, fulvous, covered with intermixed white and brown setae.

Male genitalia (Fig. 6): Superior appendages fused basally for nearly 1/2 their length. Tergum X broad, truncate from above, slightly clavate and upturned in lateral view; lateral processes finger-like, very short, arising from the lateral base of tergum X. Each inferior appendage broad in ventral view; ventral lobe short, triangular, with 5-6 thick spines in row along its dorso-lateral edge; subapico-dorsal lobe bent caudad at right angle; harpago broad basally, narrowing to ventral subapical setose lobe, apex hooked mesad; phallic guide long, sharp, sinuate in ventral view, broad in lateral view with expanded ridge from basal plate to tip. Phallic shield with pair of rounded, posterior extrinsic projections laterally; phallobase with long lower lip longitudinally divided and with short fine setae dorsally near apex; phalicata without sclerotization; pair of dorsal parameres flattened and semimembranous; lateral parameres asymmetrical with left one sinuous, right one curved ventrad; phallotremal sclerite small and inconspicuous.

Female and immature stages unknown.

Length of forewing: male - 14 mm.

Diagnosis: Morse (1975) did not see the holotype and so was not able to place this species in a species group. The cleared genitalia of this specimen reveal that it exhibits the homologues of males of the Tarsipunctata Group. The male of this species differs from those of the others by lacking the rounded, setose mesal ridge of each inferior appendage and by lacking the ventral sclerotization of the phalicata.

Distribution: Known only from the holotype collected in southern China.

Phylogenetic relationships (Fig. 49): Males of the other species of the Tarsipunctata Group have a subapical annulation on each paramere spine, absent

in this species. This suggests that C. (A.) major is the oldest known lineage in this species group; it is the sister lineage to the other species which themselves constitute a monophyletic group evidenced by that homologue.

Dissimilis Group

Diagnosis: The head and thoracic sclerites of adults in this group are reddish brown with predominately white setae. The forewings are brown, darker apically, each with a small white mark at the arculus. The males of this species group may be distinguished from those of other groups in this subgenus by the fact that in these species the superior appendages are broad basally and fused for at least half their length. Tergum X is short and generally without lateral processes. The baso-ventral lobe of each inferior appendage is obliquely truncate apically except in C. (A.) wetzeli (Ross, 1941). The phallobase is asymmetrical apically with the left lateral lobe narrower and curved ventrad, a thin sclerotized strip often extending into the endothecal membranes dorsally; the phalicata is not sclerotized; and the parameres are retracted to approximately the same depth within the phallobase when at rest (Morse, 1975).

The female of Ceraclea (Athripsodina) dissimilis (Stephens, 1836) was described by Kimmins (1964). In this species, the superior appendages are very short and triangular in dorsal view and the lamellae are small and elliptical. The apex of each of the gonopod plates is divided longitudinally, with the lateral processes curved to lie dorsad of the mesal lobes.

The larva of Ceraclea (Athripsodina) dissimilis was described by Wallace (1981). In this species, mature larvae lack mesosternal setae but have two or more pairs of metasternal setae. Setae of tergum IX are all smaller than the smallest anal proleg setae. The case is composed of closely abutted sand grains, occasionally incorporating roots at the anterior end.

Distribution: Five of the species known for this group occur in the Nearctic and Palearctic Biogeographic Regions outside of China. The sixth species, C. (A.) indistincta, is known from the Oriental and Palearctic Regions of China.

Phylogenetic relationships (Fig. 49): Evidence for the monophyly of the Dissimilis Group is the following homologue (Morse, 1975): (1) the left apex of the phallobase is narrow and downcurved. The Dissimilis Group, according to Morse (1975), is one lineage of an unresolved trichotomy. The other two lineages are, on the one hand, the Arielles Group and, on the other hand, the complex of the Diluta + Annulicornis + Riparia + Marginata Groups. The Arielles Group includes only the single northcentral Nearctic species C. (A.) arielles (Denning, 1942). Evidence for the monophyly of the four-group complex includes the following homologue (Morse, 1975): (1) the left paramere spine is positioned anteriorly inside an inverted membranous paramere lobe when the phallus is fully retracted.

Ceraclea (Athripsodina) indistincta (Forsslund, 1935)

Leptocerus indistinctus Forsslund, 1935, p. 8; holotype = male, abdomen probably lost (P.I. Persson, curator, pers. comm.); type repository = National Museum of Natural History, Stockholm, Sweden; type locality = I-chi-chang, Si-chuan Province, China (N30.50, E106.60; Fig. 1, #26), 250-400 m above sea level, 2 May 1930.

Ceraclea (Athripsodina) indistincta (Forsslund); Morse, 1975, p. 39, fig. 76, review of male genitalia.

Description: Head and thorax reddish brown, vertex and center of face with white setae, sides with brown setae. Forewings brown, darker apically, each with white mark at arculus.

Male genitalia (Fig. 7): Superior appendages broad basally, rounded apically in dorsal view. Tergum X short, with shallow median cleft in dorsal view. Baso-ventral lobe of each inferior appendage slender, as long as width of inferior appendage, projecting caudad, its apex fist-like; mesal ridge projecting as triangular lobe just below harpago; harpago short, bent mesad in middle.

Phallobase asymmetrical with left anterior part swollen (Fig. 7D'), with left apical lobe acute and narrower than right, and with dorsal apex convoluted longitudinally; parameres 2/3 as long as phallobase, curved gradually about 90° in lateral view.

Length of forewing: male - 7 mm.

Female and immature stages unknown.

Diagnosis: Ceraclea (A.) indistincta male genitalia are very similar to those of lobulata. They differ primarily in the more rounded apexes of the superior appendages in C (A.) indistincta in dorsal view, in the more nearly triangular mesal ridge of each inferior appendage, and in the more strongly curved paramere spines.

Distribution: Eastern and central China: the type locality and Wu-hu, An-hui Province (N31.23, E118.25; Fig. 1, #11), 9 August 1987.

Phylogenetic relationships (Fig. 49): The sister species for C. (A.) indistincta probably is lobulata as evidenced by the following homologue (Morse, 1974): (1) the base of the main body of each inferior appendage is slender. The sister lineage for these two species probably is C. (A.) dissimilis as is suggested by the following homologue (Morse, 1974): (1) tergum X is short and strongly upturned apically.

Ceraclea (Athripsodina) lobulata (Martynov, 1935)

Leptocerus lobulatus Martynov, 1935, pp. 223-225, figs. 16-18; holotype gender unknown, but probably = male; type series repository = Zoological Institute, U.S.S.R. Academy of Sciences, Leningrad; syntype localities = Amur, Zeja, and Bikin Rivers near Blagovestshensk, Siberia.

Ceraclea (Athripsodina) lobulata (Martynov); Morse, 1975, p. 40, fig. 77, described and illustrated syntype male.

Description: Head and thoracic sclerites reddish brown with predominately white setae. Forewings brown, darker apically, each with small white mark at arculus.

Male genitalia (Fig. 8): Superior appendages broad basally, narrower apically, fused for at least half their length. Tergum X short, without lateral processes, deeply incised laterally. Baso-ventral lobe of each inferior appendage small, upturned and obliquely truncate apically; mesal ridge with acute dorsal apex. Phallobase asymmetrical apically with left lobe narrower and sharper than right and downcurved; lateral parameres retracted to approximately same depth within phallobase.

Female genitalia (Fig. 34): Superior appendages broad basally, fused mesally. Lamellae obliquely subtruncate in dorsal and ventral views, elliptical in lateral view. Gonopod plates each with two sclerotized projections apically, mesal one lightly sclerotized and triangular, lateral one dark (conspicuous in uncleared specimens) and rectangular and positioned dorsally behind mesal lobe and lateral arm of spermathecal sclerite; gonopod plates also projecting antero-mesally into segment VIII. Spermathecal sclerite broad, with large mesal process (pr.sp.sc).

Length of forewing: male - 8.5 mm, female - 7 mm.

Immature stages unknown.

Diagnosis: Both the males and the females of this species exhibit all of the Dissimilis Group characters mentioned above. Within this group, the male of this species resembles those of C. (A.) dissimilis, indistincta, and miyakonis (Tsuda, 1942b) in the upturned tergum X, but differs from dissimilis in the relatively smaller inferior appendages, from indistincta in the narrower apex of each superior appendage and the upturned apex of the mesal ridge of each inferior appendage, and from miyakonis in the more strongly upturned tergum X and shorter baso-ventral lobe of each inferior appendage.

Distribution: Amur Region of Siberia and now China: Wu-da-lian-chi, Hei-long-jang Province (N48.45, E125.55; Fig. 1, #6), 8 August 1987.

Phylogenetic relationships (Fig. 49): The sister species of C. (A.) lobulata probably is indistincta and the sister species of the two of them probably is

dissimilis as discussed above for indistincta.

Annulicornis Group

Diagnosis: In adults of this species group, according to Morse (1975), head and thoracic sclerites are various shades of brown with light setae. In most species (except C. [A.] aurea [Pictet, 1834], sibirica [Ulmer, 1906], and hastata [Botosaneanu, 1970]), the vertex and the middle portion of the mesonotum form a dark mesal stripe with temporal regions and lateral portions of the notum lighter. The proximal antennal segments are annulated with white basally. In males, the superior appendages generally are short and tergum X is long, upturned, and usually rounded apically; a pair of processes usually is present near the base or near the middle on the lower lateral margins. Inferior appendages are either slender (most species) or broad basally (C. [A.] aurea, sibirica, and hastata), each with the baso-ventral lobe at least 1/4 as long as the main body of the appendage (up to as long as the main body, excluding the subapico-dorsal lobe); the phallic guide is usually broad basally and often rather long. In the phallus, the left paramere spine is reduced in all species and seta-like in all but the above three species; the inverted, left, membranous, paramere lobe containing this spine mostly fills the anterior portion of the phallobase which is greatly enlarged in all but the above three species; the phalicata is not sclerotized, its position suggested only by the phallotremal sclerite offset to the right of the protracted membranes.

The female of C. (A.) annulicornis (Stephens, 1836) was described by Ross (1944) and Kimmins (1964). In that species the lamellae are short and semi-circular in lateral view and the pleural regions of segment IX are concave, the concavities conspicuous in ventral view behind the lateral margins of the gonopod plates. Each of the gonopod plates extends caudally as a broad triangular projection, the two projections separated by a U- or V-shaped excision. The basal supporting bands of the spermathecal sclerite extend anteriorly beyond the sclerite into segment VII.

The mature larva of C. (A.) annulicornis was described by Lepneva (1966), Resh (1976), and Wallace (1981, also instar II), that of excisa (Fig. 48) by Lepneva (1966) and Resh (1976), and that of misca (Ross, 1941; a synonym of excisa according to Morse, 1975) by Resh (1976; considered by him as distinct from excisa). Parafrontal areas are present in these species and the antennae are long. Membranous tergum IX has one pair of long setae, three or four other pairs are short. At least in C. (A.) annulicornis, the mesosternum lacks setae and the metasternum has only one pair. The sand case of these species is cornucopia-shaped, without lateral expansions.

Lepneva (1966) and Resh (1976) described the pupae of C. (A.) annulicornis and excisa (Fig. 48) and Resh (1976) that of "misca". The mandibles each have a concave or lightly undulating mesal margin with tiny serrations. The posterior hookplates of abdominal tergum V each have 10-20 anteriorly directed hooks. The anal rods are each thick, straight and parallel-sided for the basal 1/2 or 2/3, then abruptly tapered to an acute up-turned apex, with two short projections on the mesal surface where the rod begins to taper.

Distribution: The seven species known previously for this group occur in the Nearctic and Palearctic Biogeographic Regions.

Phylogenetic relationships (Fig. 49): Evidence for the monophyly of the Annulicornis Group includes the following homologue (Morse, 1975): (1) the left (anterior) paramere spine of the male is shorter than the right (posterior) one. According to Morse (1975), the Annulicornis Group is one lineage of an unresolved trichotomy involving also, on the one hand, the Diluta Group and, on the other hand, the Riparia + Marginata Groups. Two homologues implying monophyly for the Diluta Group include the following male characters (Morse, 1975): (1) the lateral processes of tergum X are absent and (2) the phallus is especially short. A homologue implying monophyly for the Riparia + Marginata Groups includes the following (Morse, 1975): (1) the baso-ventral lobe of each inferior appendage is large. In evolutionary terms, the lobe initially became as large as the main body of the inferior appendage; the transformation series of progressively increasing size

of the baso-ventral lobe with reduction of the main body continued to the condition in which the main body was lost altogether in C. (A.) fooensis in the Marginata Group.

Ceraclea (Athripsodina) excisa (Morton, 1904)

Leptocerus excisus Morton, 1904, pp. 67-69; holotype not selected; type repository unknown; type locality = brook near Ekenäs, Finland.
Athripsodes excisus (Morton); Lepneva, 1966, larva and pupa.
Ceraclea (Athripsodina) excisa (Morton); Morse, 1975, redescription of male, also Athripsodes perplexus nordus Milne, 1934, A. miscus Ross, 1941, and A. scopulosus Leonard and Leonard, 1949, are synonyms; Resh, 1976, larva and pupa, A. miscus is not a synonym; Malicky, 1983, illustration of male.

Description: Head and thorax concolorous dark brown with relatively long white and dark brown setae intermixed. Forewing brown except small testaceous spot at arculus, with short dark brown setae.

Male genitalia (Fig. 9): Tergum X long, upturned and acute apically both in lateral and dorsal views, margined dorsally; lateral processes short. Inferior appendages slender, each with slender baso-ventral lobe 1/2 to 3/4 as long as main body of appendage and rounded apically; harpago tiny; setose median ridge about as long as broad and positioned next to harpago; phallic guide more or less triangular in caudal view, with rounded apex. Phallus strongly curved ventrad; base slightly enlarged; left paramere spine seta-like; pair of membranous dorsal parameres present.

Female genitalia (Fig. 35): Tergum IX rounded apically, with pair of small subdorsal processes; lower pleural region with shallow concavity terminating at anterior edge of segment. Superior appendages relatively long, 1/3 as long as broad, covered with long setae. Gonopod plates closely approximate on midline, each with large triangular apical projection and conspicuous dark pit at base of projection, projections separated apically by deep sinuous excision. Supporting bands of spermathecal sclerite situated internally on apical projections of gonopod plates, extending anteriorly to middle of segment VIII; spermathecal sclerite U-shaped with subparallel sides.

Length of forewing: male - 10 mm, female - 8 mm.

Larva (Fig. 48): According to Lepneva (1966) and Resh (1976), head with contrasting color pattern of spots.

Pupa Fig. 48): According to Lepneva (1966) and Resh (1976), mandibles each with middle of mesal edge nearly straight. Posterior hookplates of tergum V each with 10-14 hooks.

Habits and habitat of larva: "Solid bottom in brooks and rivulets; open littoral of lakes and rivers; phytophagous" (Lepneva, 1966).

Diagnosis: The male of this species differs from those of C. (A.) hastata and sibirica by the presence of a pair of lateral processes on tergum X and from aurea by the smaller size of those processes. From all three species it differs by the seta-like left paramere spine deeply retracted into the enlarged anterior base of the phallus. The left paramere spine is absent in annulicornis. It is present in ruthae (Flint, 1965) and shuotsuensis and the new species of this group described below, but the anterior base of the phallus is greatly enlarged in the latter four species and, in the latter three species, the baso-ventral lobe of the inferior appendage is longer, as long as the main body of the appendage.

The female of this species differs from those known for others in this group by the sinuous excision between the apical projections of the gonopod plates, the termination of the pleural concavities of segment IX at the anterior base of that segment, and the shorter supporting bands of the spermathecal sclerite.

The larva differs from that of C. (A.) annulicornis by the pattern of constrasting spots on the head, which are absent in the latter species.

Distribution: Northern Palearctic Region and northwestern Nearctic Region and now in northern China: Wu-da-lian-chi, Hei-long-jang Province (N48.45, E125.55; Fig. 1, #6), 8 August 1987.

Phylogenetic relationships (Fig. 49): The sister group of C. (A.) excisa is a monophyletic group including annulicornis, ruthae, shuotsuensis, and the new species described below. This sister group relationship is evidenced by the following homologue (Morse, 1974): (1) the left (anterior) paramere spine is seta-like. A homologue implying monophyly of the related four species is the following (Morse, 1974): (1) the anterior, basal end of the male phallobase is enlarged and subspherical. The sister group of these five species probably is the monophyletic group consisting of C. (A.) aurea, sibirica, and hastata whose monophyly is implied by the following homologues (Morse, 1974): (1) the base of each male inferior appendage is unusually large and (2) its phallic guide is strongly produced.

Ceraclea (Athripsodina) shuotsuensis (Tsuda, 1942a)

Leptocerus shuotsuensis Tsuda, 1942a, pp. 233-234, fig. 8; holotype = male; type repository presumably = presumably Nara Women's University, Nara, Japan; type locality = Shuotsu, northern Korea.

Athripsodes bicalcarata Schmid, 1970, p. 121; holotype = male; type repository = Canadian National Collection, Ottawa; type locality = River Delger Mörön, 8 km north of Somon Burenchaan, Hövsgol Province, Mongolia. NEW SYNONYM.

Athripsodes sibiricus Botosaneanu (nec Ulmer, 1906) 1970, p. 308; "A. shuotsuensis Tsuda is probably in synonymy . . ." (referring to a male from "Mts. Mjohjang-san, district Hjangsan: Hjangam-ri" in Korea).

Ceraclea (Athripsodina) shuotsuensis (Tsuda); Morse, 1975, p. 43, fig. 87, diagnosis of male.

Description: Dorsal stripe reddish-brown, lateral areas fulvous. Forewings reddish brown, with opaque testaceous stigma.

Male genitalia (Fig. 10): Superior appendages short, fused 1/2 of their length, acute apically. Tergum X upturned from middle, apex acute from dorsal view, rounded from lateral view, laterally with short processes. Baso-ventral lobe of each inferior appendage broad basally, as long as main body of appendage (excluding subapico-dorsal lobe), and acute apically; setose mesal ridge adjacent to small harpago and about as long as broad; phallic guide long, triangular. Phallus moderately enlarged basally, base about twice as broad as apical portion in lateral view; ventral margin strongly curved ventrad in lateral view; left paramere spine seta-like and withdrawn to anterior end; pair of membranous dorsal parameres present.

Female genitalia (Fig. 36): Tergum IX acute apically in both lateral and dorsal views; lower pleural regions deeply concave, the concavities extending anteriorly beyond the bases of the gonopod plates. Superior appendages short, 2/3 as long as broad. Lamellae short, semicircular in lateral view, setose. Gonopod plates each with long triangular caudal projection, plates approximate for most of their length, with subtriangular excision between their projections. Spermathecal sclerite U-shaped, with lateral arms curved mesad near the caudal end; supporting bands situated caudally above the projections of the gonopod plates and extending anteriorly to the anterior margin of segment VIII.

Length of forewing: male - 10 mm, female - 9 mm.

Immature stages unknown.

Diagnosis: The male of this species differs from those of all other species in the Annulicornis Group by the shape of the baso-ventral lobe of each inferior appendage which is broad basally, as long as the main body of the appendage, and acute apically. Also, the phallic guide of each inferior appendage is longer than for any other species in the group.

The female of this species has pleural concavities of segment IX deeper and projecting more anteriad than in known females of other species and the spermathecal supporting bands extend to the anterior margin of segment VIII, not as far as in C. (A.) annulicornis but farther than in excisa.

Distribution: North-central Mongolia, North Korea, and now China: Lang-xiang (N46.90, E128.80; Fig. 1, #7), 22 July 1986, and Wu-da-lian-chi (N48.45,

E125.55; Fig. 1, #6), 8 August 1987, Hei-long-jiang Province.

Phylogenetic relationships (Fig. 49): As discussed above for C. (A.) excisa, shuotsuensis is a member of the monophyletic group that also includes annulicornis, ruthae, and the new species described below.

Ceraclea (Athripsodina) globosa, n. sp.

Description: Body and wings light yellowish brown, covered with brown setae.

Male genitalia (Fig. 11): Superior appendages short, obtuse apically in dorsal view. Tergum X upturned from middle; apex acute in dorsal view, rounded in lateral view, margined dorsally; pair of slender processes laterally. Baso-ventral lobe of each inferior appendage directed ventrad at base, bent caudad about 1/3 distance from base, then more or less straight to dark, oblique apex, overall lobe about 2/3 as long as main body of appendage; setose mesal ridge triangular, about as long as broad basally, adjacent to small harpago; phallic guide visible in lateral view, with ridge from apex to base of baso-ventral lobe sinuous in lateral view, concave mesally in caudal view. Phallus with anterior portion globose, nearly four times as broad in lateral view as posterior, apical portion; ventral margin strongly curved ventrad about 2/3 distance from base; left paramere spine retracted to near phallic foramen.

Female and immature stages unknown.

Length of forewing: male - 11 mm.

Type material: Holotype MALE, Lang-xiang, Hei-long-jiang Province (N46.90, E128.80, Fig. 1, #7), 21 July 1986, J.A. McLean.

Etymology: Latin, "spherical," with reference to the globose anterior portion of the phallus.

Diagnosis: This is the only species whose male has both a seta-like left paramere spine and the baso-ventral lobe of each inferior appendage conspicuously bent along its length. It is the only species of the Annulicornis Group in which the male inferior appendage phallic guide is visible in lateral view and has a longitudinal, sinuous ridge.

