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Larva of *Desmidophorus crassus* and the Systematic Position of the Desmidophorini (Coleoptera: Curculionoidea)

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Abstract. Larva of Desmidophorini is described for the first time, and its systematic position among the higher weevils is discussed based on the adult and larval morphology.

Key words: Morphology, phylogeny, Ocladiinae, Brachyceridae, Curculionoidea.

Introduction

The subfamily Desmidophorinae was first proposed by Morimoto (1962) in the family Brentidae *s. lat.* based principally on the Brentid-Apionid type aedeagus and undeveloped proventriculus, and later it was transferred to the subfamily Eirrhiniinae (Kuschel, 1971), to the family Brachyceridae (Thompson, 1992), to the subfamily Brachycerinae in the family Curculionidae as a tribe (Kuschel, 1995), to near the Eirrhiniinae (Marvaldi, 1997), to the subfamily Ocladiinae in the family Brachyceridae as a tribe (Alonso-Zarazaga & Lyal, 1999; Morimoto, Kojima & Miyakawa, 2006), or to the Ocladiinae (=Desmidophorinae) in the family Curculionidae *s. lat.* (Marvaldi & Morrone, 2000). These treatments are apparently caused by the different methodology for constructing phylogeny and consequent system, and different definitions for the taxa of the Brentid-Brachycerid complex in the higher Curculionoidea having primitive features in the aedeagus, proventriculus and the larvae.

Larval studies for aiming the phylogeny of the higher taxa in the Curculionoidea have been made mostly by Emden (1938), May (1993, 1994), Kuschel (1995), Marvaldi (1997), Marvaldi & Morrone (2000), and Oberprieler (2000), but known larvae are very low in percentage at present compared to the number of species and new data must be added to the knowledge for improving the phylogenetic system of the Curculionoidea.

Present paper deals *Desmidophorus crassus* as the first treatment of the larva of Desmidophorini and discusses the phylogenetic position of this taxon based on the adult and larval morphology.

Material and methods

First instar larvae were obtained by rearing the adults in the laboratory in 1988 from May to June. Premature larvae were obtained by digging out the root of *Hibiscus mutabilis* in the campus of the University of the Ryukyus in Oct. 10, 1988 by Morimoto and in Dec. 21, 1990 by T. Ueno. Matured larvae were obtained from the pupal cells in soil in the campus of the University of the Ryukyus in March 24, 1991, together with fresh adults having mandibular appendages, but no pupa by T. Ueno. These larvae were preserved in alcohol.

Adult of *Desmidophorus (Desmidophorus) crassus* is examined in detail, and *D. (D.) cumingi*, *fasciatus*, *hebes*, and *D. (Desmidophorus) imhoffi* are also examined for obtaining the further information of the genus.

Examination and drawings were made in the ordinary methods. The gross morphological features of entire larvae were examined prior to dissection. Then, larvae were macerated in 10% KOH solution for several minutes and dissected under a stereoscopic microscope. The head capsule with attached mouthparts was first removed from the body by a cut made with a fine forceps around the head capsule along the edges of the occipital foramen. The maxillae and labium as a unit were removed from the head capsule, and remove the mandibles with attached tendons from the head capsule. Thorax and abdomen were examined under a stereoscopic microscope through the transparent light. The mouthparts and skins were mounted on the microscopic slide for a detailed examination.

Terminology adopted in this paper is in great extent

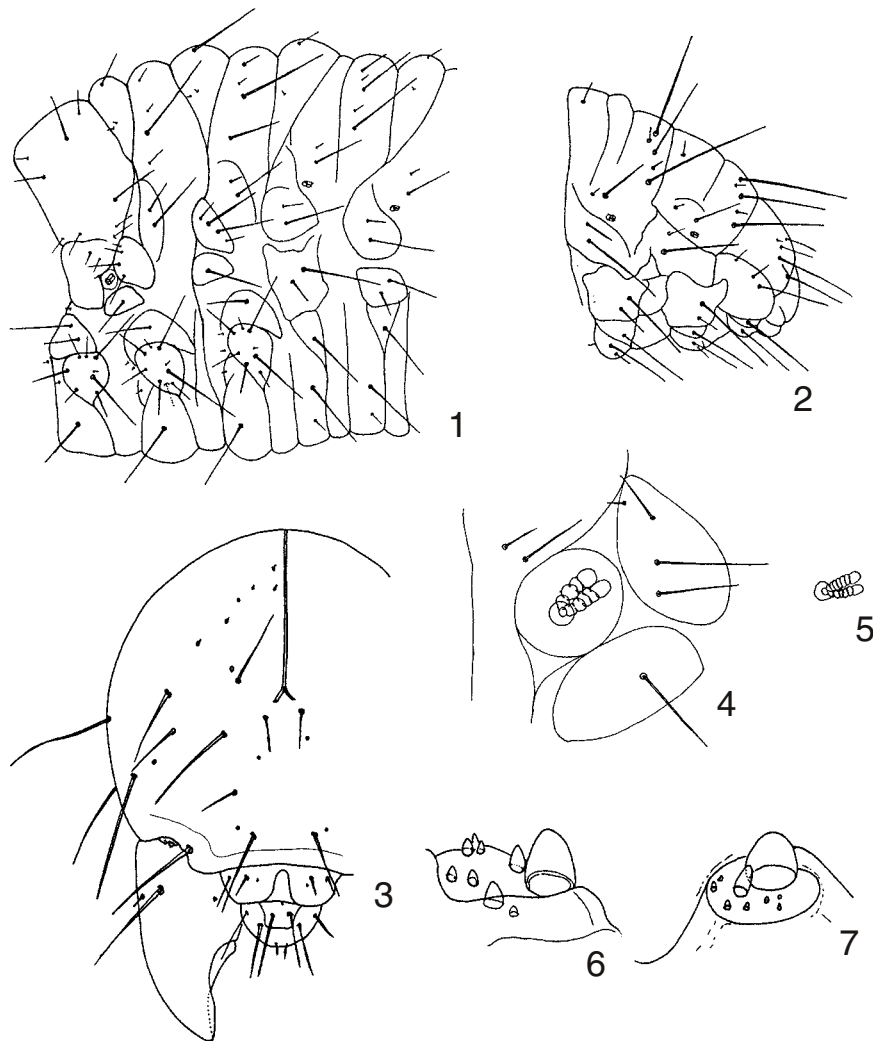
that proposed by Anderson (1947) and May (1994) for the larvae, and Morimoto, Kojima & Miyakawa (2006) for the adult.

Biology

The adults are found in Okinawa from April/May to September on branches of *Hibiscus mutabilis*, *rosa-sinensis*, *syriacus* and their cultivars on collecting data. Infestation is apt to be concentrated to a limited tree and continues several years, though *Hibiscus* spp. are commonly planted as ornamental trees. One infested tree we dug out in 1988 was transplanted 20 m distant from the original place in 1989, but no weevils have been found thenceforth on this tree. Our effort had been paid first to get the larvae from the infesting tree by splitting branches, but failed. Rearing of the adults was then initiated in

the laboratory of Kyushu University from May 10, 1988 on *Hibiscus mutabilis*. The adults were observed to make ovipositing hole into the pith of the young branches of 15 mm or more in diameter, and the hatched larvae were first found crawling on the floor of a rearing cage in a considerable speed as in the case of other adelognathous weevils in June 11, 1988. Following life cycle can be summarized from the available information at present.

