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Nipponocyphon, a New Genus of Japanese Scirtidae (Coleoptera) and its Phylogenetic Significance

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Abstract Nipponocyphon nakanei gen. et sp. nov., is described from Japan, and a new supergeneric classification of Scirtidae is proposed based on cladistic analyses of 22 scirtid genera and one genus each from Derodontidae, Eucinetidae and Decliniidae with 56 adult morphological characters. Nipponocyphoninae and Stenocyphoninae, subfam. nov., are proposed based on the genera Nipponocyphon and Stenocyphon, respectively.

Introduction

The family Scirtidae is a relatively large cosmopolitan family containing 34 described genera, but the fauna is poorly known for any but the Holarctic region and phylogenetic relationships of described genera are poorly understood. Except for the placement of *Amplectopus* SHARP (see Discussion below), monophyly of the family has never been questioned, partly due to unique features of the male genitalia and of known larvae; however, in the recently described *Stenocyphon sasajii* LAWRENCE, 2001 both male and female genitalia exhibit a radically different structure. The discovery of an unusual scirtid-like beetle from the mountains of Honshu and Shikoku, Japan, stimulated the authors to carefully reconsider family limits and relationships among genera of Scirtidae and related groups of basal Polyphaga.

Materials and Methods

The following abbreviations have been used for specimen repositories: ANIC -

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John F. LAWRENCE and Hiroyuki YOSHITOMI

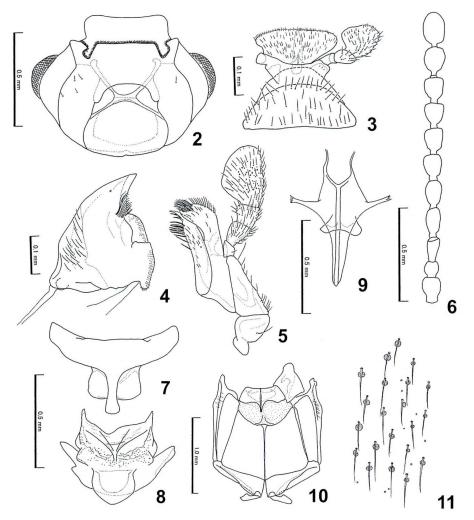


Fig. 1. Nipponocyphon nakanei sp. nov., holotype male. Photomicrograph digitally enhanced.

Australian National Insect Collection; EUM — Ehime University, Matsuyama; NMW — Natural History Museum, Wien; NSMT — Natural Museum of Nature and Science, Tokyo; NZAC — New Zealand Arthropod Collection; SEHU — Systematic Entomology, Hokkaido University — T. NAKANE Collection.

Image in Fig. 1 was enhanced using Auto-Montage software version 4.00 (Synoptics Ltd., http://www.syncroscopy.com).

Symbols used in measurements and ratios: TL=total length including head; BL=body length (excluding head, PL+EL); PL=pronotal length at midline; PW=greatest pronotal width; EL=elytral length along suture, including scutellum; EW=greatest elytral width. The terms **mesoventrite** and **metaventrite** have been used in place of mesosternum and metasternum following LAWRENCE (1999). Wing vein terminology follows that of KUKALOVÁ-PECK and LAWRENCE (1993, 2004).



Figs. 2–11. Nipponocyphon nakanei sp. nov., paratype, female; 2, head in ventral view; 3, labium; 4, mandible; 5, maxilla; 6, antenna; 7, prosternum; 8, scutellum; 9, metendosternite; 10, mesoventrite and metaventrite; 11, setae and punctures on elytra.

Nipponocyphon gen. nov.

Type species: Nipponocyphon nakanei sp. nov.

Description. Adult. Body (Fig. 1) moderately elongate and parallel-sided, somewhat flattened, clothed with suberect hairs. Head moderately strongly declined but visible from above; eyes moderately large, strongly protuberant, finely facetted; sides of head immediately behind eyes slightly inflated; transverse occipital carina absent; ventral epicranial ridges well developed; supra-antennal carinae well marked but not produced

John F. LAWRENCE and Hiroyuki YOSHITOMI

over antennal insertions, which are slightly exposed; antennal fossae moderately well developed, each extending laterally to edge of eye but not as wide as antennal insertion, continued ventrally as broad, subantennal groove; subocular carina absent. Frons barely sloping anteriorly; frontoclypeal suture well impressed, slightly curved, with distinct tentorial pits at either end; clypeus strongly transverse, slightly wider anteriorly, sides slightly rounded, apex truncate. Ventral portion of head (Fig. 2) between subgenal carinae flat to somewhat concave, except for gular area, which is slightly convex; gular sutures widely separated; corportentorial bridge very broad. Antennae (Fig. 6) relatively short, if extended posteriorly reaching just beyond elytral bases, moniliform to slightly wider than 2, 3 elongate and slender, about $2.67 \times$ as long as wide, 4 slightly wider and about $2.0 \times$ as long as wide, 5 to 8 progressively shorter and of equal width, 9 and 10 about as long as wide, 11 about $1.33 \times$ as long as wide.

Labrum completely exposed, strongly transverse, about $0.37 \times$ as long as wide, sides strongly rounded, apex subtruncate; tormae short and quadrate with acute mesal process. Mandibles (Fig. 4) slightly longer than wide at base, apex strongly and abruptly curved mesally and unidentate; basal half of outer edge with sharp dorsal carina dividing exposed surface from that concealed beneath clypeus and labrum; molae well-developed, asymmetrical, surfaces of both very finely tuberculate. Prostheca well-developed, consisting of apical tuft of hairs and membranous lobe with surface hairs at molar end. Maxillae (Fig. 5) with galea slightly expanded subapically and setose; lacinia with inner edge lined with long setae and apex bearing hook-like, tridentate uncus; apical palpomere strongly expanded and securiform. Labium (Fig. 3) with mentum transverse and trapeziform; ligula strongly expanded apically and truncate with internal longitudinal strut; apical palpomere attached at end of preapical one, strongly expanded and securiform. Cervical sclerites well developed.

Prothorax strongly transverse, about $0.5 \times$ as long as wide; sides strongly curved and explanate; anterior edge very weakly trisinuate, almost truncate; anterior angles rounded, not produced forward; posterior angles more or less right; lateral carinae complete and finely denticulate, without raised margin; base slightly produced forming broad lobe, slightly emarginate at midline, with distinct margin obliterated laterally; disc very slightly, somewhat unevenly convex with narrow, slightly curved, transverse basal groove joining pair of small, deep foveae.

Prosternum moderately well developed, almost as long as shortest coxal diameter; anterior edge slightly concave; intercoxal process long, moderately narrow and parallelsided, moderately arched but not extending below coxae, slightly expanded and truncate at apex and slightly overlapping mesoventrite. Procoxae transverse, subtriangular and strongly projecting, with weak longitudinal carina ending before apex; trochantin narrowly triangular, exposed, broadly attached to endopleuron, which is slightly expanded apically with a weak anterior projection. Procoxal cavities very broadly open internally and externally, with no trace of postcoxal, notal projections.

