Phylogenetic review of the Chinese species of *Acanthacorydalis* (Megaloptera, Corydalidae)

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The dobsonfly genus *Acanthacorydalis* Weele is a small genus which only occurs in Asia and comprises eight species. Seven species are restricted to the Oriental realm, while *A. orientalis* (McLachlan) extends into the Palaearctic realm. There are five species in China, four of which are endemic. In the present paper, the Chinese species are redescribed, illustrated, keyed, and subjected to phylogenetic and biogeographical analyses for the first time. Geographic distributions are updated. The cladistic analysis for the Chinese species was constructed by using Hennig86, based on 17 adult morphological characters. The phylogenetic relationships obtained are (*A. orientalis* + *A. yunnanensis* + *A. unimaculata* + (*A. fruhstorferi* + *A. sinensis*)). Six areas of endemism are identified based on *Acanthacorydalis* distributions: north, south-west, central and south China, north-eastern India and northern Vietnam.

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Introduction

The megalopteran genus *Acanthacorydalis* Weele is small and occurs only in Asia. Comprising eight species, it is considered to be a well established monophyletic group (Glorioso 1981). Seven species are restricted to the Oriental realm, while the range of *A. orientalis* (McLachlan) extends into the Palaearctic realm. There are five species in China, four of which are endemic. The adults are among the largest and most bizarre-appearing living insects, and the males are noted for their disproportionately large mandibles. The formidable appearance of *Acanthacorydalis* has led many collectors to regard these insects as dangerous (Glorioso 1981).

Wood-Mason (1884) and McLachlan (1899) described *A. asiatica* and *A. orientalis*, respectively, but they placed the two species in the American genus *Corydalus*, whose male mandibles are usually enlarged and elongate. Weele (1907) separated *Acanthacorydalis* from *Corydalus* as a new genus on the basis of the spines of the vertex, the toothed mandibles of the male, and the thin and short antennae, which are the same shape and length in both sexes. Weele (1907) also described a third species, *A. fruhstorferi*, from Vietnam. Weele (1910) reviewed the genus in his monograph on worldwide Megaloptera.

After the description of *A. imperatrix* and *A. horrenda* by Navás (1917, 1931) and the reviews by Lestage (1927) and Banks (1940), there were five species in the genus. Following the descriptions of three endemic Chinese species, *A. sinensis*, *A. unimaculata*, and *A. yunnanensis*, by Yang & Yang (1986, 1988) there were eight known species.

Glorioso (1981) redefined the genera of the Corydalinae and proposed a hypothesis of intergeneric relationships of the Corydalinae on the basis of a cladistic analysis. In this hypothesis, *Acanthacorydalis* and the New World lineage (*Corydalus* + *Chloronia* + *Platyneuromus*) form a monophyletic group. Penny (1993), following a rigorous cladistic analysis, concurred with this. Five years later, Contreras-Ramos (1998) proposed a second hypothesis of intergeneric relationships within this subfamily, in which *Acanthacorydalis* was sister of the lineage (*Neuromus* + *Neoneuromus*). Phylogenetic relationships among the species of *Acanthacorydalis* have not hitherto been studied.

The natural history of *Acanthacorydalis* is still poorly known. The larvae are aquatic and sensitive to environmental changes. They may be useful as biological indicators of water quality (Yang & Yang 1995). They occur in clean streams in mountainous regions and feed on a wide variety of small aquatic invertebrates. The adults emerge from late spring to early autumn and are always found near running water. Adults are readily collected nocturnally at electric lights; there is evidence indicating that they are also active in the daytime and feed on liquids from trees (Yang 1985).

In the present paper, the five Chinese *Acanthacorydalis* species are redescribed, illustrated and keyed. The first phylogenetic

analysis of all the species is also undertaken, their geographical distributions are updated, and phylogenetic relationships and biogeography are discussed.

Materials and methods

The specimens were collected mostly from light traps in mountainous regions; several were collected by the authors. Genitalic preparations were made by macerating the apex of the abdomen in 10% KOH for 8–10 h. This was then transferred to glycerine for further dissection and examination. After examination it was moved to fresh glycerine and stored in a microvial pinned below the specimen.

Identification was made on the basis of the types and original descriptions, except for *A. fruhstorferi* and *A. orientalis*, which were identified only by the original descriptions. However, there is no doubt concerning the identity of the two species because the descriptions and illustrations were very clear and detailed. Re-descriptions and new illustrations were made during the examination of the specimens under the microscope.

The cladistic analysis was conducted using Hennig86 v.1.5 (Farris 1988). The cladogram was obtained after successive weighting of characters by **mhennig*, bb*, xstep w, ccode** and unchanged weights after three iterations. Seventeen adult morphological characters were numerically coded for the five Chinese species. All specimens examined were obtained from the Insect Collection of China Agricultural University (CAU) and Institute of Zoology, Chinese Academy of Science (IZCAS) (Beijing, China).

The terminology used generally follows Glorioso (1981) except for the tenth abdominal segment, which follows Contreras-Ramos (1995).

Results

Taxonomy

Genus Acanthacorydalis *Weele, 1907*

Acanthacorydalis Weele, 1907. Not. Leyden Mus. 28: 228. Type species: *Corydalus asiatica* Wood-Mason, 1884, designated by Glorioso 1981. Syst. Ent. 6: 282.

Diagnosis. Body large. Vertex with one pair of spines. Male mandibles enlarged and much more elongate, with one large inner basal tooth and one small inner apical tooth. Costal crossveins in male forewings recticulate medially.

Description. Body length 50–105 mm; forewing length 55–95 mm, hind wing length 50–80 mm. Coloration blackish brown, often with yellowish marks on head and prothorax. Wings subhyaline, faintly washed with smoky marks; crossveins often with brownish marks.

Head large, subquadrate and moderately flattened. Postocular spines well developed, and also pair of spines present on vertex. Clypeal margin deeply incised medially. Antennae in both sexes filiform and subequal in length. Labrum triangular, deflexed between mandibles. Male mandibles enlarged and much more elongate, nearly as long as head plus prothorax, with one large inner basal tooth and one small inner apical tooth, and often with one small median tooth; female mandibles nearly as long as head with three small inner teeth. Gula T-shaped, usually with pair of acute processes on anterolateral margin in male.

Prothorax subcylindrical, much longer than wide, slightly elevated near posterolateral margins; prosternum flattened, with a pair of small medial spines on posterior margin in male. Meso- and metathorax much more robust. Wings large, about three times longer than wide; costal crossveins often recticulate on forewings; Rs 8–11-branched, last one or two branches bifurcate; 5–10 crossveins between R_1 and Rs; M_{1+2} 2–4-branched; M_{3+4} 2–3-branched; 1A 2-branched. Hind wings with short sparse yellowish setae on membrane in anal area.

Male ninth tergum entire or divided into two hemitergites, and with an angular basal notch; ninth sternum suboval, about two times wider than long, and with a pair of setiferous posterolateral lobes; ninth gonostylus short and clavate, slightly incurved at apex, with a terminal sclerotized claw; tenth tergum clavate, nearly as long as ninth tergum, often curved outwards at tip; tenth sternum arcuate, weakly sclerotized, with pair of finger-like lobes posteromedially. Female tenth tergum divided dorsally by anus, with separate semicircular ventral portions; gonocoxite valvate and membranous; lateral sclerite bandlike, much wider at middle; gonostylus present, a digitiform process basally fused with posterior tip of gonocoxite.

Distribution. Restricted to eastern and south-eastern Asia. It is known presently from China (five species), India (two species) and Vietnam (two species).

Key to Chinese species of Acanthacorydalis

1 Body blackish brown, without distinct yellowish marks on head and prothorax..... 2
Body brown to blackish brown, with distinct yellowish marks on head and prothrorax..... 3

2 Prothorax 2.0 times (male) or 1.5 times (female) longer than wide at midlength; male ninth tergum dorsally divided into a pair of hemitergites, basally with a V-shaped incision.....*A. fruhstorferi* Weele
Prothorax 1.4 times (male) or 1.1 times (female) longer than wide at midlength; male ninth tergum complete, not divided sagitally into a pair of hemitergites, basally with an arcuate incision..... *A. sinensis* Yang & Yang

3 Head with one pale yellowish circular spot around ocellar triangle; male mandible with one subapical tooth..... ..... *A. yunnanensis* Yang & Yang