Distribution: Known only from the type locality in northeastern China.

Phylogenetic relationships (Fig. 49): As discussed above for C. (A.) excisa, globosa is a member of the monophyletic group that also includes annulicornis, ruthae, and shuotsuensis.

Riparia Group

Diagnosis: According to Morse (1975), the color pattern of adults in this group is a light reddish-brown head and thorax and concolorous light brown forewings, except forewings of C. (A.) isurumuniya (Schmid, 1958) are uniformly fuscous and those of modesta (Banks, 1920) are concolorous golden brown except for white setae in a band from vein 1A to the hind margin and from the wing base to the arculus. In males, the superior appendages are relatively short and usually fused basally; tergum X usually bears a pair of slender lateral processes; the inferior appendages each have a very strong baso-ventral lobe positioned at an acute angle with respect to the main body of the appendage, this lobe having at least one and as many as three strong apical or subapical spines; paramere spines are absent in isurumuniya but in all other species of the group are lined up with the apex of the left (anterior) spine usually inserted in an elliptical opening at the base of the right (posterior) spine, the left spine bent near its base.

Females of C. (A.) ancylus (Vorhies, 1909) and flava (Banks, 1904) were described by Ross (1944), that of riparia by Kumanski and Malicky (1976; Fig. 38), and that of forcipata by Forsslund (1935). The females of C. (A.) ancylus and flava have gonopod plates that are each conspicuously concave, with the mesal and lateral edges forming ventral ridges; apparently these plates are only slightly concave in riparia and may or may not be concave at all in forcipata. Each gonopod plate has two conspicuous caudal projections in C. (A.) riparia, similar to those in the Dissimilis Group; the lateral projections of these plates are slender and appressed against the mesal projections in ancylus and flava; only one caudal

projection was mentioned by Forsslund (1935) on each gonopod plate of forcipata. In all three species the superior appendages are short and broad, forming a pair of narrow setose ridges across the posterior dorsal margin of tergum IX.

The mature larva of C. (A.) ancylus was described by Resh (1976) and that of flava by Ross (1944, as "Athripsodes species b") and Resh (1976). Larvae of these species have parafrontal regions and long antennae, no long setae on tergum IX, and the pronotum has a pair of lateral spots, each surrounded by a light corona. The larval case is made entirely of sand grains and has lateral expansions, causing it to resemble the case of Molannidae species.

Pupae of C. (A.) ancylus and flava were described by Resh (1976). Posterior hookplates of abdominal segment V each have 18 hooks. Anal rods are conical basally, slender for the remaining 3/4 of their length, each with a small mesal process.

Distribution: Species of the Riparia Group occur in the Nearctic, Oriental, and Palearctic Biogeographic Regions.

Phylogenetic relationships (Fig. 49): The Riparia Group is monophyletic as is evidenced by the following homologues: (1) multiple stout spines are present apically and subapically on the baso-ventral lobe of each inferior appendage and (2) the paramere spines are arranged end-to-end with the left (anterior) spine's tip inserted on or in a transparent "window" at the base of the right (posterior) spine. The sister group of the Riparia Group is the Marginata Group, as was discussed with the Annulicornis Group above.

Ceraclea (Athripsodina) polyacantha Yang & Tian, 1987

Ceraclea (Athripsodina) polyacantha Yang & Tian, 1987, pp. 214-216; holotype = male; type deposition = Nan-jing Agricultural University; type locality = Zi-yang, Shaan-xi Province (N32.50, E108.60; Fig. 1, #2), 6 June 1973.

Description: Head and body reddish brown, center of face with white setae, sides and vertex with white and brown intermixed. Forewings golden brown with light brown setae.

Male genitalia (Fig. 12): Superior appendages short, fused basally for about 1/3 their length. Tergum X slender, slightly clavate in both dorsal and lateral views, directed caudad (not upturned), about twice as long as superior appendages, with slender lateral processes arising near base and extending nearly to apex. Baso-ventral lobe of each inferior appendage forming angle of approximately 30° with main body of appendage, longer than main body of appendage including its subapico-dorsal lobe, bent mesad in rounded arch, oblique apex with 4-5 spines usually present asymmetrically on lobes of opposing inferior appendages; main body of appendage slender; harpago nearly as long as subapico-dorsal lobe. Phallobase very large, bean-shaped anteriorly; apico-ventral cleft situated on midline; paramere spines arranged in manner characteristic for this group.

Female and immature stages unknown.

Length of forewing: male - 8 mm.

Diagnosis: This species resembles C. (A.) trifurca, interispina, riparia, yangi, nankingensis, huangi, and modesta in the slender apex of tergum X, but differs from these and all other species of the Riparia Group in the small angle of the main body and baso-ventral lobe of each inferior appendage and in the row of stout spines at the apex of that lobe.

Distribution: Known only from the type locality in northcentral China.

Phylogenetic relationships (Fig. 49): Ceraclea (A.) polyacantha is the sister species of interispina Yang & Tian as is evidenced by the following homologue: (1) tergum X is clavate in dorsal view. Together these species are a monophyletic sister group to the remainder of the Riparia Group species. These remaining 12 species are a monophyletic group as is implied by the following homologue: (1) the baso-ventral lobe of each inferior appendage has only three stout apical and subapical spines.

Ceraclea (Athripsodina) interispina Yang & Tian, 1987

Ceraclea (Athripsodina) interispina Yang & Tian, 1987, pp. 213-214, 216; holotype = male; type deposition = Nan-jing Agricultural University; type locality = Shao-wu, Fu-jian Province (N27.21, E117.27; Fig. 1, #16), 31 July 1983.

Description: Head and body reddish brown. Forewing yellowish brown with brown setae.

Male genitalia (Fig. 13): Superior appendages short, broadly triangular, fused basally for 1/3 length. Tergum X about twice as long as superior appendages, in dorsal view triangular basally, apical portion slender and parallel-sided; lateral processes slender, slightly clavate, arising subbasally, nearly as long as tergum. Baso-ventral lobe of each inferior appendage forming angle of about 60° with main body of appendage, about as long as main body of appendage excluding subapico-dorsal lobe, slightly curved mesad in ventral view, with single stout spine apically and 1-3 spines on short median process about midlength, number of spines on median process asymmetrical on opposing appendages; main body of appendage with few normal setae but mesal ridge not conspicuous; harpago about 2/3 as long as subapico-dorsal lobe. Phallus with anterior portion 1.5 times as broad as apical portion, bent about 90° in middle; paramere spines with usual arrangement for this group.

Female genitalia (Fig. 37): Superior appendages very short, in lateral view each visible only as ridge. Longitudinal pocket near posterior end of pleural region of segment IX. Lamellae setose ventrally, elliptical in lateral view. Gonopod plates elliptical, broadest at mid-length, each bearing pair of lobes caudally with upper lateral lobe 2.5 times length of lower mesal lobe; basal half of each plate slightly concave, distal half slightly convex. Spermathecal sclerite rhomboidal.

Length of forewing: male - 6 mm, female - 5 mm.

Immature stages unknown.

Diagnosis: The short mesal projection with 1-3 stout setae on the baso-ventral lobe of each male inferior appendage and the lateral pockets of female segment IX and rhomboidal-shaped spermathecal sclerite distinguish this species from all others in the Riparia Group.

Distribution: Southeastern China: Wu-yan County, Jiang-xi Province (N29.15, E117.53; Fig. 1, #15), 6 August 1985, and the type locality, 4 August 1984.

Phylogenetic relationships (Fig. 49): Ceraclea (A.) interispina is the sister species of polyacantha as was discussed with that species above.

Ceraclea (Athripsodina) riparia (Albarda, 1874)

Leptocerus riparius Albarda, 1874, pp. 231-234, pl. IV, figs. 8-17; holotype apparently not selected; two male syntypes repository = British Museum (Natural History), London; syntype localities = Batavia and Germania.

Ceraclea (Athripsodina) riparia (Albarda); Morse, 1975, p. 43, fig. 88, redescription of male; Kumanski and Malicky, 1976, p. 115, fig. 8, illustrations of male and female genitalia; Malicky, 1983, pp. 276 and 279, illustrations of male and female genitalia.

Description: Head and thorax consistently light reddish-brown; vertex and frons with mostly white setae, sides with brown and white setae intermixed. Forewing light brown with concolorous light reddish-brown setae.

Male genitalia (Fig. 14): Tergum IX with pair of tiny dimples. Superior appendages short, narrowed subapically, fused for about half their length. Tergum X nearly parallel-sided with rounded apex in dorsal view, slightly clavate in lateral view; lateral processes moderately thick, not reaching apex of tergum. Baso-ventral lobe of each inferior appendage forming angle of about 70° with main body of appendage, about as long as main body of appendage including subapico-dorsal lobe, curved somewhat mesad, with two stout apical spines; main body of appendage curved slightly caudad; mesal ridge evident, with several normal setae; harpago about as long as subapico-dorsal lobe. Anterior portion of phallobase nearly twice

as broad as posterior portion in lateral view, with deep semicircular constriction on ventral surface in middle; paramere spines arranged normally for this group.

Female genitalia (Fig. 38): Superior appendages very short and broad. Lamellae triangular in lateral view, each with rounded apex. Gonopod plates apparently slightly concave in posterior apical half, each plate with pair of conspicuous caudal projections, lateral ones visible as oval structures through lamellae in cleared specimens. Spermathecal sclerite long, triangular, with concave lateral margins.

Length of forewing: male - 8-9 mm, female - 6-7 mm (Malicky, 1983).

Immature stages unknown.

Diagnosis: Of all known species in the Riparia Group, only C. (A.) yangi and huangi and this species have two short stout spines at or near the apex of the baso-ventral lobe of each inferior appendage. In C. (A.) huangi one of these spines is subapical on this lobe rather than apical as in this species and huangi has a stout spine at the apex of each lateral process of tergum X which is not present in this species. The anterior end of the phallobase of C. (A.) yangi is about the same size as its posterior end whereas in this species the anterior end is about twice the size of its posterior end.

We have not seen females of this species. However, the long triangular spermathecal sclerite with concave sides appears to be distinctive among the females known to us.

Distribution: Central Europe and now southeastern China: Wu-hu, An-hui Province (N31.23, E118.25; Fig. 1, #11), 9 August 1987.

Phylogenetic relationships (Fig. 49): Among the monophyletic 12 species of the Riparia Group whose baso-ventral lobe of each inferior appendage has only three stout apical and subapical spines (discussed with C. [A.] polyacantha above), C. (A.) riparia is a member of a monophyletic group which also includes yangi, brachyacantha, and nankingensis. The monophyly of these four species is evidenced by the following homologue: (1) male tergum IX has a pair of dimples antero-dorsad of the superior appendages. The four species are related in an unresolved trichotomy consisting of C. (A.) riparia as one branch, yangi as a second, and brachyacantha + nankingensis as the third. Evidence for the monophyly of the remaining eight species includes the following homologue: (1) there is only one apical stout spine on the baso-ventral lobe of each male inferior appendage.

Ceraclea (Athripsodina) yangi (Mosely, 1942)

Leptocerus yangi Mosely, 1942, p. 348, figs. 14-17; holotype = male; type deposition = British Museum (Natural History), London; type locality = Fu-zhou, Fu-jian Province, China (N26.10, E119.30; Fig. 1, #20).

Ceraclea (Athripsodina) yangi (Mosely); Morse, 1975, p. 43, fig. 89, redescription of male.

Description: Head and body light reddish-brown, mainly covered with white setae mixed sparsely with brown setae. Forewing yellowish-brown with dark brown setae.

Male genitalia (Fig. 15): Superior appendages fused only at extreme base, each with apical margin obliquely truncate. Tergum X 1.5 times as long as superior appendages, nearly parallel sided in dorsal and lateral views; lateral processes moderately thick, not quite reaching apex of tergum. Baso-ventral lobe of each inferior appendage forming angle of about 60° with main body of appendage, this lobe and main body of appendage subequal in length, lobe triangular with nearly straight sides except curved mesad at apex, two small apical spines and one small subapical spine each only slightly stouter than normal setae; main body of appendage curved somewhat caudad; mesal ridge with several thick setae; harpago slightly shorter than subapico-dorsal lobe. Phallobase with anterior and posterior portions about equal in size, moderately constricted in middle ventrally, paramere spines aligned as typical for group.

Female genitalia (Fig. 39): Superior appendages very short and broad as

typical for group, appearing triangular in lateral view. Lamellae parallel-sided and apex broadly rounded in dorsal and ventral views, triangular with rounded apex in lateral view. Gonopod plates rectangular, slightly concave , with conspicuous ridges along outer edges; each plate with two large rounded projections caudally, mesal projection nearly as broad as lateral one, lateral projection oval in vertical and lateral views and positioned dorsad of apexes of plate and supporting arms of spermathecal sclerite. Spermathecal sclerite twice as long as broad, broadest in middle, sides generally convex, process (pr.sp.sc) broad in lateral view.

Length of forewing: male - 8 mm, female - 6.7 mm.

Immature stages unknown.

Diagnosis: The male of this species resembles C. (A.) riparia and huangi in having few small stout spines at or near the apex of the baso-ventral lobe of each inferior appendage, but these spines are smaller in yangi and there is one more of them (three) than in the other two species (two). Among Riparia Group species with the characteristic end-to-end arrangement of paramere spines, this is the only species with a small anterior portion of the phallobase. Among females of this species group C. (A.) yangi is the only one with lamellae broadly triangular in lateral view.

Distribution: Southeastern China: the type locality; Wu-hu, An-hui Province (N31.23, E118.25; Fig. 1, #11), 9 August 1987; Tian-mu-shan, Zhe-jiang Province (N30.40, E119.50; Fig. 1, #12), 18 July 1965;
Guang-zhou, Guang-dong Province (N23.08, E113.20; Fig. 1, #14), 26 June 1982; and Pu-tian, Fu-jian Province (N25.32, E119.02; Fig. 1, #18).

Phylogenetic relationships (Fig. 49): Ceraclea (A.) yangi is most closely related to riparia, nankingensis, and brachyacantha as was discussed with riparia above.

Ceraclea (Athripsodina) nankingensis (Hwang, 1957)

Leptocerus nankingensis Hwang, 1957, pp. 389-390, figs. 75-78; holotype = male; type deposition = reportedly "Nanking Agricultural College Insect Museum," but no such specimen can be found now in this collection; type locality = Nan-jing, Jiang-su Province (N32.05, E118.7, Fig. 1, #10), 11 August 1948.

Ceraclea (Athripsodina) nankingensis (Hwang); Morse, 1975, p. 45, fig. 96, redescription of male.

Description: Vertex and mesonotum yellowish-brown; face and abdomen yellowish-white; hairs mostly white, intermixed brown setae only on vertex and sides of face. Forewing straw yellow with yellow-brown setae.

Male genitalia (Fig. 16): Superior appendages long, fused basally for nearly half their length. Tergum X broad, 1.3 times as long as superior appendages, parallel-sided to rounded apex in dorsal view; lateral processes slender, arising near base, extending nearly to apex of tergum. Baso-ventral lobe of each inferior appendage forming angle of about 35° with main body of appendage, about as long as main body of appendage including subapico-dorsal lobe, strongly bent obliquely ventrad and mesad about 2/3 distance from base, single stout spin apically; main body of appendage slender, sinuous, curved caudad; mesal ridge inconspicuous except for patch of stiff hairs; harpago nearly as long as subapico-dorsal lobe. Phallobase swollen anteriorly, about 2.5 times as broad as posterior apex, but expanded anteriorly only short distance; ventral surface constricted about 2/3 distance from phallic foramen.

Female genitalia (Fig. 40): Superior appendages broad but very short. Lamellae setose ventrally, somewhat bean-shaped in lateral view, with dorsal edge nearly straight to rounded apex. Gonopod plates each slightly concave with mesal and lateral edges raised; lateral edges with few longitudinal striations; each plate with two apical projections, mesal one small and triangular, lateral one longer and with rounded apex and straight mesal surface. Spermathecal sclerite about 1.6 times as long as broad, broadest in middle, convex laterally.

Length of forewing: male - 8 mm, female - 6 mm.

Immature stages unknown.

Diagnosis: The male of this species, like those of C. (A.) modesta, isurumuniya, kamonis, and ancylus, has only a single apical spine on the baso-ventral lobe of each inferior appendage; of these, only this species and kamonis have this spine strongly curved ventrad, the spine is much smaller in nankingensis than in kamonis. The female of this species most closely resembles that of C. (A.) yangi in the shapes of the caudal projections of the gonopod plates and of the spermathecal sclerite, but the lateral view of the lamellae is triangular in yangi and bean-shaped in nankingensis.

Distribution: Southeastern China: the type locality and Hong-ze Lake, Jiang-su Province (N33.30, E118.90; Fig. 1, #25), 19 July 1987.

Phylogenetic relationships (Fig. 49): Ceraclea (A.) nankingensis is closely related to riparia, yangi, and brachyacantha as was discussed with riparia above. Of these, the sister species of C. (A.) nankingensis apparently is brachyacantha as is implied by the following homologue: (1) the baso-ventral lobe of each inferior appendage has only one apical stout spine and no subapical stout spine.

Ceraclea (Athripsodina) brachyacantha Yang & Tian, 1987

Ceraclea (Athripsodina) brachyacantha Yang & Tian, 1987, pp. 213, 216; holotype = male; type deposition = Nan-jing Agricultural University; type locality = San-gang, Wu-yi Mountain, Fu-jian Province (N27.70, E117.70; Fig. 1, #17), 6 May 1986.

Description: Head and body fusco-testaceous. Forewings dark yellowish brown with brown setae.

Male genitalia (Fig. 17): Superior appendages short, separate basally. Tergum X broad, triangular with blunt apex in dorsal view, slightly clavate and upturned at middle in lateral view, about twice as long as superior appendages; lateral processes slender, not extending to apex of tergum. Baso-ventral lobe of each inferior appendage forming angle of about 45° with main body of appendage, about as long as main body including its subapico-dorsal lobe, somewhat vase-like in ventral view, broad at base, narrowed apically to neck-like constriction recurved mesad just before apex, stout spine apically; main body of appendage slender, curved caudad; mesal ridge not prominent, with row of stout setae; harpago about as long as subapico-dorsal lobe. Phallobase strongly recurved basally, anterior end about as broad as posterior end; only one paramere spine evident in retracted phallus, nearly as long as phallus; second paramere spine weakly sclerotized sheath of first spine and evident only in protracted phallus; sclerotized strip supporting endothecal membranes ventrally, evident in protracted phallus.

Length of forewing: male - 7 mm.

Female and immature stages unknown.

Diagnosis: The general shape of male tergum X and the inferior appendages clearly places this species in the Riparia Group, but in no other species in this group or elsewhere in Ceraclea is such a peculiar phallus known.

Distribution: Known only from the type locality in southeastern China.

Phylogenetic relationships (Fig. 49): Ceraclea (A.) nankingensis apparently is the sister species of brachyacantha as was discussed with nankingensis above.

Ceraclea (Athripsodina) trifurca, n. sp.

Description: Head and body uniformly brown. Forewings light brown.

Male genitalia (Fig. 18): Superior appendages each broad, triangular, with rounded apexes in dorsal view. Tergum X about 2 1/2 times as long as superior appendages, in dorsal view with subtriangular base tapering to slender, slightly clavate apex; lateral processes slender, upcurved, each nearly reaching tip of tergum X, together with tergum X forming three slender processes in dorsal view. Baso-ventral lobe of each inferior appendage forming angle of about 45° with remainder of appendage, as long as remainder of appendage including its subapico-dorsal lobe, nearly straight, tapering from broad base to retrocurved apex with single large spine; main body of appendage curved somewhat caudad in lateral view; mesal ridge straight, extending from base nearly to harpago, with paired short

spines; harpago nearly as long as subapico-dorsal lobe. Phallus enlarged and projecting anteriorly such that phallic foramen positioned ventrally about 1/3 distance from anterior end; apico-ventral cleft asymmetrically arising on left side about 2/3 distance from anterior end; phallic paramere spines aligned in manner typical for group.

Length of forewing: male - 7 mm.

Female and immature stages unknown.

Type material: Holotype MALE, Nan-jing, Jiang-su Province (N32.05, E118.70, Fig. 1, #10), 15 July 1981, Tian Li-xin.

Etymology: Latin, "three-forked," with reference to the appearance of tergum X in dorsal view.

Diagnosis: The male of this species resembles those of C. (A.) riparia, yangi, modesta, nankingensis, huangi, polyacantha, and interispina in the narrow apex of tergum X in dorsal view, but the apex is even narrower in this species than in any of these others. The baso-ventral lobe of each inferior appendage is relatively straight until a sharp bend just before the apex in this species and in yangi, modesta, brachyacantha, huangi, and nankingensis, but tergum X is much longer in this species than in yangi, brachyacantha, huangi, and nankingensis, and this species lacks the large subapical spine of each lateral process of tergum X found in modesta.

Distribution: Known only from the type locality in southeastern China.