The adults are found from April/May to September, and feed on young branches of *Hibiscus* spp. They make oviposition holes on the branch into the pith and lay some eggs in a hole. Hatched larvae fall on the ground, crawl into soil, and feed on the root of *Hibiscus* spp. Larvae feed on roots externally in soil by making feeding groove and half burying the body in the groove. They make pupal cells in soil in the late winter, and the pupal duration must be short. New adults have been ob-



Figs. 1-7. First instar larva.
 1: Thorax and abd. I, lateral. 2: Abd. VII-X, lateral. 3: Head, dorsal. 4: Thoracic spiracle. 5: Abd. II spiracle. 6, 7: Antenna, seen in two angles.

served in February and March. The mandibular appendages break off soon after emergence from soil.

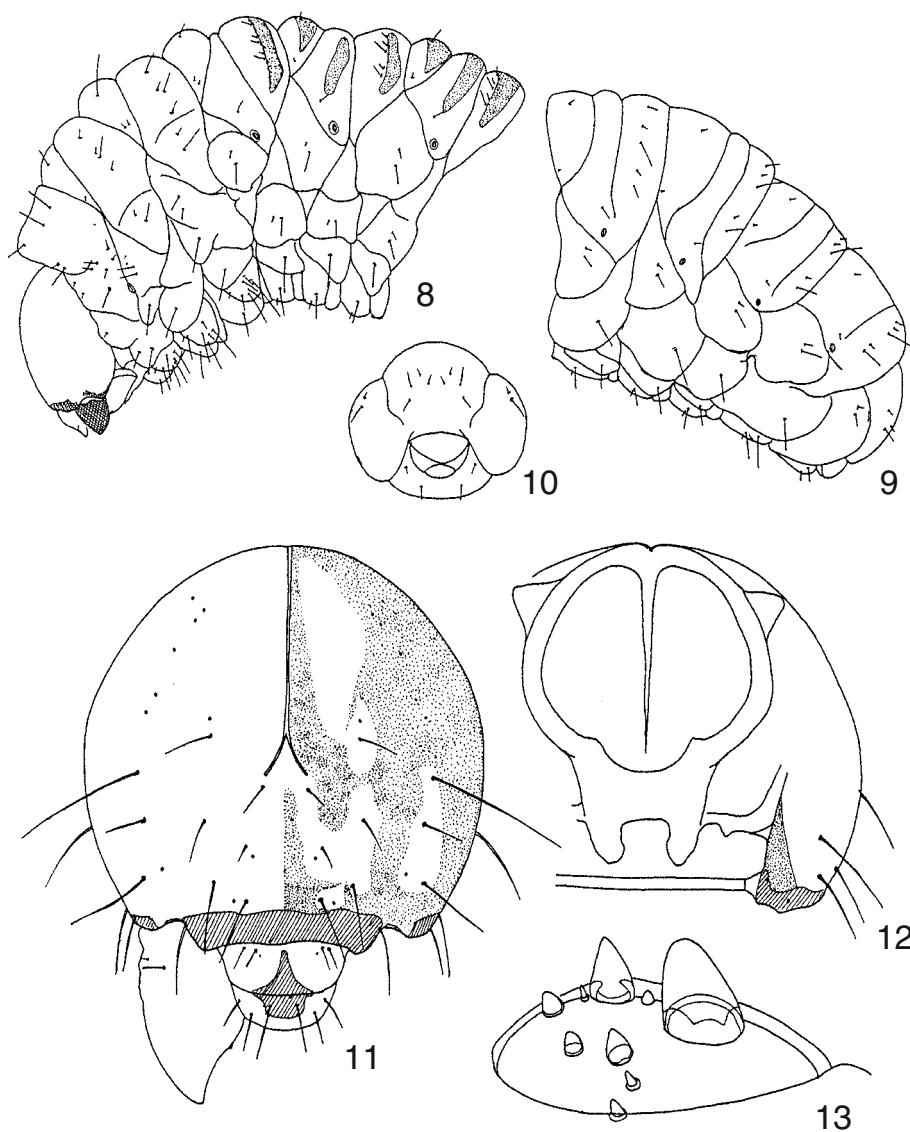
Host trees confirmed are *Hibiscus mutabilis*, *rosasinensis*, *syriacus* and their cultivars. *Hibiscus mutabilis* and *syriacus* are reported also as the hosts of *Desmidophorus hebes* in China (Chao & Chen, 1980).

Description of larva

First instar larva. Head pale milky white, catapophyses brown, anterior margin between ventral receptacles of mandibles via frontoclypeal margin pale brownish, narrow ridges along sides of maxillae from ventral receptacles brownish; mandibles with dorsal and

ventral margins and apical half brownish, basal area pale brownish; body whitish from pronotum to anus.

Head 0.54~0.58 mm in length to clypeus, 0.50~0.56 mm in maximum width; free, evenly rounded. Ocelli absent. Antenna ogival, as long as broad, with 8 minute appendages on basal membrane. Catapophyses in the same plane as frons. Hypopharyngeal bracon readily discernible. Frontal suture vestigial excepting short base. Epicranial suture about one-half as long as head. Endocarina absent. Frons with four pairs of setae, fs 2 usually absent, fs 1 and fs 3 moderately long, fs 4 and fs 5 long. Dorsal epicranial setae long, des 3 a little shorter, des 5 longest; posterior epicranial setae minute, six in all, of which five on a line. Lateral epicranial setae long, les 1 a



Figs. 8-13. Last instar larva.

8: Head to abd. III, lateral. 9: Abd. V-X, lateral. 10: Abd. IX-X, caudal. 11: Head, dorsal. 12: Head, ventral. 13: Antenna.

Characters	First instar larvae	Mature larvae
setae	longer	shorter
spiracles	bicameral	ovate, no air tubes, slit
fs 2	usually absent	present
spiracular area of Th II & III	4 setae	2 setae
pronotum	11 setae	13 setae (two minute)

little longer than les 2. Two ventral epicranial setae present, shorter than les 2. Clypeus not pigmented at basal margin, with two setae and a sensillum close to cls 1, cls 1 shorter than cls 2. Labrum with three setae of the equal length and a median sensillum, lateral sensilla absent. Labral rods distinct, subparallel, not reaching clypeus. Epipharynx with three anterolateral setae and three anteromedian setae, of which one on dorsal side close to anterior margin, and with four median spines close to anterior end of labral rods, epipharyngeal sensory pores in two-paired, anterior pair between the middle of labral rods, with cluster of three sensory pores, posterior pair on the underside of clypeus, with cluster of two sensory pores. Mandibles clearly distinguish the apical brownish part in contrast to basal pale part, with an obtuse tooth in the middle close to the base of brownish part on the dorsal cutting edge, no tooth at apex, with one short and one long setae, and three sensilla near base, inner surface smooth, no ridge, evenly concave, dorsal and ventral cutting edges longitudinally sulcate, the dorsal sulcus on apical half before tooth, the ventral sulcus from near apex to before base. Maxillae with three long and one short setae and two sensory pores on stipes, mala with eight dorsal setae, which are all sharply tapered apically, and five ventral setae, of which one rounded at apex and one short, maxillary palpi with two articles, basal article with one short seta and two sensory pores, apical article without seta, with one sensory pore and an elongate accessory process. Postmentum with three pairs of setae, pms 1 narrowly distant than psm 2. Prementum with one pair of long setae and one pair of sensory pores on basal area and two pairs of short setae near apex, premental sclerite complete, pigmented, with short posterior extension into transparent triangular area.