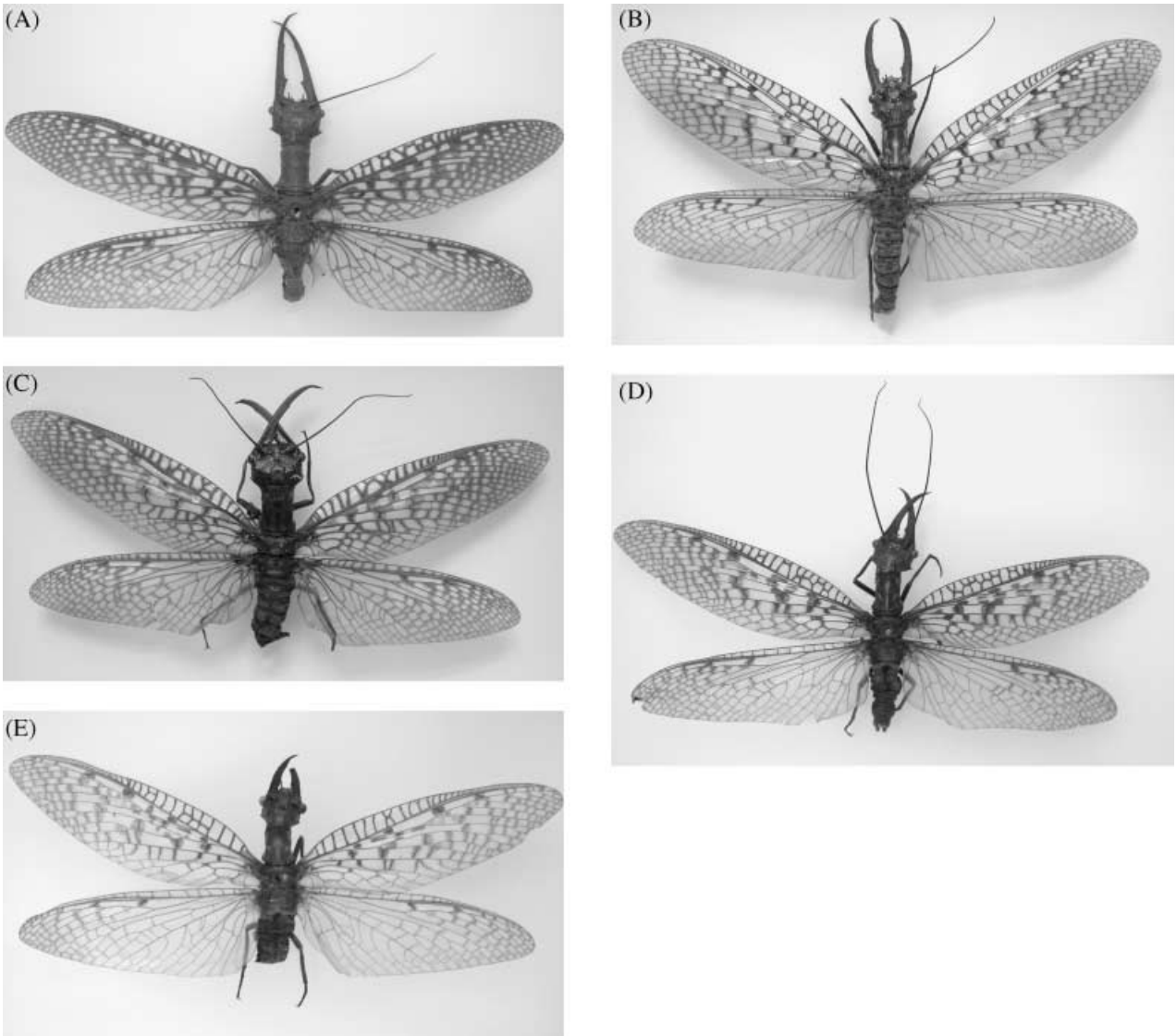

Fig. 1 A–E. Habitus photographs of the five Chinese *Acantha-corydalis* species. —A. *Acanthacorydalis fruhstorferi* Weele. —B. *A. orientalis* (McLachlan). —C. *A. sinensis* Yang & Yang, holotype. —D. *A. unimaculata* Yang & Yang, holotype. —E. *A. yunnanensis* Yang & Yang, holotype.

Head with three yellowish spots near ocellar triangle or only one spots before ocellar triangle; male mandible without subapical tooth 4

4 Head with one yellowish spot before ocellar triangle, without any spots behind ocellar triangle; male mandible without median tooth .....*A. unimaculata* Yang & Yang

Head with one yellowish spot before ocellar triangle, and two yellowish spots behind ocellar triangle; male mandible with a median tooth .....*A. orientalis* (McLachlan)

Acanthacorydalis fruhstorferi *Weele, 1907 (Figs 1A and 2).* *Acanthacorydalis fruhstorferi* Weele, 1907. Not. Leyden Mus. 28: 233. Type locality: Vietnam (Than-Moi).

Material examined. 1♂, CHINA, Yunnan, Malipo, 23°07′N, 104°41′E, 1650 m, 11 May 1979, Anpei Zhang (CAU); 1♂, CHINA, Fujian, Wuyi, Sangang, 27°45′N, 117°40′E, 4 July 1986, Qixian Chen (CAU); 1♂, CHINA, Fujian, Wuyi, Sangang, 27°45′N, 117°40′E, 4 July 1986, Fushui Cai (CAU); 1♀, CHINA, Fujian, Shaowu, Dazhulan, 27°02′N, 117°29′E, 10 July 1945, Xiufu Zhao (CAU); 1♀, CHINA, Fujian, Wuyishan, 26°54′N, 116°42′E, 4 July 1986, Xianliang Chen (CAU); 1♀, CHINA, Fujian, Yongan, Tianbaoyan, 26°39′N, 118°53′E, 15–18 July 2001, Zaifu Xu (CAU); 1♂, CHINA, Guangdong, Chebaling, 24°58′N, 114°02′E, 19–21 April 2002 (CAU); 1♂1♀, CHINA, Zhejiang, Anji, Longwangshan, 30°39′N, 119°41′E, 18 August 1995, Hong Wu

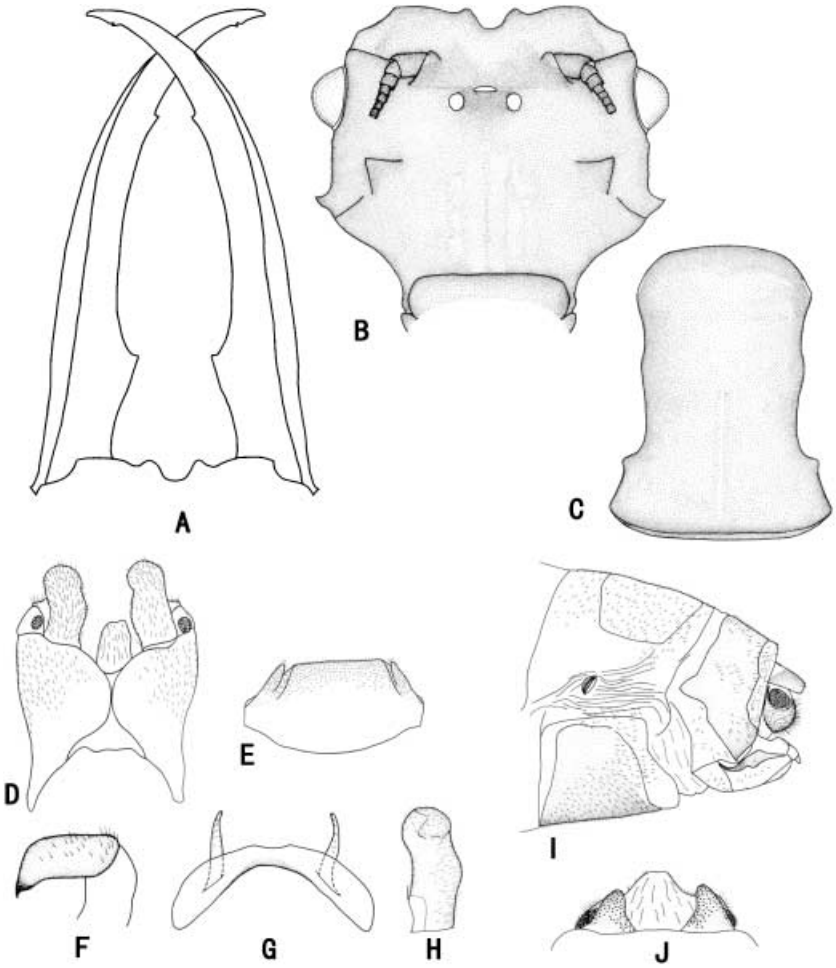

Fig. 2 A–J. *Acanthacorydalis fruhstorferi* Weele —A. Male mandibles. —B. Male head, dorsal view. —C. Male pronotum. —D. Male genitalia, dorsal view. —E. Male ninth sternum, ventral view. —F. Male ninth gonostylus, ventral view. —G. Male tenth sternum, ventral view. —H. Male tenth tergum, ventral view. —I. Female genitalia, lateral view. —J. Female genitalia, dorsal view.

(CAU); 2♀♀, CHINA, Zhejiang, Anji, Longwangshan, 30°39′N, 119°41′E, 20 August 1995, Hong Wu (CAU); 1♀, CHINA, Zhejiang, Anji, Longwangshan, 30°39′N, 119°41′E, 27 August 1995 (CAU), Hong Wu; 1♀, CHINA, Zhejiang, Anji, Longwangshan, 30°39′N, 119°41′E, 27 August 1996, Hong Wu (CAU); 1♀, CHINA, Zhejiang, Anji, Longwangshan, 30°39′N, 119°41′E, 28 August 1996, Hong Wu (CAU); 1♀, CHINA, Zhejiang, Gutianshan, 29°16′N, 118°06′E, 28 July 1992, Hong Wu (CAU). 15♀♀, CHINA, Fujian, Chong-an, Xingcun, Sangang, 27°45′N, 117°40′E, 740 m, 14–15 July 1960, Yiran Zhang (IZCAS); 1♀, CHINA, Fujian, Chong-an, Xingcun, Tongmuguan, 27°45′N, 117°40′E, 850–970 m, 8 July 1960, Yiran Zhang (IZCAS); 1♀, CHINA, Fujian, Chong-an, Xingcun, Qiliqiao, 27°45′N, 117°40′E, 840 m, 12 July 1960, Youwei Zhang (IZCAS); 1♀, CHINA, Fujian, Shaowu, Tongmuguan, 27°45′N, 117°40′E, 28 July 1979, Linyao Wang (IZCAS); 1♀, CHINA, Guizhou, Jiangkou, Fanjingshan, 27°55′N, 108°41′E, 550 m, 11 July 1988, Xiaochun Zhang (IZCAS); 1♀, CHINA, Guizhou, Jiangkou, Fanjingshan, 27°55′N, 108°41′E, 530 m, 13 July 1988 (IZCAS), Xingke Yang; 1♀, CHINA, Guizhou, Jiangkou, Fanjingshan, 27°55′N, 108°41′E, 530 m, 13 July 1988, Shuyong Wang (IZCAS); 2♀♀, CHINA, Guangxi, Jinxiu, Linhaishanzhuang, 24°08′N, 110°11′E, 1000 m, 2 July 2000, Jun Chen (IZCAS); 1♂, CHINA, Jiangxi, Dayu, Neiliang, 25°23′N, 114°22′E, 550 m (IZCAS); 3♀♀, CHINA, Guangxi, Fangcheng, Banbaxiang, 21°37′N, 108°20′E, 250 m, 3 June 2000, Wenzhu Li (IZCAS); 3♀♀, CHINA, Guangxi, Fangcheng, Fulong, 21°37′N, 108°20′E, 500 m, 25 May 1999, Xuezhong Zhang (IZCAS); 1♀, CHINA, Fangcheng, Fulong, 21°37′N, 108°20′E, 350 m, 23 May 1999, Guoqing Zhang (IZCAS); 5♀♀, CHINA, Fangcheng, Fulong, 21°37′N, 108°20′E, 350 m, 23 May 1999, Wenzhu Li (IZCAS).