Phylogenetic relationships (Fig. 49): Ceraclea (A.) trifurca is a member of a monophyletic group of eight species within the Riparia Group as was discussed with riparia above. Among these eight species, C. (A.) trifurca is one lineage of an unresolved trichotomy; the other two lineages including modesta, isurumuniya, and huangi on the one hand and forcipata, flava, kamonis (Tsuda, 1942b), and ancylus on the other. A homologue implying the monophyly of C. (A.) modesta, isurumuniya, and huangi is the following: (1) the lateral processes of tergum X each have a stout apical spine. A homologue implying the monophyly of forcipata, flava, kamonis, and ancylus is the following: (1) the baso-ventral lobe of each inferior appendage is situated laterally on the base of the main body of the appendage and then curved posteriorly and mesally.

Ceraclea (Athripsodina) huangi (Tian, 1981),
NEW COMBINATION

Leptocerus huangi Tian, 1981, pp. 1-2, figs. 1-4; holotype = male; type deposition = Nan-jing Agricultural University; type locality = Nan-jing, Jiang-su Province (N32.05, E118.70; Fig. 1, #10), 6 July 1981.

Description: Head and thorax moderate brown. Forewings light yellowish brown, with brown setae dense from anastomosis to apex.

Male genitalia (Fig. 19): Superior appendages short, separated basally, rounded apically. Tergum X more than twice as long as superior appendages, narrowly triangular in dorsal view with slender distal 1/3 nearly parallel-sided to blunt apex, bent upward about 30° in middle in lateral view; lateral processes arising from extreme base of tergum X, nearly as long as tergum, curved dorsad about 90° in middle such that apexes above lateral profile of tergum, apex of each process with stout spine. Baso-ventral lobe of each inferior appendage forming angle of about 50° with main body of appendage, as long as main body of appendage including subapico-dorsal lobe, vase-like in ventral view with broad base and narrow apex curved mesad, one stout spine apically and one stout spine subapically on mesal surface; main body of appendage slender, curved caudad; mesal ridge inconspicuous broad bump; harpago about as long as subapico-dorsal lobe. Posterior sclerotized lobes of phallobase relatively long and asymmetrical with right lobe about 1.5 times as wide in lateral view as left lobe; anterior portion of phallobase about twice as broad as right apical lobe of posterior portion, anterior portion only slightly projecting anteriorly; deep V-shaped constriction of ventral surface evident in lateral view; left (anterior) paramere spine much more slender and shorter than right spine.

Female genitalia (Fig. 41): Superior appendages short and broad, triangular in lateral view. Lamellae long, apically blunt in dorsal and ventral views, trapezoidal in lateral view with dorsal apex obliquely truncate, ventral margin straight and setose. Gonopod plates each subrectangular;, slightly concave in middle with prominent mesal and lateral edges; two caudal projections near meson with mesal projection triangular and half as long as elliptical lateral projection. Spermathecal sclerite nearly twice as long as broad, broadest in posterior 1/3, sides convex.

Length of forewing: male - 6.5 mm, female - 6 mm.

Immature stages unknown.

Diagnosis: The male of this species resembles C. (A.) modesta and isurumuniya in bearing a stout spine at the apex of each lateral process of tergum X and, like isurumuniya, tergum X and its lateral processes are very long; however, the lateral processes are strongly curved dorsad in this species, not straight (modesta) or curved ventrad (isurumuniya) as in those species, the anterior end of the phallobase is only slightly enlarged and projecting anteriorly (vs. greatly enlarged and projecting in modesta) and both paramere spines are present (vs. absent in isurumuniya).

The female of this species differs from all known females of the Riparia Group by the trapezoidal appearance of the lamellae in lateral view and in the egg-shaped spermathecal sclerite in ventral view.

Distribution: This species has long been collected in and near the type locality in Nan-jing, Jiang-su Province, in southeastern China, with flight dates as early as 6 July and as late as 15 August.

Phylogenetic relationships (Fig. 49): This species is a member of the monophyletic group that also includes C. (A.) modesta and isurumuniya as was discussed with trifurca above. Ceraclea (A.) isurumuniya is the sister species of huangi as is implied by the following homologue: (1) male tergum X and its lateral processes are very long.

Ceraclea (Athripsodina) forcipata (Forsslund, 1935)

Leptocerus forcipatus Forsslund, 1935, pp. 9-11, fig. 9; holotype = male (abdomen missing); type deposition = National Museum of Natural History, Stockholm; type locality = Pe-lin-kou [unable to locate on available maps], southeastern Si-chuan Province, 25 May 1930.

Ceraclea (Athripsodina) forcipata (Forsslund); Morse, 1975, p. 44, fig. 92, redescription of male.

Description: Head and thorax brownish-yellow with white-gray setae, middle part of mesonotum darkened.

Male genitalia (Fig. 20): Superior appendages 2/3 as long as tergum X, fused for half their length, rounded apically. Tergum X upturned at extreme apex, broadly rounded apically in dorsal view; lateral processes very slender, especially apically, not quite as long as tergum. Baso-ventral lobe of each inferior appendage forming angle of about 90° with base of main body of appendage in lateral view, arising on caudo-lateral base of main body of appendage, excluding its apical spine about as long as main body of appendage, bent somewhat mesad about 2/3 distance from base, subapical spine positioned at bend and about half as long as lobe, huge apical spine nearly as long as lobe; main body of appendage arched about 45° caudad; mesal ridge small triangular projection near base of main body of appendage; harpago about as long as subapico-dorsal lobe. Phallobase conspicuously enlarged anteriorly such that phallic foramen positioned on ventral surface nearly half distance from anterior end; phallobase broadest at level of phallic foramen, about twice as broad as posterior portion, about 1.5 times as broad as anterior portion; posterior portion conspicuously asymmetrical, with apical cleft offset to left and with left side of apex narrower than right; paramere spines aligned as typical for group.

Female genitalia (Forsslund, 1935, from German; Fig. 42):

"Female. Segment IX very broad laterally, continuous on posterior edge; dorsally proximal edge broadly excised; distal edge in the middle with

slender pointed tooth (from lateral view appearing broader with sharp point), above and on the side of this are two small protuberances and even further laterally a triangular hump on either side; ventrally the segment is divided by a proximal broad cleft; inner hind edge continuous as a rounded projection. Segment X with two vertical, short lanceolate lobes, whose tips and dorsal edges are sewn to each other."

Length of forewing: Wingspread male - 17-19 mm, female - 14.5 mm (Forsslund, 1935).

Immature stages unknown.

Diagnosis: The male of this species most closely resembles C. (A.) flava and ancylus in the shape of tergum X; it most closely resembles flava in the arrangement of spines at and near the apex of the baso-ventral lobe of each inferior appendage. However, these spines are relatively much larger in C. (A.) forcipata than in either of these species. The apical spine of this lobe in C. (A.) kamonis is about the same size as that in forcipata, but the lobe is longer and more slender in forcipata and bears a large subapical spine apparently not present in kamonis.

We have not seen a female of this species. However, it appears distinctive from other females of this group known to us in its lanceolate lamellae and the single caudal projection of each gonopod plate.

Distribution: Southcentral China: the type locality; "Pao-ning-fu" (Forsslund, 1935; unable to locate on available maps), 17 May 1930; and Chin-chin-kai, southeastern Si-chuan Province (N29.00, E106.60, Fig. 1, #27), 8 May 1930.

Phylogenetic relationships (Fig. 49): Ceraclea (A.) forcipata is a member of a monophyletic group which also includes flava, kamonis, and ancylus as was discussed with trifurca above. Within this group, C. (A.) forcipata is one lineage of an unresolved trichotomy which also includes flava, on the one hand, and kamonis + ancylus, on the other. Evidence for the sister group relationship of C. (A.) kamonis and ancylus includes the following homologue: (1) the subapical spine of the baso-ventral lobe of each inferior appendage is absent.

Marginata Group

Diagnosis: According to Morse (1975), the head and thorax of adults is light reddish-brown except in C. (A.) martynovi (Forsslund, 1940) they are dark reddish fuscous. Forewings have light and medium brown setae in patches, especially along veins, forming an irrorate pattern. Ceraclea (Athripsodina) marginata (Banks, 1911) and martynovi have white setae in the anal region of the forewings and dark apical fringes similar to the pattern in modesta. The main body of each inferior appendage is very reduced, semimembranous and inconspicuous in most species, absent in C. (A.) fooensis. Superior appendages are long and tapered. Tergum X is short and without lateral processes. Paramere spines are about the same size and are retracted to about the same depth, except they are fused in C. (A.) fooensis.

The female or immature stages of none of the species of this species group have been described.

Distribution: Southeastern China, northeastern India, and Sri Lanka.

Phylogenetic relationships (Fig. 49): The Marginata Group is monophyletic as is implied by the following male homologues (Morse, 1975): (1) the main body of each inferior appendage is reduced to an inconspicuous, semimembranous finger-like process; (2) the paramere spines are retracted to approximately the same level within the phallobase; and (3) tergum X has no lateral processes. The sister group of the Marginata Group is the Riparia Group according to Morse (1975), as was discussed with the Annulicornis Group above.

Ceraclea (Athripsodina) lirata, n. sp.

Ceraclea (Athripsodina) marginata Yang & Tian (nec Banks), 1988, in press.

Description: Head and thorax reddish-brown. Forewings straw yellow colored,

cell Cu_2 darker beyond arculus; hairs rubbed away in alcohol.

Male genitalia (Fig. 21): Superior appendages slightly longer than tergum X and acute apically; fused only at extreme base. Tergum X with pair of prominent longitudinal ridges dorsally, fused apically in small, acute apical process in caudo-ventral view (Fig. 21E'); lateral edges of tergum each with rounded excision in lateral view. Baso-ventral lobe of each inferior appendage huge, sinuous in lateral view; somewhat enlarged in middle in caudal view, with broad subrectangular setose base having angled ridge mesally, and with 5-6 seta-bearing protuberances apically; main body of appendage slender, semimembranous and nearly obscured by baso-ventral lobe, 2/3 as long as baso-ventral lobe. Phallobase tubular, with pair of tapered apico-ventral lobes about as long as remainder of phallobase; paramere spines subequal in length and depth of retraction; pair of dorsal membranous lobes exposed dorsally.

Female and immature stages unknown.

Length of forewing: male - 7.8 mm.

Type material: Holotype MALE, Meng-xing, Yun-nan Province (N21.90, E101.40; Fig. 1, #5), 20 April 1982, Jing Geng-tao.

Etymology: Latin, "with a ridge," referring to the pair of ridges on male tergum X.

Diagnosis: This species most closely resembles C. (A.) marginata in the structures of their inferior appendages and the general shape of their phalluses. However, in C. (A.) lirata the longitudinal pair of ridges on tergum X are distinctive, the baso-ventral lobe of each inferior appendage is longer and lacks the bare subapico-ventral projection seen in marginata, and the apico-ventral lobes of the phallobase are longer.

Distribution: Known only from the type specimen captured in extreme southcentral China. Contrary to the reference by Yang & Tian (1988), C. (A.) marginata (Banks) is not known from China.

Phylogenetic relationships (Fig. 49): Ceraclea (A.) marginata is the sister species of lirata as is evidenced by the following homologue: (1) the base of the baso-ventral lobe of each inferior appendage has an angled setose ridge, such that in caudal view this region appears subrectangular. The sister lineage of these two species is C. (A.) fooensis, as is indicated by the following homologue: (1) the apex of the baso-ventral lobe of each inferior appendage bears numerous protuberances, most of which have an apical seta.

Ceraclea (Athripsodina) fooensis (Mosely, 1942)

Leptocerus fooensis Mosely, 1942, p. 348, figs. 18-21; holotype = male; type repository = British Museum (Natural History), London; type locality = Fu-zhou, Fu-jian Province, China (N26.10, E119.30; Fig. 1, #20).

Ceraclea (Athripsodina) fooensis (Mosely); Morse, 1975, p. 46, fig. 97, redescription of male.

Description: Forewing reddish-brown, with small dark patch at distal hind edge (Mosely, 1942; apparently similar in this respect to preceding species).

Male genitalia (Fig. 22): Tergum X abruptly narrowed and nearly acute in dorsal view, with pair of transverse, subapico-dorsal, sensilla-bearing ridges. Baso-ventral lobe of each inferior appendage enlarged and recurved apically; apex with crown of small protuberances, most of them bearing apical seta; mesal margin with four ridges, including (a) ventral ridge with long setae, (b) longitudinal ridge with short stout setae, (c) narrow projecting inconspicuous transverse ridge without setae, and (d) dorsal longitudinal ridge without setae; main body of appendage and its harpago absent. Phallobase long, without anterior enlargement; paramere spines fused for entire length.

Female genitalia (Fig. 43): Pleural regions of segment IX broad, each semimembranous except for sclerotized anterior bridge, anterior portion of semimembranous area concave. Lamellae semi-elliptical in lateral view, setose ventrally, with longitudinal-oblique ridge laterally. Gonopod plates very long and approximate on midline, each plate more than 3 times as long as broad; apex

tapered to meson, subacute. Spermathecal sclerite in ventral view nearly as broad as long, anterior apex truncate, anterior half concave laterally, posterior half broadest with round margins; large membranous mass ventrally over posterior half.

Length of forewing: male - 9 mm, female - 7 mm.

Immature stages unknown.

Diagnosis: The male of C. (A.) fooensis resembles lirata and marginata in the protuberances of the apex of the baso-ventral lobe of each inferior appendage and lirata in the possession of a pair of subapico-dorsal ridges on tergum X. It resembles C. (A.) martynovi in the lack of an angled ridge at the mesal base of this baso-ventral lobe. It differs from all of these in the lack of a main body of each inferior appendage, in the broad and recurved apex and the presence of a bare transverse ridge on the baso-ventral lobe of this appendage, and in the fused condition of the paramere spines.

The females of no other species of the Marginata Group have been described before now. Superficially the female of C. (A.) fooensis resembles that of dingwuschanella below (Fig. 46) in the concave pleural regions of segment IX and the long gonopod plates, but this species lacks longitudinal ridges on the gonopod plates and the spermathecal sclerite is relatively shorter and broader.

Distribution: Known only from the type series in southeastern China.

Phylogenetic relationships (Fig. 49): The sister group relationship of C. (A.) fooensis with marginata + lirata was discussed with lirata above. Together these three species are the sister lineage of C. (A.) martynovi, their monophyly as the Marginata Group having been discussed with the Group above.

Kolthoffi Group, C. (A.) Incertae Sedis

Diagnosis: Male tergum X is slender and slightly clavate in dorsal view, similar to that in some species of the Riparia Group. There is no evidence of a baso-ventral lobe of each male inferior appendage, similar in this respect to the Spinosa Group. The left (anterior) paramere spine is small and seta-like, as in males of the Annulicornis Group, but unlike species with that character, the anterior end of the phallobase is not spherically enlarged nor is the phallobase constricted ventrally in its midregion. In females, these species have very small lamellae, a pair of longitudinal ridges are present on the gonopod plates, the gonopod plates extend as concave pockets deeply within segment VIII, and the spermathecal sclerite is unusually long and with a pair of curved bands mesally at the posterior end.

Distribution: The two species of this group occur at least from the Amur Region of Siberia to southeastern China.

Phylogenetic relationships (Fig. 49): The two species of this group probably are sister species based on the following homologues: (1) male tergum X is long and slender in lateral view; (2) the lateral processes of male tergum X are short and thick, oblique apically; (3) the mesal ridge of each male inferior appendage has a prominent acute projection; (4) the female lamellae are small, only slightly larger than the superior appendages; (5) the female gonopod plates each have a longitudinal ridge near the posterior apex; (6) the female gonopod plates are invaginated anteriorly as concave sclerotized pockets with the posterior margin of segment VIII; and (7) the spermathecal sclerite is long and (8) with a pair of curved, postero-mesal bands. Character information is insufficient presently to determine the sister group of the Kolthoffi Group within Ceraclea (Athripsodina) subgenus.

Ceraclea (Athripsodina) ensifera (Martynov, 1935)

Leptocerus ensifer Martynov, 1935, pp. 228-230; holotype gender unknown, but probably = male; type series repository = Zoological Institute, U.S.S.R. Academy of Sciences, Leningrad; type locality = River Lefu, near Lake Chanka, Amur, Siberia.

Leptocerus kashingensis Tsuda, 1943, pp. 105-106; holotype gender unknown, but probably = male; type series repository presumably = Nara Women's University, Nara, Japan; type locality = Jia-xing ("Kashing"), Zhe-jiang Province, China

(N30.51, E120.52; Fig. 1, #23), 25-26 September 1942. NEW SYNONYM.
Ceraclea (Athripsodina) ensifera (Martynov); Morse, 1975, p. 47, fig. 101, redescription of male.
Ceraclea (Athripsodina) kashingensis (Tsuda); Morse, 1975, p. 47, fig. 102, review of male description.

Description: Head and thorax mostly light reddish-brown with white and brown setae. Forewings light brown with white and reddish-brown setae thoroughly intermixed.

Male genitalia (Fig. 23): Sclerotization of sternum IX discontinuous with narrow membranous strip dividing it entirely, posterior ventral corners greatly elongate. Superior appendages long, fused basally about 1/3 their length, tapering to blunt apexes. Tergum X narrow, slightly clavate in dorsal view; lateral processes thick, compressed, oblique apically, with tiny subapico-dorsal triangular projection. Inferior appendages narrow in lateral view, broad in caudal view; baso-ventral lobe absent from each appendage; mesal ridge with small triangular projection; phallic guide long and saber-like; harpago as long as subapico-dorsal lobe of appendage. Phallobase broad, tubular anteriorly, posterior lobes asymmetrical with left lobe half as broad as right lobe and slightly shorter; left (anterior) paramere spine seta-like, 2/3 as long as thick right (posterior) spine.

Female genitalia (Fig. 44): Slightly depressed. Tergum IX short, broad, with conspicuous superior appendages. Lamellae only slightly larger than superior appendages, each subtriangular with rounded apex in lateral view. Gonopod plates nearly twice as long as tergum IX; each plate with diagonal, sinuous ridge from base of lamella nearly to middle of anterior margin, plates concave mesally between ridges; anterior mesal margin of each plate projecting anteriorly into segment VIII; sternum VIII broad and projecting caudally under gonopod plates. Spermathecal sclerite twice as long as broad, with posterior portion 2.5 times as broad as anterior portion; spermathecal process greater than half as long as sclerite; pair of postero-mesal bands curved ventrad.

Length of forewing: male - 10 mm, female - 9 mm.

Immature stages unknown.

Diagnosis: Among males of Ceraclea species, the divided sternum IX with its long projecting processes is unique and conspicuous. Among females of Ceraclea species, only C. (A.) kolthoffi and this species such small lamellae, longitudinal ridges on the gonopod plates, gonopod plates invaginated into segment VIII, sternum VIII projecting caudally, or spermathecal sclerite at least twice as long as broad. From C. (A.) kolthoffi, the female of ensifera differs in its longer, sinuous ridges of the gonopod plates; mesal (rather than lateral) projections of the gonopod plates into segment VIII; and broader posterior region of the spermathecal sclerite.

Distribution: Siberia (Amur Region) and eastern China: Tian-jing (N39.08, E117.20; Fig. 1, #8), 14 May 1965; Xing-hua, Jiang-su Province (N32.90, E119.80; Fig. 1, #9), 13 June 1987; Wu-hu, An-hui Province (N31.23, E118.25; Fig. 1, #11), 9 August 1987; and C. (A.) kashingensis type locality.

Phylogenetic relationships (Fig. 49): The sister lineage of C. (A.) ensifera is kolthoffi, as was discussed above for the Kolthoffi Group.

Ceraclea (Athripsodina) kolthoffi (Ulmer, 1932)

Leptocerus kolthoffi Ulmer, 1932, pp. 55-57; holotype = male; type deposition = National Museum of Natural History, Stockholm; Jiang-su Province, China.
Leptocerus inchinus Mosely, 1942, pp. 347-348, figs. 9-13; holotype = male; type deposition = British Museum (Natural History), London; type locality = Fu-zhou, Fu-jian Province, China (N26.10, E119.30; Fig. 1, #20); Morse, 1975, p.47, synonym of C. (A.) kolthoffi.
Ceraclea (Athripsodina) kolthoffi (Ulmer); Morse, 1975, pp. 47-48, fig. 103, redescription of male.

Description: Head and thorax brown with white and brown setae intermixed. Forewings yellowish-brown with white and brown setae thoroughly intermixed.

Male genitalia (Fig. 24): Superior appendages long, fused for short distance basally but widely divergent and acute apically. Tergum X extending just beyond superior appendages, narrowed conspicuously subapically in dorsal view; lateral processes arising from base, short and thick, nearly 1/2 as long as tergum, with depressed slightly upturned apexes. Subapico-dorsal lobe of each inferior appendage about as long as main body of appendage; mesal ridge with protracted, dagger-like process; harpago 2/3 as long as subapico-dorsal lobe; baso-ventral lobe entirely absent. Phallobase relatively large, somewhat swollen anteriorly, narrowing to pair of heavily sclerotized, asymmetrical postero-ventral lobes with left lobe narrower, subacute and more dorsal than right lobe; left paramere spine retracted anteriorly and seta-like, right spine thick, 2/3 as long as phallobase, and with convoluted plate anteriorly.

