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# A review of the genus *Satonius* (Coleoptera: Myxophaga: Torridincolidae): taxonomic revision, larval morphology, notes on wing polymorphism, and phylogenetic implications

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Abstract. The genus Satonius Endrödy-Younga, 1997, is revised. Three new species are described from China: Satonius schoenmanni sp. nov. (Hunan province), S. stysi sp. nov. (Yunnan province), and S. wangi sp. nov. (Zhejiang province). Two additional new species from the Chinese provinces Fujian and Anhui are left undescribed pending the collection of complete specimens and males, respectively. Metathoracic wing venation of S. stysi sp. nov. is shown to differ from the remaining Myxophaga in the presence of the bifurcation of AA<sub>3+4</sub>, which updates the venation groundplan of the suborder. Anterolateral spine-like projection of the metaventrite and the increased number of apical setae on parameres are defined as adult autapomorphies of the genus. Larvae of S. stvsi sp. nov. are described and compared with the larvae of the Japanese S. kurosawai (Satô, 1982). Characters shared by larval Satonius and Ytu Reichardt, 1973 (extremely flattened body covering legs, and modified orientation and unusual morphology of legs) are supposed as parallel adaptations for the larval environment – very thin film of water in seepage habitats. Interspecific wing polymorphism of Satonius is briefly discussed and possible reasons of the wide distribution of the apterous S. kurosawai are hypothesized.

**Keywords.** Coleoptera, Myxophaga, Torridincolidae, *Satonius, Ytu*, new species, larva, Oriental region, Palaearctic region, China, Japan, wing venation, phylogeny, hygropetric habitats.

## Introduction

The Torridincolidae represent the youngest but currently most speciose group of the Myxophaga, comprising about 60 species in seven genera (BEUTEL & VANIN 2005). The family was established by STEFFAN (1964) for a single Afrotropical species *Torridincola rhodesica* Steffan, 1964. Later on, STEFFAN (1973) added two other *Torridincola* species and a new genus and species *Incoltorrida madagassica* Steffan, 1973, from Madagascar, and REICHARDT (1976) described a third Afrotropical genus *Delevea* Reichardt, 1976, with a single species *D. bertrandi* Reichardt, 1976, from South Africa. REICHARDT & COSTA (1967) discovered the Torridincolidae also in the Neotropical region and described a new genus and species *Ptyopteryx britskii* Reichardt & Costa, 1967 (species placed originally in *Ptyopteryx* are currently classified in the genus *Iapir* Py-Daniel, Fonseca & Barbosa, 1993). Subsequently, REICHARDT (1973) described a new genus and species *Claudiella ingens* Reichardt & Vanin, 1976, was described by REICHARDT & VANIN (1976).

The genus *Satonius* Endrödy-Younga, 1997, was erected for *Delevea kurosawai* Satô, 1982, which is the only Japanese species of the family. ENDRÖDY-YOUNGA (1997) confirmed the similarity of adult *Satonius* with the African *Delevea* (based mainly on the 11-segmented antenna, abdominal ventrites without plastron, and elytra without serial punctures) but distinguished *Satonius* on the basis of the sharply crested mesocoxal edge of the metaventrite, discal emargination of the female apical tergite, and reduced hind wings. Moreover, ENDRÖDY-YOUNGA (1997) placed both genera in a new subfamily Deleveinae, defined by the presence of respiratory flaps in *Delevea*. These respiratory flaps are however missing in *Satonius*, which was considered as a plesiomorphic condition by the same author. Subsequent phylogenetic analyses (BEUTEL 1999, BEUTEL et al. 1999) demonstrated that the Deleveinae are a paraphyletic taxon and showed that *Delevea* is a sister group to all remaining Torridincolidae, and *Satonius* a sister group of the Torridincolinae.