Scutellum (Fig. 8) subpentagonal, with apex somewhat rounded; anterior edge

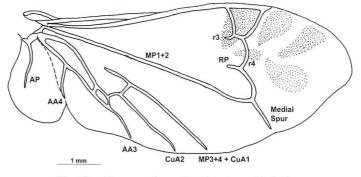


Fig. 12. Nipponocyphon nakanei sp. nov., hind wing.

abruptly raised, straight, simple. Elytra elongate, $1.85-2.25 \times$ as long as wide, only slightly wider at base than prothorax, parallel-sided for basal two-thirds, then gradually narrowed to conjointly rounded apices; humeri well-developed, lying just above sharp carina extending from sides of scutellum to elytral apices; epipleura narrow and extending almost to apex; punctation (Fig. 11) seriate, each elytron with 10 puncture rows and scutellary striole, each interval with additional puncture row.

Mesoventrite (Fig. 10) strongly transverse; sides moderately oblique; anterior edge with pair of narrow, slightly curved and strongly elevated coxal rests; discrimen complete to base of mesoventral process, anterior portion slightly widened forming narrow, shallow groove for reception of short keel lying above prosternal process; mesoventral process short and acute not extending to metaventrite; mesepisternum sharply elevated anteriorly to form narrow procoxal rest; mesepimeron slightly shorter, separated by deep groove (pleural suture); mesocoxal cavities confluent, open laterally (partly closed by mesepimeron); internal meso-metathoracic joint membranous; mesocoxae conical and projecting; mesotrochantin moderately well-developed and exposed, elongate.

Metaventrite slightly transverse, about $0.75 \times$ as long as wide, slightly convex; discrimen complete to base of metaventral process; transverse (katepisternal) suture well developed, extending on each side to about middle of metacoxa; metanepisternum subrectangular, about 3.5 times as long as wide; metepimeron not visible. Metacoxae moderately large, only slightly oblique, extending laterally to elytral epipleura; metacoxal plate complete but more well developed mesally. Metendosternite (Fig. 9) with long stalk, moderately long arms, well-developed ventrolateral processes, long but broad anterior process and well separated anterior tendons.

Hind wing (Fig. 12) about 2.25 times as long as wide; apical field about 0.25 times total wing length, with three broad pigment patches and a narrower, longitudinal one crossing r4; radial cell subtriangular, shorter than broad, its lumen entirely obscured by pigment, which extends beyond the cell basally and posteriorly; cross-vein r3 short, slightly curved, arising separately from r4, which is strongly curved and complete; basal portion of **RP** very short and straight; radio-medial loop broad; medial spur straight,

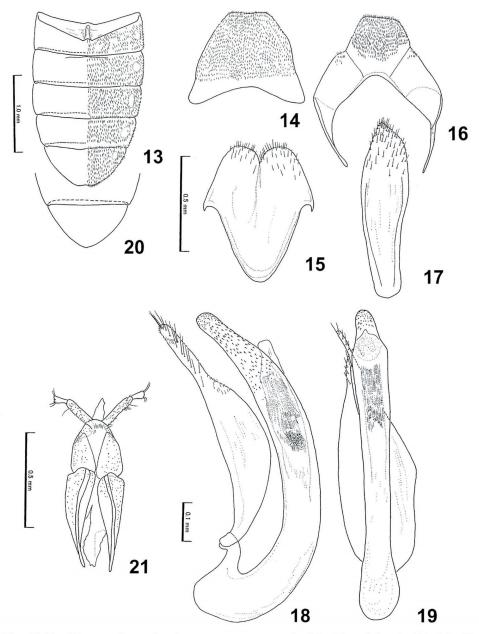
almost reaching wing margin, where there is a slight embayment; medial field with 4 free veins, $MP_{3+4}+CuA_1$, CuA_2 , AA_3 and AA_4 , the last of which extends to anal fold; MP_{3+4} without basal spur or cross-vein; wedge cell small, about half as long as medial spur, obliquely truncate at apex, with CuA_{1+2} arising at about apical third and subequal in length to CuA1; anal notch deep; AP_{3+4} simple.

Legs moderately long and slender; trochanter moderately long; trochanterofemoral joint oblique but well removed from coxa; femora and tibiae subequal in length, the former slightly enlarged at middle, the latter slender and only barely expanded apically; tibial surfaces without longitudinal carinae or spines; tibial spurs short, simple, subequal; tarsus about half as long as tibia, tarsomere 1 about as long as 2 and 3 combined, slightly expanded ventrally; tarsomeres 2 to 4 more strongly expanded ventrally forming lobes, those on 2 and 3 more or less truncate, that on 4 distinctly emarginate; tarsomere 5 longest, tarsomeres 1–4 setose below; pretarsal claws simple; empodium not apparent.

Abdomen (Fig. 13) about 2.35 times as long as wide, flattened; ventrites 1–4 more or less equal in length, 5 slightly longer; all freely articulated; laterosternites sharply delimited, narrow. Tergites I–VIII lightly sclerotized; spiracles located in pleural membrane, absent on segment VIII; tergite VIII in male (Fig. 14) broadly truncate and densely setose apically and broadly emarginate at base, sternite VIII (Fig. 15) with median apical incision separating two broadly rounded lobes, basally with broadly rounded plate sclerotized rim. Tergite VIII in female slightly emarginate apically, basally with paired, slightly divergent, lateral struts, sternite VIII deeply emarginate apically forming pair of widely separated laterotergites, but fused at base with tergite X, which is truncate and setose at apex; sternite IX (Fig. 17) elongate asymmetrical, with obliquely truncate apex and broadly rounded basal plate with sclerotized rim. Rectum with 6 cuticular rings.

Aedeagus (Figs. 18–19) lying on its side when retracted; penis somewhat compressed laterally, curved so that when protracted the apex is slightly curved dorsally and the base more strongly curved dorsally, with a narrow projection to which the symmetrical parameres are attached; each paramere long and moderately narrow, expanded at middle and narrowed again apically to form narrowly rounded lobe with few setae at apex; apex of penis bearing several spicules; endophallus with mass of longitudinally oriented setae or spicules.

Ovipositor (Fig. 21) slightly shorter than as last two ventrites combined and 2.7 times as long (excluding styli) as greatest width, widest at middle; lightly sclerotized except for baculi. Proctiger (tergite X) lightly sclerotized, broadly rounded and densely setose at apex; paraprocts almost as long as gonocoxites, parallel-sided, with ventral sinuate bacula slightly converging apically; proximal gonocoxites about as long as combined width, with transverse, slightly oblique bacula, and sides strongly converging apically; distal gonocoxites each about 6 times as long as wide, parallel-sided and palpiform; styli apical, expanded and truncate, each bearing 2 setae, one at each apical angle.



Figs. 13-21. *Nipponocyphon nakanei* sp. nov., paratype, male (13-19) and female (20-21); 13, abdomen; 14, tergite VIII; 15, sternite VIII; 16, tergite IX-X; 17, sternite IX; 18, aedeagus in lateral view; 19, aedeagus in ventral view; 20, sternite VII; 21, ovipositor.

Gender. Masculine.

Nipponocyphon nakanei sp. nov.