Diagnosis. Body colour almost black. Hemitergites of male ninth tergum with arched inner margins. Male tenth sternum with arched basal incision.

Description. Body length 67–105 mm; forewing length 68–95 mm, hindwing length 63–80 mm.

Head brownish black, with one indistinct reddish brown or yellowish brown spot before ocellar triangle, and some females with reticulate brownish marks on vertex. Compound eyes brown, ocelli yellow. Antennae black. Mouthparts blackish brown or reddish brown, bearing short yellowish setae; labrum sometimes yellow, galea yellow; male mandibles enlarged, with one large inner basal tooth, one small inner median tooth and one small inner apical tooth. Male gula with a pair of acute processes on anterolateral margins.

Thorax blackish brown; prosternum reddish brown or yellowish brown, with anterior margin and posterior margin black. Prothorax 2.0 (male) or 1.5 (female) times longer than wide at midlength. Setae on prothorax pale yellow; setae on meso- and metathorax dark yellow and long. Legs brown, with short dense golden setae; trochanters, bases of femora and inner surfaces of fore coxae dark yellow; tarsal claws dark red. Wings subhyaline; veins brown, with dark brownish marks bordering crossveins; Rs 9–11-branched, last one or two branches bifurcate distally, sometimes last three branches bifurcate; 7–10 crossveins between R_1 and Rs; M_{1+2} 2–3-branched; M_{3+4} 2-branched; 1A 2-branched.

Abdomen blackish brown, with dark yellowish setae. Male ninth tergum (Fig. 2D) dorsally divided into a pair of hemitergites, each with an arched inner margin; ninth sternum (Fig. 2E) suboval, with truncate posterior margin, its posterolateral lobes tapering toward tip; ninth gonostylus (Fig. 2F) short and clavate, and apically slightly incurved; tenth tergum (Fig. 2H) clavate, and apically curved outwards, with tip incised; tenth sternum (Fig. 2G) arcuate, with arched basal margin and shallow apical notch; lobes of tenth sternum digitiform, more than 1/2 length of lateral arm. Female tenth tergum (Fig. 2I, J) sagitally divided by anus, and with free semicircular ventral portion; gonocoxite valvate and membranous, with apical portion subquadrate; tip of gonostylus digitiform.

Distribution. China (Yunnan, Guizhou, Guangxi, Guangdong, Fujian, Jiangxi, Zhejiang); northern Vietnam.

Remarks. The body coloration of *A. fruhstorferi* is sometimes unusual; in this instance the head and thorax has yellowish marks. However, these marks are not so distinct as in *A. orientalis* or *A. unimaculata*. The species seems to be closely related to *A. sinensis* because of the dark body and wing coloration, but in *A. fruhstorferi* the male ninth tergum is dorsally divided into a pair of hemitergites and in *A. sinensis* it is entire, without a sagittal dorsal division.

Acanthacorydalis orientalis *McLachlan, 1899 (Figs 1B and 3).*
Corydalis orientalis McLachlan, 1899. Trans. Entomol. Soc. Lond. 1899 (3): 281. Type locality: China: Sichuan (Chia-Ting-Fu).
Acanthacorydalis kolbei Weele, 1907. Not. Leyden Mus. 28: 230. Type locality: China: Sichuan (Emei-Shan).

Material examined. 1♂, CHINA, Yunnan, Yanjin, 28°04′N, 104°16′E, 700 m, 8 June 1980, Guozhi Song (CAU); 1♂, CHINA, Yunnan, Yiliang, 27°37′N, 104°03′E, 1100 m, 16 June 1980, Zhengyu Luo (CAU); 1♂, CHINA, Sichuan, Qingchengshan, 30°58′N, 103°31′E, 23 May 1983, Youxin Zhao (CAU); 1♂, CHINA, Sichuan, Ya-an, 29°59′N, 102°59′E, May 1957 (CAU); 2♀♀, CHINA, Hubei, Shennongjia, Dayanwu, 31°45′N, 110°40′E, 29 June 1984, Xinli Wang (CAU); 1♀, CHINA, Hubei, Xingshan, Longmenhe, 31°14′N, 110°44′E, 18 June 1993, Jian Yao (CAU); 1♀, CHINA, Gansu, Wenxian, 32°39′N, 104°41′E, June 1964, Yao Zhou & Shaoyou Liu (CAU); 1♀, CHINA, Shaanxi, Foping, 33°32′N, 108°00′E, 17 July 1985, Fasheng Li (CAU); 1♂, CHINA, Shaanxi, Zhen-an, 33°26′N, 109°10′E, 30 May 1981 (CAU); 1♂, CHINA, Shanxi, Xiaoyi, Nanyao, 37°08′N, 111°48′E, 26 August 1949, Yao Zhou (CAU); 1♂ 1♀, CHINA, Henan, Songxian, Baiyunshan, 34°08′N, 112°05′E, 18 June 2001, Xiaocheng Shen (CAU); 1♀, CHINA, Henan, Huangshian, 33°40′N, 111°37′E, 16 June 1998, Xiaocheng Shen (CAU); 2♂♂, CHINA, Hebei, Xinglong, 40°24′N, 117°30′E, 20–30 June 1971 (CAU); 1♀, CHINA, Tianjin, Jixian, Mashenqiao, 40°02′N, 117°24′E, July 1975 (CAU); 1♀, CHINA, Beijing, Pinggu, 40°08′N, 117°07′E, 1976 (CAU). 1♂, CHINA, Sichuan, Emeishan, 29°32′N, 103°19′E, 600 m, 20 June 1955 (IZCAS); 1♀, CHINA, Sichuan, Qingchengshan, Tianshidong, 30°58′N, 103°31′E, 1000 m, 4 June 1979, Ping Gao (IZCAS); 1♀, CHINA, Sichuan, Qingchengshan, 30°58′N, 103°31′E, 1000 m, 2 June 1979, Jinwen Gao (IZCAS); 1♂, CHINA, Sichuan, Mianyang, 31°30′N, 104°42′E, May 1985 (IZCAS); 2♂♂, CHINA, Sichuan, Qingchengshan, Tianshidong, 30°58′N, 103°31′E, 23 May 1979, Ping Gao (IZCAS); 3♀♀, CHINA, Hubei, Shennongjia, Songluo, 900 m, 16–18 June 1981, Yinheng Han (IZCAS); 1♂, CHINA, Sichuan, Emeishan, Baoguosi, 29°32′N, 103°19′E, 550–750 m, 9 June 1957, Youcai Yu (IZCAS); 1♂, CHINA, Sichuan, Emeishan, Baoguosi, 29°32′N, 103°19′E, 550–750 m, 15 June 1957, Zongyuan Wang (IZCAS); 1♀, CHINA, Sichuan, Pengshui, 29°19′N, 108°10′E, 750 m, 9 July 1989, Long-long Yang (IZCAS); 1♂, CHINA, Hubei, Xuanen, 29°59′N, 109°28′E, 26 May 1989, Wenzhen Ma (IZCAS); 2♀♀, CHINA, Shannxi, Taibai, 34°04′N, 107°18′E, 1350 m, 11 July 1980, Yinheng Han (IZCAS); 3♀♀, CHINA, Shannxi, Liuba, Miaotaizi, 33°38′N, 106°57′E, 1470 m, 1 July 1999, Tongli He (IZCAS); 2♀♀, CHINA, Shannxi, Foping, 33°32′N, 108°00′E, 900 m, 27 June 1999, Yaojian (IZCAS); 1♀, CHINA, Shannxi, Foping, 33°32′N, 108°00′E, 900 m, 26 June 1999, Tongli He (IZCAS); 1♀, CHINA, Shannxi, Zhouzhi, Houshenzi, 34°10′N, 108°12′E, 1350 m, 24 June 1999, Chaodong Zhu (IZCAS); 1♀, CHINA, Shannxi, Taibai, Huangbaiyuan, 34°04′N, 107°18′E, 14 July 1980; 1♀, CHINA, Beijing, Baihuashan, 39°52′N, 115°36′E, 16 July 1973, Yinheng Han & Youqiao Liu (IZCAS).