Detailed information on the morphology of adults and larvae, biology, and phylogeny of the family was summarized by BEUTEL & VANIN (2005). All known species of the Torridincolidae inhabit aquatic or hygropetric habitats. Specimens of *Delevea* were collected in permanent, fast-flowing mountain streams with rich submerged vegetation (ENDRÖDY-YOUNGA 1997); the remaining torridincolid taxa are most frequently found in aquatic and hygropetric habitats on rocks in stream rapids, alongside streams and waterfalls or below seepages, often on sites covered with algae (REICHARDT 1973, BEUTEL & VANIN 2005). LÉONARD & DESSART (1994) published an observation of African Torridincolidae pollinating the flowers of riverweeds (Podostemaceae). The representatives of this plant family usually grow on rocks in rapids and waterfalls of rivers.

The immature stages of the family are reasonably well known – the larvae of all described genera except of *Incoltorrida* are known at present, especially since they are usually collected with the adults. Publications concerning the immature stages are summarised in Table 1. Immature stages of some additional Neotropical species of the genera *Iapir* and *Ytu* are also available but their descriptions have not been published (COSTA & VANIN 2001). Larval

Table 1. State of knowledge on the immature stages of the Torridincolidae. Abbreviations: L1-L4 – first to fourth larval instars; Lm and Lpm – mature and premature larva (i.e., last and penultimate larval instar, respectively, in species with unknown number of larval instars); L? – larva of unknown instar; P – pupa.

Genus / species	Described stages	Reference			
Claudiella Reichardt & Vanin, 1976					
<i>Claudiella ingens</i> Reichardt & Vanin, 1976	Lm (detailed description)	Vanin & Costa (2001)			
Delevea Reichardt, 1976					
Delevea bertrandi Reichardt, 1976 (?)	L? (brief description)	BERTRAND (1962) as 'Hydraeni- dae genus, groupe <i>Prosthetops</i> '			
Delevea namibiensis Endrödy- Younga, 1997	L1-L4 (brief description, photo, bionomy)	Endrödy-Younga (1997)			
	Lm (detailed description)	BEUTEL et al. (1999)			
<i>Iapir</i> Py-Daniel, Fonseca & Barbosa, 1993					
Iapir britskii (Reichardt &	L1-L4, P (brief description, bionomy)	Reichardt (1973)			
Costa, 1967)	L4 (detailed description)	Costa et al. (1988)			
	L4 (detailed description in character matrix)	BEUTEL et al. (1999)			
Satonius Endrödy-Younga, 199	7	•			
Satonius kurosawai (Satô,	Lpm, Lm (detailed description)	Beutel (1998)			
1982)	L? (photo)	Науазні (2007)			
	P (photo)	Науазні (2008)			
	Lpm, Lm (chaetotaxy)	this paper			
Satonius stysi sp. nov.	Lpm (detailed description)	this paper			
Torridincola Steffan, 1964					
Torridincola rhodesica Stef-	L? (brief description)	Steffan (1964)			
fan, 1964	Lm (detailed description in character matrix)	BEUTEL et al. (1999)			
Ytu Reichardt, 1973					
Ytu athena Reichardt, 1973	L? (figure, number of instars)	Reichardt (1973)			
Ytu zeus Reichardt, 1973	Lm (brief description)	Reichardt (1973)			
	Lm (detailed description)	Costa et al. (1988)			
	Lm (detailed description in character matrix)	BEUTEL et al. (1999)			

characters were even used for the reconstruction of the phylogenetic relationships within the family (BEUTEL et al. 1999) and provided results identical to the analysis based on adults (BEUTEL 1999).

The study of recently collected *Satonius* material housed in the Natural History Museum in Vienna and National Museum in Prague enables us to improve the knowledge on the taxonomy, distribution, and larval morphology of the genus: three new species are described including the larva of one of them.