(Figs. 1-21)

Description. Male. Length 4.3-4.45 mm. Body about 2.5 times as long as wide, more or less parallel-sided and flattened, clothed with suberect, yellow hairs. Coloration vellow to reddish-brown or dark brown; head, prothorax, undersides, antennae and legs somewhat lighter than elytra, which may be lighter mesally than laterally. Head (without labrum) $0.80 \times as$ long as wide, more or less flattened, slightly, irregularly concave at middle, finely and densely punctate; eyes prominent. Antennae moderately long, extending posteriorly to about basal fourth of elytra; antennomeres 3-11 distinctly longer than wide, 11 more than 1.5 times as long as 10 and more than twice as long as wide. Pronotum about 0.5 times as long as wide, sides explanate and subsinuate, widest just in front of middle; disc somewhat uneven, with transverse groove joining pair of broad, weak impressions behind anterior edge, pair of weak, paramedial elevations separated by longitudinal groove just in front of middle, pair of longitudinally oval impressions just behind middle, and slender transverse groove joining pair of small, sublateral pits just in front of posterior edge; punctation fine and dense. Elytral about twice as long as wide and 5 times as long as pronotum, with rows with punctures which are coarser and more densely packed than on pronotum, but with rows of smaller punctures in intervals; interspaces smooth and shiny. Ventrite V moderately evenly rounded except at apex, where there is a narrow, shallow emargination.

F e m a l e. Length 4.6 mm. Antennae somewhat shorter than in male, with antennomere 11 less than 1.5 times as long as 10 and less than 1.5 times as long as wide. Body 2.34 times as long as wide. Pronotum 0.51 times as long as wide. Elytra 1.96 times as long as wide and 5.11 times as long as pronotum. Ventrite 5 evenly, narrowly rounded at apex.

Measurements and ratios. Measurements in mm: TL (male) 4.3-4.45 (4.36), PL 0.6-0.68 (0.65), PW 1.16-1.36 (1.26), EL 3.12-3.6 (3.4), EW 1.44-1.88 (1.66 ± 0.19). Ratios: BL/EW 2.21-2.63 (2.46); PL/PW 0.50-0.53 (0.52), EL/EW 1.85-2.24 (2.06); EL/PL 4.88-5.67 (5.24). Ratio of antennomere lengths: male: 1.12 : 1.00 : 1.75 : 1.75 : 1.62 : 1.50 : 1.50 : 1.50 : 1.50 : 2.40; female: 1.43 : 1.00 : 1.71 : 1.57 : 1.43 : 1.43 : 1.43 : 1.29 : 1.29 : 1.29 : 1.86. Antennomere length-width ratios: (male) 1.12 : 1.33 : 1.75 : 1.55 : 1.44 : 1.33 : 1.33 : 1.33 : 1.33 : 2.22; (female) 1.25 : 1.16 : 2.00 : 1.57 : 1.25 : 1.25 : 1.11 : 1.00 : 1.00 : 1.00 : 1.44.

Type material. Holotype: Male, Nikko, Tochigi Pref., 11~13-VI-1967, H. TAKIZAWA leg. (NSMT). Paratypes: 1 female, Tashiroyama-rindô, 1,300 m, Kuriyama, Tochigi Pref., 6-VI-1982, N. MORISHIMA leg (ANIC, dry wing slide and dissection in glycerine); 1 male, Mt. Gomadan, Wakayama Pref., 22-V-1997, I. MATOBA leg. (NSMT); 1 male, Chû-zenji, Tochigi Pref., 9-VII-1917, Edme GALLOIS (SEHU); 1 male, Jôju, Iyo, 1~3-VI-1967, T. KOSAKA (SEHU); 1 female, Shôbugahama, Nikkô-

shi, Tochigi Pref., 11–VI–2005, S. MAEHARA leg. (NMW); 1 male, Mt. Jirôgyû (F.I.T), Kisawa-son, Tokushima Pref., $4\sim13$ –VI–2004, K. TANAKA leg. (NZAC); 1 female, Hikawa-path, Daibosatsu Mts., Yamanashi Pref., 14–VI–1992, S. TSUYUKI leg. (EUM); 1 male, Okuyarito (FIT), Kisawa-son, Tokushima Pref., 31–V ~4 –VI–2004, K. TANAKA leg. (EUM); 1 male, Mt. Maruzasayama, near Mt. Tsurugi, Tokushima Pref., 11–VI–1972, M. YOSHIDA leg. (EUM); 1 female, Oodaigahara, Kamikitayama-mura, Nara Pref., $21\sim24$ –VI–2005, T. KISHIMOTO leg. (NSMT); 1 male & 1 female, Otomedani (alt. 1,260 m), Higashiiya, Miyoshi, Tokushima Pref., 28–V ~5 –VI–2006 (FIT), K. TANAKA leg. (EUM); 1 male, Minokoshi (alt. 1,360 m), Higashiiya, Miyoshi, Tokushima Pref., 28–V ~5 –VI–2006 (FIT), K. TANAKA leg. (NMW).

Distribution. Japan (Honshu, Shikoku).

Etymology. The species is named after the late Dr. Takehiko NAKANE, who gave us the opportunity to study this species.

Cladistic Analysis

In order to assess the phylogenetic relationships of *Nipponocyphon* to selected genera of Scirtidae and members of related families of basal Polyphaga, 56 adult morphological characters were coded for *Nipponocyphon*, 21 genera of Scirtidae, and one taxon each from the families Derodontidae, Eucinetidae and Decliniidae (see Appendices 1 and 2). The data were initially coded in Delta format using the Delta Editor (DALLWITZ *et al.*, 2000 a, 2000 b) and converted to Hennig86 (FARRIS, 1988) files for use with Winclada (NIXON, 1999) and Nona (GOLOBOFF, 1999). All characters were treated as unordered. With all taxa and characters included and *Derodontus* as outgroup, a heuristic search using multiple TBR + TBR with 95 replications produced three shortest trees with a length of 169, consistency index of 41 and retention index of 59. A strict consensus of these trees is shown in Fig. 22 with Bremer support values given for the major nodes; the same tree showing unambiguous character changes is shown in Fig. 23.

In all trees, *Nycteus* is basal to three unresolved clades: *Declinia*, *Nipponocyphon* and remaining Scirtidae; *Stenocyphon* is basal to the remaining 20 scirtid genera (hereafter referred to as Scirtidae MP), a clade is formed with *Hydrocyphon*, *Amplectopus*, *Sarabandus*, *Sacodes* and *Elodes*, and the following generic pairs are recognized: *Sacodes* +*Elodes*, *Atopida* +*Byrrhopsis*, *Macrodascillus* +*Prionocyphon* and *Scirtes* +*Ora*. In one of the trees *Nipponocyphon* or *vice versa*. The *Declinia* +*Nipponocyphon* + *Scirtidae* clade has a Bremer value of 4 and is supported by seven synapomorphies, but only three, 39–1 (metendosternite with ventrolateral processes), 41–1 (AA₄ meeting anal fold) and 51–1 (loss of spiracles on segment VIII) are unique and unreversed. Of the three changes supporting *Stenocyphon* + *Scirtidae* MP, 52–2 (fusion of tergites IX and X) is unique and unreversed and 53–0 (absence of rectal rings) is a reversal to the condition in *Derodontus*. There appears to be more substantial support for the Scirtidae MP clade,