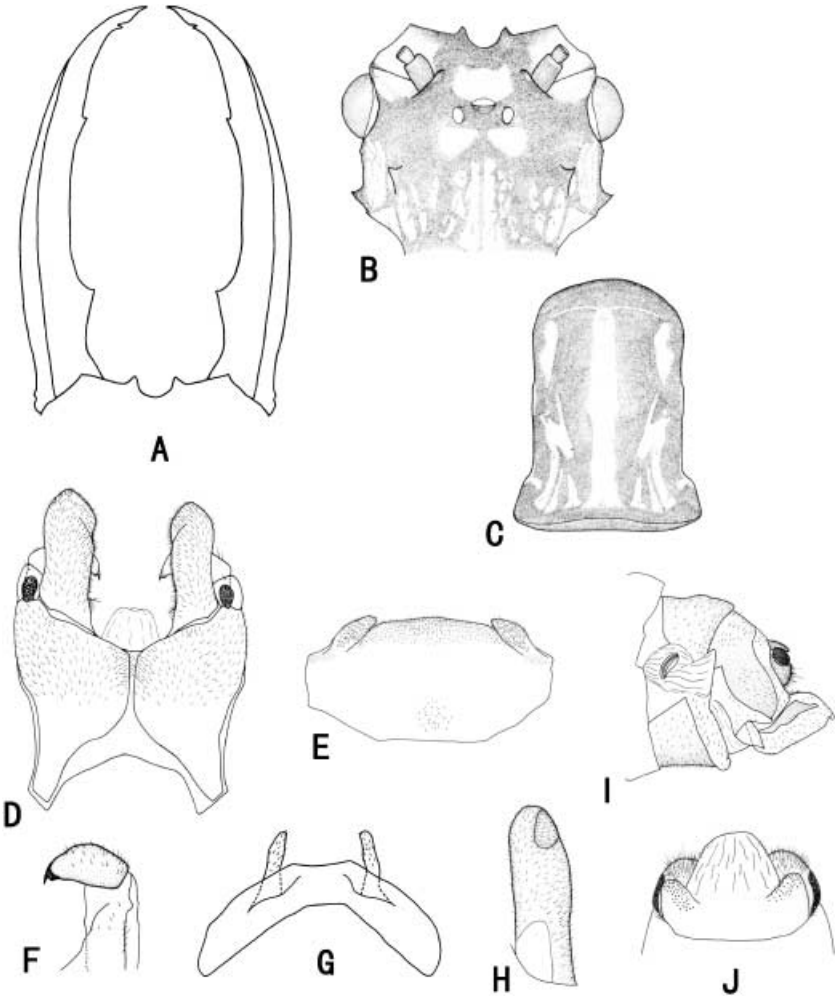

Fig. 3 A–J. *Acanthacorydalis orientalis* McLachlan. —A. Male mandibles. —B. Male head, dorsal view. —C. Male pronotum. —D. Male genitalia, dorsal view. —E. Male ninth sternum, ventral view. —F. Male ninth gonostylus, ventral view. —G. Male tenth sternum, ventral view. —H. Male tenth tergum, ventral view. —I. Female genitalia, lateral view. —J. Female genitalia, dorsal view.

Diagnosis. Body brownish black with distinct yellowish marks on head and prothorax. Head with one large yellowish spot before, and two large yellowish spots behind, ocellar triangle. Male ninth gonostylus clavate, extremely short and inflated near base of terminal sclerotized claw. Male tenth tergum clavate, slightly curved outwards apically, with feebly incised tip.

Description. Body length 51–83 mm; forewing length 70–81 mm, hindwing length 60–70 mm.

Head brownish black, with one large yellowish spot before, and two large yellowish spots behind, ocellar triangle; vertex and ventral surface with reticulate yellowish marks; anterolateral corners yellow. Compound eyes brown, ocelli yellow. Antennae blackish brown. Occiput yellow, dorsally with a pair of cuneate blackish marks near lateral margin and one blackish mark medially. Mouthparts reddish brown, bearing short yellowish setae; membrane between labrum and clypeus, galea and lacinia yellow, maxillary palpi black; male mandibles enlarged, with one large inner basal tooth, one small inner median tooth and one small inner apical tooth. Male gula with pair of acute processes on anterolateral margins.

Thorax blackish brown. Prothorax 2.0 (male) or 1.5 (female) times longer than wide at midlength. Pronotum with one comma-shaped yellowish spot near each anterolateral corner, followed by one long hook-shaped yellowish mark and with one longitudinal yellowish mark on lateral margin; central yellow mark spear-shaped, extending nearly to anterior margin, and with pair of triangular marks basally; posterolateral portion yellow, slightly elevated. Prosternum with pair of small yellowish spots on anterior margin and two yellowish spots on lateral margin. Mesonotum with one or two yellowish spots on anterior margin. Setae on prothorax pale yellow; setae on meso- and metathorax dark yellow and long. Legs blackish brown, with dense short golden setae; trochanters, bases of femora and inner surfaces of fore coxae dark yellow; tarsal claws dark red. Forewings

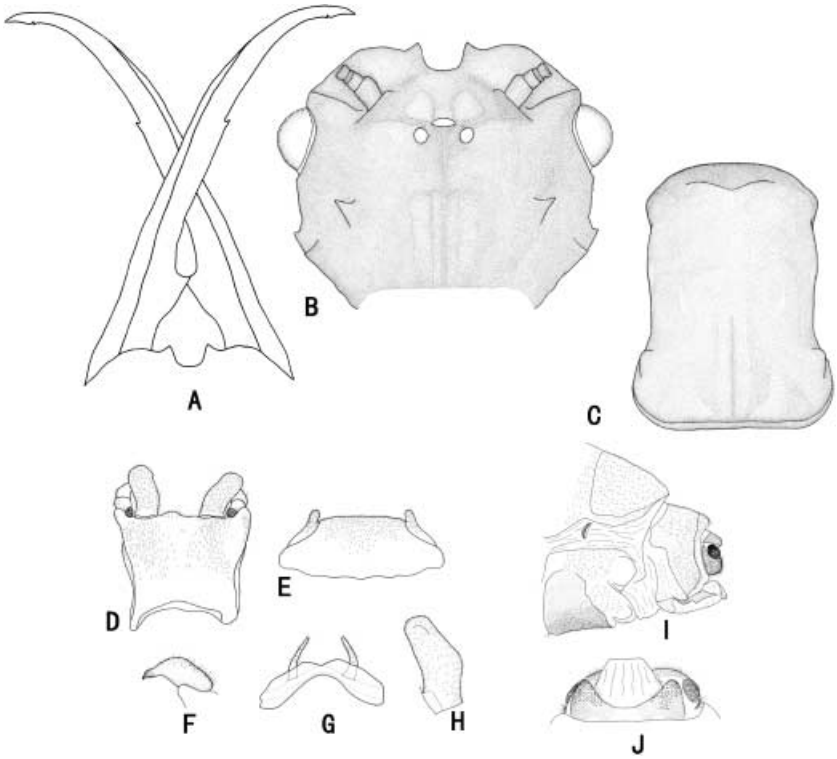

Fig. 4 A–J. *Acanthacorydalis sinensis* Yang & Yang. —A. Male mandibles. —B. Male head, dorsal view. —C. Male pronotum. —D. Male genitalia, dorsal view. —E. Male ninth sternum, ventral view. —F. Male ninth gonostylus, ventral view. —G. Male tenth sternum, ventral view. —H. Male tenth tergum, ventral view. —I. Female genitalia, lateral view. —J. Female genitalia, dorsal view.

pale brown; veins blackish brown, with brownish marks bordering crossveins; Rs 8–10-branched, last branches bifurcate; 5–9 crossveins between R_1 and Rs; M_{1+2} and M_{3+4} 2-branched, 1A 2-branched. Hindwings almost hyaline, without distinct brownish marks.

Abdomen blackish brown with dorsal surface dark yellow, bearing short dark yellow setae. Male ninth tergum (Fig. 3D) dorsally divided into a pair of hemitergites, and with V-shaped basal notch; ninth sternum (Fig. 3E) suboval, with shallowly arcuate posterior margin, and its posterolateral lobes tapering toward tip; ninth gonostylus (Fig. 3F) clavate and extremely short, inflated near base of terminal sclerotized claw, apically slightly incurved; tenth tergum (Fig. 3H) clavate, apically slightly curved outwards with shallowly incised tip; tenth sternum (Fig. 3G) arcuate, with trapezoid basal incision and shallow apical incision; lobes of tenth sternum digitiform, less than 1/2 length of lateral arm. Female tenth tergum (Fig. 3I,J) sagitally divided by anus, with semicircular ventral portions; gonocoxite valvate and membranous with subquadrate apical portion; tip of gonostylus digitiform.

Distribution. China: Yunnan, Sichuan, Hubei, Fujian, Shaanxi, Shanxi, Henan, Hebei, Tianjin, Beijing.

Remarks. This species was established by McLachlan (1899) based on a specimen from Sichuan, China. *Acanthacorydalis kolbei* Weele, 1907 was synonymized under *A. orientalis* by Banks (1940). In all specimens examined the pattern of the marks on the head and prothorax corresponds to the original description of *A. kolbei*. The pattern of the marks on the prothorax in *A. orientalis*, as recorded in original description, was not found, so McLachlan's type might be aberrant.

Acanthacorydalis sinensis *Yang & Yang, 1986 (Figs 1C and 4).* *Acanthacorydalis sinensis* Yang & Yang, 1986. Entomotaxonomia 8 (1–2): 86. Type locality: China: Guangxi (Jinxiu).

Material examined. Holotype ♂, allotype 1♀, CHINA, Guangxi, Jinxiu, 24°08′N, 110°11′E, 720 m, 10 June 1982, Fasheng Li (CAU); paratypes 2♀♀, CHINA, Guangxi, Jinxiu, 24°08′N, 110°11′E, 720 m, 10 June 1983, Xinli Wang (CAU). Other material: 1♀, CHINA, Guizhou, Fanjingshan, 27°55′N, 108°41′E (CAU); 1♀, CHINA, Guangdong, Chebaling, 24°58′N, 114°02′E, 19–21 April 2002 (CAU).

Diagnosis. Body slightly flattened; colour almost black. Male ninth tergum complete, not sagitally divided, with shallowly arcuate basal incision.