Pronotum with 11 setae. Thoracic spiracle on intersegmental area, bicameral. Prodorsum of meso- and metathorax with one long and two minute setae. Postdorsum of meso- and metathorax with four setae, pds 1 and 2 short. Alar area with two setae. Spiracular area with four setae. Epipleurum with one seta on meso- and metathorax. Pleurum with one seta. Epipleurum and

pleurum conjoined on prothorax. Pedal area with eight setae, often with one additional seta. Three minute setae in front of pedal area. Eusternum with one long seta. Sternellum without seta.

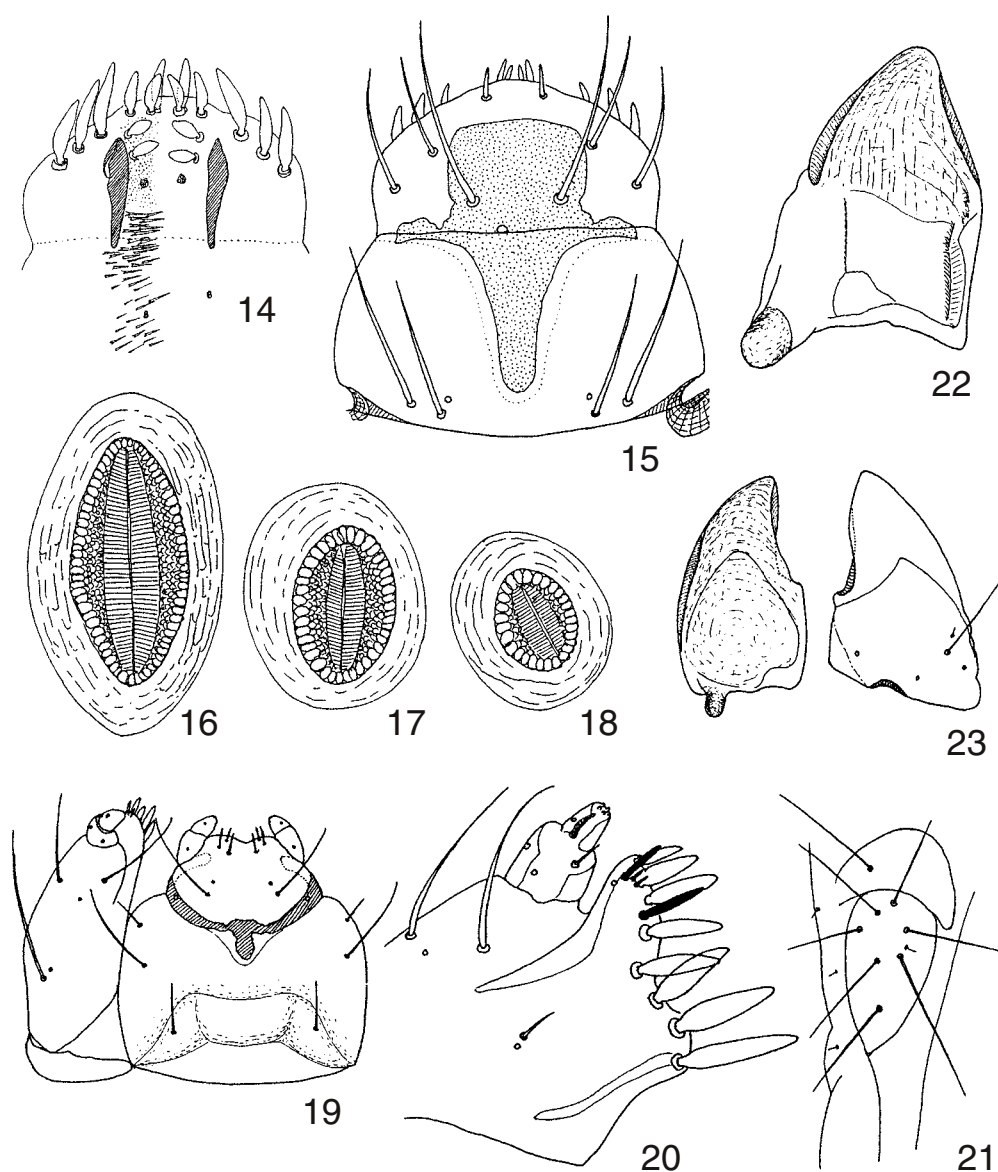
Abdomen with eight pairs of spiracles. Spiracles all lateral, bicameral, air tubes subequal in length, much longer than diameter of circular peritreme. Typical abdominal segment with three dorsal folds; prodorsum with one short and one additional minute setae; postdorsum with five setae, pds 2 and 3 short; spiracular area with one short and one long setae; epipleurum with two setae; pleurum with two setae; pedal area with one seta; eusternum with two setae; sternellum present, without seta. Caudal segments not sclerotized. Anus terminal, consisted of four lobes. Asperities generally distributed on tergal area including epipleurum, pointed; those on pleural and sternal areas and caudal segments pustulate.

Mature larva. Body cylindrical, curved, 12.0~13.5mm in length along spiracular line. Head 3.1~3.5mm in length to clypeus, 3.0~3.2 mm in maximum width, free, evenly rounded, indefinitely infuscate on cranium. Ocelli absent. Antennae ogival, with rounded apex, a little longer than broad, with 8 minute appendages on basal membrane. Catapophyses in the same plane as frons. Hypopharyngeal bracon readily discernible, without hypopharyngeal sclerome. Frontal suture obsolete excepting short base. Epicranial suture about as long as frons. Endocarina absent. Frons with five pairs of setae and two pairs of sensory pores, fs 2 short. Dorsal epicranial setae long, des 2 longest; posterior epicranial setae minute, six in all, of which five on a line. Lateral epicranial setae long, les 1 a little longer than les 2. Two ventral epicranial setae present, about as long as les 1. Clypeus not sclerotized at base, thus two pairs of setae and a pair of sensory pores on unsclerotized part, cls 1 and 2 equal in length. Labrum with three setae, lms 1 longest, lms 2 and lms 3 equal in length, with a median sensillum, lateral sensilla absent, subquadrate sclerite in the middle, which produced laterally at base and subtriangularly invaded into clypeus in middle. Labral rods distinct, subparallel, not reaching clypeus. Epipharynx