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Table

CHARACTERS	01	02	03	04	05	90	07	08 (09 1	10 1		12 13	F	4 15	16	17	18	19	20	21	22	23	24	25	26	27 2	28
Derodontus	0	0	0	0	0	0	0	0	0 0		0 0	0	0	0	0	0	0	0	0	0	0	-	0	-	0	-	
Nycteus	0	-	-	0	0	-	0	0	1 0		0 0	0	0	0	0	0	0	0	0	0	-	0	0	0	0	-	
Declinia	-	0	-	0		0	0	0	0 1		0	0 (0	0	-	0	0	0	0	0	0	0	1	1	0	0 0	-
Nipponocyphon	-	0	1	0	0	0	0	0	0 1	0	0 0	0	0	0	-	0	0	-	0	0	0	-	1	1	0	0 1	
Stenocyphon	1	0	1	0	0	0	1	0	0 0	0 (0 (1	0	0	0	0	0	0	0	-	0	0	1	1	0	0	-
Cyphotelus	0	0	1	0	0	0	0	0	1	0	1	-	2	-	0	-	-	0	1	0	0	0	1	1	0	-	
Atopida	0	1	1	0	0	0	0	0	2 1	0	1	2	2	1	0	1	1	0	1	0	2	0	1	0	1	0 1	
Veronatus	0	-	1	0	0	0	1	0	2 1	0	1	2	2	-	0	0	0	0	0	0	1	0	1	0	-	0 1	
Amplectopus	0	-	1	0	-	0	0	0	0 1		0) 2	2	-	0	0	0	0	0	0	2	0	1	0	0	1	
Macrohelodes	0	0	1	0	0	0	1	0 (0 1	0	1	2	0	1	0	0	0	0	0	0	1	0	0	0	1	0 1	
Macrodascillus	0	0	1	-	0	1	2	1	1	0	1	2	2	-	0	-	0		0	0	1	0	0	0	1	0 1	
Macrocyphon	0	-	1	0	0	0	1	0	1	0	1	2	2	1	0	0	0	0	0	0	2	0	1	0	1 0	0 1	
Pseudomicrocara	0	0	1	0	0	0	1	0 (0 1	0	1	2	0	1	0	-	0	1	0	1	0	0	0	1	1	0 1	
Byrrhopsis	0	-	1	0	0	0	1	0	1	0	1	2	2	-	0	-	0	0	0	0	2	0	1	0	1	0 1	
Heterocyphon	0	0	1	0	0	0	0	0	1	0	1	2	1	1	0	0	0	0	0	1	0	0	1	1	1	0 1	
Cyphanus	0	-	1	0	0	0	1	0	2 1	0	1	2	2	-	0	2	0	-	0	0	0	0	0	0	1) 1	
Prionocyphon	0	0	1	1	0	1	1	1	1	0	1	2	2	1	0	2	0	0	0	0	0	0	0	0	0	0 1	
Sarabandus	0	0	1	0	0	0	1	0 (0 1	0	0 () 2	2	1	0	0	0	1	0	1	0	0	1	1	0	-	
Microcara	0	0	1	0	0	0	1	0 (0 1	0	0 () 2	2	1	0	2	0	1	0	1	0	0	0	0	1	0 1	
Sacodes	0	0	1	0	0	1	2	0 (0 1	0	0 (1	2	1	0	2	0	1	0	1	0	0	2	1	0	-	
Elodes	0	0	1	0	0	1	2	0	0 1		0 0	-	2		0	2	0	1	0	1	0	0	2	1	0	1	
Scirtes	0	0	1	0	0	1	0	0	0 1	0	0 () 2	2	1	0	2	0	1	0	0	0	0	2	0	0	0 1	
Ora	0	0	1	0	0	0	0	0	0 1		0 0) 2	2	1	0	2	0	1	0	0	1	0	2	0	0	0 1	
Hydrocyphon	0	0	-	0	0	-	0	0	0	0	0	-	-	-	0	0	0	0	0	0	0	0	-	1	0	-	
Cyphon	0	0		0	0	0	-	0	0	0	-	2	2	-	0	0	0	0	0	0	-	0	_	-	0	0 1	

CHARACTERS	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43 4	44 4	45 4	46 47	7 48	8 49	50	15 (52	53	54	55	56
Derodontus	-	0	0	-	1	1	0	0	0	0	0	_	0	-	0 0	-	0	0	0	0	0	0	-	0	0	0	0
Nycteus	0	0	0	0	0	-	1	2	0	0	0	0	0	0	0 0	-	0	0	-	0	0	0	-	0	0	-	0
Declinia	-	-		0	0	5	1	1	1	0	1	0	0	0	-	-	-	0	0	-	0	-	-	0	0	-	0
Nipponocyphon	0	0	0	0	-	1	0	0	0	1	1	0	0	1	0	-	0	0	0	0	0	-	0	0	-	-	0
Stenocyphon	0	-	0	0		0		0	0	2	1	_	0	-	1	-	0	0	-	0	0	-	0	0	2	0	0
Cyphotelus	0	1	0	-	0	1	1	0	0	1	1	0	-	_	-	-	5	0	0	0	0	-	-	-	2	0	-
Atopida	-	-	0	-	0			2	0	1	1	0	1	_	-	-	1	0	0	0	0	-	-	-	2	0	-
Veronatus	-	-	0	0	0	-	-	0	0	_	1	0	-	_	-	-	2	0	0	0	0	-	-	-	0	0	-
Amplectopus	-	-		-	-	2	0	1	1	0	1	0	-	_	1 1	-	-	0	0	-	0	-	-	-	2	0	-
Macrohelodes	-	-	0	-	0	-	-	0	0	1	1	0	1	-	-	0	2	0	0	0	0	-	-	-	2	0	-
Macrodascillus	-	-	0	0	0	-	-	-	0		-	0	1	-	1	0	2	0	0	0	0	-	-	-	2	0	
Macrocyphon	-	-	0	-	0	1	-	_	0	-	-	0	-		1	-	2	0	0	2	0	-	-	-	5	0	-
Pseudomicrocara	-	-	0	0	0	-	-	-	0	-	1	0	1	-	1	0	2	0	0	0	0		-	-	0	0	-
Byrrhopsis	-	-	0		0	-	-		0	1	1	0	1	-		-	2	0	0	0	0			-	2	0	-
Heterocyphon	-	-	0	-	0	-	_	_	0	_	-	0	-	_	-	0	2	0	0	0	0			-	5	0	-
Cyphanus	-	-	0	0	0	_		-	0	_	-	0	-	1	1	1	2	0	0	0	0	-	-	-	0	0	-
Prionocyphon	-	-	0	0	0	-	-	-	0	_	1	0	_	_	1	0	2	0	0	0	0	-	-	-	5	0	-
Sarabandus	0	-	0	-	-	0	0	_	0	_	1	0	1	1	-	0	2	0	0	0	0	-	-	-	5	0	-
Microcara		-	0	-	-	0	0	-	0		1	0	1	1	1	0	2	0	0	0	0		-		2	0	-
Sacodes	0	-	0	-	-	0	0	0	0	_	-	0	-	-	1	1	2	0	0	0	-	-	-	-	5	0	-
Elodes	0	-	0	-	-	0	0	0	0	_	-	0	-	1	1	1	2	0	0	0	-	-	-	-	5	0	-
Scirtes	-	-	0	0	0	-	_	0	0	5	-	0	-	-	1	1	2	-	-	0	0	-	-	-	5	0	-
Ora		-	0	0	0	-	_	_	0	5	-	0	-	-	1	1	2	-	-	0	0	-	-	-	5	0	-
Hydrocyphon	0	-	0	0	0	-	0	-	0	1	1	0	-	_	-	-	5	0	0	0	0		-	-	5	0	-
Cyphon	0	-	0	0	0	-	-	0	0	-	-	0	_	-	1	1	2	0	0	0	0	-	-	-	5	0	-

Table 1 b. Continued.