Description. Body length 78–100 mm; forewing length 89–91 mm, hindwing length 80–81 mm.

Head black, with one indistinct reddish brown spot before ocellar triangle. Compound eyes pale yellowish brown, ocelli pale yellow. Antennae black. Mouthparts reddish brown, bearing short dark yellow setae; male mandibles enlarged, with one large inner basal tooth, one small inner median tooth and one small inner apical tooth. Male gula with a pair of acute processes on anterolateral margins.

Thorax blackish brown; pronotum dark reddish brown, sometimes with several small orange spots near anterolateral corners and lateral margin. Prothorax 1.4 (male) or 1.1 (female) times longer than wide at midlength. Setae on prothorax pale yellow; setae on meso- and metathorax dark yellow and long. Legs brown, with short dense yellowish setae; trochanters, bases of femora dark yellowish brown; tarsal claws dark red. Wings subhyaline; veins blackish brown, with dark brownish marks bordering crossveins; Rs 11 branched, last two branches bifurcate; 7–9 crossveins between R_1 and Rs; M_{1+2} 2–4-branched; M_{3+4} 2–3-branched; 1A 2-branched.

Abdomen blackish brown, bearing dark yellowish setae. Male ninth tergum (Fig. 4D) complete, not sagitally divided, with shallowly arcuate basal incision; ninth sternum (Fig. 4E) suboval, and its posterolateral lobes rounded at tip; ninth gonostylus (Fig. 4F) clavate and short, apically moderately incurved, with a terminal sclerotized claw; tenth tergum (Fig. 4H) clavate, apically curved outwards, with slightly incised tip; tenth sternum (Fig. 4G) arcuate with U-shaped basal incision; lobes of tenth sternum digitiform, more than 1/2 length of lateral arm. Female tenth tergum (Fig. 4I, J) dorsally divided by anus, with semicircular ventral portion; gonocoxite valvate and membranous with subquadrate apical portion; tip of gonostylus digitiform.

Distribution. China: Guangxi, Guangdong, Guizhou.

Remarks. This species seems to be closely related to *A. fruhstorferi* because of its large body size and dark body coloration. In addition, it is very difficult to distinguish females of these two species from each other by morphological characters. However, males can be easily distinguished by the complete male ninth tergum, while in *A. fruhstorferi* the male ninth tergum is dorsally divided into a pair of hemitergites.

Acanthacorydalis unimaculata *Yang & Yang, 1986 (Figs 1D and 5).* *Acanthacorydalis unimaculata* Yang & Yang, 1986. Entomotaxonomia 8 (1–2): 85. Type locality: China: Guangxi (Guilin).

Material examined. Holotype ♂, paratypes 3♂♂, CHINA, Guangxi, Guilin, 25°17′N, 110°17′E, 150 m, 8 June 1984, Ding Yang (CAU); allotypes 1♀, paratypes 8♀♀, CHINA, Guangxi, Lingchuan, Longkou, 22°40′N, 109°45′E, 250 m, 5 June 1984, Ding Yang (CAU); allotypes 1♂, 3♀♀, CHINA, Guangxi, Lingchuan, Longkou, 22°40′N, 109°45′E, 250 m, 5 June 1984, Fasheng Li (CAU); allotypes 6♂♂, 5♀♀, CHINA, Zhejiang, Lishui, 28°27′N, 119°54′E, 18–23 June 1982, Huizhen Chen (CAU); paratypes 2♀♀, CHINA, Guangxi, Jinxiu, 24°08′N, 110°11′E, 11 June 1982, Jikun Yang (CAU); paratypes 1♂, 1♀, CHINA, Zhejiang, Lin-an, Hongling, 30°14′N, 119°43′E, 23 May 1981, Jinzhang Chen (CAU); paratype 1♀, CHINA, Guizhou, Sinan, 27°57′N, 108°14′E, 30 August 1974 (CAU); paratypes 1♂, 1♀, CHINA, Fujian, Shaowu, 27°20′N, 117°29′E, 23 May 1965, Shengli Liu (CAU). Other material: 1♂, CHINA, Guangxi, Baise, 24°18′N, 106°14′E, 27 May 1982, Jikun Yang (CAU); 1♂, 1♀, CHINA, Guizhou, Luodian, 25°25′N, 106°44′E, 500–1000 m, 5 June 1981, Fasheng Li (CAU); 1♂, 14♀♀, CHINA, Guangdong, Chebaling, 24°58′N, 114°02′E, 19–21 April 2002 (CAU). 1♂, CHINA, Guangxi, Jinxiu, Luoxiang, 24°08′N, 110°11′E, 400 m, 15 May 1999, Dajun Liu (IZCAS); 1♀, CHINA, Guangxi, Jinxiu, Luoxiang, 24°08′N, 110°11′E, 400 m, 15 May 1999, Mingyuan Gao (IZCAS); 1♀, CHINA, Guangxi, Jinxiu, Luoxiang, 24°08′N, 110°11′E, 400 m, 15 May 1999, Xuezhong Zhang (IZCAS); 1♂, CHINA, Guangxi, Jinxiu, Shengtangshan, 24°08′N, 110°11′E, 900 m, 17 May 1999, Xuezhong Zhang (IZCAS); 1♀, CHINA, Guangxi, Xing-an, 25°37′N, 110°40′E, 5 June 1984 (IZCAS); 1♀, CHINA, Guangdong, Lianping, 24°21′N, 114°29′E, 16 May 1973 (IZCAS); 2♀♀, CHINA, Guizhou, Leishan, 26°22′N, 108°03′E, 900 m, 28 June 1988, Decheng Yuan (IZCAS); 1♀, CHINA, Jiangxi, Xinfeng, 27°07′N, 116°12′E, May 1980 (IZCAS); 2♀♀, CHINA, Zhejiang, Tianmushan, 30°26′N, 119°34′E, 9 June 1964 (IZCAS); 1♂, CHINA, Zhejiang, Moganshan, 30°37′N, 119°51′E, 10 June 1937 (IZCAS); 1♂, CHINA, Anhui, 1 July 1977 (IZCAS).

Diagnosis. Body brownish black with distinct yellowish marks on head and prothorax. Head with one large yellowish spot before, and without any spot behind, ocellar triangle. Apical half of male mandibles with only one small apical tooth and without median tooth. Male ninth gonostylus clavate and very short, with inflated middle portion. Male tenth tergums clavate, apically inflated and curved outwards. Male tenth sternum arcuate, with deep arcuate incision basally.

Description. Body length 55–82 mm; forewing length 57–78 mm, hindwing length 50–70 mm.

Head brownish black, with one large yellowish spot before ocellar triangle; vertex and ventral surface with reticulate yellowish marks. Compound eyes brown, ocelli yellow. Antennae blackish brown. Occiput yellow, dorsally with a pair of cuneiform blackish marks near lateral margin and one blackish mark medially. Mouthparts reddish brown, bearing short yellowish setae; galea, lacinia and membrane between

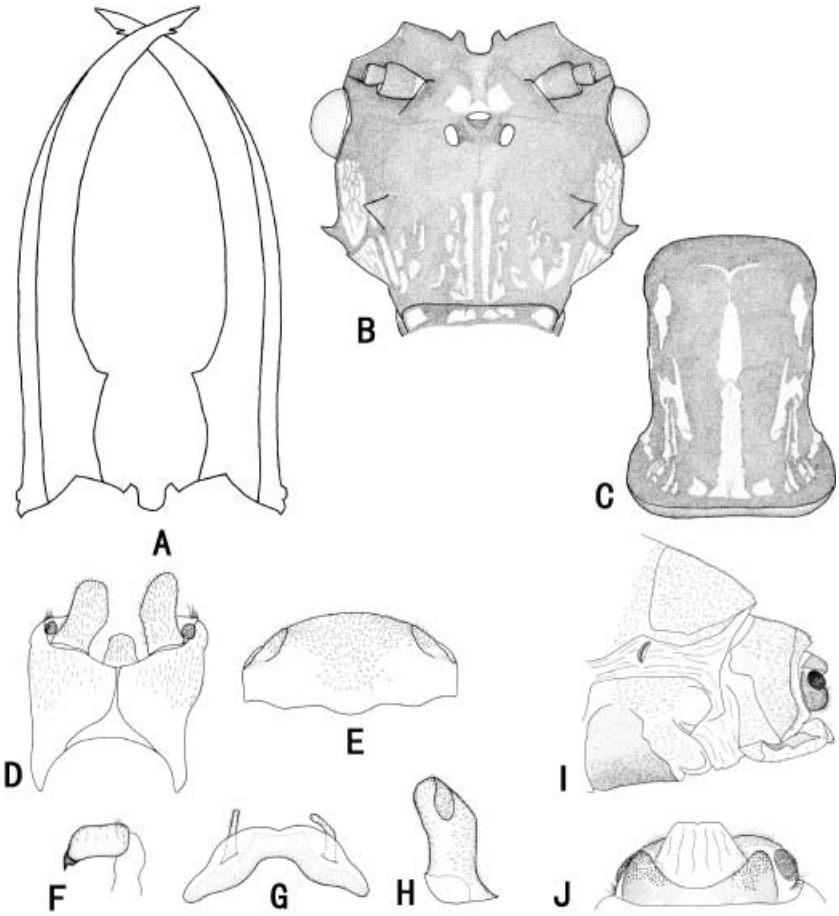

Fig. 5 A–J. *Acanthacorydalis unimaculata* Yang & Yang. —A. Male mandibles. —B. Male head, dorsal view. —C. Male pronotum. —D. Male genitalia, dorsal view. —E. Male ninth sternum, ventral view. —F. Male ninth gonostylus, ventral view. —G. Male tenth sternum, ventral view. —H. Male tenth tergum, ventral view. —I. Female genitalia, lateral view. —J. Female genitalia, dorsal view.

labrum and clypeus yellow, maxillary palpi black; male mandibles enlarged, with one large inner basal tooth and one small inner apical tooth. Male gula with a pair of acute processes on anterolateral margins.