Female genitalia (Fig. 45): Anterior pleural regions of segment IX conspicuously narrower than gonopod plates, concave. Superior appendages broadly triangular, conspicuous. Lamellae about same size as superior appendages. Gonopod plates projecting antero-laterally into segment VIII and sternum VIII extended ventrally below anterior half of plates; plates converging posteriorly to blunt apexes; each plate with short ridge from ventral edge of lamella concave mesally, space between ridges concave. Spermathecal sclerite 2.5 times as long as wide in ventral view, sides straight and almost parallel, tapering slightly from posterior to anterior; posterior bands short and convex mesally; spermathecal process 1/4 as long as sclerite.

Length of forewing: male - 10.5 mm, female - 9.5 mm.

Immature stages unknown.

Diagnosis: Ceraclea (A.) kolthoffi males most closely resemble those of ensifera in the general shape of the superior appendages, tergum X and its lateral processes, and phallus. It differs from that species, however, in its solid sternum IX without posterior projections and its dagger-like process on the mesal ridge of each inferior appendage. The similarities and differences between the females of these two species were discussed with C. (A.) ensifera above.

Distribution: Southeastern China: Hong-ze, Jiang-su Province (N33.30, E118.90; Fig. 1, #25), 19 July 1987; Shang-hai (N31.13, E121.50, Fig. 1, #19), 16 May 1972; and the type localities of C. (A.) kolthoffi and inchinus.

Phylogenetic relationships (Fig. 49): The sister lineage of C. (A.) kolthoffi is ensifera, as was discussed for the Kolthoffi Group above.

Dingwuschanella Group, C. (A.) Incertae Sedis

Diagnosis: This group of four species resembles the Kolthoffi Group in that the males lack baso-ventral lobes on their inferior appendages and the females have longitudinal ridges on their gonopod plates. However, males of this group have no lateral processes on tergum X, have a relatively short and slender subapico-dorsal lobe on each inferior appendage, and the harpago is oriented longitudinally with the appendage. Females have lamellae twice as large as superior appendages, pleural regions of segment IX are concave, and the region of the gonopod plates between the longitudinal ridges is more or less flat.

Distribution: Central and southeastern China.

Phylogenetic relationships (Fig. 49): Monophyly for the four species of the Dingwuschanella Group is evidenced by the following male homologues: (1) subapico-dorsal lobe of each inferior appendage slender and curved caudad and (2) harpago aligned longitudinally with main body of appendage and curved dorsad, crossing the subapico-dorsal lobe. Evidence presently is not sufficient to infer the sister lineage of this species group.

Ceraclea (Athripsodina) brachycera Yang & Tian, 1988

Ceraclea (Athripsodina) brachycera Yang & Tian, 1988, in press; holotype = male; type deposition = Nan-jing Agricultural University, Nan-jing; type locality = Hua-xi, Gui-zhou Province, China (N26.25, E106.40; Fig. 1, #4), 27 April 1980.

Description: Head and thorax dark brown with white and dark brown setae

intermixed. Forewings dark brown with brown setae.

Male genitalia (Fig. 25): Superior appendages short, widely diverging in dorsal view, blunt apically. Tergum X twice as long as superior appendages, with short cleft on meson of otherwise rounded apex in dorsal view; pair of finger-like processes on dorsal surface about middle of length of tergum; latero-ventral margins convex basally in lateral view, concave in apical 1/3 of length of tergum. Inferior appendages dark brown; main body broad, especially basally; mesal ridge wide basally with numerous stout setae on edge and surface; subapico-dorsal lobe slender, curved caudad, with sensory setae apically; harpago about as long as subapico-dorsal lobe, aligned with main body and curved dorsad in lateral view, rounded apically. Phallobase long, with small bulbous anterior enlargement; apico-ventral lobes long and narrow; paramere spines nearly identical and retracted to approximately same depth within phallobase.

Female and immature stages unknown.

Length of forewing: male - 7.6 mm.

Diagnosis: Among males of the Dingwuschanella Group, that of C. (A.) brachycera has shorter and more widely diverging superior appendages, broader inferior appendages whose mesal ridges lack any triangular projections, and more nearly equal paramere spines. The pair of vertical finger-like projections on the dorsal surface of tergum X is unique for this species.

Distribution: Known only from the type locality in southcentral China.

Phylogenetic relationships (Fig. 49): Within the monophyletic Dingwuschanella Group, C. (A.) brachycera is the sister lineage to the other three species, curva, dingwuschanella, and acutipennis. Monophyly for those three species is indicated by the following male homologues: (1) superior appendages are unusually long, overarching tergum X and (2) the mesal ridge of each inferior appendage has an apical triangular projection near the harpago.

Ceraclea (Athripsodina) curva Yang & Tian, 1988

Ceraclea (Athripsodina) curva Yang & Tian, 1988, in press; holotype = male; type deposition = Nan-jing Agricultural University, Nan-jing; type locality = Wu-yuan, Jiang-xi Province, China (N29.15, E117.53; Fig. 1, #15), 6 August 1985.

Description: Head and thorax brown with white and dark brown setae. Forewings light golden brown with dark brown setae.

Male genitalia (Fig. 26): Superior appendages long, parallel-sided, overarching tergum X, fused at extreme base for short distance then gradually diverging to rounded outcurved apices. Tergum X nearly as long as superior appendages; with conspicuous mid-dorsal ridge; apical 1/2 somewhat sinuous and directed dorsad about 45°. Inferior appendages narrow in lateral view, with subapico-dorsal lobe nearly as broad as main body of appendage; mesal ridge with slender, blunt triangular projection apically just proximad of harpago; harpago narrow basally, broad and flat and curved mesad apically, not quite as long as subapico-dorsal lobe. Phallobase swollen dorsally; apico-ventral lobes short and slender, 1/7 as broad as anterior portion in lateral view; paramere spines stout, one spine 1.3 times as long as other and retracted somewhat more anteriorly.

Female and immature stages unknown.

Length of forewing: male - 7 mm.

Diagnosis: Among males of the Dingwuschanella Group, the long overarching superior appendages, the slender inferior appendages each with a narrow mesal ridge and its blunt triangular projection, and the dorsally swollen phallobase are distinctive characters.

Distribution: Known only from the type locality in southeastern China.

Phylogenetic relationships (Fig. 49): The monophyly of C. (A.) curva, dingwuschanella, and acutipennis was discussed with brachycera above. The sister lineage of C. (A.) curva is dingwuschanella + acutipennis whose monophyly is implied by the following homologues: (1) tergum X short and (2) with divided, recurved, sensilla-bearing pads apically.

Ceraclea (Athripsodina) dingwuschanella (Ulmer, 1932)

Leptocerus dingwuschanellus Ulmer, 1932, pp. 57-59, figs. 26-28; holotype = male; type deposition presumably = Hamburg Museum, Hamburg, Federal Republic of Germany; type locality = "Dingwuschan," China (locality not recognizable on available maps); Schmid, 1965, p. 147, figs. 4-6, description of variation in males.

Ceraclea (Athripsodina) dingwuschanella (Ulmer); Morse, 1975, pp. 46-47, fig. 100, redescription of male.

Description: Head and thorax reddish-fuscous with white and brown setae. Forewings dark brown with gold-red to gold-yellow setae along posterior basal quarter, gold-yellow at arculus and a large patch of gold-yellow at apex.

Male genitalia (Fig. 27): Superior appendages broad and separate basally, apical half slender, blunt apically. Tergum X short, broad, subtriangular, 2/3 as long as superior appendages; without lateral processes; in dorsal view, apex broad with shallow, narrow excision on meson; pair of transverse, subapical carina on either side of excision defining pair of thick pads bearing 3-13 sensilla. Inferior appendages without baso-ventral lobes; mesal ridge broad and setose, with short triangular projection just proximad of harpago; subapico-dorsal lobe slender, curved caudad, 2/3 as long as harpago; harpago about as broad as subapico-dorsal lobe, aligned longitudinally with main body of appendage in lateral view and curved dorsad, rounded apically. Phallobase tubular, with apico-ventral lobe 2/3 as broad as anterior portion in lateral view; paramere spines bent and arranged as in Riparia Group; dorsal parameres present with left membranous lobe apparently much longer than right one, each paramere lobe with short sclerotized hook apically.

Variation: Ulmer's (1932) illustrations and discussion depict tergum X apex "somewhat broadened and rounded" and the harpago of each inferior appendage is "set in the middle of the main body of the appendage, just as broad as the subapico-dorsal lobe, somewhat shorter, rising in an S-shape, directed dorso-mesad and more pointed" (freely translated from German). Schmid (1965) noted in his specimens that "the apical lobes of tergum X are thin and separated by a broad circular space" and that "the harpago of each inferior appendage is shorter than seen in Ulmer's figure and rounded apically" (freely translated from French); his illustration shows the harpago much farther from the base of the appendage than Ulmer did. Our specimens seem to be rather intermediate between these two extremes in these characters: the apex of tergum X is divided, but not as broadly as seen by Schmid, and the apical lobes do not project so far above the tergum; the harpago arises farther from the base of the main body of the inferior appendage than shown by Ulmer, is shorter, not S-shaped, and somewhat rounded apically, but not so far from the base as shown by Schmid and longer.

Female genitalia (Fig. 46): Genital capsule somewhat compressed. Segment IX lower pleural regions concave, defined especially well ventrally by subventral carinae which parallel lateral margins of gonopod plates; tergum IX projecting caudally between conspicuous superior appendages nearly to their apexes. Gonopod plates together about twice as long as broad; postero-mesal apex of each plate prolonged in slender process; each plate with longitudinal ridge from near ventral edge of lamella to about middle of plate, otherwise plate flat to convex. Spermathecal sclerite relatively small, shape and structure superficially similar to those in Riparia Group except dorsal bridge triangular.

Length of forewing: male - 8.0 mm, female - 7.5 mm. Wingspread of male is 17 - 24 mm (Schmid, 1965).

Immature stages unknown.

Diagnosis: Among males of the Dingwuschanella Group, that of C. (A.) dingwuschanella differs from that of brachycera by the former's superior appendages much longer than tergum X, the triangular process present on the mesal ridge of each of its inferior appendages, and the end-to-end alignment of its paramere spines; from that of curva by its shorter and apically cleft tergum X and its harpago larger than the subapico-dorsal lobe of each inferior appendage; and from acutipennis by the larger harpago and much shorter projection of the

mesal ridge of each of its inferior appendages. No females of the Dingwuschanella Group have been described previously. The genitalia of the female of C. (A.) dingwuschanella superficially resembles that of fooensis, but the gonopod plates of the latter species lack longitudinal ridges and its spermathecal sclerite is much broader.

Distribution: Although we cannot locate the type locality on available maps and Schmid (1965) did not mention his Chinese collection locality(ies?), our records indicate a distribution at least in northcentral and southeastern China: An-kang, Shaan-xi Province (N32.50, E109.00; Fig. 1, #1), 22 April 1980; Wen-zhou, Zhe-jiang Province (N28.02, E120.40; Fig. 1, #21), 17 April 1939.

Phylogenetic relationships (Fig. 49): The monophyly of C. (A.) curva, dingwuschanella, and acutipennis was discussed with brachycera above. C. (A.) dingwuschanella and acutipennis are sister species as evidenced by the following male homologue: (1) tergum X has a pair of setose, apico-dorsal pads set off by a pair of transverse carinae.

Ceraclea (Athripsodina) acutipennis Yang & Tian, 1988

Ceraclea (Athripsodina) acutipennis Yang & Tian, 1988, in press; holotype = male; type deposition = Nan-jing Agricultural University, Nan-jing; type locality = Wang-jiang, An-hui Province (N30.10, E116.44; Fig. 1, #13), 7 May 1982.

Description: Head and thorax dark brown, vertex and frons mostly with white setae. Forewings light yellow-brown, golden at stigma, anal region slightly expanded with relatively long, dark brown fringe, giving triangular appearance.

Male genitalia (Fig. 28): Superior appendages long, triangular, fused basally for about half their length, blunt apically. Tergum X broad basally, compressed in dorsal view and somewhat attenuated in lateral view about 1/3 its length; divided apically by narrow, shallow cleft on meson; pair of large lateral, sensilla-bearing lobes on either side of cleft defined anteriorly by pair of transverse carinae. Inferior appendages sub-rectangular in lateral view; mesal ridge of each appendage broad and with surface setae in middle, apically with slender, outcurved, acute process 2/3 as long as harpago; harpago slender, longer than subapico-dorsal lobe, and with acute apical hook recurved mesad. Phallobase tubular, curved ventrad about 80°, with relatively narrow apico-ventral lobes; one paramere spine 1.5 times longer than other and retracted much further into phallobase.

Length of forewing: male - 10 mm.

Female and immature stages unknown.

Diagnosis: The slender acute process of the mesal ridge of each inferior appendage distinguishes this species from all others of the Dingwuschanella Group. A superficially similar process occurs in C. (A.) kolthoffi, but acutipennis lacks lateral processes of tergum X, its superior appendages are longer than tergum X, the shape of the apical region of its tergum X is much more complex, and the harpago of each inferior appendage is much more slender.

Distribution: Known only from the type locality in southeastern China.

Phylogenetic relationships (Fig. 49): The sister group relationship of this species with C. (A.) dingwuschanella was discussed with that species above.

Ungulifera Group, C. (A.) Incertae Sedis

Diagnosis: The similarities between males of the two species in this group are remarkable. Both C. (A.) ungulifera (Kimmins, 1963) and omeiensis have short, rounded superior appendages, long tergum X with slender arching apex and long lateral processes arising from the base, relatively simple inferior appendages each with setose mesal ridge in the middle, and a tubular phallobase with broad apico-ventral lobes. In the general shape of tergum X and its lateral processes, these species resemble those of the Tarsipunctata Group, but the absence of a sclerotized phalicata and the deeply retracted paramere spines are very different from characters in that group.

Distribution: Northeastern Burma and southcentral China.

Phylogenetic relationships (Fig. 49): The sister-group relationship of C. (A.)

ungulifera and omeiensis is implied by the following homologues: (1) tergum X is long and with a slender arching apex and (2) lateral processes of tergum X are long, slightly capitate and originating at the base of the tergum.

Ceraclea (Athripsodina) omeiensis Yang & Tian, 1988

Ceraclea (Athripsodina) omeiensis Yang & Tian, 1988, in press; holotype = male; type deposition = Nan-jing Agricultural University, Nan-jing; type locality = E-mei Mountain, Si-chan Province (N29.36, E103.29; Fig. 1, #3), 29 April 1957.

Description: Head and thorax brownish-black with dark brown setae. Forewings dark brown with brown setae.

Male genitalia (Fig. 29): Tergum IX forming narrow band projecting caudad in round arch in dorsal view. Superior appendages separated basally. Tergum X 1.5 times as long as superior appendages; in lateral view parallel-sided basally, abruptly narrowed near apexes of superior appendages, apex arching caudad and ventrad, sub-deltoid in dorsal view; lateral processes originating basally, about 4/5 as long as tergum, widely separated from tergum, apex of each slightly enlarged, setose and upturned. Subapico-dorsal lobe of each inferior appendage as long as main body of appendage, curved caudad; mesal ridge broad in middle, surface setose; phallic guide short and acute in ventral view; harpago shorter than subapico-dorsal lobe, its apex acute and recurved. Phallobase with anterior portion nearly twice as broad as posterior apical lobes in lateral view and about 1.5 times as long; one paramere spine present, about 3/4 as long as phallobase. retracted.

Length of forewing: male - 8 mm.

Female and immature stages unknown.

Diagnosis: Ceraclea (A.) omeiensis is very similar to ungulifera in the characters discussed for the species group. The former species, however, has tergum X more abruptly narrowed from about 2/3 length and there is only one paramere spine evident in the phallus.

Distribution: Known only from the type locality in southcentral China.

Phylogenetic relationships (Fig. 49): The sister-group relationship of this species with C. (A.) ungulifera was discussed with the species group above.

Ceraclea (Athripsodina) Incertae Sedis

Ceraclea (Athripsodina) signaticornis (Ulmer, 1926)

Leptocerus signaticornis Ulmer, 1926, pp. 64-66, figs. 46-48; holotype = male; type deposition presumably = Zoological Museum, Berlin; type locality = "Lotosteiche," Guang-zhou, Guang-dong Province (N23.08, E113.20; Fig. 1, #14), 12 April 1920.

Description (Ulmer, 1926, from German):

"In the structure of the inferior appendage standing near Leptocerus annulicornis [= Ceraclea (Athripsodina) annulicornis]. Head and thorax light yellowish brown, nearly cream-color, with grayish white hairs. Abdomen darker yellowish brown, dark brown on the side line. Antenna dark brown, except that the uniformly dark apical part distinctly, but narrowly, ringed snow-white; the first 3 or 4 segments colored as the head. Maxillary palp grayish brown (somewhat darker than the head), with whitish gray or brownish white hairs. Legs light ocher (yellowish white), the tarsi, especially on the fore and middle legs, darker (grayish brown), ringed white; also the coxae darker. Forewing fairly broad; membrane light gray, with thick brownish gold (dull rust color or light cinnamon brown) hairs, just as the fringe; veins somewhat darker golden brown, conspicuous. Hindwing broad (male), light gray, with gray bronze-like shining hairs (scattered) and fringe; veins gold-brownish, scarcely as visible as in the forewing. In the latter the first crossvein of the anastomosis is positioned approximately its length further apical than

either of the following, which are formed in a straight line. In the male (Fig. 30A, 30B, 30C) tergum IX bluntly projecting in the middle, not cleft; the preanal appendages originating from the common area under tergum IX situated on a broad short plate and being narrow and long; in dorsal view (Fig. 30B) reaching the apex of the inferior appendages, being slender ribbon-like, straight and extending to a postero-mesal bend, abruptly narrowing apically; in lateral view (Fig. 30A) appearing somewhat broader, with curved edges and truncated apex; the posterior sclerite of tergum X (Figs. 30A, 30B) is long and narrow and ending in a thick knob shape; the phallus is visible beneath it (Fig. 30A), narrow, provided with a spine; the inferior appendage persists as a basal, strongly bent main body (Fig. 30A) and a long subapico-dorsal lobe, with its rounded end lying over tergum X; the baso-ventral lobe is elongated in a bluntly pointed process (e.g., Fig. 30C, ventral), the harpago ending almost truncated and bearing an undivided short tooth on the ventral edge of the apex (Fig. 30A, lateral, Fig. 30B, dorsal). Superior appendages and inferior appendages with long hairs, the apex of tergum X bearing isolated shorter sensillae.

"Body length: 10 mm, length of the forewings: 11 mm; wingspan thus about 23 mm."

Female and immature stages unknown.

Diagnosis: Resembling members of the Annulicornis Group, especially in the shape of the inferior appendages and tergum X. A pair of lateral processes for tergum X were even illustrated by Ulmer (Fig. 30B), although not mentioned in the text. However, the superior appendages are much longer than those of any other species known for this group, much more divergent from the base, and bent mesad apically. The general structure of the phallus is unknown.

Distribution: Known only from the type locality in southeastern China.

Phylogenetic relationships (Fig. 49): Until specimens of this species are seen, it will not be possible to confirm its affinity with the Annulicornis Group and its relationship with the species included in that group.

BIOGEOGRAPHY

Procedures for discovering patterns of historical relationships among the regions that organisms inhabit were reviewed by Nelson and Platnick (1981) and Wiley (1981). In essence, the procedure is to (1) note the distributions of organisms to discover "areas of endemism" or replicated regions where endemism is common (Candolle, 1820), (2) infer the phylogenetic relationships of those organisms and refer the resulting inferences to an "area cladogram" or phylogeny of the areas of endemism (Rosen, 1978, 1979), (3) identify "tracks" of modern or historical relationships of the organisms between areas of endemism across uninhabited regions or area boundaries (Croizat, 1964), and (4) relate "generalized tracks" or frequently replicated tracks with modern and historical geological and ecological information.

Areas of endemism: The Ceraclea species of the world generally inhabit the traditional Ethiopian, Nearctic, Oriental, and Palearctic continental or subcontinental areas of endemism identified by Wallace (1876), with the further refinement that these species usually are confined to either eastern or western portions of those regions. For purposes of this discussion, we use the traditional interpretation that the division between the Oriental and Palearctic regions in eastern China occurs along the Chang-jiang (Yang-tze) River. (Coincidentally, this division is consistent with the observation that only one rice crop is usually possible each year north of that river and two rice crops south of it).

Of the 29 species of Ceraclea presently known from China, 22 are apparently endemic to it. As can be seen in Figs. 1 and 49, 13 species of Ceraclea are endemic to Oriental China, four to Palearctic China, five to both Oriental and Palearctic China, and three to Palearctic China and non-Chinese parts of the

eastern Palearctic Region. One species each has an Oriental China - western Palearctic (riparia), Oriental & Palearctic China - eastern Palearctic (ensifera), eastern & western Palearctic (including Palearctic China, alboguttata), and eastern & western Palearctic (including Palearctic China) - western Nearctic (excisa) distribution. Considering the distributions presently known for the 29 Ceraclea species, only six species (21%) occur in both Oriental and Palearctic areas of endemism.