LARVA OF *DESMIDOPHORUS CRASSUS*

with three anterolateral setae and three anteromedian setae, of which one on dorsal side close to anterior margin, and with two pairs of median spines close to anterior end of labral rods, epipharyngeal sensory pores two paired, anterior pair between the middle of labral rods, with cluster of three sensory pores, posterior pair on the underside of clypeus with cluster of two sensory pores. Mandibles with apical dorsal and ventral areas dark brown, basal areas on exterior and interior surfaces pale brown, rounded at apex, with an obtuse tooth in the middle of dorsal cutting edge, no apical tooth, dorsal and ventral cutting edges longitudinally sulcate, exterior

surface flat and transversely corrugated, with one long and one short setae and three sensory pores, interior surface smooth, evenly concave, no ridge. Maxillae with three long and one short setae and two sensory pores on stipes, mala with eight dorsal setae, which are blunt at tip, and four ventral setae, of which two short, with a sclerotized brown stripe from the most basal dorsal seta inwards, maxillary palp with two articles, basal article with one short seta and two sensory pores, apical article without seta, with one sensory pore and an elongate accessory process. Postmentum with three pairs of setae, psm 1 narrowly distant than psm 2. Prementum with one



Figs. 14-23. Last and first instar larvae (14-22: last instar; 23: first instar).
 14: Epipharynx. 15: Clypeus and labrum. 16-18: Spiracles (16: thorax; 17: abd. I; 18: abd. VIII). 19: Labium and maxilla. 20: Maxilla, apical part. 21: Pedal lobe of mesothorax. 22: Mandible, internal. 23: Mandibles, internal and external.

Table 1. Data matrix

	1														2													
	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8
Caridae	1	0	0	0	0	1	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
Apioninae	0	0	2	0	0	2	2/3	0	1	0	0	0	0	1	0	0	0	0	1	1	0	1	1	0	0	0	0	1
Nanophyinae	0	0	2	0	0	2	2	0	1	0	0	0	0	1	1	1	0	0	1	1	0	1	1	0	0	0	0	1
Brentinae	0	0	3	1	0	0	2	0	0	0	0	0	0	1	0	0	0	1	1	0	0	1	1	0	0	0	0	1
Cyladinae	0	0	2	0	1	1	2	0	0	0	0	0	0	1	0	0	0	1	1	0	0	1	1	0	0	0	0	1
Antliarhininae	0	0	1/2	0	0	1	2/3	0	1	0	0	0	0	1	1	1	0	0	1	0	0	1	0	0	0	0	0	1
Ithycerinae	1	0	1	0	1	0	2	0	0	0	0	0	0	1	1	0	0	0	0	0	1	2	0	0	0	0	0	1
Microcerinae	0	1	3	0	?	?	?	?	0	0	?	0	0	?	1	0	0	1	0	0	1	1	1	?	0	0	0	1
Brachycerini	1	2	2	1	1	1	0	0	2	1	0	1	0	1	1	1	1	0	0	0	1	2	0	0	0	0	0	0
Ocladiini	1	1	3	1	1	1	2	0	2	1	?	1	1	?	1	1	0	0	0	0	1	?	0	?	0	0	0	?
Desmidophorini	2	1	3	1	0	1	2	1	2	0	0	1	1	0	1	1	1	0	0	0	1	2	0	0	0	0	0	0
Dryophthorinae	1	0	2	0/1	1	1	0/1	0	2	1	1	1	0	1	1	1	0	0	0	0	1	2	0	0/1	0	0	1	0
Eriirhininae	1	0	2	0	0	1	1	0	2	1	1	1	0/1	1	1	1	0	0	0	0	1	2	0	0/1	0/1	0	1	0
Curculioninae	1	0	2	0/1	1	1	?	0	2	1	1	1	0/1	1	1	1	0/1	0	0	0	0/1	2	0	1	1	1	1	0

pair of long setae and one pair of sensory pores on behind the middle and three pairs of short setae near apex, premental sclerite complete, pigmented, with short posterior extension into triangular transparent area.

Prothorax with 13 setae on pronotum, one seta on epipleurum, two setae on pleurum. Meso- and metathorax with one and one or two additional minute setae on prodorsum, four setae on postdorsum, two setae on alar area, two setae on spiracular area, one setae on epipleurum, one seta on pleurum. Each segment of thorax with eight setae on pedal area, of which one very short, three minute setae in front of pedal area, one long seta on eusternum, and no seta on sternellum. Thoracic spiracles on intersegmental area, ovate, no air tube, surrounded around by a chain of small cells at periphery, with dense spicules directing interiorly toward longitudinal slit on internal surface, peritreme completely ringed, weakly wrinkled.

Abdomen with eight pairs of spiracles. Spiracles all lateral, similar to those on thorax but smaller and roundish. Typical abdominal segment with three dorsal folds; prodorsum with one short and one or two additional minute setae; postdorsum with five setae, pds 2 and pds 3 short; spiracular area with a seta; epipleurum with two setae; pleurum with two setae; pedal area with a seta;

eusternum with two setae; sternellum present, without seta. Anus terminal, consisted of four lobes. Each lobe on dorsum from postdorsum of Abd I to postdorsum of Abd IV transversely pigmented in pale brownish, each pigmented area surrounded around by brownish margin and often narrowly divided on prodorsum of Abd II at middle. Asperities generally distributed on over whole body, indistinct. Alimentary canal with six Malpighian tubules in number.

Notes. The first instar larva is similar to the mature larva in fundamental structures, but is different in the following points excepting the size:

As mentioned above, drastic change of the spiracular structure is characteristic to this taxon and no such data have been noticed on the weevil larvae up to the present. Absence of the lateral sensilla on labrum of weevil larvae was discussed by Sanborne (1981) from the view point of phylogeny, and the intersegmental position of thoracic spiracles is regarded as one of the primitive features. The sulcate both cutting edges of mandibles are characteristic to this taxon. The head cranium is concolorous pale brown except for the anterior margin and the body from pronotum to anus is also concolorous milky white in most larvae, but the head is indefinitely mottled