John F. LAWRENCE and Hiroyuki YOSHITOMI

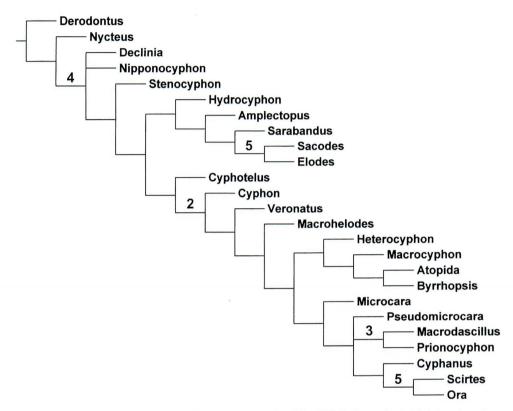


Fig. 22. Strict consensus of three shortest trees produced by NONA from the total data set, using multiple TBR + TBR (mult*max*) with 95 replications and one starting tree per replication, showing Bremer support values of 2 or more. Length=169 (CI=41, RI=59).

but its Bremer support is only one. Of the eight unambiguous changes, 15,1 (loss of lacinial uncus), 41–1 (reduction of veins in medial field), 52–0 (parallel or diverging basal struts on sternite VIII), 53–1 (base of segment IX open) and 56–1 (fusion or loss of parameres) are unique and unreversed. Within the clade containing most scirtid genera, the only clades with relatively strong Bremer support are *Sacodes* + *Elodes* (5), *Scirtes* + *Ora* (5) and *Macrodascillus* + *Prionocyphon* (3). The low support value for Scirtidae MP appears to be associated with the inclusion of *Amplectopus*, a genus which is discussed further below. When the analysis is run with this genus excluded and with five uninformative characters deactivated, the resulting copnsensus of 9 shortest trees has a similar topology, but Scirtidae MP has a Bremer value of 4 and a clade formed by *Sarabandus* + *Elodes* + *Sacodes* has a value of 2. A final analysis excluding *Derodontus*, with *Nycteus* as outgroup, produced the single shortest tree shown in Fig. 24; here again the Bremer value was 4 for Scirtidae MP, with *Declinia* basal to *Nipponocyphon* + Scirtidae MP.

518

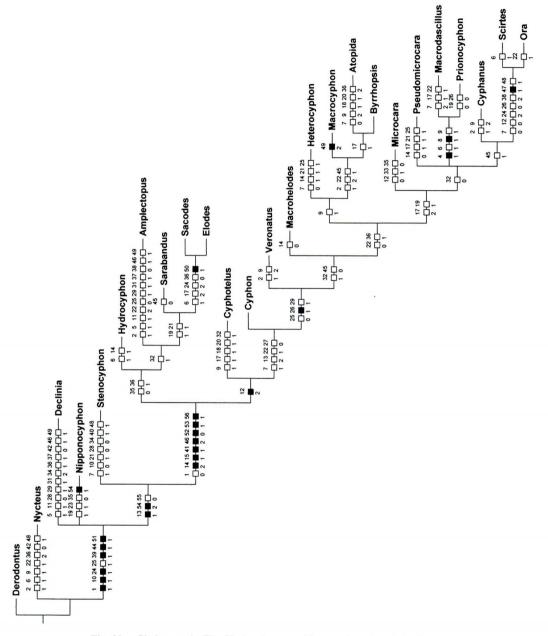


Fig. 23. Cladogram in Fig. 22 showing unambiguous character state changes.

Discussion

Phylogenetic relationships of the family Scirtidae and other members of the superfamily Scirtoidea (=Eucinetoidea of CROWSON, 1960) have been reexamined in several recent works. LAWRENCE et al. (1995) included Scirtoidea at the base of the series Elateriformia (Dascilliformia of CROWSON, 1950, 1955), but since then it has become apparent through both morphological (LAWRENCE, 2001) and molecular (CATERINO et al., 2002) studies that both Scirtoidea and Derodontidae may occupy a more basal position within Polyphaga. In their study of the pterothorax of selected Scirtidae (species of Elodes, Cyphon, Pseudomicrocara and Ora), FRIEDRICH and BEUTEL (2006) failed to find support for a basal position of Scirtoidea within Polyphaga except for the absence of a hind wing "bending zone" in all other elateriform lineages; however an inclusion of this superfamily within Elateriformia was only weakly supported by an elongate metanepisternum, triangular radial cell and reduction of RP branches in the apical field of the hind wing. The absence of a bending zone cannot be considered a synapomorphy for Elateriformia excluding Scirtoidea, since this occurs at least in some Artematopodidae. However, those features used to unite scirtoids with Elateriformia are either unclear or just incorrect: a short, broad metanepisternum occurs both in the scirtoid family Eucinetidae and in some Rhipiceridae among the basal Elateriformia, the boundary between "rounded" and "triangular" radial cells appears to break down in various Elateriformia, as well as in Bostrichiformia - Cucujiformia, and RP branches in the apical field are quite obvious at least in Dascillidae. The position of the Scirtoidea continues to remain ambiguous, and will hopefully be clarified by the use of a larger morphological character set combined with DNA data.

The discovery of the family Decliniidae (NIKITSKY et al., 1994) reinforced the link between Scirtidae and Eucinetidae, since *Declinia* shared a type of aedeagus and the presence of rectal rings with Eucinetidae, while the wing venation and loss of the eighth spiracles were more reminiscent of Scirtidae. The unusual Chilean genus *Stenocyphon* (LAWRENCE, 2001) has a large exposed protrochantin like that in *Declinia* and trilobate aedeagus with a distinct phallobase; however the reduced prosternum, projecting procoxae, reduced eighth spiracles and wing venation are more typical of the family Scirtidae, in which the genus was placed. In *Nipponocyphon*, we have yet another transitional form, which, like *Stenocyphon*, lacks the two tibial carinae present in almost all scirtids and has an atypical aedeagus, which lacks a phallobase but has articulated parameres. Furthermore, it has the rectal rings found in Eucinetidae and Decliniidae and 10 distinct elytral puncture rows plus a scutellary striole, which occur in no other scirtid.