Tracks: In addition to the tracks recognizable from contemporary species distributions, the phylogeny of Fig. 49 permits identification of three to four historical tracks between Oriental China and the eastern Nearctic Region: one in the Fulva Group (cama and the remainder of the Group), one in the Tarsipunctata Group (major and the remainder of the Group), and one or two in the Riparia Group (forcipata and flava and possibly ancylus). One or two historical track occurs between Palearctic China and the Nearctic Region in the Fulva Group (alboguttata and transversa-latahensis, possibly also alboguttata and alces-resurgens-vertreesi). Three historical tracks occur between the Chinese and non-Chinese portions of the Oriental Region, one in the Riparia Group (huangi and isurumuniya) and two in the Marginata Group (lirata and marginata, fooensis and martynovi). One historical track occurs between Palearctic China and the non-Chinese Oriental Region in the Ungulifera Group (omeiensis and ungulifera). Additionally, two historical tracks between the Oriental and Palearctic portions of China are identifiable besides those seen in contemporaneous distributions, one in the Fulva Group (spinulicolis and alboguttata) and one in the Riparia Group (polyacantha and interispina).

Generalized Tracks: From this analysis, it can be concluded that generalized tracks occur between China and the non-Chinese Oriental Region (four tracks), the non-Chinese Palearctic Region (six tracks), and the Nearctic Region (six or seven tracks). There are no tracks inferred for Ceraclea species between China and the Australian, Ethiopian, or Neotropical Biogeographic Regions. Conclusions regarding the causes of these biogeographic relationships are not possible without research into the contemporary and historical geology and ecology of these regions, research outside the scope of this work.

KEY TO SPECIES OF CHINESE CERACLEA

1. Genitalia with inferior appendages and phallus (Figs. 2A, 2D) . . . . . (males) 2
   Genitalia with lamellae and internal spermathecal sclerite (Figs. 31A, 31D). . . . . (females) 30

2. Phallobase entire apico-ventrally, with well-sclerotized phalicata (Fig. 2D) . . . . . (Subgenus Ceraclea) 3
   Phallobase with a longitudinal cleft apico-ventrally; without separate, well-sclerotized phalicata (Fig. 8D). . . . . (Subgenus Athripsodina) 6

3. Superior appendages broad, fused basally for a short distance (Fig. 2B); tergum X upturned in middle (Fig. 2A); harpago with triangular, subapical projection (Fig. 2C) 4
   Superior appendages small, separated basally (Fig. 4B); tergum X straight (Fig. 5A'); harpago without subapical projection (Fig. 4C). 5

4. Tergum X truncate apically, with pair of ear-like ridges laterally in middle (Fig. 3A); each inferior appendage with spine-bearing baso-ventral lobe (Fig. 3A) and strong spine on caudal face of mesal ridge (Fig. 3C). . . . . alboguttata (Hagen)

Tergum X rounded apically, without lateral ridges (Fig. 2A); each inferior appendage without baso-ventral lobe (Fig. 2A) or strong spine on mesal ridge (Fig. 2C). . . . spinulicolis, n. sp.

5. Tergum X no longer than superior appendages, without spine-bearing lateral processes (Fig. 4A); each harpago longer than main body of its inferior appendage (not including subapico-dorsal lobe, Figs. 4A, 4C); paramere spines longer than phalicata (Fig. 4D) . . . . . superba (Tsuda)
Tergum X twice as long as superior appendages, with spine-bearing lateral processes (Fig. 5A', 5B); each harpago about 1/2 as long as main body of its inferior appendage (Fig. 5C); paramere spines shorter than phalicata (Fig. 5D) . . . . . sinensis (Forsslund)

6. Lateral processes of tergum X small, finger-like (Fig. 6A); baso-ventral lobe of inferior appendage with row of 5-6 stout spines (Fig. 6A); dorsal parameres present (Fig. 6D) . . . . . major (Hwang)
Genitalia without such structures. 7

7. Main body of each inferior appendage inconspicuous (Fig. 21C) or absent (22C), harpago absent 8
Main body of inferior appendage at least 1/2 has large as its baso-ventral lobe (Figs. 12A, 20A), harpago present 9

8. Main body of inferior appendage slender, semi-membranous and baso-ventral lobe with tapered apex in ventral view (Fig. 21C); phallus with two separate paramere spines (Fig. 21D). . . . . lirata, n. sp.
Main body of inferior appendage absent and baso-ventral lobe with broad apex in ventral view (Fig. 22C); phallus with single fused paramere spine (Fig. 22D). . . . . fooensis (Mosely)

9. Each inferior appendage with distinct baso-ventral lobe (Fig. 7A, 12A). 10
Each inferior appendage without baso-ventral lobe (Figs. 23A, 24A). 24

10. Tergum X without slender lateral processes (Fig. 8A) 11
Tergum X with slender lateral processes (Figs. 10A, 19A) 12

11. Superior appendages rounded apically in dorsal view (Fig. 7B); mesal ridge of each inferior appendage subtriangular (Fig. 7C); paramere spines 2/3 as long as phallobase (Fig. 7D). . . . . indistincta (Forsslund)
Superior appendages nearly acute in dorsal view (Fig. 8B); mesal ridge hooked dorsad (Fig. 8C); paramere spines 1/2 as long as phallobase (Fig. 8D) . . . . . lobulata (Martynov)

12. Superior appendages at least as long as tergum X (Figs. 30A, 30B). . . . . signaticornis (Ulmer)
Superior appendages no more than 2/3 as long as tergum X (Fig. 9A) 13

13. Baso-ventral lobe of each inferior appendage without stout apical spines, although normal hairs often present (Fig. 9A); one paramere spine far anterior of other one and much smaller, seta-like (Fig. 9D) 14

Baso-ventral lobe of each inferior appendage with stout apical spine (Fig. 16A, 16C') or spines (Figs. 12A, 12C'); paramere spines subequal and arranged end-to-end (Fig. 12D) 16

14. Baso-ventral lobe of each inferior appendage broad basally, tapering to acute apex (Figs. 10A, 10C) . . . . . shuotsuensis (Tsuda)
Baso-ventral lobe of each inferior appendage more slender basally, with blunt apex in lateral view (Figs. 9A, 11A) 15

15. Baso-ventral lobe of each inferior appendage straight (Fig. 9A); phallic guide of inferior appendage without sinuous caudal ridge and not visible in lateral view (Fig. 9A) . . . . . excisa (Morton)
Baso-ventral lobe of each inferior appendage bent caudad (Fig. 11A); phallic guide with sinuous caudal ridge visible in lateral view (Figs. 11A, 11C) . . . . . globosa, n. sp.

16. Baso-ventral lobe of each inferior appendage with huge apical spine at least 2/3 as long as lobe, with slender spine subapically (Figs. 20A, 20C) . . . . . forcipata (Forsslund)
Baso-ventral lobe of each inferior appendage with only short apical spine or spines no more than 1/4 as long as lobe (Figs. 14C, 16C); with or without subapical spine or spines 17

17. Baso-ventral lobe of each inferior appendage with 1-3 stout spines on short median process (Fig. 13C') . . . . . interispina Yang & Tian
Baso-ventral lobe of each inferior appendage without spine-bearing median process (Fig. 12C') 18

18. Baso-ventral lobe of each inferior appendage with 4-5 stout apical and subapical spines (Fig. 12C') . . . .polyacantha Yang & Tian
Baso-ventral lobe of each inferior appendage with no more than 2 apical spines (Figs. 14A, 14C) 19

19. Baso-ventral lobe of each inferior appendage with one or two apical spines, one subapical spine (Figs. 15C, 19C') 20
Baso-ventral lobe of each inferior appendage with one apical spine, no subapical spine (Fig. 18C') 21

20. Lateral processes of tergum X upturned about 90°, each with stout apical spine (Fig. 19A) . . . . . huangi (Tian)
Lateral processes of tergum X straight, without stout apical spines (Fig. 15A) . . . . . yangi (Mosely)

21. Baso-ventral lobe of each inferior appendage with two apical spines (Figs. 14A, 14C) . . . . . riparia (Albarda)
Baso-ventral lobe of each inferior appendage with only one apical spine (Fig. 16C') 22

22. Tergum X slender in apical 1/3 in dorsal view (Fig. 18B); its lateral processes upturned about 60°, reaching dorsal profile of tergum in lateral view (Fig. 18A) . . . . . trifurca, n. sp.
Tergum X broad apically in dorsal view (Fig. 17B); its lateral processes nearly straight, parallel with lateral edges of tergum (Fig. 17A) 23

23. Baso-ventral lobe of each inferior appendage with apical spine about 1/8 as long as lobe (Fig. 17C'); paramere spine apparently single in normal retracted position (Fig. 17D). . . . . brachyacantha Yang & Tian
Baso-ventral lobe of each inferior appendage with apical spine about 1/3 as long as lobe (Fig. 16C'); two paramere spines aligned end-to-end (Fig. 16D) . . nankingensis (Hwang)

24. Tergum X with lateral processes (Fig. 23A) 25
Tergum X without lateral processes (Fig. 27A') 27

25. Lateral processes of tergum X 1.5 times as long as superior appendages, widely separated from tergum basally, upturned about 45° apically (Fig. 29A); tergum X abruptly narrower beyond superior appendages (Fig. 29A), with apex deltoid in dorsal view (Fig. 29B) . . .omeiensis Yang & Tian
Lateral processes of tergum X no longer than superior appendages, closely applied to tergum basally, thick and blunt and little if any upturned apically (Fig. 23A); tergum X narrowed only slightly apically in lateral view (Fig. 23A), with apex blunt and subparallel-sided in dorsal view (Fig. 23B). 26

26. Sternum IX completely divided longitudinally, its posterior ventral corners elongated, twice as long as rest of sternum (Fig. 23A); phallic guide of each inferior appendage long, saber-like (Fig. 23C), mesal ridge with small truncate projection . . . . . .ensifera (Martynov)
Sternum IX not divided and without long apical processes (Fig. 24A); phallic guide not saber-like, mesal ridge with dagger-like process (Fig. 24C) . . . . . kolthoffi (Ulmer)

27. Superior appendages finger-like, divergent (Fig. 26B); tergum X apex not cleft on meson (Fig. 26B). . . . . .curva Yang & Tian
Superior appendages triangular and straight or convergent (Figs. 27B, 25B). 28

28. Superior appendages shorter than tergum X (Fig. 25A); tergum X with pair of dorso-lateral finger-like processes (Fig. 25B). . . . . .brachycera Yang & Tian
Superior appendages longer than tergum X (Fig. 28A); tergum X without pair of finger-like processes but with pair of thick, recurved, apical sensilla-bearing pads (Fig. 27B') 29

29. Mesal ridge of each inferior appendage with apical process falcate (Fig. 28C). . . . . .acutipennis Yang & Tian
Mesal ridge of each inferior appendage with apical process blunt and subtriangular (Fig. 27C). . . . . dingwuschanella (Ulmer)

30. Lamellae semicircular in lateral view (Fig. 31A); gonopod plates with evident longitudinal striae laterally and each plate convex with single caudal projection (Fig. 31C). 31
Lamellae semicircular (Fig. 35A) or elliptical (Fig. 40A) in lateral view, but if semicircular then gonopod plates without lateral striae (Fig. 35C); gonopod plates with or without lateral striae, but if with striae then each plate concave and with two caudal projections (Fig. 40C). 32

31. Lamellae without ventral striae (Figs. 31A, 31C); superior appendages very short transverse ridges (Fig. 31B). . . . . spinulicolis, n. sp.
Lamellae with ventral striae (Figs. 32A, 32C); superior appendages longer than tergum IX and semicircular in dorsal view (Fig. 32B). . . . . alboguttata (Hagen)

32. Tergum IX dorsal process truncate apically in dorsal view, with pair of small lateral protuberances (Fig. 42B) . . . . . forcipata (Forsslund)
Tergum IX dorsal process rounded (Fig. 33B) or cleft (Fig. 44B) apically in dorsal view. 33

33. Spermathecal sclerite with long, sclerotized supporting ribbons extending anteriorly beyond sclerite (Figs. 35A, 35D) 34
Spermathecal sclerite without ribbons anterior of sclerite (Figs. 33A, 33D). 35

34. Anterior supporting ribbons of spermathecal sclerite extending only to middle of abdominal segment VIII (Fig. 35A); gonopod plates each with dark pit apico-mesally (Fig. 35C). . . . . excisa (Morton)
Anterior supporting ribbons of spermathecal sclerite extending to anterior end of segment VIII (Fig. 36A); gonopod plates without pits (Fig. 36C). . . . . shuotsuensis (Tsuda)

35. Each gonopod plate with two posterior processes, with lateral process sometimes partly hidden above mesal one (Fig. 34C) or with mesal process sometimes much smaller than lateral one (Fig. 37C). 36
Each gonopod plate with one posterior process (Figs. 43C, 45C) or none (Fig. 33C) 41

36. Gonopod plate lateral posterior processes square, partly hidden above larger triangular mesal processes (Fig. 34C). . . . . lobulata (Martynov)
Gonopod plate lateral posterior processes elliptical and larger than mesal processes (Fig. 37C). 37

37. Abdominal segment IX pleural regions concave, with conspicuous lateral pockets above gonopod plates (Figs. 37A, 37C); spermathecal sclerite diamond-shaped (Fig. 37D). . . . . interispina Yang & Tian
Abdominal segment IX pleural regions convex (Figs. 38A, 38C); spermathecal sclerite triangular (Fig. 38C) or elliptical (Fig. 39D) 38

38. Gonopod plate mesal caudal projections rounded (Fig. 39C). . . yangi (Mosely)
Gonopod plate mesal caudal projections acute (Figs. 38C, 40C). 39

39. Gonopod plates broadest in middle (Fig. 40C); spermathecal sclerite broadest in middle (Fig. 40D). . . . . nankingensis (Hwang)
Gonopod plates broadest anteriorly (Fig. 41C); spermathecal sclerites broadest posteriorly (Figs. 38C, 39D) 40

40. Lamellae triangular in lateral view, each with dorsal edge straight to rounded apex (Fig. 38A) . . . . . riparia (Albarda)

Lamellae quadrilateral in lateral view, each parallel-sided basally with dorsal apex oblique (Fig. 41A) . . . . . huangi (Tian)

41. Gonopod plates each with transverse ridge near middle (Fig. 33C); spermathecal sclerite ovoid to pear-shaped, broadest near middle, rounded anteriorly in ventral view (Fig. 33D) . . . . . sinensis (Forsslund)
Gonopod plates without ridges (Fig. 43C) or each with longitudinal ridge (Fig. 46C); spermathecal sclerite broadest posteriorly, blunt (Fig. 44D) truncate (Fig. 43D) or with small projection (Fig. 46D) anteriorly 42

42. Gonopod plates without ridges (Fig. 46C); spermathecal sclerite rounded laterally and truncate anteriorly (Fig. 43D). . . . . fooensis (Mosely)
Gonopod plates each with longitudinal ridge from base of lamella to middle of sclerite (Fig. 46C); spermathecal sclerite nearly straight-sided, blunt anteriorly (Fig. 44D). 43

43. Abdominal segment IX pleural regions concave (Fig. 46A); gonopod plates convex between longitudinal ridges, with long and slender apico-mesal projections (Fig. 46C) . . . . . dingwuschanella (Ulmer)
Abdominal segment IX pleural regions convex (Fig. 44A); gonopod plates concave between longitudinal ridges, with triangular (Fig. 45C) or inconspicuous (Fig. 44C) apico-mesal projections 44

44. Gonopod plate anterior margins projecting antero-mesally into abdominal segment VIII and anterior ends of longitudinal ridges divergent (Fig. 44C) . . . . . ensifera (Martynov)
Gonopod plate anterior margins projecting antero-laterally into abdominal segment VIII and anterior ends of longitudinal ridges convergent (Fig. 45D) . . . . . kolthoffi (Ulmer)

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FIGURES

Fig. 1. Map of collection sites in China, with Chang-jiang (Yang-tze) River indicated. The sites are named in the text on page 4.

Figs. 2-4. Male genitalia of Ceraclea spp. (abbreviations explained on p. 5):
2, C. (C.) spinulicolis, n. sp., holotype;
3, C. (C.) alboguttata (Hagen), specimen from Wu-da-lian-chi, Hei-long-jiang Province;
4, C. (C.) superba (Tsuda), specimen from Wu-da-lian-chi, Hei-long-jiang Province;
A = left lateral view (phallus omitted), B = dorsal view, C = caudal view of left inferior appendage (baso-ventral lobe omitted from alboguttata), D = left lateral view of phallus, E = caudal view of tergum X.

Figs. 5-7. Male genitalia of Ceraclea spp. (abbreviations explained on p. 5):
5, C. (C.) sinensis (Forsslund), specimen from Shao-wu, Fu-jian Province;
6, C. (Athripsodina) major (Hwang), holotype;
7, C. (A.) indistincta (Forsslund), specimen from Wu-hu, An-hui Province;
A = left lateral view (phallus omitted), A' = detail of left lateral view of tergum X, B = dorsal view, C = caudal view of left inferior appendage (baso-ventral lobe omitted from indistincta), C' = detail of caudo-ventral view of baso-ventral lobe of left inferior appendage, D = left lateral view of phallus, D' = dorsal view of phallus.

Figs. 8-10. Male genitalia of Ceraclea spp. (abbreviations explained on p. 5):
8, C. (Athripsodina) lobulata (Martynov), paratype (from paper by Morse, 1975);
9, C. (A.) excisa (Morton), specimen from Wu-da-lian-chi, Hei-long-jiang Province;
10, C. (A.) shuotsuensis (Tsuda), paratype of bicalcarata (from paper by Morse, 1975);
A = left lateral view (phallus omitted), B = dorsal view, C = caudal view of left inferior appendage (baso-ventral lobe omitted from excisa), C' = detail of ventral view of baso-ventral lobe of left inferior appendage, D = left lateral view of phallus.

Figs. 11-13. Male genitalia of Ceraclea spp. (abbreviations explained on p. 5):
11, C. (Athripsodina) globosa, n. sp., holotype;
12, C. (A.) polyacantha Yang & Tian, holotype;
13, C. (A.) interispina Yang & Tian, paratype from Wu-yuan, Jiang-xi Province;
A = left lateral view (phallus omitted), B = dorsal view, C = caudal view of left inferior appendage (baso-ventral lobe omitted), C' = ventral view of baso-ventral lobe of left inferior appendage, D = left lateral view of phallus.

Figs. 14-16. Male genitalia of Ceraclea spp.:
14, C. (Athripsodina) riparia (Albarda), specimen from France (from paper by Morse, 1975);
15, C. (A.) yangi (Mosely), paratype (from paper by Morse, 1975);
16, C. (A.) nankingensis (Hwang), specimen from Hong-ze, Jiang-su Province;
A = left lateral view (phallus omitted), B = dorsal view, C = caudal view of inferior appendages (both appendages in 14C and 15C and right appendage of these with baso-ventral lobe omitted, left appendage of 16C and baso-ventral lobe omitted), C' = ventral view of baso-ventral lobe of left inferior appendage, D = left lateral view of phallus.

Figs. 17-19. Male genitalia of Ceraclea spp.:
17, C. (Athripsodina) brachyacantha Yang & Tian, holotype;
18, C. (A.) trifurca, n. sp., holotype;
19, C. (A.) huangi (Tian), specimen from Nan-jing, Jiang-su Province;
A = left lateral view (phallus omitted), B = dorsal view, C = caudal view of left

inferior appendage (baso-ventral lobe omitted), C' = ventral view of baso-ventral lobe of left inferior appendage, D = left lateral view of phallus, D' = protracted phallus.

Figs. 20-22. Male genitalia of Ceraclea spp. (abbreviation explained on p. 5):
20, C. (Athripsodina) forcipata (Forsslund), holotype (from paper by Morse, 1975);
21, C. (A.) lirata, n. sp., holotype;
22, C. (A.) fooensis (Mosely), holotype (from paper by Morse, 1975);
A = left lateral view (phallus omitted), B = dorsal view, C = caudal view of left inferior appendage, D = left lateral view of phallus, E = left dorsal oblique view of tergum X, E' = caudoventral view of tergum X.

Figs. 23-25. Male genitalia of Ceraclea spp. (abbreviations explained on p. 5):
23, C. (Athripsodina) ensifera (Martynov), paratype (from paper by Morse, 1975);
24, C. (A.) kolthoffi (Ulmer), holotype (from paper by Morse, 1975);
25, C. (A.) brachycera Yang & Tian, holotype;
A = left lateral view (phallus omitted), A' = left dorsal oblique view of tergum X, B = dorsal view, C = caudal view of left inferior appendage, D = left lateral view of phallus.

Figs. 26-28. Male genitalia of Ceraclea spp.:
26, C. (Athripsodina) curva Yang & Tian, holotype;
27, C. (A.) dingwuschanella (Ulmer); 27A, 27B, 27C, 27D, specimen from Zhe-jiang, China (from paper by Morse, 1975); 27A', 27B', specimen from An-kang, Shaan-xi Province, China;
28, C. (A.) acutipennis Yang & Tian, holotype;
A = left lateral view (phallus omitted), A' = left lateral view of tergum X illustrating variation, B = dorsal view, B' = dorsal view of tergum X illustrating variation, C = caudal view of left inferior appendage, D = left lateral view of phallus.

Figs. 29-31. Male (29-20) and female (31) genitalia of Ceraclea spp. (abbreviations explained on p. 5):
29, C. (Athripsodina) omeiensis Yang & Tian, holotype;
30, C. (A.) signaticornis (Ulmer), holotype (from paper by Ulmer, 1926);
31, C. (C.) spinulicolis, n. sp., paratype;
A = left lateral view (phallus omitted from 29A); B = dorsal view; C = caudal view of left lateral inferior appendage (29C) or both inferior appendages (30C) or ventral view (31C); D = left lateral view of phallus (29D) or ventral view of spermathecal sclerite (31D).