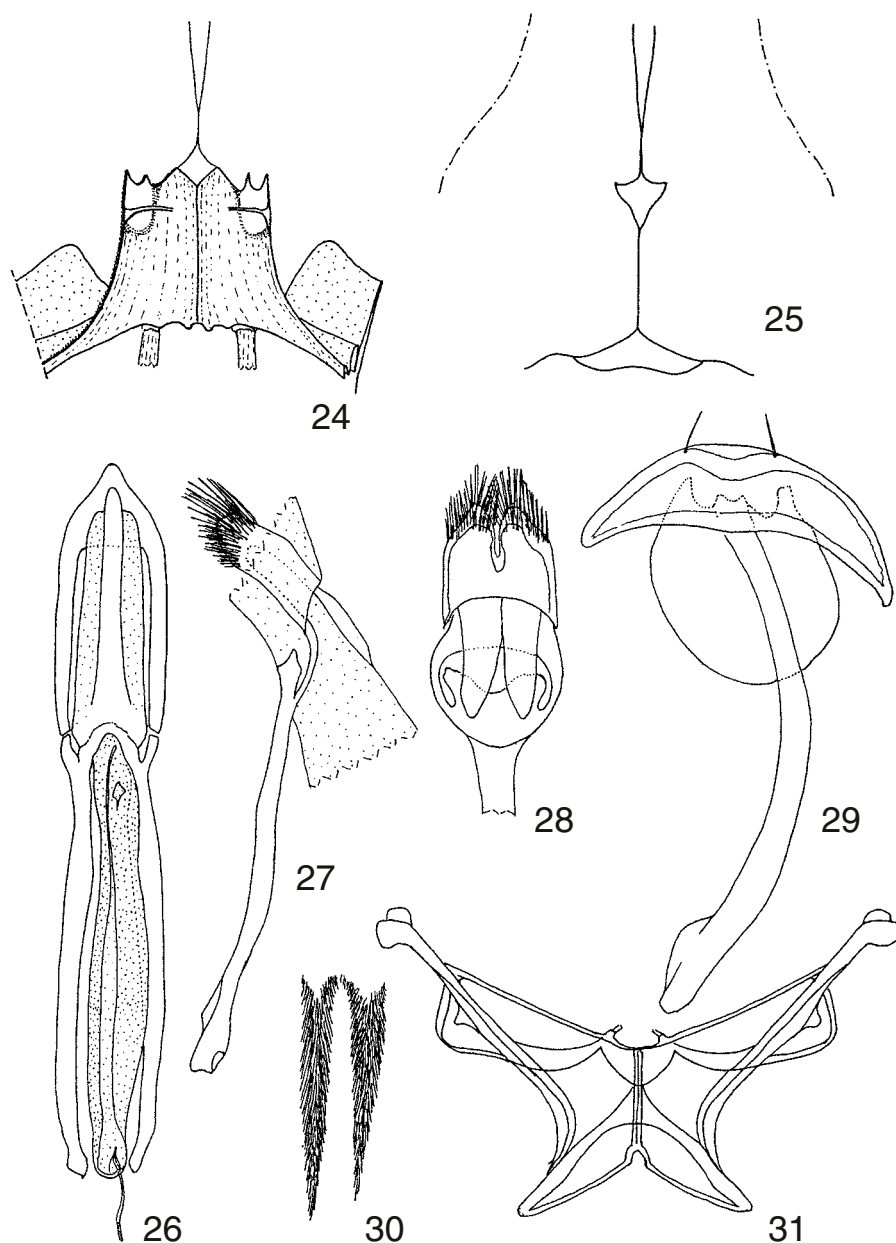
and the dorsal folds of abdomen from the postdorsum of the first segment to the postdorsum of the fourth segment have transverse band, ten bands in all, in the mature larvae in the pupal chamber.

Some comments on the adult structures

Among the higher weevils including Brentidae and Curculionidae, *Desmidophorus* has the following fea-

tures in adult:

Head hemiglobular; eyes weakly convex, partly concealed by ocular lobes when rostrum reposed; rostrum robust, reaching shallow concavity between mesocoxae, roughly punctate dorsally as on head; antennal insertions subterminal, antennal scrobes oblique from a little above the middle of lateral surface to the underside of base and continuous to each other, distant from eyes at base; antennae with seven segments in funicle, club compact,

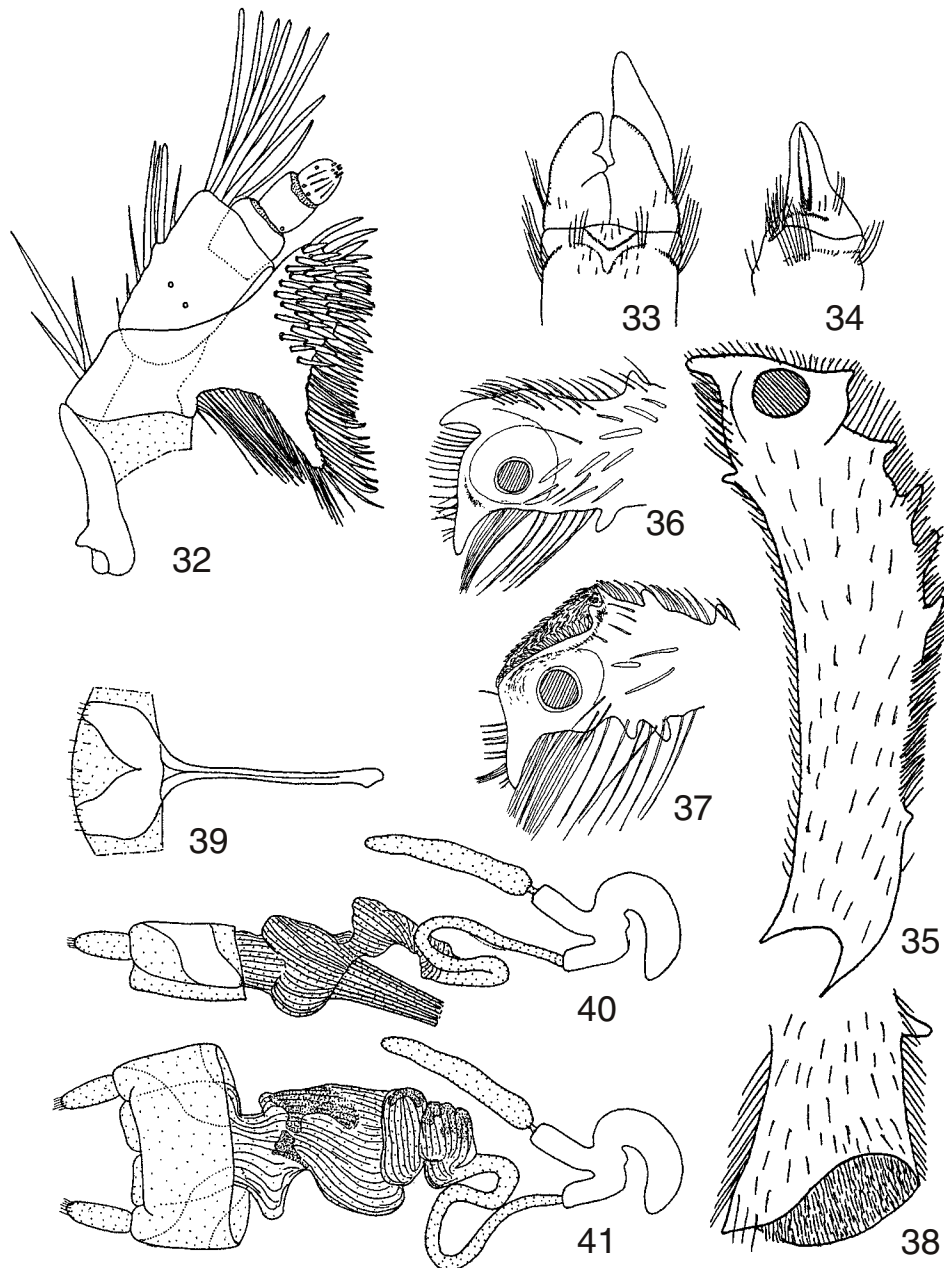


Figs. 24-31. Adult.
 24: Tentorium, dorsal. 25: Head, ventral, notice the Y-shaped gular suture, comp. w. fig.24. 26: Aedeagus, dorsal. 27: Tegmen and cap-piece, lateral. 28: Ditto, dorsal. 29: Sternites 8 and 9, and spiculum gastrale, ventral. 30: Proventriculus, part. 31: Metendosternite.

ovate, first segment shorter than the rest; mandibles move almost in a horizontal plane and occlude medially, triangular, slender and more than twice as long as basal width when viewed dorsally, with median sharp tooth, then dorsal cutting edge almost straight to base on left mandible, arcuate to base on right mandible, with deciduous appendage conspicuous on both mandibles, which has a broad base along the whole lateral edge of mandible, thus the mandibular scar linear; maxillary

sinus weakly narrowed basally; maxillae with galea and lacinia fused, with three segments in palpi; labial palpi three-segmented on anterior margin of prementum; postmentum slender, very narrow, tapered basally. Tentorium with gular margins narrowly and shortly divaricate at apex. Pronotum with ocular lobes and short vibrissae. Scutellum evident. Elytra conjointly rounded at apex, with distinct humeri.