Based on the above analyses, *Nipponocyphon* either lies outside the family Scirtidae or forms the most basal scirtid clade. Although it forms a monophyletic group with *Declinia* in one of the three trees produced with the total data set, it never clusters with *Stenocyphon*. The latter genus is weakly attached to a strongly supported main scirtid clade in all trees. The present data set does not support any strongly supported clades

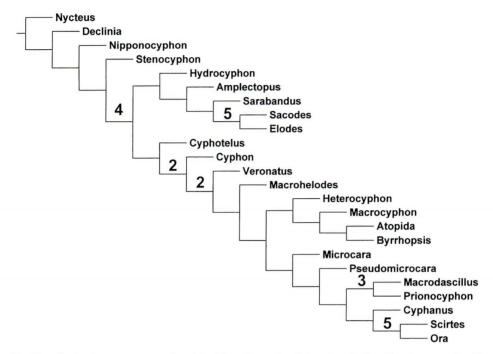


Fig. 24. Single shortest tree produced by Nona from the data set excluding *Derodontus* and with *Nycteus* as outgroup, using the same search strategy and showing Bremer support values of 2 or more. Length=153 (CI=41, RI=58).

within Scirtidae proper, except for the generic pairs Elodes + Sacodes, Scirtes + Ora and possibly Macrodascillus + Prionocyphon.

Currently available data on phylogenetic relationships within the family Scirtidae, as summarized by YOSHITOMI (2005), are based primarily on Palaearctic genera and rely to a great extent on characters of the larvae. Unfortunately, larvae are unknown for critical taxa discussed above and none of the Southern Hemisphere larvae described by HANNAPEL and PAULUS (1991) have been associated with adults. The cladogram produced by HANNAPEL and PAULUS (1987), based on larval characters only, and that of YOSHITOMI (2005), based on both larvae and adults, agree in the separation of an *Elodes* + *Sacodes* clade from a clade containing the remaining Palaearctic genera with *Hydrocyphon* at its base. The cladograms produced here contain the same two clades, but with *Hydrocyphon* attached to the former rather than the latter.

The most problematic genus within the main body of Scirtidae is the New Zealand *Amplectopus*, which was moved to the family Chelonariidae by KASAP and CROWSON (1975), based mainly on the fusion of the first three ventrites, and returned to Scirtidae by LAWRENCE *et al.* (1995). Although the reduced prosternum, type of metendosternite and wing venation in *Amplectopus* are typical of Scirtidae, several divergent features are similar to those in *Declinia*. These include the 5-segmented antennal club, distinctive

pedicel shape, dorsal mandibular carina, apically widened epipleura, mid leg impressions on metaventrite, mesepisternum and epipleura, single tibial carina, and fusion of the basal three ventrites. As pointed out by LAWRENCE et al. (1995), some of these features differ in detail. The Amplectopus antenna, for instance, lacks the specialized sensilla found in Declinia. Furthermore, the aedeagus is of a distinctive type found only in the family Scirtidae (NYHOLM, 1972, 2000; YOSHITOMI, 2005). The tegmen is dorsoventrally flattened and deeply emarginate, with a broad base but no indication of a separate phallobase, and the penis is also flattened, with styliform parameroids and a prostheme bearing a pair of short lateral hooks.

The information presented above presents us with the following nomenclatural options: 1) to include Declinia in a more broadly defined Scirtidae, also including Nipponocyphon and Stenocyphon, 2) to place Nipponocyphon in a new family, 3) to propose new scirtid subfamilies for both Nipponocyphon and Stenocyphon, or 4) to include Nipponocyphon in Scirtidae but make no changes at the supergeneric level. We hesitate to make family level changes at this time, especially when immature stages are known for none of these taxa. On the other hand, we feel that some changes in classification should reflect the basal positions of both Nipponocyphon and Stenocyphon and the number of important adult features uniting the remaining scirtid genera. We therefore propose the following new taxa: Nipponocyphoninae subfam. nov. and Stenocyphoninae subfam. nov., for the genera Nipponocyphon and Stenocyphon, respectively. At the present time, there are no other subfamilies or tribes within Scirtidae, except for Atopidini proposed without justification by PIC (1914) for the New Zealand genus Atopida. The subfamilies of Scirtidae may be separated by the following key:

1. Prosternum in front of coxae at least half as long as prosternal process; elytra with 10 distinct puncture rows and scutellary striole; mandible with well developed mola and membranous prostheca; apical maxillary palpomere strongly expanded apically, subtriangular; sides of pronotum broadly explanate with denticulate edges; hind wing with wedge cell; tergite X at least partly free from tergite IX; aedeagus with phallobase absent and parameres articulated to base of penis.Nipponocyphoninae

- Prosternum in front of coxae less than half as long as prosternal process; elytra punctation not seriate; mandibular mola, if present, not accompanied by membranous prostheca; apical maxillary palpomere not or only slightly expanded apically; sides of pronotum, if explanate, not denticulate; hind wing without wedge cell; tergite X completely fused to tergite IX; parameres articulated to
- 2. Frontoclypeal suture distinctly impressed; mandible bidentate; lacinia with uncus; protrochantin large, quadrate and broadly exposed; hind wing with 4 free veins in medial field; outer edge of tibia without longitudinal carina; aedeagus laterally compressed with distinct phallobase and articulated parameres. Stenocyphoninae

522

Frontoclypeal suture vaguely impressed or absent; mandible unidentate; lacinia without uncus; protrochantin slender and usually more or less concealed by strongly declined head; hind wing with 3 or fewer free veins in medial field; outer edges of tibiae almost always with paired longitudinal carinae (rarely with single carina); aedeagus dorsoventrally flattened, without phallobase and with parameres fixed or absent.

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Appendix 1. Taxa for Cladistic Analyses

Amplectopus SHARP, 1886. Based on Amplectopus ovalis SHARP (New Zealand).

Atopida WHITE, 1846. Based on Atopida lawsoni BROUN and Atopida sp. (New Zealand).

Byrrhopsis CHAMPION, 1913. Based on B. gravidus (SHARP) (New Zealand).

Cyphanus SHARP, 1878. Based on Cyphanus sp. (New Zealand).

Cyphon PAYKULL, 1799. Based on C. brevicollis LECONTE (western North America), C. collaris (GUÉRIN-MÉNEVILLE) (eastern North America), C. concinnus LECONTE (western North America) and Cyphon spp. and descriptions and illustrations in YOSHITOMI (2005).

Cyphotelus SHARP, 1878. Based on C. angustifrons SHARP 1878, 58 (New Zealand).

Declinia NIKITSKY et al., 1994. Based on females of *D. relicta* NIKITSKY et al. (eastern Russia) and *D. versicolor* SAKAI et SATÔ (Japan) and descriptions and illustrations in SAKAI & SATÔ (1996).

Derodontus LECONTE, 1861. Based on Derodontus spp. (North America).

Elodes LATREILLE, 1796. Based on *E. apicalis* LECONTE (North America) and descriptions and illustrations in YOSHITOMI (2005).

Heterocyphon ARMSTRONG, 1953. Based on H. australis (ERICHSON) (Australia).

- Hydrocyphon REDTENBACHER, 1858. Based on H. satoi YOSHITOMI (Japan) and descriptions and illustrations in YOSHITOMI (2005).
- Macrocyphon PIC, 1918. Based on M. spencei ARMSTRONG (Australia).