## Material and methods

The habitus of *Satonius* is generally very similar among species. Therefore, we provide only diagnostic characters concerning the size, body shape, bordering of pronotum and elytra, size of hind wings, and male genitalia for each species. Nomenclature of hind wing venation follows KUKALOVÁ-PECK & LAWRENCE (1993, 2004). As most known diagnostic characters are based on the male genitalia, the taxonomy is based on males only.

Male genitalia were mounted in DMHF (dimethyl hydantoin formaldehyde resin) on a clear celluloid label pinned under the beetle or on the same card as the beetle. Drawings of the general shape of male genitalia were traced from photographs made with Olympus Camedia-5050 camera attached to Olympus SZX-ILLK200 binocular microscope; details of parameres were drawn using a drawing tube attached to Olympus BX40 compound microscope. Exact label data are cited for the type material; a forward slash (/) separates different lines of data; additional remarks are found in square brackets. Holotypes of the newly described species are provided with one red label with the following printed text: 'HOLOTYPE / SATONIUS / 'name of the species' sp. nov. / J. Hájek & M. Fikáček det. 2007'. Each paratype is provided with a red label similar to that of the holotype, except 'PARATYPE' instead of 'HOLOTYPE', and the respective tag number.

Larvae of the following torridincolid genera were studied for comparative purposes of this study:

*Delevea namibiensis* Endrödy-Younga, 1997: 'Delevea, S. A., Endrödy-Younga', 3 larvae (ISZE). No detailed data were available to these larvae, but the material most probably comes from the larval samples published by ENDRÖDY-YOUNGA (1997).

*Iapir britskii* (Reichardt & Costa, 1967): 'Hintonia, Brazil, C. Costa', 3 larvae (ISZE). No detailed data were available to these larvae, but the material most probably comes from larval samples published by Costa et al. (1988).

*Torridincola rhodesica* Steffan, 1964: 'Republic of South Africa, Rustenburg Nature Reserve, xii.2000, V. Grebennikov lgt. and det.', 7 larvae (NMPC).

*Ytu zeus* Reichardt, 1973: 'Ytu, Brazil, C. Costa', 1 larva (ISZE). No detailed data were available to this larva, but the material most probably comes from larval samples published by COSTA et al. (1988).

The larvae were examined in temporary slides using glycerol without any previous treatment or in permanent slides using Euparal after clearing them in cold 10% KOH solution and transferring through alcohol-isopropanol solution to pure isopropanol (HANLEY & ASHE 2003). The slides were examined under Olympus BX40 compound microscope and drawings were prepared using the drawing tube attached to this microscope. Measurements were done using QuickPhoto Micro 2.3 software after taking photographs of the larvae using the same compound microscope as for adults.

The specimens are deposited in the following collections:

- BMNH The Natural History Museum [former British Museum], London, Great Britain (Maxwell V. L. Barclay);
- CASS Chinese Academy of Sciences, Institute of Applied Ecology, Shenynag, China (Lanzhu Ji);
- CZUG Entomological Collection of the Universidad de Guadalajara, Mexico (José L. Navarrete-Heredia);
- ISZE Institut für spezielle Zoologie und Evolutionsbiologie, Friedrich Schiller Universität, Jena, Germany (Rolf G. Beutel);
- KSEM Natural History Museum, University of Kansas, Lawrence, USA (Andrew E. Z. Short);
- NHMW Naturhistorisches Museum, Wien, Austria (Manfred A. Jäch);
- NMPC Národní Muzeum, Praha, Czech Republic (Jiří Hájek, Martin Fikáček);
- TMSA Transvaal Museum, Pretoria, South Africa (Ruth Müller).

## **Taxonomy**

## Satonius Endrödy-Younga, 1997

Satonius ENDRÖDY-YOUNGA, 1997: 317 (original description; gender masculine).

Type species: Delevea kurosawai Satô, 1982 (by original designation).

Description. Modified from Satô (1982), and ENDRÖDY-YOUNGA (1997).