Legs robust, femora weakly clavate, not sulcate,



Figs. 32-41. Adult.

32: Maxilla. 33, 34: Mandibles, dorsal and lateral. 35: Fore tibia. 36: Apex of middle tibia. 37, 38: Apex of hind tibia, notice the enclosed oval bevel. 39: Female sternite 8 and spiculum ventrale. 40, 41: Female reproductive tract, lateral and dorsal.

toothed; tibiae flattened, denticulate externally, uncinata at inner apical corner and further in male uncinata near outer apical corner from the keeled flange, the latter unci small and obtuse on fore and hind tibiae, sharp on middle tibiae; hind tibiae with enclosed oval bevel surrounded by sharp keel and densely setose inside, similar but smaller bevel present on fore and middle tibiae in *D. imhoffi*; tarsi with third segment deeply bilobate, claws simple, free.

Prosternum deeply and U-shapedly concave between ocular lobes at anterior margin, pectoral canal deep, bare, bordered laterally with sharp carina in front of fore coxae, and terminate at a shallow bare concavity between middle coxae on metasternum; fore coxae as widely distant as middle coxae. Venter with first ventrite behind coxa as long as second, as long as third and fourth combined, first suture deep, entire. Tergum with first to sixth tergites weakly pigmented, each with scattered sensory organs visible as brown small spots, spicule patches indefinite, each tergite with spiculate transverse area on basal half; seventh and eighth ter-

gites in male sclerotized, the latter only covered by the former at base, truncate at apices; in female, seventh tergite broadly rounded at apex, eighth tergite broadly rounded at apex, completely covered with seventh; without stridulation organ in both sexes. Genitalia in male with eighth sternite undivided, crescent; ninth sternite ovate, lamellar; spiculum gastrale curved; aedeagus with dorsal plate, tegmen with large cap-piece, manubrium almost as long as apodeme; in female eighth sternite subquadrate, spiculum ventrale straight, ovipositor with styli, bursa copulatrix indefinite, spermathecal duct robust, spermatheca with curved cornu, straight ramus and long collum. Malpighian tubules six in number, of which three close or contiguous at base on each lateroventral side. Rectal plates on hind gut absent. Proventriculus with 8 rows of aggregated setae.

Comparison

Owing to the absence of the frontal sutures in larval head, *Desmidophorus* is unable to assign whether it be-

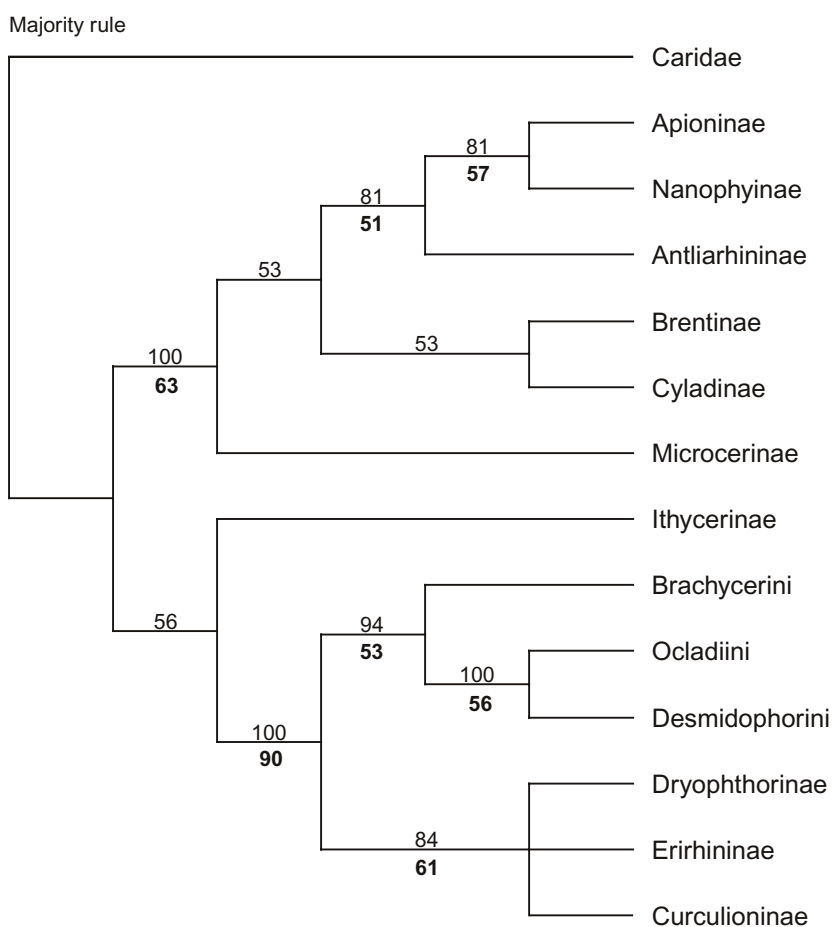


Fig. 42. 50% majority-rule consensus tree of 32 most-parsimonious trees. Tree length = 55, CI = 0.65, RI = 0.75, RC = 0.49. Numbers below nodes are bootstrap value.

longs to the primitive families or to the Curculionidae *s. lat.* in the key of May (1994). In order to investigate the systematic position of *Desmidophorus*, following larval and adult characters, those are coded principally after Marvaldi & Morrone (2000) and Oberprieler (2000) and also cited from other previous works (see references) were employed in the phylogenetic analysis. Character states of *Desmidophorus* are indicated in brackets after every character. Common characters in the Apionid-Brentid-Curculionid taxa are omitted from the following character list.

Phylogenetic reconstruction was accomplished by using PAUP version 4 (Swofford, 2002). Branch and bound search algorithm was used to guarantee discovery of the shortest trees, and the trees were rooted using Caridae.