Macrodascillus CARTER, 1935. Based on M. denticornis CARTER (Australia).

Macrohelodes BLACKBURN, 1892. Based on M. crassus BLACKBURN (Australia).

Microcara THOMSON, 1859. Based on M. explanata (LECONTE) (northern North America) and M. testacea (LINNAEUS) (Europe).

Nipponocyphon gen. nov. Based on N. nakanei sp. nov. (Japan).

Nycteus LATREILLE, 1829. Based on N. infumatus (LECONTE) (North America).

Ora CLARK, 1865. Based on Ora spp. (Florida and Brazil) and descriptions and illustrations in YOSHITOMI (2005).

Prionocyphon REDTENBACHER, 1858. Based on P. discoideus (SAY) (eastern North America) and P. niger KITCHING et ALLSOPP (Australia) and descriptions and illustrations in YOSHITOMI (2005).

Pseudomicrocara ARMSTRONG, 1953. based on P. orientalis ARMSTRONG and P. variabilis ARMSTRONG (Australia).

Sacodes LECONTE, 1853. Based on S. pulchella (GUÉRIN-MÉNEVILLE) and S. thoracica (GUÉRIN-MÉNEVILLE) (North America) and descriptions and illustrations in YOSHITOMI (2005).

Sarabandus LEECH, 1955. Based on S. robustus (LECONTE) (eastern North America).

Scirtes ILLIGER, 1807. Based on Scirtes spp. (North America and Australia) and descriptions and illustrations in YOSHITOMI (2005).

Stenocyphon LAWRENCE, 2001. Based on S. sasajii LAWRENCE (Chile).

Veronatus SHARP, 1878. Based on V. tricostellus (WHITE) and Veronatus sp. (New Zealand).

Appendix 2. Characters and Character States for Cladistic Analyses

- 1. Frontoclypeal suture: 0, vaguely impressed or absent; 1, distinctly impressed.
- 2. Subocular carina: 0, absent; 1, present. This refers to a sharp ridge lying between the subgenal ridge and the eye, thus forming one edge of the subantennal groove.
- 3. Subgenal ridge: 0, absent; 1, less sharply defined and located immediately beneath and behind eye; 2, more sharply defined and extending well behind eye.
- 4. Antennomere 1: 0, not or only slightly inflated, not carinate; 1, strongly inflated and more or less carinate.
- 5. Antennomere 2: 0, not wider at base than at apex; 1, distinctly wider at base than at apex.
- 6. Antennomere 3: 0, not distinctly shorter than 2; 1, distinctly shorter than 2.
- Antennomere 4: 0, shorter than 2 and 3 combined; 1, between 1 and 2 times as long as 2 and 3 combined; 2, more than 2 times as long as 2 and 3 combined.
- 8. Antennomeres 4 to 10: 0, neither serrate nor pectinate; 1, serrate or pectinate.
- 9. Apex of labrum: 0, subtruncate to slightly convex; 1, slightly concave or emarginate; 2, deeply emarginate or bilobed.
- 10. Mandible: 0, bidentate; 1, unidentate.
- 11. Dorsal surface of mandible: 0, without carina fitting over sides of labrum; 1, with carina fitting over sides of labrum.
- 12. Mesal edge of mandible: 0, without teeth or retinacula; 1, with two or more teeth or retinacula.
- 13. Mesal edge of mandible: 0, with membranous prostheca (sometimes accompanied by fringe of hairs); 1, with fringe of hairs only; 2, with neither prostheca nor fringe of hairs.
- 14. Mandibular mola: 0, well developed (occupying basal fifth or more); 1, very small (occupying basal tenth); 2, absent.
- 15. Lacinial apex: 0, with uncus; 1, without uncus. This refers to a sclerotized, hook-like process, usually tridentate.
- 16. Apical maxillary palpomere: 0, cylindrical to fusiform, not apically expanded; 1, apically expanded and subtriangular.

- 17. Preapical labial palpomere: 0, not distinctly enlarged or oblique at apex, apical palpomere arising from about middle of apical edge; 1, distinctly enlarged and oblique at apex, apical palpomere arising near inner portion of apical edge; 2, highly distorted, so that apical palpomere arises at middle or near base and palpi appears bifurcate.
- 18. Prothorax: 0, not widest anteriorly; 1, widest anteriorly.
- 19. Sides of prothoracic disc: 0, not or slightly explanate; 1, distinctly explanate.
- 20. Base of prothorax: 0, not or slightly narrower than elytral bases; 1, distinctly narrower than elytral bases.
- 21. Anterior edge of pronotum: 0, truncate or emarginate, not forming continuous curve with lateral edges; 1, strongly rounded, forming continuous curve with lateral edges.
- 22. Anterior angles of pronotum: 0, absent or not produced forward; 1, produced and rounded or broadly angulate; 2, produced and acute.
- 23. Lateral pronotal carinae: 0, simple or minutely crenulate; 1, denticulate.
- 24. Posterior angles of pronotum: 0, absent or broadly rounded; 1, obtuse or right; 2, moderately to strongly acute.
- 25. Pronotal disc just in front of posterior edge: 0, without pair of small pits; 1, with a pair of small pits.
- 26. Prosternal process: 0, not abruptly bent, broadened and flattened at apex; 1, abruptly bent, broadened and flattened at apex.
- 27. Prosternal process ventrally: 0, extending almost to coxal apex; 1, ending well before coxal apex.
- 28. Protrochantin: 0, large and subquadrate, lying between coxa and edge of notum, forming part of lateral thoracic wall; 1, small and narrow, lying in front of coxa and not forming part of thoracic wall.
- 29. Anterior edge of scutellum: 0, not or gradually elevate; 1, abruptly elevated forming sharp ridge.
- 30. Elytral punctation: 0, distinctly seriate; 1, not distinctly seriate.
- 31. Elytral epipleuron: 0, narrowed apically; 1, slightly widened at apex.
- 32. Mesoventrite: 0, divided by longitudinal groove or discrimen; 1, not divided by longitudinal groove or discrimen.
- 33. Mesoventral cavity: 0, present; 1, absent. This refers to a distinct depression lying between and in front of the mesocoxal cavities and not just a slight widening of the mesothoracic discrimen.
- 34. Mesocoxal cavities: 0, contiguous; 1, narrowly separated; 2, moderately to widely separated (more than $0.4 \times$ shortest diameter of coxal cavity).
- 35. Apex of mesoventral process: 0, not cleft or emarginate; 1, cleft or emarginate.
- 36. Metathoracic discrimen: 0, complete to base of intercoxal process; 1, incomplete but more than half median length of ventrite (excluding intercoxal process); 2, less than half median length of ventrite (excluding intercoxal process).
- 37. Metaventrite, metepisternum and anterior portion of epipleuron: 0, without impressions for housing mid legs; 1, with impressions for housing mid legs.
- 38. Metacoxal plate: 0, extending to lateral edge of coxa; 1, extending beyond middle of coxa but not to lateral edge; 2, not extending to middle of coxa.
- 39. Metendosternite: 0, without ventrolateral processes; 1, with ventrolateral processes.
- 40. Radial cell of hind wing: 0, forming equilateral triangle; 1, forming elongate triangle.
- 41. Medial field of hind wing: 0, with 4 or more terminal veins; 1, with 3 or fewer terminal veins.