Body evenly ovate. Coloration black, ventral part somewhat lighter, brownish. Integument microsculptured, reticulation composed of moderately deeply impressed isodiametric polygonal meshes. Entire surface covered with short semi-erected setae, without discernible basal punctures. Female without conspicuous differences from male (except for morphology of abdominal segments VIII-IX and genitalia).

Head. Frons gently and evenly convex; without dorsal impressions. Eyes moderately large, coarsely facetted, separated by  $3.5-4.0\times$  of width of one eye. Clypeus transverse, ca.  $2.5\times$  as broad as long. Frontoclypeal suture finely traced. Labrum about  $1.5-1.6\times$  as broad as long, with long stiff setae along anterior margin. Antennae inserted in front of eyes. Antenna with 11 antennomeres, short, club-shaped. Scapus robust; pedicel smaller, stout; antennomeres III-X compact, distinctly transverse; antennomere XI long, about  $3\times$  longer than preceding antennomere, bearing a few papillae at apex. Mandibles with movable subapical tooth and cutting tooth. Maxilla with galea and lacinia fused to mala. Maxillary palps trimerous, with clubbed palpomeres; palpomere I shortest, palpomere III longest, about  $2\times$  as long as palpomeres I-II



Figs. 1-2. *Satonius stysi* sp. nov., general habitus. 1 – imago (length: 2.2 mm); 2 – larva of penultimate instar (length: 1.7 mm).



Fig. 3. Jade Dragon waterfall (China, Yunnan province), type locality of *Satonius stysi* sp. nov. Arrows indicate the places at which the specimens were collected.



Fig. 4. Jan Růžička collecting Satonius stysi sp. nov. at the Jade Dragon waterfall.

combined. Submentum fused with head capsule, mentum slightly longer than broad. Labial palps short, bimerous; palpomere I long, palpomere II very small. Gula distinct, elongate.

Prothorax. Pronotum trapezoid, transverse, broadest at base,  $2 \times$  as broad as long. Posterolateral angles truncate, covered by humeral angles. Sides of pronotum narrowly to broadly bordered; anterior and posterior margins slightly sinuate. Pronotal disc with short and very fine median sagittal furrow. Prosternum with crenulate anterior margin. Prosternal process broad with arcuate apical margin.

Mesothorax. Scutellar shield small, triangular. Elytra broadest in basal two fifths, lacking striae, lateral margin at least basally with well visible rim. Epipleuron with large basal cavity; wide in anterior half, then abruptly narrowing and narrow in posterior half. Mesoventrite narrow, its anterior margin receding for reception of prosternal process; mesocoxal line well defined.