Larvae

Head

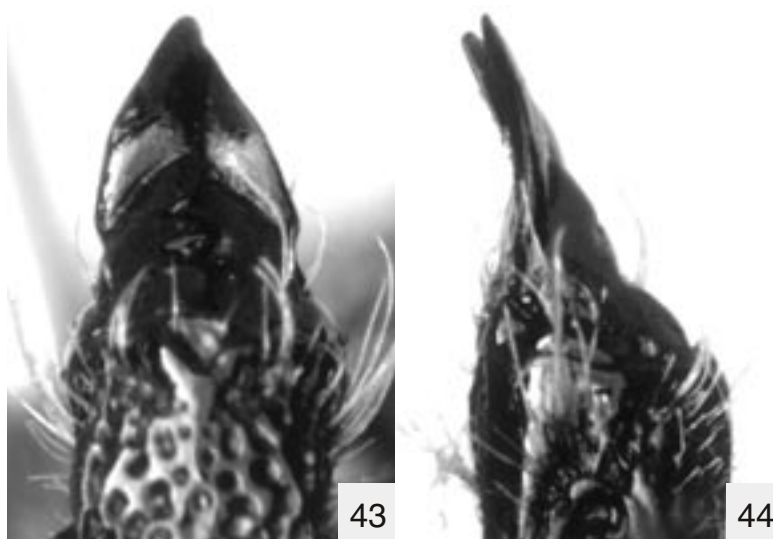
1. Frontal sutures (0) complete, reaching articulating membrane of mandibles; (1) incomplete, ending at antennae; (2) obsolete. [2]. Last state has a possibility to be derived from (0) or (1), but several genera of Entiminae as well as some Brentinae and Microcerinae (Oberprieler, 2000) are known to have this state.
2. Antennal sensorium: (0) convex, protruding, much longer than wide; (1) conical, ogival or semiellipsoidal, not or hardly longer than wide, with collar-like structure at base; (2) flat, not protruding. [1]. State (1) is seen in Alophini, Emphyastina, Amycterini, and Episomini, and (2) in bulk of Entiminae, Ceuto-

rhynchinae, and *Lissorhoptrus*.

3. Number of stemmata or ocelli: (0) 6-4; (1) 3; (2) 1 or 2; (3) 0. [3]. Stemmata are grouped in two in primitive families, and the anterior group comprises three stemmata. The latter is usually diminished in size and fused to form the anterior ocellus comprising three black pigments in some taxa, but the pigments are completely conglutinate to form a black spot in bulk of Curculionidae.
4. Endocarinal line: (0) present; (1) absent. [1].
5. Clypeus with basal sclerotized area: (0) absent; (1) present. [0]. Clypeus is divided into basal sclerotized part and distal unpigmented part, and clypeal setae and sensilla are usually born on the former.
6. Clypeus: (0) with three setae on each side; (1) with two setae and a sensillum on each side; (2) one seta and a sensillum on each side. [1].
7. Labrum: (0) with one or two pairs of sensilla; (1) with a median sensillum and a pair of lateral sensilla; (2) with a median sensillum, no lateral sensilla; (3) no sensillum. [2]. (2) is seen in Ithycerinae, Brentinae and some Apioninae (Sanborne, 1981).
8. Mandibles along ventral cutting edge: (0) not sulcate; (1) sulcate. [1]. This is presently autapomorphic to *Desmidophorus*. Similar but shorter sulcus is present on the distal half of the dorsal cutting edge in this genus, but the similar sulcus is also present in some species of Entiminae.

Thorax

9. Legs: (0) present, segmented; (1) vestigial with faint segmentation; (2) absent. [2].
10. Thoracic spiracles: (0) on mesothorax or interseg-



Figs. 43-44. Photographs of adult mandibles and its appendages (43: dorsal; 44, lateral).

mental; (1) on prothorax. [0].

11. Thoracic and abdominal spiracles: (0) same type from first to last instars; (1) different type from second instar. [1]. Drastic change of spiracular type from first instar to the second is characteristic to *Desmidophorus*.

Abdomen

12. Typical segments: (0) with two dorsal folds; (1) with three or four dorsal folds. [1].

Adults

13. Rostrum in repose: (0) not retractable; (1) retractable in prosternal furrow. [1].
14. Gular sutures: (0) Y-shaped; (1) completely fused. [0].
15. Scrobe shape: (0) foveiform; (1) sulciform. [1].
16. Type of antennae: (0) orthocerous; (1) geniculate. [1].
17. Deciduous processes on mandibles: (0) absent; (1) present. [1].
18. Labial palpi: (0) free; (1) set in pits or grooves. [0]
19. Labial palpi: (0) 3; (1) 2 or 1. [0].
20. Trochanter: (0) short; (1) long. [0].
21. Tibial apex: (0) without mucro or uncus; (1) mucronate and/or uncinat. [1].
22. Metendosternite: (0) belid-type; (1) brentid-type; (2) curculionid-type. [2].
23. Ventrites: (0) ventrites 1-2 at same level with 3; (1) ventrites 1-2 more convex, more protruding than 3 in lateral view. [0].
24. Male sternite 8: (0) undivided; (1) divided into a paired sclerites. [0].
25. Male aedeagus: (0) orthocerous type; (1) gonatocerous type. [0].
26. Insertion of apodeme into aedeagal body in lateral aspect: (0) dorsal; (1) median to ventral. [0].
27. Proventricular blades: (0) not developed; (1) well developed. [0].
28. Number of Malpighian tubules: (0) 6; (1) 4. [0].

Data matrix is compiled from the aforementioned characters and character states in Table 1, and the reconstructed relative relationships of the taxa are represented in Fig. 42. Our result obtained is roughly concordant with those of previous authors in the phylogenetic sequence, and Brachycerini, Ocladiini and Desmidophorini became sister to Dryophthorinae + Erihrininae + Curculioninae. Monophyly of Ocladiinae including Desmidophorini was supported, and that of Brachyceridae sensu Thompson (1992) and Alonso-Zarazaga & Lyal (1999) including Ocladiinae was also supported, but not so robust. However, Microcerinae was excluded from

Brachyceridae and belonged to Brentidae as showed by Oberprieler (2000). Further studies will be required to confirm the monophyly of Brachyceridae as well as to resolve the basal relationships of Curculionidae *s. lat.*