Figs. 32-34. Female genitalia of Ceraclea spp. (abbreviations explained on p. 5):
32, C. (C.) alboguttata (Hagen), specimen from Wu-da-lian-chi, Hei-long-jiang Province;
33, C. (C.) sinensis (Forsslund), specimen from Shao-wu, Fu-jian Province;
34, C. (Athripsodina) lobulata (Martynov), specimen from Wu-da-lian-chi, Hei-long-jiang Province;
A = left lateral view; B = dorsal view; C = ventral view; D = ventral view of spermathecal sclerite.

Figs. 35-37. Female genitalia of Ceraclea spp.:
35, C. (Athripsodina) excisa (Morton), specimen from Gogebi County, Michigan, United States of America;
36, C. (A.) shuotsuensis (Tsuda), specimen from Lang-xiang, Hei-long-jiang Province;
37, C. (A.) interispina Yang & Tian, paratype from Shao-wu, Fu-jian Province;
A = left lateral view, B = dorsal view; C = ventral view; D = ventral view of spermathecal sclerite.

Figs. 38-40. Female genitalia of Ceraclea spp.:
38, C. (Athripsodina) riparia (Albarda), from paper by Kumanski and Malicky (1976);
39, C. (A.) yangi (Mosely), specimen from Tian-mu-shan, Zhe-jiang Province;
40, C. (A.) nankingensis (Hwang), specimen from Hong-ze, Jiang-su Province;
A = left lateral view, B = dorsal view, C = ventral view, D = ventral view of spermathecal sclerite.

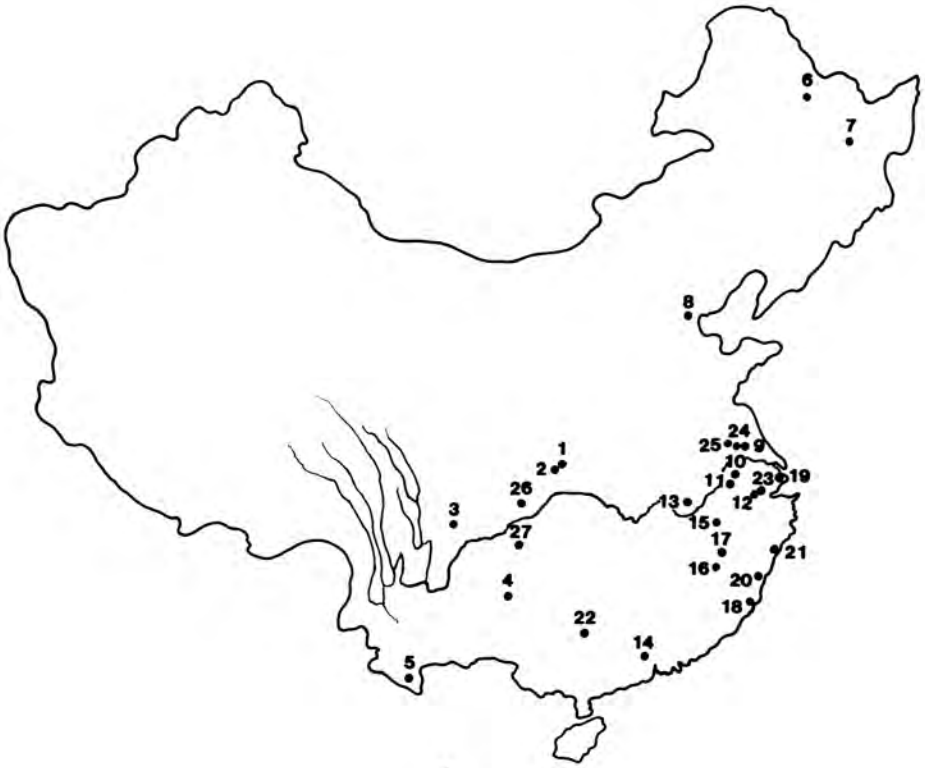
Figs. 41-43. Female genitalia of Ceraclea spp.:
41, C. (Athripsodina) huangi (Tian), specimen from Nan-jing, Jiang-su Province;
42, C. (A.) forcipata (Forsslund), paratype (from paper by Forsslund, 1935);
43, C. (A.) fooensis (Mosely), paratype;
A = left lateral view, B = dorsal view, C = ventral view, D = ventral view of spermathecal sclerite.

Figs. 44-46. Female genitalia of Ceraclea spp.:
44, C. (Athripsodina) ensifera (Martynov), specimen from Xing-hua, Jiang-su Province;
45, C. (A.) kolthoffi (Ulmer), specimen from Hong-ze, Jiang-su Province;
46, C. (A.) dingwuschanella (Ulmer), specimen from An-kang, Shaan-xi Province;
A = left lateral view, B = dorsal view, C = ventral view, D = ventral view of spermathecal sclerite, D' = caudodorsal view of spermathecal sclerite.

Figs. 47-48. Larval and pupal structures of Ceraclea spp.:
47, C. (C.) alboguttata (Hagen), larva and its case (from paper by Tsuda, 1954);
48, C. (Athripsodina) excisa (Morton), larva, larval case, and pupa (from paper by Lepneva, 1966);
A and A-1 = dorsal view of larval head, A-2 = ventral view of larval head, A-3 = left lateral view of larval head, A-4 = dorsal view of larval labrum, B = dorsal view of pro- and mesonota, B-1 = dorsal view of pronotum, B-2 = dorsal view of mesonotum, C = dorsal view of larval habitus, C-1 = posterior view of tibia and tarsus and claw of [right] mesothoracic leg, C-2 = left lateral view of claw of left anal leg, D and D-1 = ventral view of larval case (47D with larva), D-2 = right lateral view of larval case, E-1 = ventral view of left pupal mandible, E-2 = [right] lateral view of [right] process of pupal abdominal segment I, E-3 = dorsal view of anal rods of male pupa.

Fig. 49. Phylogeny and distribution of Chinese Ceraclea species and their relatives. Species groups and subgenera are indicated on the right. Homologues providing evidence for these phylogenetic relationships are discussed in the text. Areas of endemism are as follows:

CHINA-O = Oriental portion of China
CHINA-P = Palearctic portion of China
E = Ethiopian Biogeographic Region
N = Nearctic Biogeographic Region
O = Oriental Biogeographic Region
P = Palearctic Biogeographic Region
c = central
e = eastern
w = western



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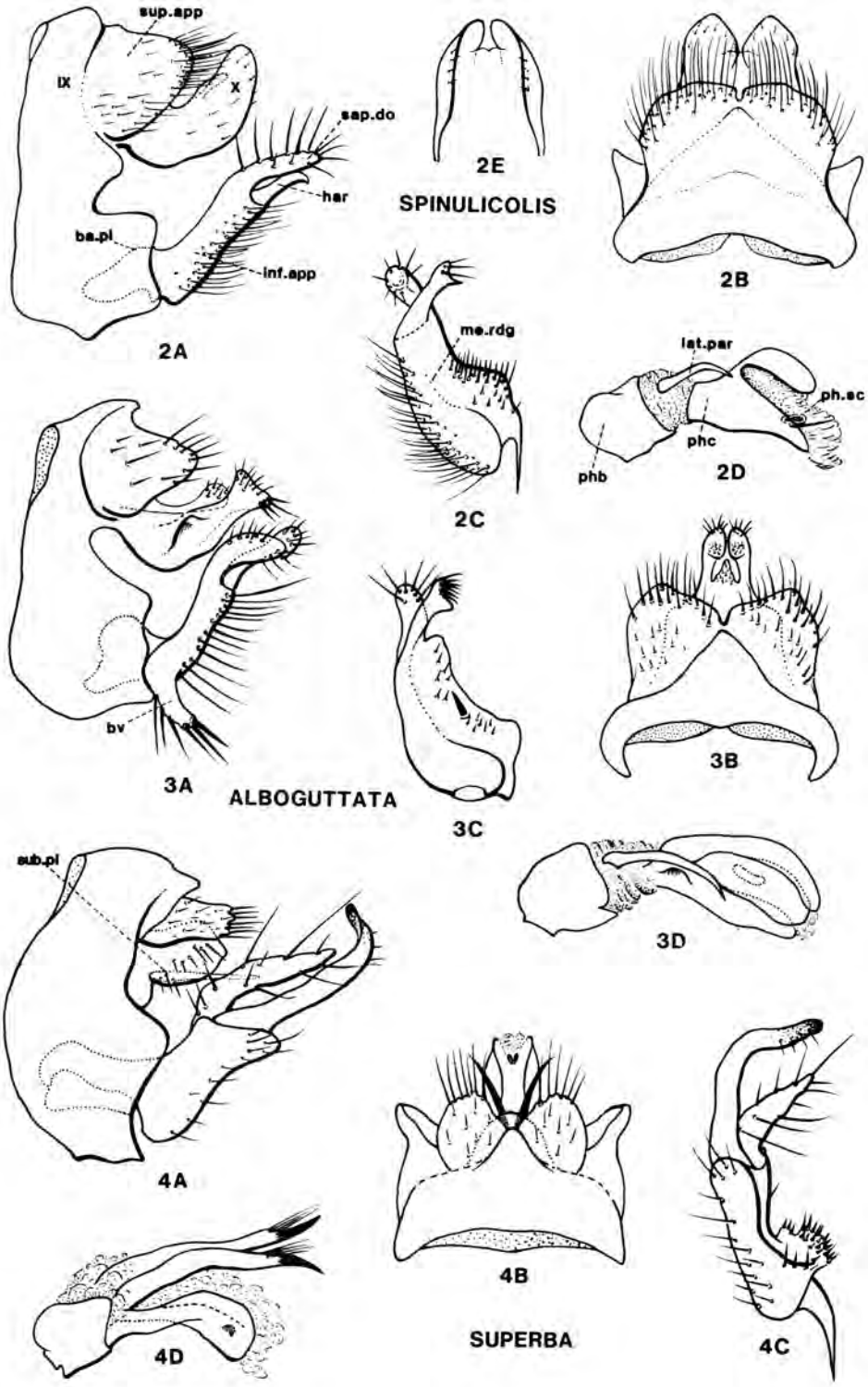
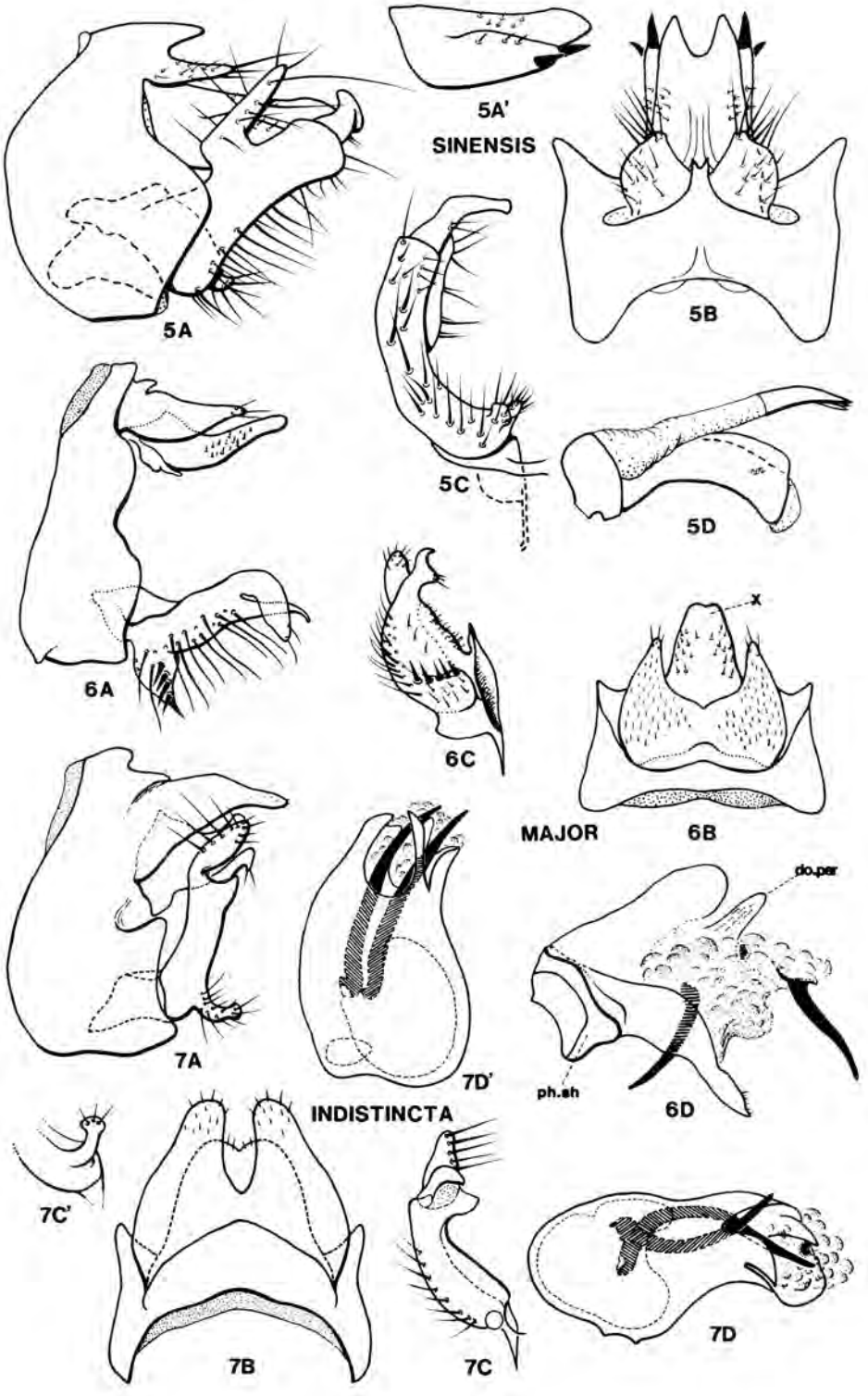
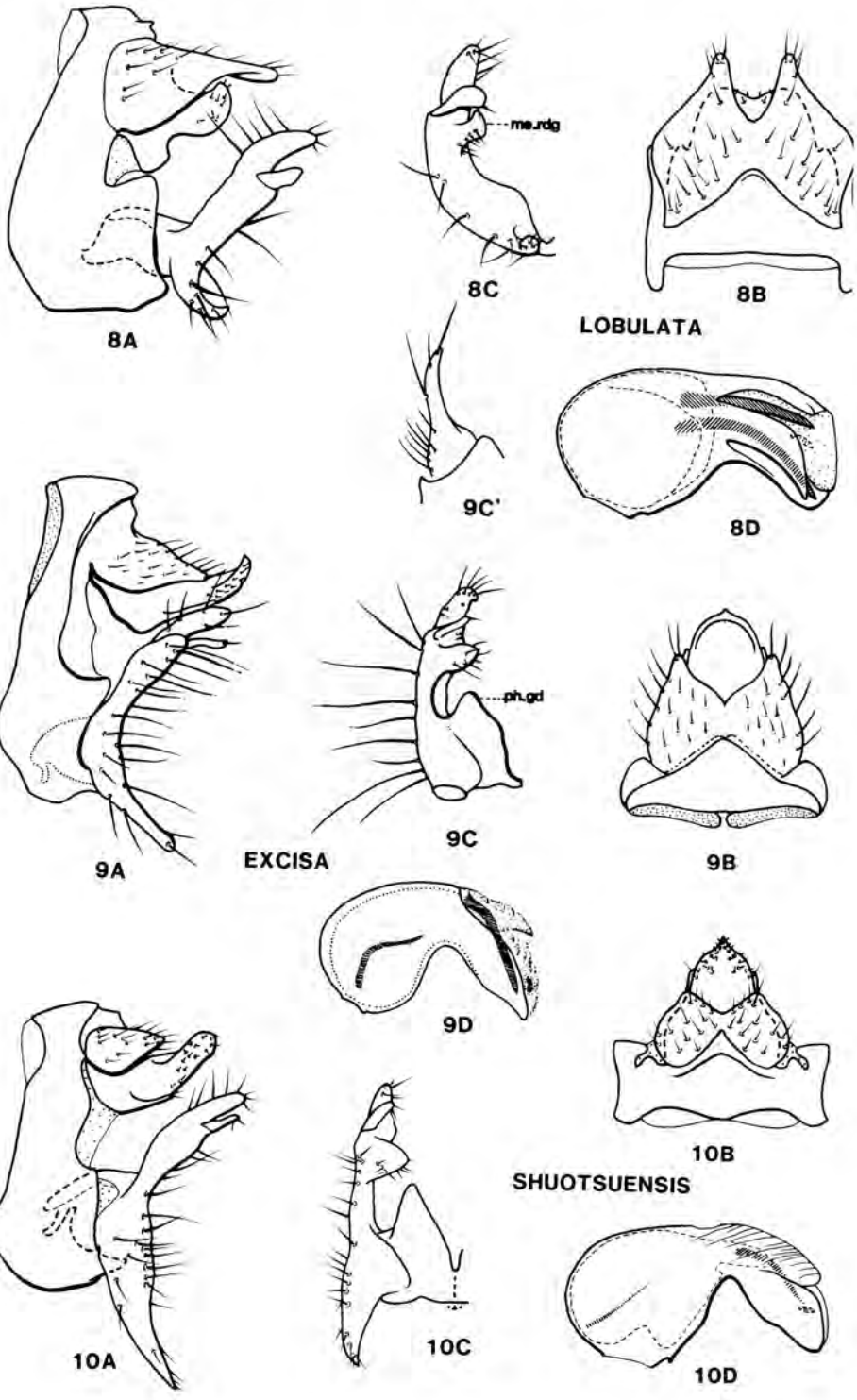
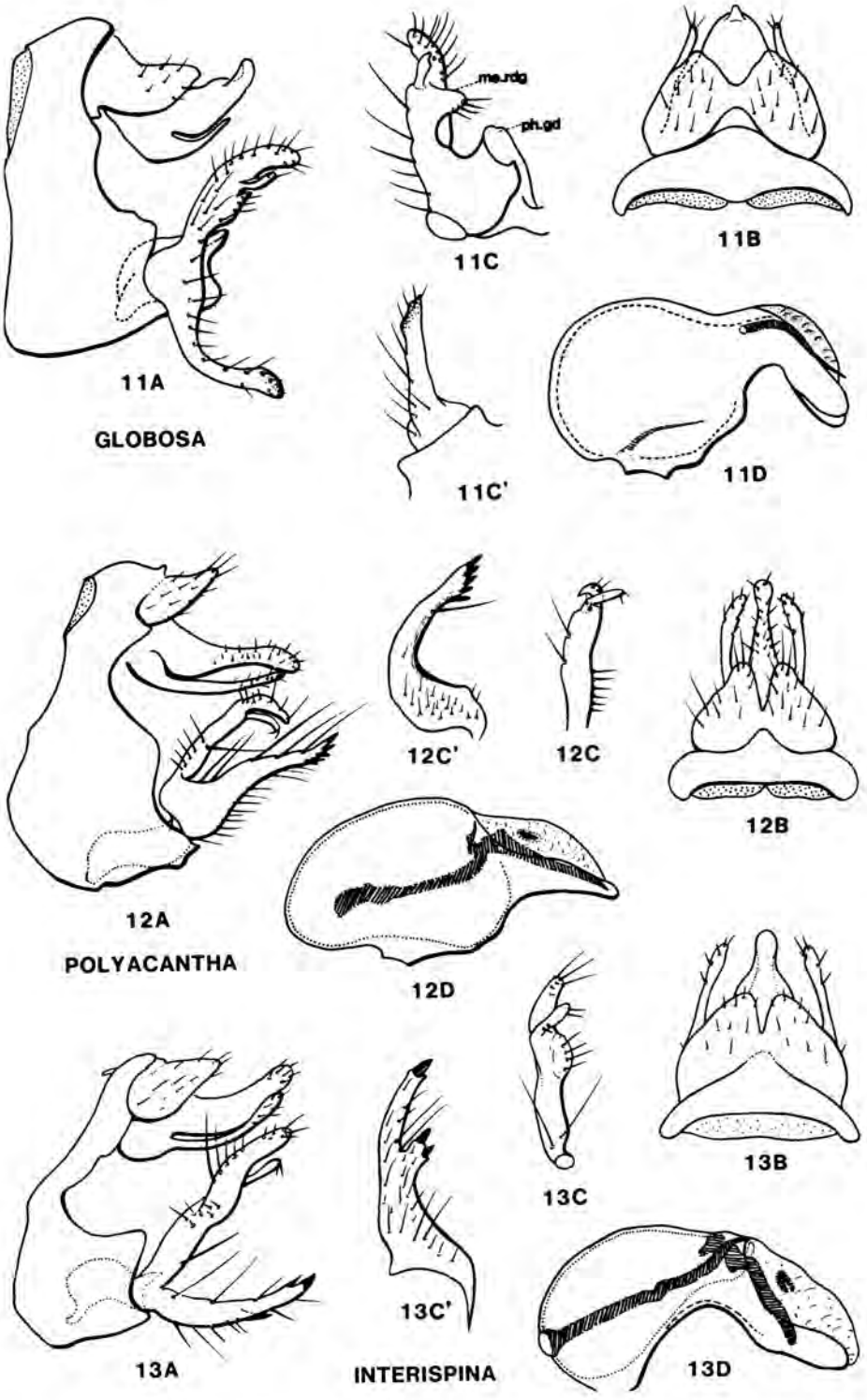

sup.app
IX
X
sap.do
har
ba.pl
inf.app
2A
2E
SPINULICOLIS
2B
me.rdg
2C
lat.par
ph.sc
phc
phb
2D
bv
3A
ALBOGUTTATA
3C
3B
3D
sub.pl
4A
4B
SUPERBA
4C
4D