Thorax blackish brown, but sometimes male prosternum yellow. Prothorax 2.0 (male) or 1.5 (female) times longer than wide at midlength. Pronotum with one comma-shaped yellowish spot near each anterolateral corner, followed by one long hook-shaped yellowish mark and one longitudinal yellowish mark on lateral margin; central mark cuneiform, extending nearly to anterior margin, and with a pair of triangular marks basally; posterolateral portion yellow, slightly elevated. Prosternum with two small yellowish spots on anterior margin and each lateral margin, and also with a pair of subquadrate yellowish marks on lateral margin. Mesonotum with two oval yellowish spots on anterior margin. Setae on prothorax pale yellow; setae on meso- and metathorax dark yellow and long. Legs blackish brown, with short dense golden setae; trochanters, bases of femora and inner surfaces of fore coxae yellow; tarsal claws dark red. Forewings pale brown; veins blackish brown, with distinct brownish marks bordering crossveins; Rs 8–10-branched, last branches bifurcate; 5–12 crossveins between R_1 and Rs; M_{1+2} and M_{3+4} 2-branched; 1A 2-branched. Hindwings much lighter than forewings, with basal half almost hyaline.

Abdomen blackish brown with dorsal surface dark yellow, bearing short dark yellow setae. Male ninth tergum (Fig. 5D) dorsally divided into a pair of hemitergites, and with a V-shaped basal incision; ninth sternum (Fig. 5E) suboval with arcuate posterior margin, its posterolateral lobes tapering toward tip; ninth gonostylus (Fig. 5F) clavate and very short, inflated near base of terminal sclerotized claw, and apically slightly incurved; tenth tergum (Fig. 5H) clavate, its apical portion apparently curved outwards with slightly incised tip; tenth sternum (Fig. 5G) arcuate, with semicircular basal incision and shallow apical incision; lobes of tenth sternum digitiform, more than 1/2 length of lateral arm. Female tenth tergum (Fig. 5I,J) sagitally divided by anus, with separate semicircular ventral portion; gonocoxite valvate and membranous, with subtriangular apical portion; tip of gonostylus digitiform.

Distribution. China: Guizhou, Guangxi, Guangdong, Jiangxi, Fujian, Zhejiang, Anhui.

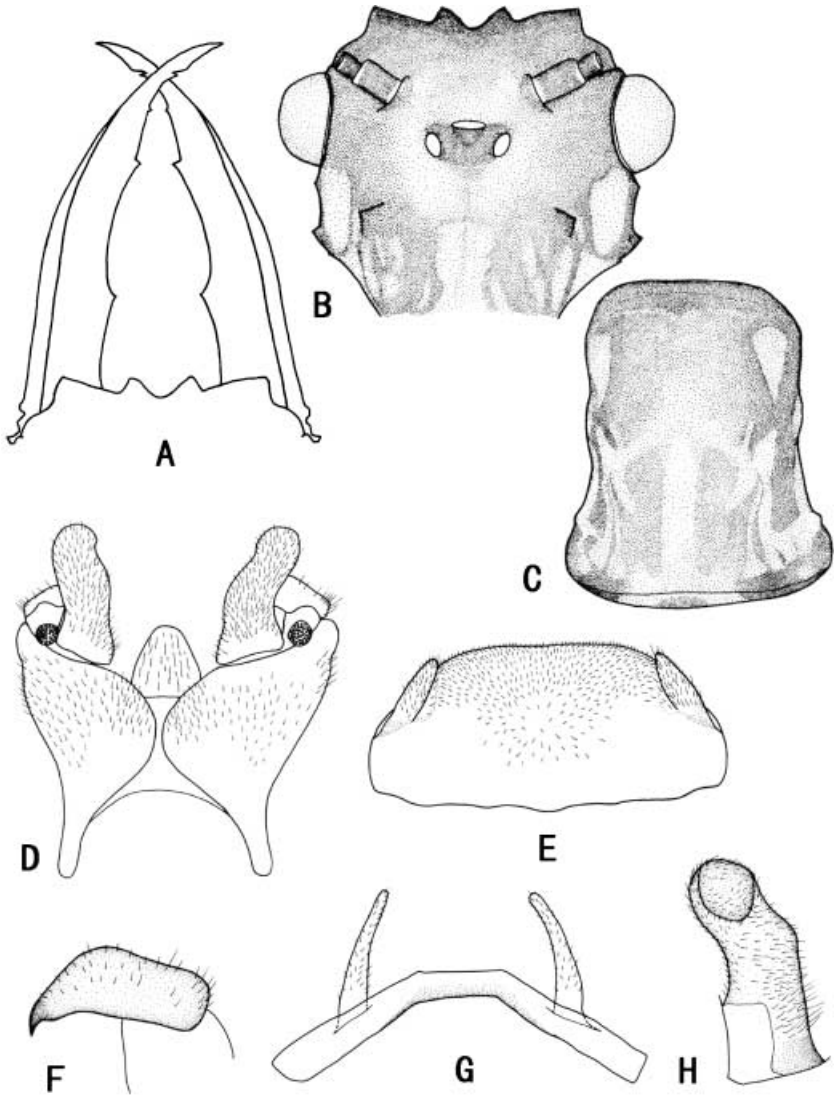

Fig. 6 A–H. *Acanthacorydalis yunnanensis* Yang & Yang. —A. Male mandibles. —B. Male head, dorsal view. —C. Male pronotum. —D. Male genitalia, dorsal view. —E. Male ninth sternum, ventral view. —F. Male ninth gonostylus, ventral view. —G. Male tenth sternum, ventral view. —H. Male tenth tergum, ventral view.

Remarks. This species is distinguished from other *Acanthacorydalis* species by the male mandibles having no median tooth, the marks on the head, the shape of the male tenth sternum, and the subtriangular female gonocoxite.

Acanthacorydalis yunnanensis *Yang & Yang, 1988 (Figs 1E and 6).* *Acanthacorydalis yunnanensis* Yang & Yang, 1988. Zoological Research 9 (1): 45. Type locality: China: Yunnan (Jingdong).

Material examined. Holotype ♂, CHINA, Yunnan, Jingdong, 24°26′N, 100°50′E, 1170 m, 31 May 1956 (IZCAS).

Diagnosis. Relatively small body size. Body brown with distinct yellowish marks on head and prothorax. Apical half of male mandibles with three small teeth: median tooth, subapical tooth and apical tooth. Male tenth sternum with trapezoidal basal incision.

Description. Body length 48 mm; forewing length 57 mm, hindwing length 51 mm.

Head brown, with reticulate yellowish marks on vertex and a large yellowish circular spot around ocellar triangle; ventral surface yellow, with one brownish vitta near each lateral margin. Compound eyes brown, ocelli yellow. Antennae with blackish brown scape and pedicel, flagellum colour unknown (flagella lost in unique holotype). Mouthparts blackish brown, bearing dark short yellowish setae; labrum and maxilla mostly yellow; male mandibles enlarged, with one large inner basal tooth, one small inner median tooth, one small inner subapical tooth and one small inner apical tooth. Male

gula T-shaped, without acute processes on anterolateral margins.

Thorax brown. Prothorax 1.5 times longer than wide at midlength in male. Pronotum with one comma-shaped yellowish spot near antero-lateral margin, followed by one long hook-shaped yellowish mark and one longitudinal yellowish mark on lateral margin; central mark umbrella-shaped with a pair of triangular spots basally; posterolateral portion yellow, slightly elevated. Prosternum with anterior and posterior margins brown and with two dark yellowish spots, which extend toward each other. Meso- and metathorax brown with dark black lateral margins; mesonotum with two oval yellowish spots on anterior margin. Setae on prothorax pale yellow; setae on meso- and metathorax dark yellow and long. Legs brown, with reddish brown setae on fore and middle legs, but with yellowish setae on hind leg; trochanters, bases of femora and inner surfaces of fore coxae yellow; tarsal claws dark red. Forewings pale brown; veins pale brown, with indistinct brownish marks on crossveins; Rs 9-branched, last branches bifurcate; 6–8 crossveins between R_1 and Rs; M_{1+2} and M_{3+4} 2-branched; 1A 2-branched. Hind wings hyaline, with anterior margin and tip pale brown.

Abdomen brown with short dark yellow setae. Male ninth tergum (Fig. 6D) dorsally divided into a pair of hemitergites, and with a V-shaped basal notch; ninth sternum (Fig. 6E) suboval, with posterior margin almost truncate, and its posterolateral lobes tapering toward tip; ninth gonostylus (Fig. 6F) clavate and moderately elongated, and apically slightly incurved, with a terminal sclerotized claw; tenth tergum (Fig. 6H) clavate, apically contracted and apparently curved outwards, with incised tip; tenth sternum (Fig. 6G) arcuate, with trapezoidal basal incision and shallow arcuate apical incision; lobes of tenth sternum digitiform, longer than 1/2 of lateral arm.

Female. Unknown.

Distribution. China (Yunnan).

Remarks. Specimen of this species is the smallest of the five Chinese species of *Acanthacorydalis* and it is distinguished by the shape of the marks on head and prothorax, by the male mandibles with four teeth, the moderately elongate male ninth gonostylus, and by the structure of the male tenth sternum.

Cladistic analysis

Having closely examined many morphological features of the head, thorax and abdomen, we found 17 characters which are informative in a phylogenetic analysis of the Chinese *Acanthacorydalis* (see Appendix 1). *Corydalus crossi* Contreras-Ramos was selected as the outgroup because it belongs to the New World lineage which was the sister of the *Neuromus* lineage, and its genitalia retain some features apparent in *Acanthacorydalis* (Contreras-Ramos 2002; Glorioso 1981). *Neoneuromus ignobilis* Navás was chosen as another outgroup because it belongs to the lineage which was sister to *Acanthacorydalis* in the hypothesis proposed by Contreras-Ramos (1998). The character state matrix is given in Table 1.