Metathorax. Metaventrite large, with anterolateral margin projecting into a spine along mesocoxal cavity. Hind wing reduced to small, slightly sclerotized scale-like structure (S. *kurosawai*), membranous but small with reduced venation (S. schoenmanni sp. nov.), or fully developed (S. stysi sp. nov., S. wangi sp. nov.). Wing venation (based on S. stysi sp. nov., Fig. 5): ScA bulge long, relatively narrow. Anterior margin PC+C broad near wing base. ScP weak, concavely arched in basal 0.15, then fused with anterior margin and RA into radial bar. RA thin and weak up to basal 0.15, then joining radial bar. Distal tip of RA<sub>1+2</sub> diverging from anterior margin. Radian bar before wing midlength reinforced posteriorly by sclerotized strip. RP<sub>3+4</sub> weakly indicated distally from tip of folding triangle. RA, weakly sclerotized, long, reaching anterior wing margin. Pigmented pterostigma absent, replaced by weakly sclerotized, slightly darker area between anterior margin, radial bar, RA3+4 and RA3. RA4 weakly sclerotized, broad, concavely curved, ending above wing apex. RP thin and weak, ending at basal 0.3. RP, weakly sclerotized, dark, almost straight, directed towards but not reaching posteroapical wing margin. RP3+4 limited to a short and disconnected pigmented strip in membrane posteriorly from RP,. Cross-vein r1 well developed, bifurcated anteriorly (probably at meeting point with reduced basal portion of RA<sub>3+4</sub>) and partly reduced posteriorly. MP<sub>1+2</sub> thick and strongly sclerotized, with median hinge in distal 0.65 of its length. Oblongum closed, with short spur of  $MP_{1+2}$  projecting from its postero-distal corner.  $MP_{3+4}$ base, MP<sub>3+4</sub>+CuA<sub>1+2</sub> followed by MP<sub>4</sub>+CuA<sub>1+2</sub> weakly preserved but distinct. Cu thick and strongly sclerotized basally; CuP reduced. CuA forked into weak CuA<sub>1+2</sub>, broadly interrupted by a fold proximally, and fused first to  $MP_{3+4}$ , then to  $MP_4$  distally, and finally to strongly sclerotized, curved CuA<sub>3+4</sub> ending on AA<sub>3</sub>. AA<sub>3+4</sub> thick, sclerotized, forked into long and strong AA, reaching posterior margin of wing and short, weak AA, AP forked basally into thicker and pigmented AP<sub>1+2</sub> curved towards posterior margin of wing at about midlength of anal fold, and thin and weak AP3++4 running along entire posterior margin of anal lobe. Wing margin fringed by sparsely arranged, moderately long setae. Wings reduced in S. kurosawai and S. schoenmanni sp. nov. (see their respective descriptions).

Legs rather short and flattened. Pro- and mesocoxae suboval, metacoxae transverse; pro- and mesotrochanters subtriangular, metatrochanter elongate; femora stout; tibiae elongated, with four rows of setigerous punctures and apical cluster of spines; tarsi tetramerous, tarsomeres I-II very short, tarsomere IV distinctly longer than tarsomeres I-III combined; tarsomeres



Fig. 5. Metathoracic wing of *Satonius stysi* sp. nov. Abbreviations: AA – anterior anal vein; AP – posterior anal vein; C – costa; Cu – cubitus; CuA – anterior cubitus; MP – posterior media; PC – precosta; r – cross-vein connecting branches of radius; RA – anterior radius; RP – posterior radius; r-mp – radio-median cross-vein; ScA – anterior subcosta; ScP – posterior subcosta. Subscript numbers refer to the branches of the respective vein. Dashed lines: wing folds.

I-III with two setae ventro-apically; tarsomere IV with one seta ventrally; claws curved and slightly dilated basally.

Abdomen with five visible ventrites. Ventrite I (= sternite III) depressed laterally to receive metafemora, anteriorly with long and acute process separating metacoxae. Posterior margin of each ventrite finely crenulate. Male sternite VIII subdivided, tergite VIII with longitudinal cleft at apex. Female tergite VIII deeply emarginate at apex. Male tergite IX rounded at apex, with elongated paraprocts.

Male external genitalia. Aedeagus well sclerotized. Median lobe simple, gently tapered, usually slightly curved in lateral view. Phallobase large. Parameres short and slender, bearing 3-6 long setae apically and a group of rounded pores (most probably campaniform sensilla) at base.

Female external genitalia. Coxites elongate with rounded apex, without styli; vulva sclerotized, ring-shaped.

#### Satonius kurosawai (Satô, 1982)

(Fig. 6)

Delevea kurosawai Satô, 1982: 279 (original description).

Satonius kurosawai: ENDRÖDY-YOUNGA (1997: 318) (new combination, redescription); BEUTEL (1998: 54) (description of larva); HAYASHI (2007: 77) (faunistics, photographs of imago and larva); HAYASHI & KADOWAKI (2007: 149) (faunistics, photograph of imago); HAYASHI (2008: 61) (faunistics, photographs of pupa).

Type locality. Japan, Honshū Is., Yamagata Prefecture, Mt. Maya-san.