5A'
SINENSIS
5A
5B
5C
5D
6A
6C
x
MAJOR
6B
7A
7D'
INDISTINCTA
do.per
ph.sh
6D
7C'
7B
7C
7D


me.rdg
8A
8C
8B
LOBULATA
9C'
8D
ph.gd
9A
EXCISA
9C
9B
9D
10B
SHUOTSUENSIS
10A
10C
10D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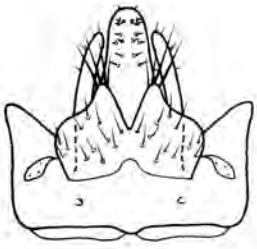
ph.gd
11A
GLOBOSA
11C
11B
11C'
11D
12A
POLYACANTHA
12C'
12C
12B
12D
13C
13B
13A
13C'
INTERISPINA
13D

14A

RIPARIA 14C



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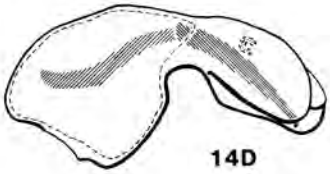


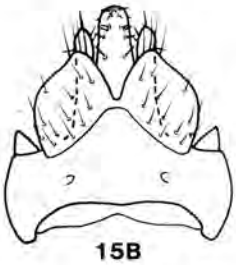
14D

15C

YANGI

15A

15D



15B

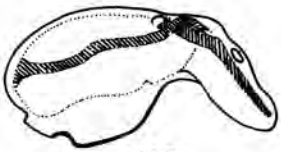
16C

16C'

NANKINGENSIS

16A

16B



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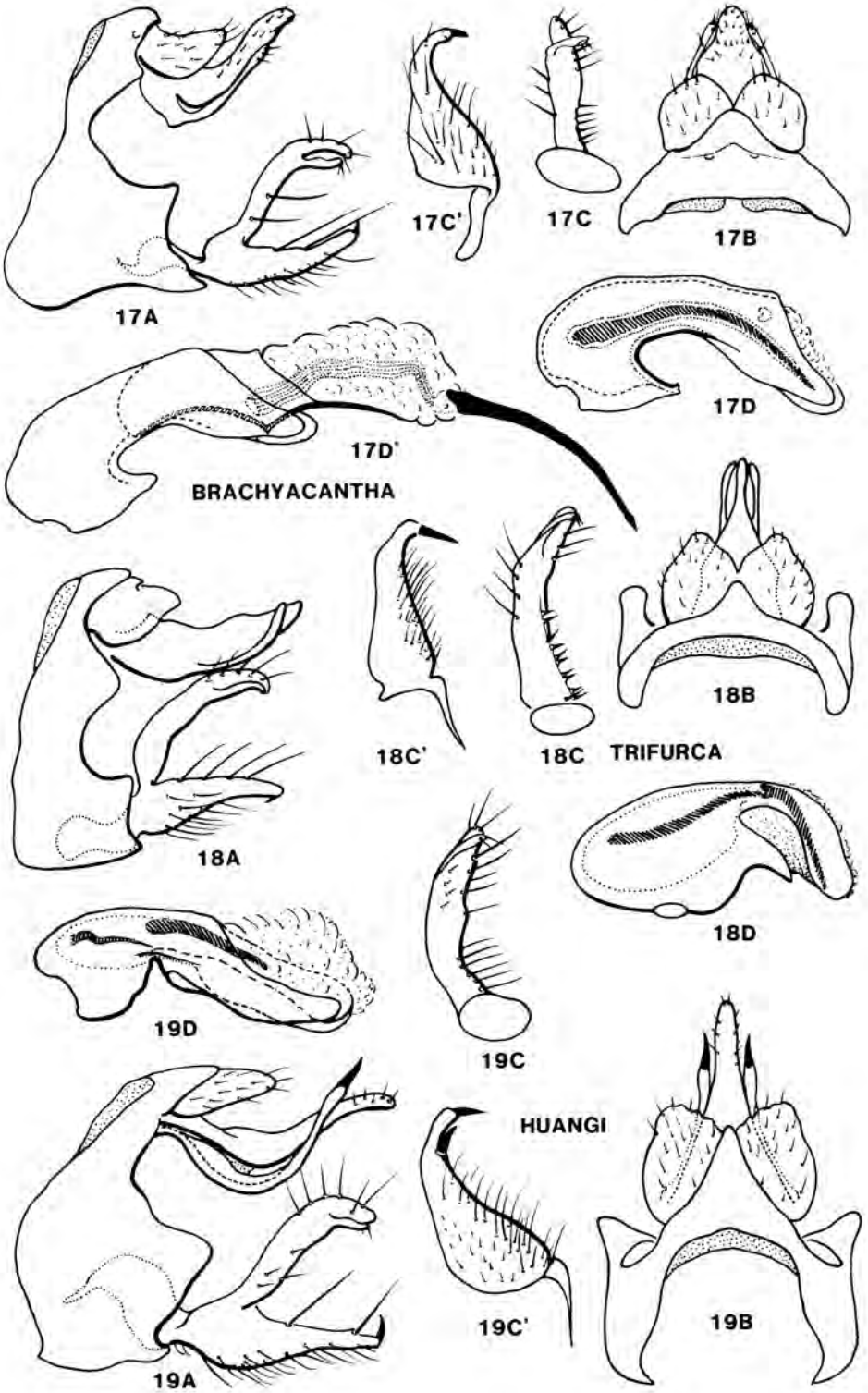
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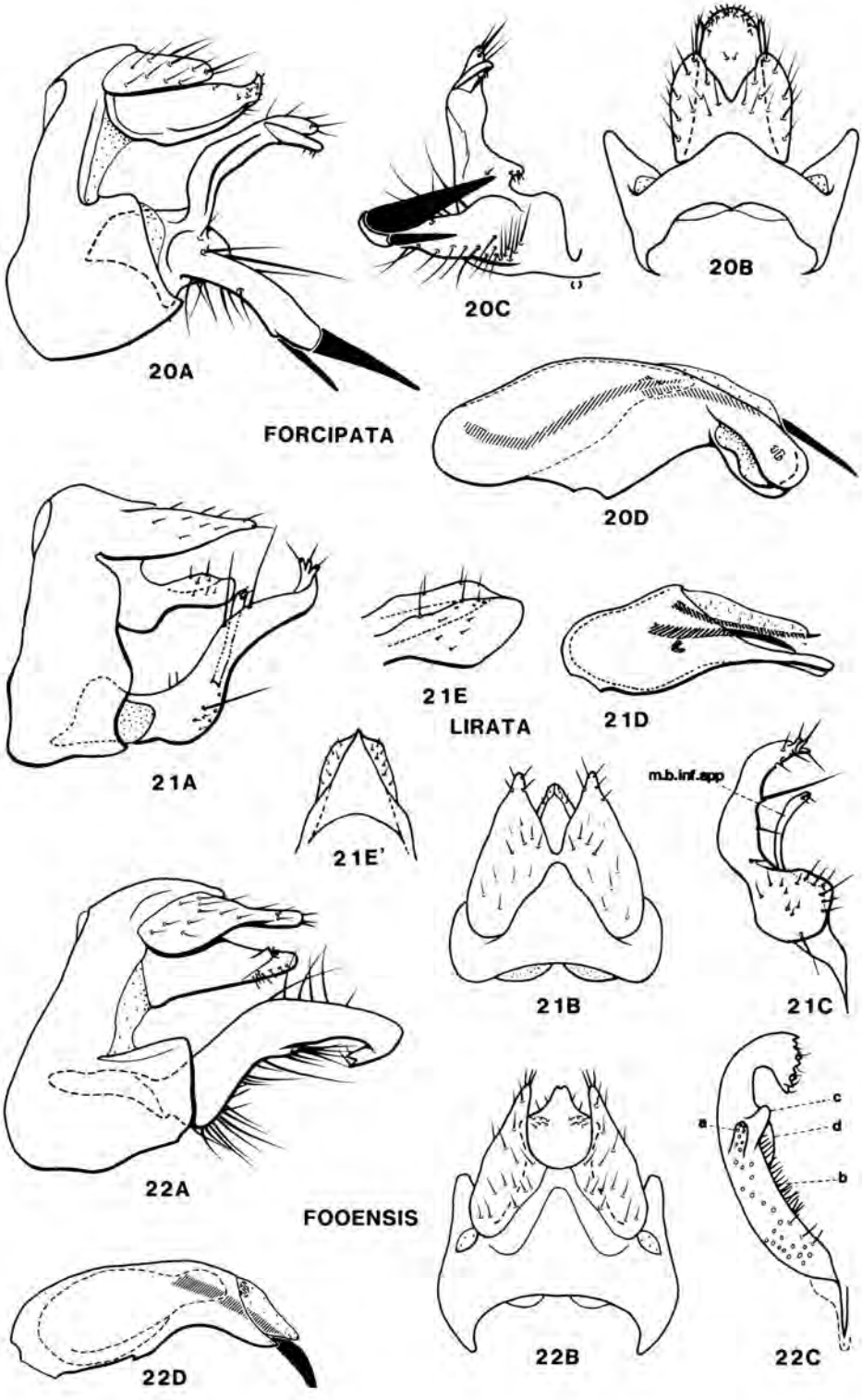
17C'
17C
17B
17D
17D'
BRACHYACANTHA
18A
18C'
18C
18B
TRIFURCA
18D
19D
19C
HUANGI
19C'
19B
19A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20C
20B
FORCIPATA
20D
21A
21E
LIRATA
21D
21E'
m.b.inf.app
21B
21C
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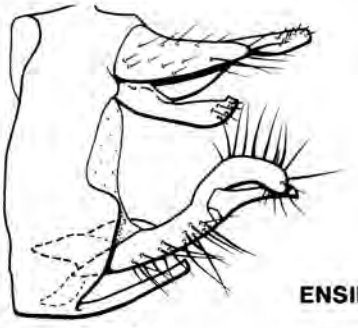
22D
a
c
d
b

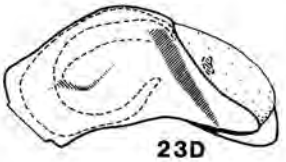


ENSIFERA

23A

23C

23B



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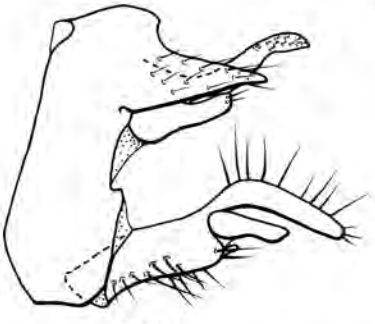
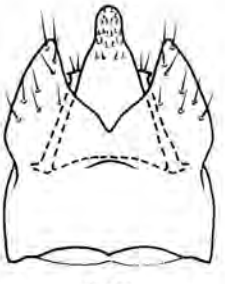


24A

KOLTHOFFI

24C



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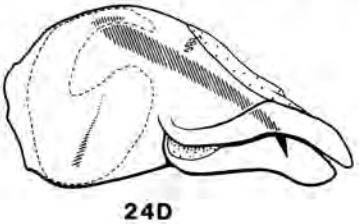

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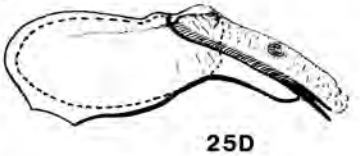
25A'



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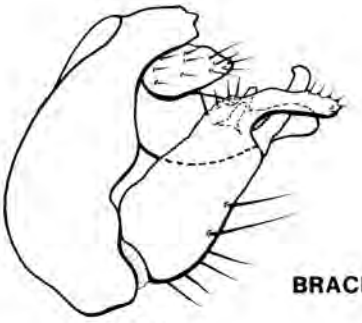
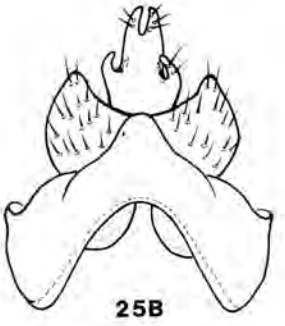


25A

BRACHYCERA

25C



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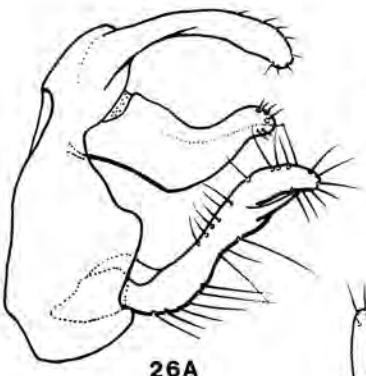

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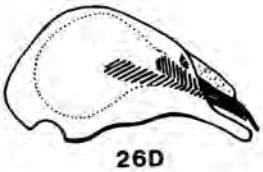
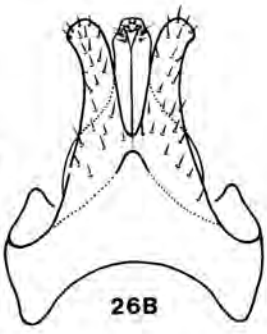


26D

CURVA



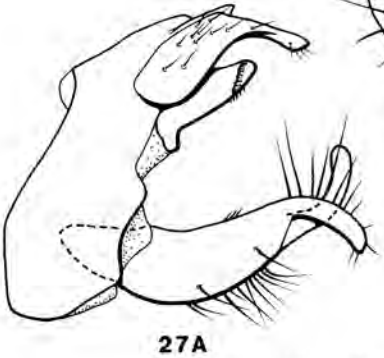
26B

26C

26E

27B'

27A'

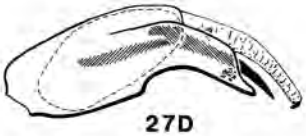


27A

DINGWUSCHANELLA

27B

27C

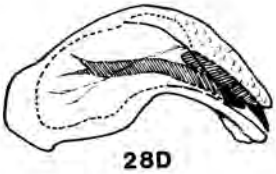


27D

28A

ACUTIPENNIS

28C



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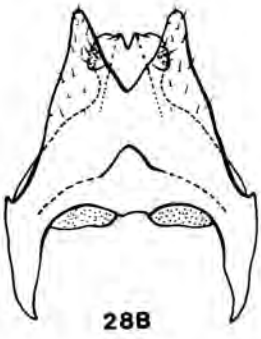

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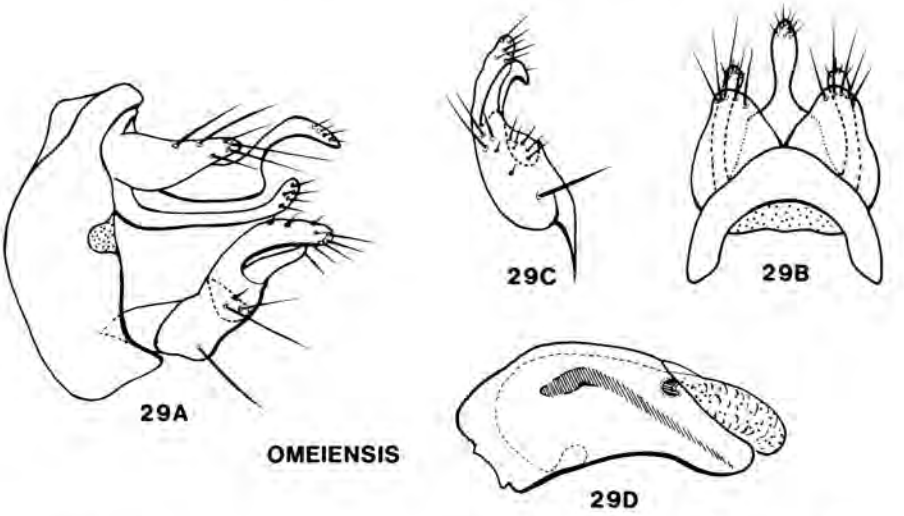


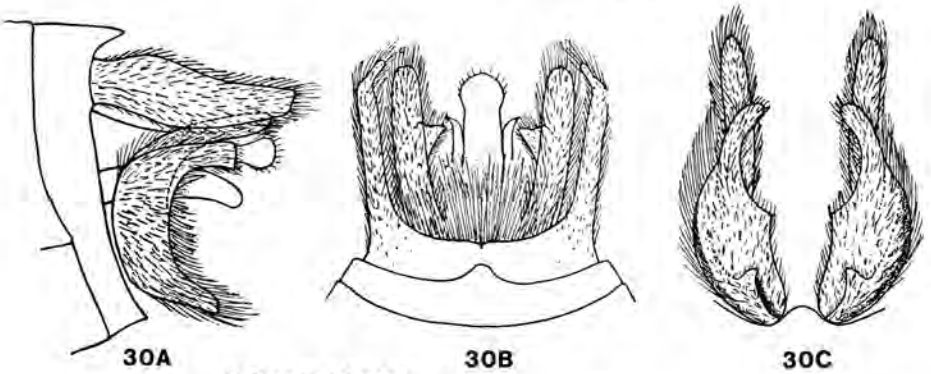
29A

29C

29B

OMEIENSIS

29D

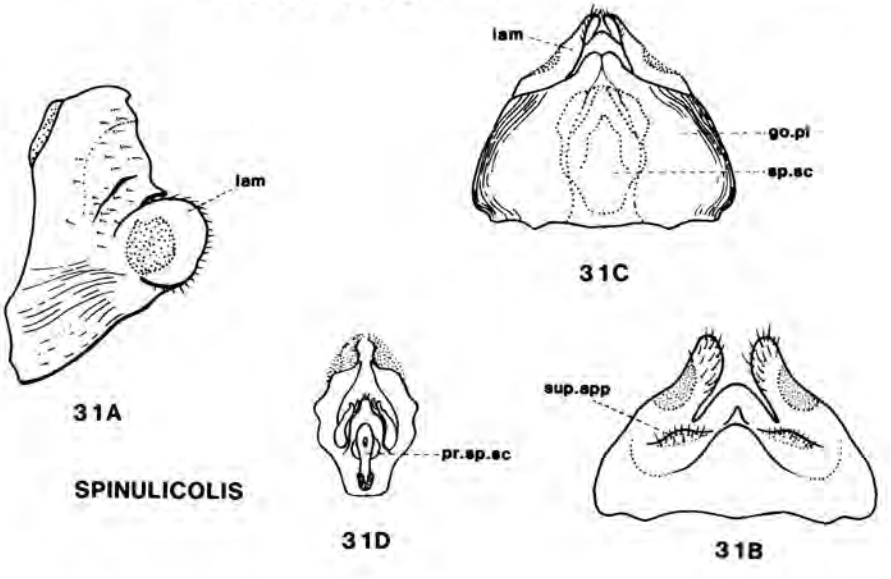


30A

30B

30C

SIGNATICORNIS



31C

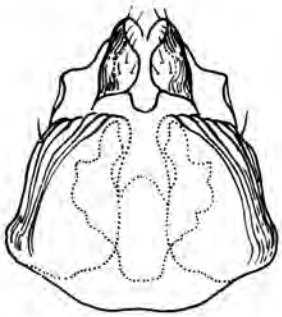
31A

SPINULICOLIS

31D

31B

32A



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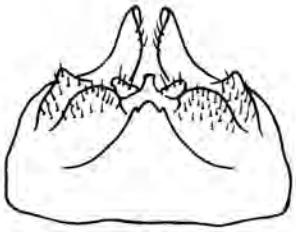

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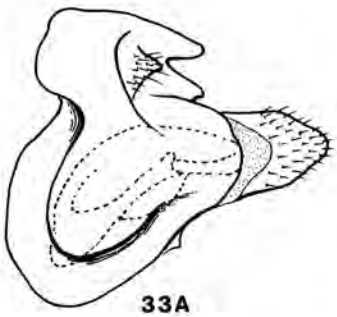
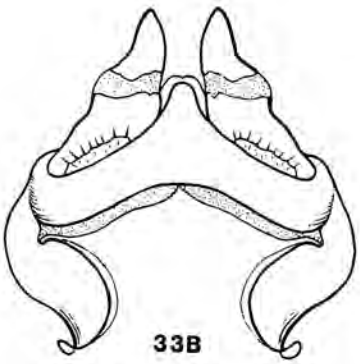


33A

32D



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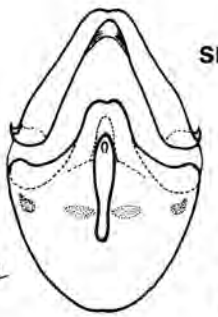

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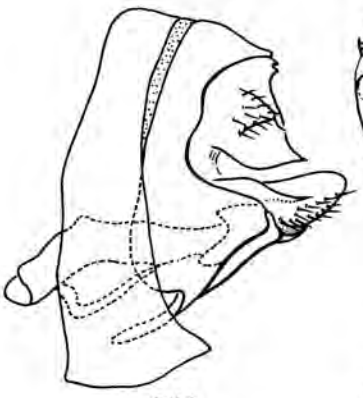