The cladistic analysis produced four equally parsimonious trees (L = 22, Ci = 86, Ri = 76). The strict consensus tree is shown in Fig. 7. In the cladogram the five Chinese *Acanthacorydalis* species form a monophyletic group which is well supported by characters 1, 6, 8, 11, and 13. Within this group, *A. fruhstorferi* and *A. sinensis* form a monophyletic group based on their dark head and prothorax without distinct light marks, while character 14: 1 is derived in parallel in this subclade and *A. unimaculata*. The relationship among the three species, *A. orientalis*, *A. unimaculata*, and *A. yunnanensis*, is

Table 1 Character state distribution of characters used in cladistic analysis.

	Characters
	1
Taxa	0 1 2 3 4 5 6 7 8 9 0 1 2 3 4 5 6
C. crossi	1 0 1 1 0 0 0 1 0 1 0 0 0 0 0 1 0
N. ignobilis	0 0 0 0 0 0 0 0 0 0 ? 0 0 0 0 0 0
A. fruhstorferi	2 1 1 0 0 0 1 2 1 1 0 1 0 1 1 0 0
A. orientalis	1 1 1 0 0 0 1 1 1 1 1 1 1 0 0 0 1
A. sinensis	2 1 1 0 0 0 1 2 1 0 ? 1 0 1 1 0 0
A. unimaculata	1 1 1 0 1 0 1 1 1 1 1 1 1 1 1 0 0
A. yunnanensis	1 1 1 0 0 1 1 1 1 1 0 1 0 1 0 0 0

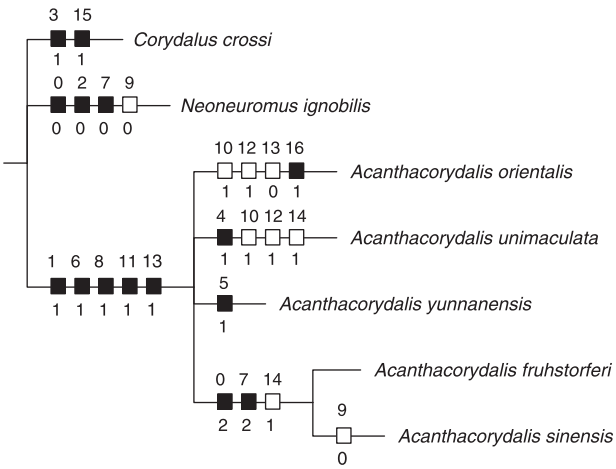

Fig. 7 Strict consensus of four most parsimonious trees of Chinese *Acanthacorydalis* species (L = 22, Ci = 86, Ri = 76). Numbers above squares correspond to characters as described in the text; numbers below squares correspond to states. Synapomorphies (■), parallelism (□).

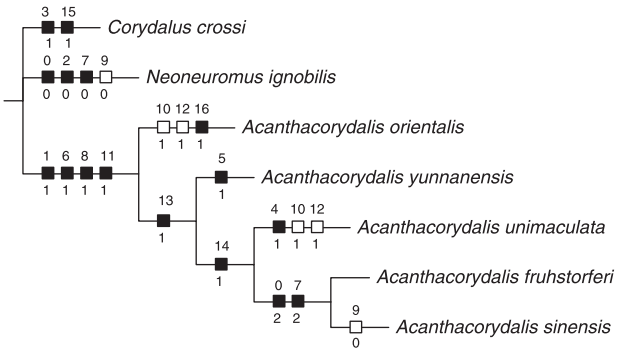

Fig. 8 Most parsimonious tree of Chinese *Acanthacorydalis* species reflecting geographical distribution.

unresolved. However, one of the four most parsimonious trees (Fig. 8) is felt to be better in that it reflects the geographical distributions of the five species.

Discussion

Phylogenetic considerations

The monophyly of the genus *Acanthacorydalis* is well supported by the following five characters: (1) the well developed spines on the vertex of the head; (2) the female mandible equal in length to the head; (3) the costal crossveins of the forewings reticulate medially; (4) the presence of posterolateral lobes on the male ninth sternum, and (5) the apically outcurved male tenth tergum.

Other characters that support monophyly in Penny's (1993) review are somewhat doubtful. For instance, the enlarged male mandibles, which are also present in most *Corydalus* species, and the posterolateral lobes and the setiferous lateral protuberances could be the same character (character 11).

The five Chinese species can be easily divided into two groups based on body coloration, the first with light marks and the second dark coloured. In the cladistic analysis the relationships of the first group are unresolved. An explanation for this might be that the group represents a clade of closely related species; alternatively, it may be simply a basal paraphyletic group 'unified' by symplesiomorphies.

The few morphological characters which can be used in the analysis might be another explanation for this result. The reason for there being so few useful characters might be the fact that the structure of the male genitalia is so similar among different species in the genus. The morphological similarity in male genitalia can be found in other megalopteran insects, and this phenomenon has been explained by Contreras-Ramos (1998).

In addition, the position of the three species not found in China is difficult to define because their types are not accessible. Useful genitalic characters of these species have not been clearly described or illustrated. *A. asiatica* (Wood-Mason) seems to be closely related to *A. horrenda* Navás in having a remarkably similar pattern of marks on the head and prothorax and a similar male genitalic structure. In addition, the basal tooth of the male mandible is also feebly developed in both species. Both type localities are in the Naga Hills in north-eastern India. Therefore, *A. horrenda* might be the same species as *A. asiatica*.

A. imperatrix Navás was established only from one female specimen from Vietnam. According to its original description, it appears to be closely related to *A. fruhstorferi* and *A. sinensis* because of the dark body coloration and large body size. In the original illustration, *A. imperatrix* has some yellowish marks on the vetex of the head, like the unusual individuals of *A. fruhstorferi*. Hence, there might be some synonyms within the three species.

From the foregoing, it would appear that in order to obtain better supported phylogenetic relationships of all the *Acanthacorydalis* species the following conditions should be fulfilled: (1) proof of the validity of the dubious species; (2) substantiation of full membership in the genus, and (3) provision of a stronger basis for a phylogenetic analysis, especially the addition of molecular and morphological data of immature animals.

Biogeographical considerations

Most *Acanthacorydalis* species are mainly distributed in the Oriental realm, in China, Vietnam and north-eastern India. It has not been recorded from the major islands such as Taiwan, Hainan and Indonesia. The majority of species are found in southern China, and four (*A. orientalis*, *A. unimaculata*, *A. sinensis*, and *A. yunnanensis*) are endemic to China.

Southern China can be subdivided into three regions: south-west, central and south (Zhang 1998). Four species — *A. unimaculata*, *A. orientalis*, *A. fruhstorferi*, and *A. sinensis* — are distributed in the central region. Three of these are also distributed in the south. *A. orientalisis* is also associated with the south-west and is the only species that extends northward into the Palaearctic realm. *A. fruhstorferi* also occurs in Vietnam. *A. orientalis* and *A. unimaculata* are widely distributed, while *A. fruhstorferi* and *A. sinensis* are relatively narrowly distributed. *A. yunnanensis* is recorded in only one locality from Yunnan (Jingdong) in the south.

Penny (1993) hypothesized a Gondwanan distribution to explain the distributional pattern of Megaloptera. According to this, the five Asian genera of Corydalinae originated from a single ancestor or multiple ancestors in the Indian subcontinent as it drifted northward. The distributional pattern of the Chinese *Acanthacorydalis* species, and the most parsimonious tree shown in Fig. 8, appears to support this theory. This suggests that the genus might have originated in north-eastern India or south-western China, where the

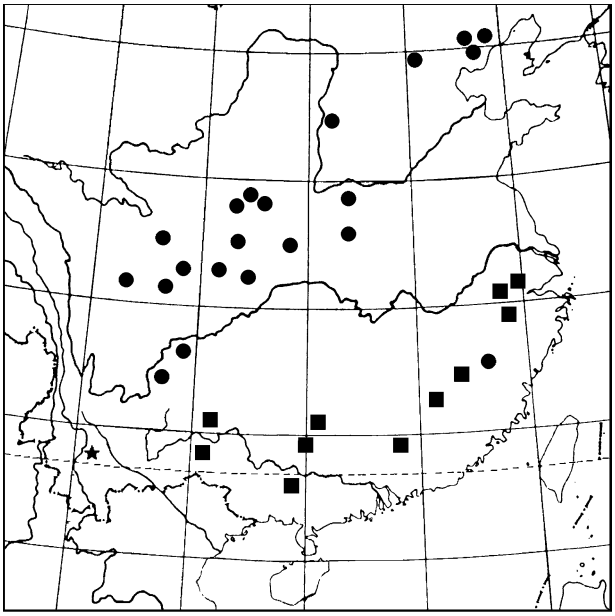

Fig. 9 Distribution of *A. orientalis* (●), *A. unimaculata* (■) and *A. yunnanensis* (★), showing the pattern from north-eastern India, through south-western and central China to north China.