Material examined. JAPAN: HONSHŪ: Nara Pref., Shakagateyama, Asahigawa valley, 1600 m a s.l., 28.vi.2002, 1  $\stackrel{?}{\circ}$  1  $\stackrel{?}{\circ}$ , Bolm leg. (NMPC).

**Diagnosis.** Small and broad species; body length 1.4-1.7 mm, width 0.9-1.1 mm. Sides of pronotum broadly bordered. Lateral margin of elytra visible in the basal fourth in dorsal view. Micropterous species; hind wing reduced to small, slightly sclerotized scale-like structure.

Male genitalia. Median lobe of aedeagus nearly evenly curved from base to apex, with small spur subapically. Parameres rather wide, with four long setae apically, base with long field of pores along ventral surface reaching basal half of length of paramere (Fig. 6). **Bionomics.** Hygropetric, collected on wet surfaces of rocks in streams and seepage habitats

(Satô 1982, Hayashi 2007, Hayashi & Kadowaki 2007).

**Distribution.** Widely distributed in the Japanese islands of Honshū (Prefectures Aichi, Fukui, Fukushima, Hyôgo, Miyagi, Naga, Niigata, Shimane, Tottori, Yamagata) and Shikoku (Ehime Prefecture) (Satô 1982; Hayashi 2007, 2008; Hayashi & Kadowaki 2007) (Fig. 32).

#### Satonius schoenmanni sp. nov.

(Fig. 7)

**Type locality.** China, Hunan province, ca. 25 km N Pingjiang, ca.  $28^{\circ}50'10''$ N,  $113^{\circ}38'05''$ E, ca. 200 m a s.l. **Type material.** HOLOTYPE:  $3^{\circ}$  (CASS), 'CHINA: Hunan, 20.3.2003 / ca. 25 km N Pingjiang City,  $113^{\circ}38'05''$ E  $28^{\circ}50'10''$ N / ca. 200 m, leg. Schönmann, / Komarek & Wang (CWBS 499)'. PARATYPES:  $3^{\circ}$ , same label data as holotype (CASS, NHMW, NMPC).

**Diagnosis.** Small and broad species; body length 1.6 mm, width 1.0 mm. Sides of pronotum broadly bordered. Lateral margin of elytra visible only in humeral part. Brachypterous species; hind wing membranous, 0.35 mm long (elytron 1.00 mm long), venation reduced.

Male genitalia. Median lobe of aedeagus with dorsal side slightly rounded in basal two thirds, straight in apical third; ventral side slightly concave, apex with minute hook. Parameres rather wide, with four long setae apically, base with short field of pores along ventral surface (Fig. 7).

**Bionomics.** At the type locality, water beetles were collected in a 3-5 m wide stream with boulders on cliffs, between sparse riparian vegetation and in flood debris (H. Schönmann, pers. comm. 2008). No detailed data on the precise microhabitat of this species are known.

**Etymology.** The new species is dedicated to one of its collectors, Heinrich Schönmann (NHMW), a specialist on the Hydrophilidae.

Distribution. So far known only from the type locality in Hunan province, China (Fig. 32).

#### Satonius stysi sp. nov.

(Figs. 1, 5, 10)

**Type locality.** China, Yunnan province, Shanzhi env., Jizu Shan Mt., Jade Dragon waterfall, ca. 27°57.6'N, 100°23.2'E, 2250 m a.s.l.

**Type material.** HOLOTYPE: ♂ (NMPC), 'CHINA: Yunnan province, / SHANZHI env., 23.-24.VI.2007, / Jizu SHAN Mt., / Jade Dragon waterfall / 27°57.6′N 100°23.2′E, 2250 m, / J. Hájek & J. Růžička leg.' PARATYPES: 10 ♂♂ 5 ♀♀ and 26 unsexed spec., same label data as holotype (BMNH, CASS, CZUG, KSEM, NHMW, NMPC, TMSA).