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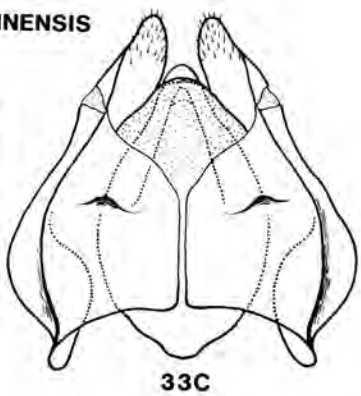

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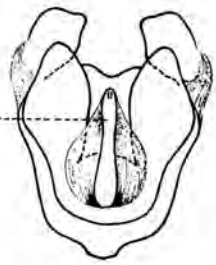
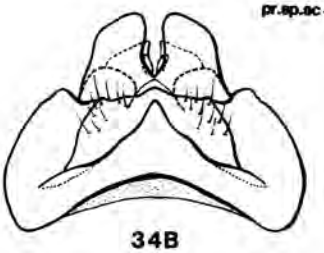


pr.sp.sc

34D

LOBULATA



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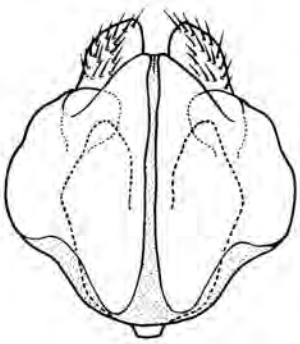

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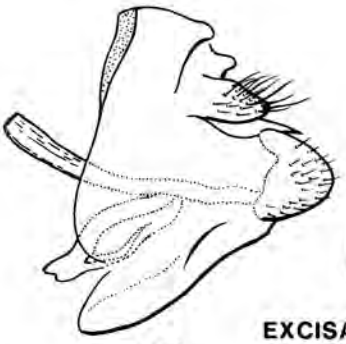

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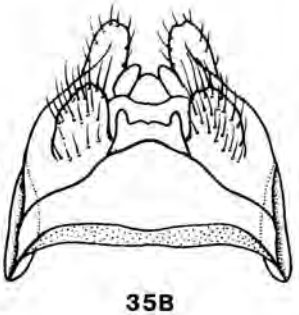

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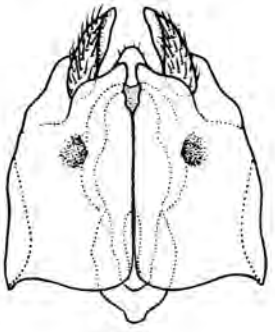

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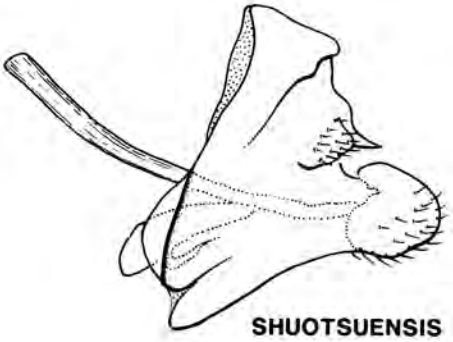
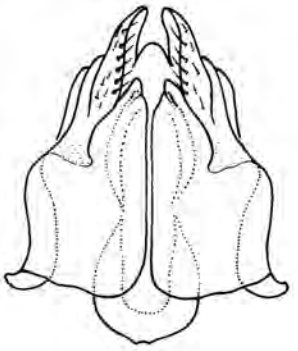
EXCISA



36A

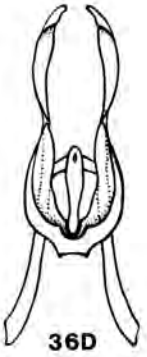
35D



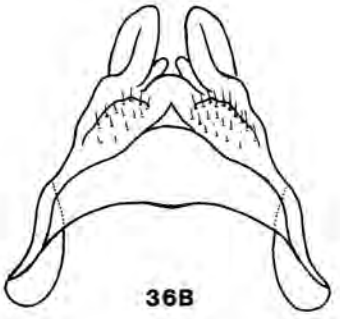
36C

SHUOTSUENSIS

37A

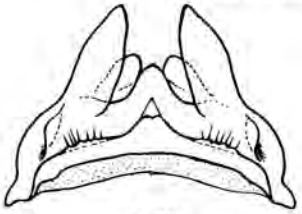


36D



36B

INTERISPINA



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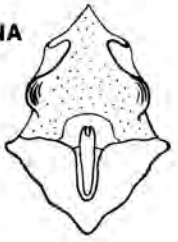
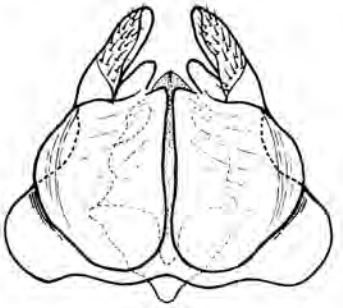
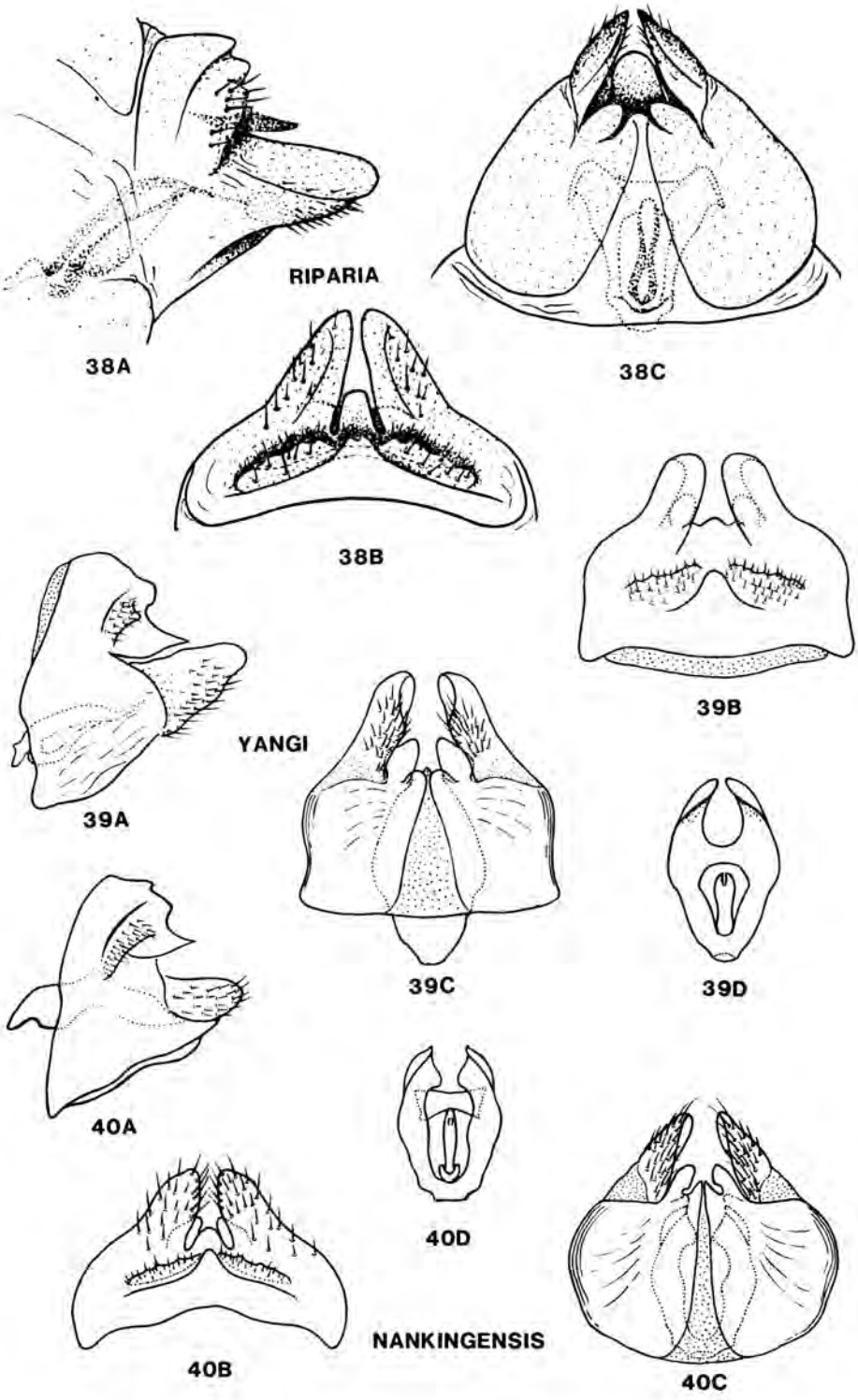


37D



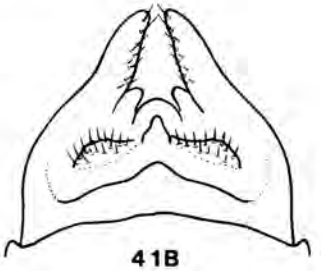
37C


RIPARIA
38A
38C
38B
39B
YANGI
39A
39C
39D
40A
40D
40B
NANKINGENSIS
40C

HUANGI

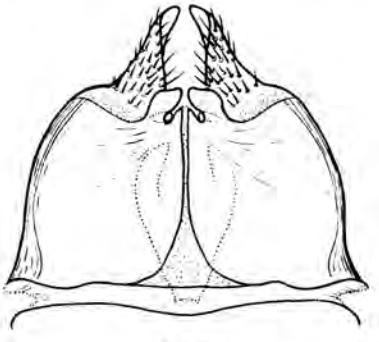
41A

41D



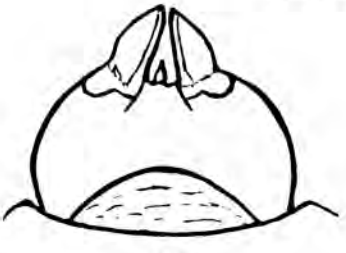
41B

42A

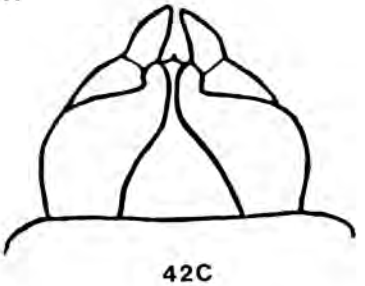


41C

FORCIPATA



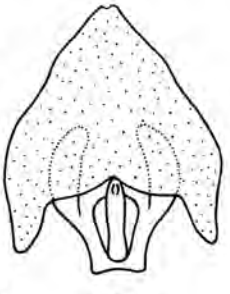
42B



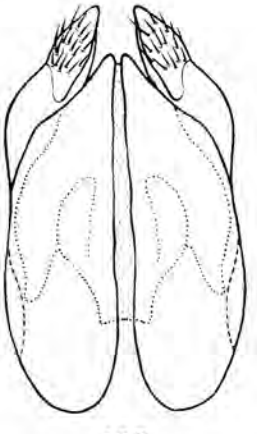
42C

FOOENSIS

43A



43D



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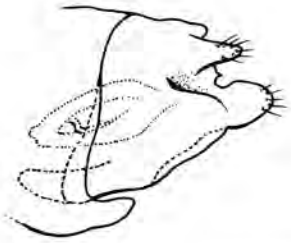
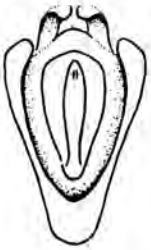
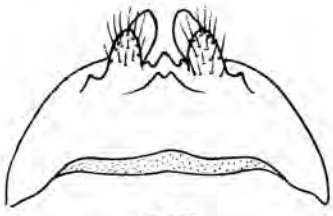


44A



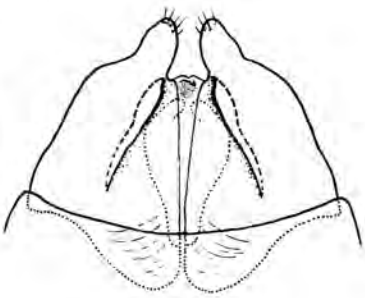
44D



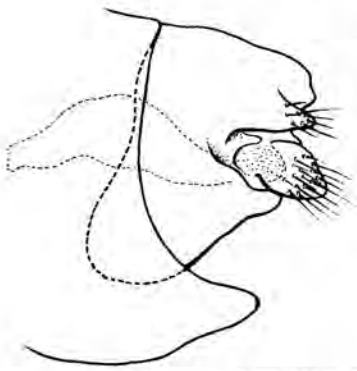
44B

ENSIFERA

44D'



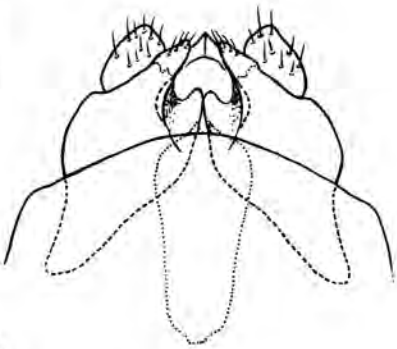
44C



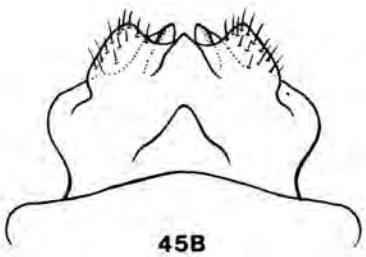
45A

KOLTHOFFI

45D



45C



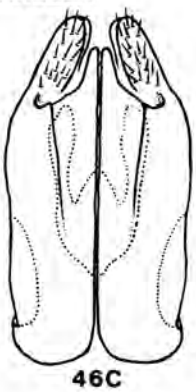
45B

46D

DINGWUSCHANELLA

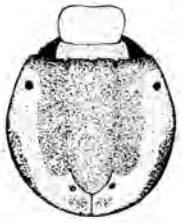
46A

46B

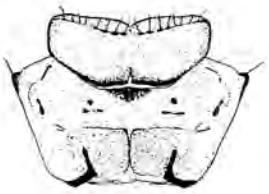


46C

ALBOGUTTATA



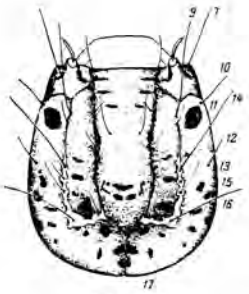
47A



47B

47C

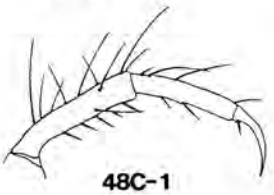
47D



48A-1

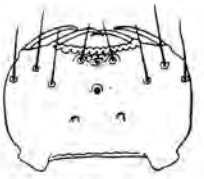
48A-2

48A-3



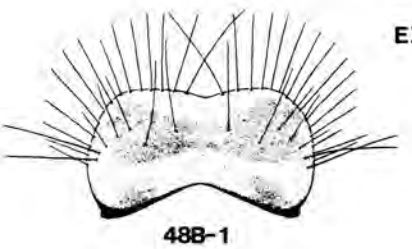
48C-1

48C-2

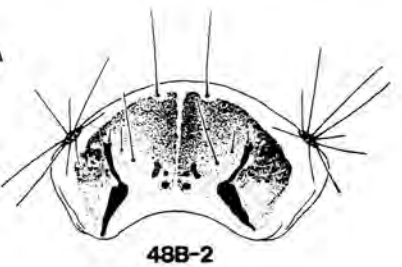


48A-4

EXCISA



48B-1



48B-2

48D-1

48D-2

48E-1

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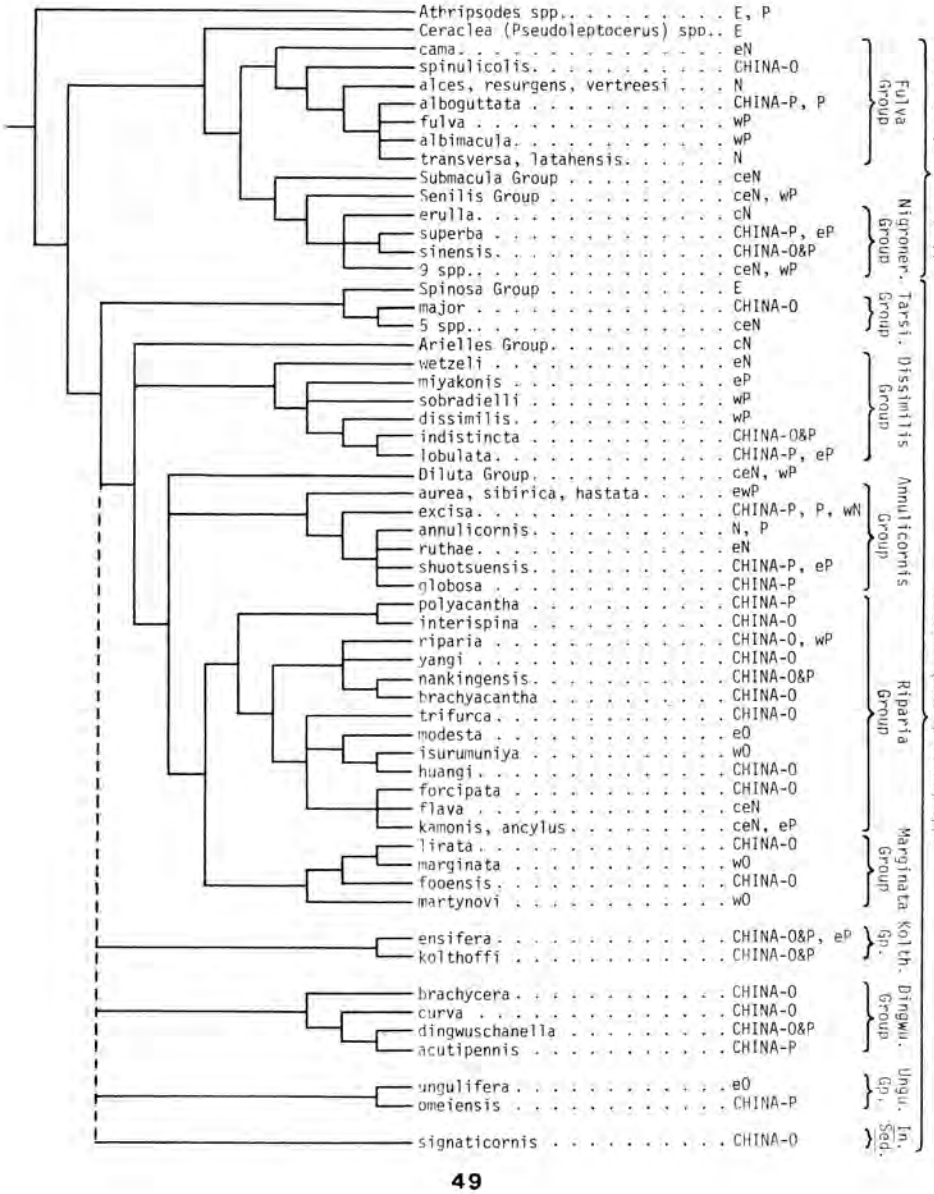
Athripsodes spp. E, P
Ceraclea (Pseudoleptocerus) spp. E
cama eN
spinulicolis CHINA-O
alces, resurgens, vertreesi N
alboguttata CHINA-P, P
fulva wP
albimacula wP
transversa, latahensis N
Submacula Group ceN
Senilis Group ceN, wP
erulla cN
superba CHINA-P, eP
sinensis CHINA-O&P
9 spp. ceN, wP
Spinosa Group E
major CHINA-O
5 spp. ceN
Arielles Group cN
wetzeli eN
miyakonis eP
sobradielli wP
dissimilis wP
indistincta CHINA-O&P
lobulata CHINA-P, eP
Diluta Group ceN, wP
aurea, sibirica, hastata ewP
excisa CHINA-P, P, wN
annulicornis N, P
ruthae eN
shuotsuensis CHINA-P, eP
globosa CHINA-P
polyacantha CHINA-P
interispina CHINA-O
riparia CHINA-O, wP
yangi CHINA-O
nankingensis CHINA-O&P
brachyacantha CHINA-O
trifurca CHINA-O
modesta eO
isurumuniya wO
huangi CHINA-O
forcipata CHINA-O
flava ceN
kamonis, ancylus ceN, eP
lirata CHINA-O
marginata wO
fooensis CHINA-O
martynovi wO
ensifera CHINA-O&P, eP
kolthoffi CHINA-O&P
brachycera CHINA-O
curva CHINA-O
dingwuschanella CHINA-O&P
acutipennis CHINA-P
ungulifera eO
omeiensis CHINA-P
signaticornis CHINA-O
Fulva Group
Nigromer. Group
Tarsi. Group
Dissimilis Group
Annulicornis Group
Riparia Group
Marginata Group
Kolth. Gp.
Dingwu. Group
Ungu. Gp.
In. Sed.
Ceraclea (Ceraclea) spp.
Ceraclea (Athripsodina) spp.

INDEX OF SPECIES

Each synonym is marked with an asterisk. The underlined pages are those which concern the primary treatment of the species. Numbers in parentheses refer to the figures illustrating the species.