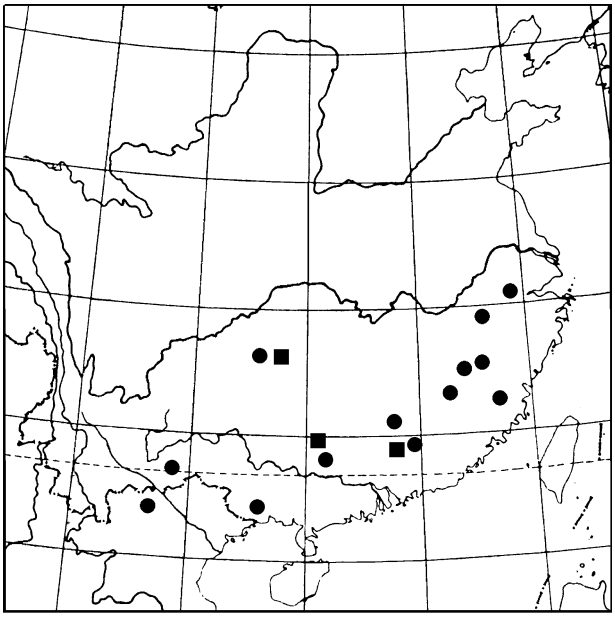

Fig. 10 Distribution of *A. fruhstorferi* (●) and *A. sinensis* (■), showing the pattern from south China and northern Vietnam to central China.

ancestral species *A. orientalis*, and its probable close relatives (*A. asiatica* and *A. horrenda*) are distributed.

Two main distribution patterns have been established in the present study, based on the cladogram shown in Fig. 8. The first extends from south China and northern Vietnam to central China, the second from north-eastern India, through south-western and central China to north China (Figs 9, 10). Taiwan and Hainan have been joined to the Chinese mainland many times over historical time, through episodic lowering of sea levels. The absence of the genus from these islands suggests that *Acanthacorydalis* might not be adapted to the current climates of these islands. Its absence from southern and central India may be due to vicariance caused by the collision between the Indian subcontinent and Eurasia, so that modern species have not been reintroduced since the extinction of their ancestor.

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Appendix 1

Characters and character states employed in the cladistic analysis of the Chinese *Acanthacorydalis* species. Character states were scored 0–2, ? (0 = plesiomorphic state, 1–2 = apomorphic state, ? = state inapplicable).

0 *Head*, *coloration*. (0) Pale yellow, with distinct dark marks (Liu & Yang 2004: 149, fig. 1). (1) Dark, with distinct light marks (Figs 3B, 5B, 6B). (2) Almost dark, without distinct light marks (Figs 2B and 4B). *Comments:* in *Neoneuromus ignobilis* the coloration of the head is pale yellow with distinct dark marks near the lateral margins. *Corydalus crossi*, *A. orientalis*, *A. unimaculata* and *A. yunnanensis* have distinct light marks on the dorsal surface of the head. However, in *A. fruhstorferi* and *A. sinensis* the light marks are absent.

1 *Head*, *spines on vertex*. (0) Absent (Liu & Yang 2004: 149, fig. 1). (1) Present (Figs 2B, 3B, 4B, 5B, 6B). *Comments:* all of the *Acanthacorydalis* species have a pair of spines on the vertex, while in *Neoneuromus*, *Corydalus*, and the other genera of Corydalinae, the vertexal spines are absent.

2 *Male mandible*, *modification in length*. (0) Not enlarged (Liu & Yang 2004: 149, fig. 1). (1) Enlarged (Figs 2A, 3A, 4A, 5A, 6A; Contreras-Ramos 2002: 57, fig. 5). *Comments:* the male mandible is not enlarged in *N. ignobilis*, but is in *C. crossi* and the five Chinese *Acanthacorydalis* species.

3 *Male mandible*, *inner basal tooth*. (0) Acute (Figs 2A, 3A, 4A, 5A, 6A). (1) Blunt (Contreras-Ramos 2002: 57, fig. 5). *Comments:* in *N. ignobilis* and the five Chinese *Acanthacorydalis* species the male mandible has a large acute basal tooth while in *C. crossi* the inner basal tooth of the male mandible is blunt, showing a degree of reduction.

4 *Male mandible*, *median tooth*. (0) Present (Figs 2A, 3A, 4A, 6A; Contreras-Ramos 2002: 57, fig. 5). (1) Absent (Fig. 5A). *Comments:* the median tooth is the second tooth from the base of the mandible. In the two outgroup and four of the Chinese *Acanthacorydalis* species the median tooth is present; the exception is *A. unimaculata*.

5 *Male mandible*, *subapical tooth*. (0) Absent (Figs 2A, 3A, 4A, 5A; Contreras-Ramos 2002: 57, fig. 5). (1) Present (Fig. 6A). *Comments:* the subapical tooth is between the median and apical tooth. It is only present in *A. yunnanensis*. It is absent in *N. ignobilis*, *C. crossi* and the other four Chinese *Acanthacorydalis* species.

6 *Female mandible*, *length*. (0) Less than 3/4 the length of the head. (1) Equal to the length of the head. *Comments:* in the five Chinese *Acanthacorydalis* species the female mandibles are equal to the length of the head, while in *N. ignobilis* and *C. crossi* they are much shorter and less than 3/4 the length of the head.

7 *Pronotum*, *coloration*. (0) Pale yellow, with distinct dark vittae (Liu & Yang 2004: 149, fig. 1). (1) Dark, with distinct light marks (Figs 3B, 5B, 6B). (2) Almost dark, without distinct light marks (Figs 2B, 4B). *Comments:* in *N. ignobilis* the coloration of the pronotum is pale yellow with distinct dark vittae near the lateral margins of the prothorax. *C. crossi*, *A. orientalis*, *A. unimaculata* and *A. yunnanensis* have distinct light marks on the prothorax; these are absent in *A. fruhstorferi* and *A. sinensis*.

8 *Forewing*, *costal crossveins*. (0) Parallel (Glorioso 1981: 260, fig. 21; Contreras-Ramos 2002: 57, fig. 5). (1) Recticulate medially (Fig. 1). *Comments:* in *N. ignobilis* and *C. crossi* the costal crossveins of the forewings are parallel, while in the five Chinese *Acanthacorydalis* species the costal crossveins of the forewings are recticulate medially.

9 *Male genitalia*, *shape of ninth tergum*. (0) Sagitally divided into a pair of hemitergites (Figs 2D, 3D, 5D, 6D; Contreras-Ramos 2002: 66, fig. 22). (1) Complete, not sagitally divided into a pair of hemitergites (Fig. 4D; Liu & Yang 2004: Fig. 2). *Comments:* most *Acanthacorydalis* species have the ninth tergum sagitally divided into a pair of hemitergites, as well as *C. crossi*. In *N. ignobilis* and *A. sinensis*, the ninth tergum is complete.

10 *Male genitalia*, *inner margin of ninth hemitergite*. (0) Arched (Figs 2D, 6D). (1) Nearly trapezoidal (Figs 3D, 5D). *Comments:* in *C. crossi*, *A. fruhstorferi* and *A. yunnanensis* the inner margin of the hemitergum is arched, while in *A. orientalis* and *A. unimaculata* it is nearly trapezoidal.

11 *Male genitalia*, *ninth sternum*. (0) Without the posterolateral lobes (Liu & Yang 2004: 149, fig. 3; Contreras-Ramos 2002: 66, fig. 23). (1) With a pair of posterolateral lobes. *Comments:* in the two outgroups the male ninth sternum has no posterolateral lobes while in the five Chinese *Acanthacorydalis* species these lobes are present.

12 *Male genitalia*, *ninth gonostylus.* (0) Not inflated (Figs 2F, 4F, 6F; Liu & Yang 2004: 149, fig. 4; Contreras-Ramos 2002: 66, fig. 25). (1) Inflated (Figs 3F, 5F). *Comments:* the male ninth gonostylus in *Acanthacorydalis* spp. is short and much thicker than the one in *N. ignobilis* and *C. crossi*. In *A. orientalis* and *A. unimaculata* the thick male ninth gonostylus is still inflated, especially near the base of the terminal claw. However, in *A. yunnanensis*, *A. fruhstorferi* and *A. sinensis*, it is not inflated.

13 *Male genitalia*, *apical half of tenth tergum.* (0) Not curved outwards (Fig. 3H; Liu & Yang 2004: 149, fig. 2; Contreras-Ramos 2002: 66, fig. 22). (1) Curved outwards (Figs 2H, 4H, 5H, 6H). *Comments:* in *C. crossi*, *N. ignobilis* and *A. orientalis* the apical half of the male tenth tergum is not curved outwards, whereas it is in the other four *Acanthacorydalis* species.

14 *Male genitalia*, *basal margin of tenth sternum.* (0) Trapezoidal (Figs 3G, 6G; Liu & Yang 2004: 149, fig. 5; Contreras-Ramos 2002: 66, fig. 24). (1) Arched (Figs 2G, 4G, 5G). *Comments:* in *C. crossi*, *N. ignobilis*, *A. orientalis* and *A. yunnanensis* the basal margin of the tenth sternum is trapezoidal, while it is arched in *A. fruhstorferi*, *A. sinensis* and *A. unimaculata*.

15 *Male genitalia*, *style of the lobes of tenth sternum.* (0) Slightly sclerotized. (1) Strongly sclerotized. *Comments:* in *C. crossi* the lobes of the male tenth sternum are strongly sclerotized while in *N. ignobilis* and the five Chinese *Acanthacorydalis* species they are slightly sclerotized.

16 *Male genitalia*, *length of the lobes of tenth sternum.* (0) Less than half the length of the lateral arm (Fig. 3G; Liu & Yang 2004: 149, fig. 5; Contreras-Ramos 2002: 66, fig. 24). (1) More than half the length of the lateral arm (Figs 2G, 4G, 5G, 6G). *Comments:* the length of the lobes of the male tenth sternum is measured from the base to the tip. The length of the lateral arm is measured from the mid point to the lateral point of the tenth sternum. In *A. orientalis* the lobes of the male tenth sternum are much shorter, less than half the length of the lateral arm, while in the two outgroup species and the other four Chinese *Acanthacorydalis* species they are more than half the length of the lateral arm.