**Diagnosis.** Large and elongate species (Fig. 1); body length 2.0-2.4 mm, width 1.2-1.4 mm. Sides of pronotum narrowly bordered. Lateral margin of elytra visible in dorsal view



Figs. 6-10. Aedeagus and details of parameres of *Satonius* Endrödy-Younga, 1997 in lateral view. 6 - S. *kurosawai* (Satô, 1982); 7 - S. *schoenmanni* sp. nov.; 8 - S. *wangi* sp. nov.; 9 - S. sp. 1; 10 - S. *stysi* sp. nov. Scales: a – aedeagus; b – detail of paramere.

only in basal fifth. Macropterous species (for description of hind wing venation see generic description, Fig. 5).

Male genitalia. Median lobe of aedeagus evenly curved to apex. Parameres long and narrow, with four long and two shorter setae apically, base with short field of pores along ventral surface (Fig. 10).

**Bionomics.** *Satonius stysi* sp. nov. was collected in hygropetric habitats in the spray zone along the Jade Dragon waterfall and on a seepage near the waterfall but not connected to the stream (Figs. 3-4). Both microhabitats had only a thin film of water (up to 2 mm) and were covered with a macroscopic algal mat. The new species was collected together with unidentified species of *Anacaena* Thomson, 1859 (Hydrophilidae) and *Cephalobyrrhus* Pic, 1923 (Limnichidae).

**Etymology.** The new species is dedicated to Prof. Pavel Štys (Charles University, Prague, Czech Republic), our teacher and a specialist on the Heteroptera.

Distribution. So far known only from the type locality in Yunnan province, China (Fig. 32).

## Satonius wangi sp. nov.

(Fig. 8)

**Type locality.** China, Zhejiang province, 5 km N Lishui, Baiyunshan Forest Park, ca. 270 m a.s.l.. **Type material.** HOLOTYPE: ♂ (CASS), 'CHINA: Zhejiang prov. / 5 km N Lishui City / ca. 270 m, 1.4.2001 / leg. M. Wang (CWBS 412)'. PARATYPES: 6 ♂♂ 7 ♀♀ and 33 unsexed spec., same label data as holotype (BMNH, CASS, CZUG, KSEM, NHMW, NMPC).

**Diagnosis.** Small and broad species; body length 1.4-1.8 mm, width 0.9-1.1 mm. Sides of pronotum fairly broadly bordered. Lateral margin of elytra visible throughout elytral length except for apex. Macropterous species.

Male genitalia. Median lobe of aedeagus with dorsal side slightly curved in basal half, almost straight in apical half; ventral side slightly concave, with small spur subapically. Parameres short and stout, with two setae on apex and one located subapically, base with long field of pores along ventral surface reaching basal half of length of paramere (Fig. 8).

**Bionomics.** Collected in a small, ca. 1 m wide stream with small rocks, flowing fast through a *Cunninghamia* forest (JACH & JI 2003).

**Etymology.** The new species is dedicated to its collector Miao Wang (Shenyang, China). **Distribution.** So far known only from the type locality in Zheijang province, China (Fig. 32).

## Satonius sp. 1

(Fig. 9)

**Material examined.** 1  $\Diamond$  1  $\Diamond$ , 'CHINA: Fujian, Chong'an, Wuyi Shan, 1 km W Wuyi Gong, 250 m, 15.-18.i.1997, H. Schönmann leg. (CWBS 240)' (NHMW).

**Notes.** The torso of a *Satonius* male specimen lacking head was already mentioned by JÄCH (1998). It represents without any doubt an undescribed species, which differs from all other taxa by a very convex body, sides of pronotum very narrowly bordered, and characteristic shape of male aedeagus (median lobe with apical portion bent dorsad; paramere narrow, with four apical setae, basal portion with wide field of pores on lateral surface, Fig. 9). The female collected with the male differs from it and is almost identical to *S. wangi* sp. nov. We are

not able to decide whether it is a sexual dimorphism or both specimens represent different taxa. In accordance with JACH (1998), we refrain from their description until more material becomes available.