- 42. Cross-vein joining MP_{1+2} and MP_{3+4} : 0, present; 1, absent.
- 43. Wedge cell of hind wing: 0, present; 1, absent.
- 44. Wing vein AA₄: 0, not meeting to anal fold; 1, meeting anal fold.
- 45. Wing vein AP_{3+4} : 0, forked to form AP_3 and AP_4 ; 1, simple or absent.
- 46. Mesotibia: 0, without longitudinal carina; 1, with single longitudinal carina; 2, with paired longitudinal carinae.
- 47. Metafemur: 0, not much wider than mesofemur; 1, much wider than mesofemur.
- 48. Metatibial spurs: 0, more or less equal in length; 1, greatly differing in length.
- 49. Number of basal ventrites connate: 0, none or two; 1, three; 2, four.
- 50. Anterior edge of ventrite 1 (sternite III): 0, with intercoxal process; 1, without intercoxal process.
- 51. Spiracles on segment VIII: 0, present; 1, absent.
- 52. Base of sternite VIII in male: 0, with parallel or diverging lateral struts; 1, with lateral struts meeting to form closed basal rim.
- 53. Base of segment IX in male: 0, closed forming genital ring; 1, open with separate basal struts.
- 54. Proctiger (tergite X) in male: 0, completely free from tergite IX; 1, partly fused to tergite IX; 2. completely fused to tergite IX.
- 55. Rectal rings: 0, absent; 1, present. These structures are illustrated in LAWRENCE et al. (1995, fig. 17).
- 56. Parameres: 0, basally articulated; 1, fixed or absent.

要 約

John F. LAWRENCE・吉富博之:新属 Nipponocyphon の日本からの発見とその系統的位置. — 日本からたいへん特徴的なマルハナノミ科の新属新種ナガマルハナノミ Nipponocyphon nakanei gen. et sp. nov. を記載した. 本属を含め、マルハナノミ科 22 属と外群 3 科 (Derodontidae, Eucinetidae, Decliniidae) に対して成虫の外部形態 56 形質を用い系統解析を行った. その結果、ナガ マルハナノミ属は南米の Stenocyphon 属を含めたマルハナノミ科と姉妹群関係になることが判明 した. そこで、ナガマルハナノミ属と Stenocyphon 属それぞれに Nipponocyphoninae と Stenocyphoninae の新亜科を創設した. また、残りのマルハナノミ科に対して、Scirtinae 亜科を提唱した.

References

CATERINO, M. S., V. S. SHULL, P. M. HAMMOND & A. P. VOGLER, 2002. Basal relationships of Coleoptera inferred from 18S rDNA sequences. *Zool. Scripta*, 31: 41–49.

CROWSON, R. A., 1950. The classification of the families of British Coleoptera (part). Ent. monthly Mag., 86: 327–344.

1955. The Natural Classification of the Families of Coleoptera. 187 pp. N. Lloyd, London.

———— 1960. The phylogeny of Coleoptera. Annual Rev. Ent., 5: 111–134.

DALLWITZ, M., T. A. PAINE & E. J. ZURCHER, 2000 a. 'Principles of interactive keys'. http://biodiversity. uno.edu/delta/.

_____, _____ & _____ 2000 b. User's Guide to the Delta Editor. Edition 1.03. CSIRO Division of Entomology, Canberra, 34 pp.

- FRIEDRICH, F., & R. G. BEUTEL, 2006. The pterothoracic skeletomuscular system of Scirtoidea (Coleoptera: Polyphaga) and its implications for the high-level phylogeny of beetles. J. Zool. Syst. Evol. Res., 44: 290– 315.
- HANNAPPEL, U., & H. F. PAULUS, 1987. Arbeiten zu einem phylogenetischen System der Helodidae (Coleoptera) Feinstrukturuntersuchungen an europäischen Larven. Zool. Beitr., (N. F.), 31: 77–150.
 & 1991. Some undetermined Helodidae larvae from Australia and New Zealand: fine structure of mouthparts and phylogenetic position, pp. 89–128. In: ZUNINO, M., X. BELLÉS & M. BLAS (eds.), Advances in Coleopterology, A. E. C., Barcelona.
- KASAP, H., & R. A. CROWSON, 1975. A comparative anatomical study of Elateriformia and Dascilloidea (Coleoptera). Trans. r. ent. Soc. Lond., 126: 441–495.
- KUKALOVÁ-PECK, J., & J. F. LAWRENCE, 1993. Evolution of the hind wing in Coleoptera. Can. Ent., 125: 181–258.

& _____ & 2004. Relationships among coleopteran suborders and major neopteran lineages: Evidence from hind wing characters. Eur. J. Ent., 101: 95–144.

- LAWRENCE, J. F., 1999. The Australian Ommatidae (Coleoptera: Archostemata): new species, larva and discussion of relationships. *Invert. Tax.*, **13**: 369–390.
 - 2001. A new genus of Valdivian Scirtidae (Coleoptera) with comments on Scirtoidea and the beetle suborders. In MORIMOTO, K., K. MIZUNO, Y. HAYASHI, T. Ito, N. ITO, K. ANDO, M. TANIKADO & S. SHIYAKE, S. (eds.), Sukunahikona. Spec. Publ. coleopterol. Soc., Osaka, (1): 351–361.
 - , N. B. NIKITSKY, & A. G. KIREJTSHUK, 1995. Phylogenetic position of Decliniidae (Coleoptera: Scirtoidea) and comments on the classification of Elateriformia (sensu lato), In PAKALUK, J., & S. A. ŚLIPIŃSKI (eds), Biology, Phylogeny, and Classification of Coleoptera. Papers Celebrating the 80th Birthday of Roy A. Crowson, 375–410. Muzeum i Instytut Zoologii Polska Akademia Nauk, Warsaw.
- NIKITSKY, N. B., J. F. LAWRENCE, A. G. KIREJTSHUK & W. G. GRATSHEV, 1994. A new beetle family, Decliniidae fam. n., from the Russian Far East and its taxonomic relationships (Coleoptera Polyphaga). *Russ. Ent. J.*, 2: 3–10.
- NYHOLM, T., 1972. Zur Morphologie und Funktion des Helodiden-Aedoeagus (Col.). *Ent. Scand.*, 3: 81–119.
 2000. New species, taxonomic notes, and genitalia of New Zealand *Cyphon* (Coleoptera: Scirtidae).
 N. Z. Ent., 22: 45–67.

PIC, M., 1914. Dascillidae, Helodidae, Eucinetidae. Coleopterorum Catalogus, pars 58. 65 pp. W. JUNK, Berlin.

SAKAI, M., & M. SATÔ, 1996. The coleopteran family Decliniidae (Elateriformia, Scirtoidea) new to Japan, with description of its second representative. *Elytra, Tokyo*, 24: 103–111.

YOSHITOMI, H., 2005. Systematic revision of the family Scirtidae of Japan, with phylogeny, morphology and bionomics (Insecta: Coleoptera, Scirtoidea). Jpn. J. Syst. Ent., Mon. Ser., (3), 212 pp. Matsuyama.