References

- Alonso-Zarazaga, M. A., 1989. Revision of the supraspecific taxa in the Palaearctic Apionidae Schoenherr, 1823. 1. Introduction and subfamily Nanophyinae Seidlitz, 1891 (Coleoptera, Curculionoidea). *Fragm. Ent. Roma*, **21**: 205-262.
- Alonso-Zarazaga, M. A., 1990. Revision of the supraspecific taxa in the Palaearctic Apionidae Schoenherr, 1823 (Coleoptera, Curculionoidea). 2. Subfamily Apioninae Schoenherr, 1823: Introduction, keys and descriptions. *Graellsia*, **46**: 19-156.
- Alonso-Zarazaga, M. A. & C. H. C. Lyal, 1999. *A World Catalogue of Families and Genera of Curculionoidea (Insecta: Coleoptera) (Excepting Scolytidae and Platypodidae)*. 315 pp., Entomopraxis, Barcelona, Spain.
- Anderson, W. H., 1947. A terminology for the anatomical characters useful in the taxonomy of weevil larvae. *Proc. Ent. Soc. Wash.*, **49**: 123-132.
- Anderson, R. S., 1995. An evolutionary perspective on diversity in Curculionoidea. *Mem. Ent. Soc. Wash.*, **14**: 103-114.
- Aslam, N. A., 1961. An assessment of some internal characters in the higher classification of the Curculionidae *s. l.* (Coleoptera). *Trans. R. Ent. Soc. Lond.*, **113**: 417-489.
- Calder, A. A., 1989. The alimentary canal and nervous system of Curculionoidea (Coleoptera): gross morphology and systematic significance. *J. Nat. Hist.*, **23**: 1205-1265.
- Calder, A. A., 1990. Gross morphology of the soft parts of the male and female reproductive systems of Curculionoidea (Coleoptera). *J. Nat. Hist.*, **24**: 453-505.
- Chao, Y-C. & Y-Q. Chen, 1980. *Economic Insect Fauna of China*, **20: Coleoptera, Curculionidae (1)**. ix+184, 14 pls. Science Press, Beijing. (In Chinese.)
- Emden, F. van, 1938. On the taxonomy of Rhynchophora larvae (Coleoptera). *Trans. R. Ent. Soc. Lond.*, **87**: 1-37.
- Emden, F. van, 1952. On the taxonomy of Rhynchophora larvae: Adelognatha and Alophinae (Insecta: Coleoptera). *Proc. Zool. Soc. Lond.*, **122**(3): 651-795.
- Farrell, B. D., 1998. "Inordinate fondness" explained: Why are there so many beetles? *Science*, **281**: 555-559.
- Haaf, E., 1957. Revision der äthiopischen und madagassischen Arten der Gattung *Brachycerus* Ol. (Col. Curc.). *Ent. Arb. Mus. Frey*, **8**: 1-274.
- Howden, A. T., 1986. Note on the biology of *Ocladius* (Coleoptera, Curculionidae). *J. Ent. Soc. S. Afr.*, **49**: 394-395.
- Hubenthal, W., 1917. Die indomalaiischen Arten der Curculionidengattung *Desmidophorus* Schönherr. *Ent. Blätt.*, **13**: 103-227.
- Kuschel, G., 1971. Entomology of the Aucklands and other islands south of New Zealand: Coleoptera: Curculionidae. *Pacific Ins. Monogr.*, **27**: 225-259.
- Kuschel, G., 1995. A phylogenetic classification of Curculionoidea to families and subfamilies. *Mem. Ent. Soc. Wash.*, **14**: 4-33.
- Lacordaire, T., 1866. *Histoire naturelle des insectes. Genera*

- des Coléoptères, VII*. 620 pp., Paris.
- Louw, S., 1986. Revision of the Microcerinae (Coleoptera: Curculionidae) with an analysis of their phylogeny and zoogeography. *Mem. Nas. Mus. Bloemfontein*, **21**: 1-331.
- Louw, S., 1990. The life history and immature stage of *Brachycerus ornatus* Drury (Coleoptera: Curculionidae). *J. Ent. Soc. S. Afr.*, **53**: 27-40.
- Louw, S., 1995. Systematics and biogeography of the subfamily Microcerinae (Coleoptera: Curculionidae): A re-evaluation based on larval morphology. *Mem. Ent. Soc. Wash.*, **14**: 169-174.
- Marvaldi, A. E., 1997. Higher level phylogeny of Curculionidae (Coleoptera: Curculionoidea) based mainly on larval characters, with special reference to broad-nosed weevils. *Cladistics*, **13**: 285-312.
- Marvaldi, A. E., 2000. Morphologic characters of the immature stages of *Ocladius dianthi* Marshall (Coleoptera: Curculionidae: Ocladiinae), with phylogenetic implications. *Coleopt. Bull.*, **54**: 325-331.
- Marvaldi, A. E. & J. J. Morrone, 2000. Phylogenetic systematics of weevils (Coleoptera: Curculionoidea): a reappraisal based on larval and adult morphology. *Ins. Syst. Evol.*, **31**: 43-58.
- May, B. M., 1993. *Larvae of Curculionoidea (Insecta: Coleoptera): A systematic overview*. Fauna of New Zealand, No. 29. 226 pp., Manaaki Whenuta Press, Lincoln, New Zealand.
- May, B. M., 1994. An introduction to the immature stages of Australian Curculionoidea. pp.365-721. In Zimmerman (ed.), *Australian Weevils., II*. CSIRO, Australia.
- Morimoto, K., 1962. Comparative morphology and phylogeny of the superfamily Curculionoidea of Japan. *J. Fac. Agr., Kyushu Univ.*, **11**: 331-373.
- Morimoto, K., 1962. Key to families, subfamilies, tribes and genera of the superfamily Curculionoidea of Japan excluding Scolytidae, Platypodidae and Cossoninae. *J. Fac. Agr., Kyushu Univ.*, **12**: 21-66.
- Morimoto, K., 1964. Key and illustrations for the identification of the Curculionid- beetles of Japan and the Ryukyus. I. Subfamily Nanophyinae. *Kontyû*, **32**: 81-90.
- Morimoto, K., 1976. Notes on the family characters of Apionidae and Brentidae, with a key to the related families. *Kontyû*, **44**: 469-476.
- Morimoto, K., 1986. Phylogeny and classification. pp.142-201. In Morimoto & Hayashi (eds.), *The Coleoptera of Japan in color, I*. Hoikusha, Osaka. (In Japanese.)
- Morimoto, K. & H. Kojima, 2003. Morphologic characters of the weevil head and phylogenetic implications (Coleoptera, Curculionoidea). *Esakia*, (43): 133-169.
- Morimoto, K., H. Kojima & S. Miyakawa, 2006. *The Insects of Japan, No.3. Superfamily Curculionoidea: General introduction and family Curculionidae: Entiminae (Part 1): Phyllobiini, Polydrusini and Cyphicerini*. 406 pp. (in press.)
- Oberprieler, R., 2000. The larvae of the weevil tribe Eurhynchini and the phylogeny of the Brentidae (Coleoptera: Curculionoidea). *Inverte. Taxon.*, **14**: 753-770.
- Pajni, H. R. & B. R. Bhateja, 1982. Indian Apionidae (Coleoptera: Curculionoidea). I. Taxonomic studies on subfamily Nanophyinae. *Orient. Ins.*, **16**: 431-490.
- Sanborne, M., 1981. Biology of *Ithycerus noveboracensis* (Forster) (Coleoptera) and weevil phylogeny. *Evolution. Monogr.*, **4**: 1-80.
- Swofford, D. L., 2002. PAUP*, version 4. Sinauer Associates, Massachusetts.
- Thompson, R. T., 1992. Observations on the morphology and classification of weevils (Coleoptera: Curculionoidea) with a key to major groups. *J. Nat. Hist.*, **216**: 835-891.
- Ting, P. C., 1936. The mouth parts of the Coleopterous group Rhynchophora. *Microent.*, **1**: 93-114.
- Zherikhin, V. V. & V. G. Gratsev, 1995. A comparative study of the hind wing venation of the superfamily Curculionoidea, with phylogenetic implications. In Pakaluk, J. & Slipinski (eds.), *Biology, Phylogeny and Classification of Coleoptera*. Papers Celebrating the 80th Birthday of Roy A. Crowson, **2**: 633-777.