#### Satonius sp. 2

Material examined. 1 ♀, 'CHINA: Anhui, Huang Shan, 60 km NNW Tunxi, nr. Tang Kou, 900-1000 m, 31.x.1997, H. Schönmann leg. (CWBS 292)' (NHMW).

**Notes.** A single macropterous female from Anhui province differs from all other *Satonius* species by its very broadly bordered sides of pronotum and most probably represents an undescribed species. However, until a male will be found, we refrain from its description.

## Larval morphology

#### Satonius stysi Hájek & Fikáček, 2008

(Figs. 2, 11-17, 20-26, 28, 30)

**Material examined.** 13 larvae of penultimate instar (NMPC): **CHINA:** YUNNAN: Shanzhi env., Jizu Shan Mt., Jade Dragon waterfall, 27°57.8'N 100°23.2'E, 2250 m a.s.l., 23.-24.vi.2007, J. Hájek & J. Růžička leg. Larvae collected together with the adults designated above as type specimens.

**Description.** Body oniscoid, strongly flattened and ovoid in shape (Fig. 2), dorsal surface distinctly sclerotized. Head partly covered by pronotum. Legs not visible in dorsal view.

Measurements. Head width 0.52 mm; body length 1.50-1.80 mm; maximum body width 1.20-1.32 mm.

Head capsule (Fig. 12) subprognathous, transverse, ca. 2× as wide as long. Dorsal surface brown, ventral parts paler, weakly sclerotized. Clypeus separated from frons by narrow 'suture'; trapezoid in shape, with distinct darker attachment of anterior tentorial arms. Frontal sutures lyriform, joining clypeofrontal membrane at clypeal sides anteriorly; sulci distinctly shifted mesally by attachments of dorsal tentorial arms. Coronal suture short but distinct. Four stemmata situated on lateral prominence. Antenna inserted on anterolateral part of parietale, insertion area not connected with frontal suture or clypeofrontal membrane. Maxillary groove large, anteriorly limited by narrow projection of parietale with ventral mandibular articulation. Gula broad, trapezoid, not separated from submentum; laterally with posterior tentorial pits. Chaetotaxy of head capsule consisting of numerous short setae dorsally, with longer setae situated only on anterior parts of clypeus and frons; each lateral prominence with one short stout seta among stemmata; posterior part of parietale with two stout setae dorsally; ventral surface with few long hair-like setae anterolaterally.

Labrum (Figs. 13-14) transverse, separated from clypeus by membranous fold. Chaetotaxy of disc consisting of eight pores and eight short setae; lateral margin with two long hair-like setae and one long and stout seta situated on angle of lateral labral fold. Anterior part with transverse ridge; three pairs of small stout setae situated posteriorly of this ridge. Surface between the ridge and anterior margin of labrum finely longitudinally ridged with two small submedian pores. Anterior margin with two pairs of small stout setae. Frayed setae absent. Ventral surface (epipharynx) membranous, with anterior area covered with microtrichia; posterior part with semicircular microtrichial area and dense mesal cluster of microtrichia situated posteriorly.



Figs. 11-19. Larvae of *Satonius* Endrödy-Younga, 1997. 11-17 – *S. stysi* sp. nov., penultimate instar; 18-19 – *S. kurosawai* (Satô, 1982), ultimate instar. 11 – right antenna, dorsal view; 12 – head, dorsal view; 13 – labrum, dorsal view; 14 – labrum, ventral view (epipharynx); 15 – maxilla, ventral view; 16 – maxilla, dorsal view; 17-18 – apical portion of mala; 19 – detail of maxillary palpus and basolateral portion of mala, ventral view.

Antenna (Fig. 11) directed anterolaterally, composed of two antennomeres. Antennomere I short, ring-like, bearing a pore dorsally. Antennomere II  $10.5 \times$  as long as antennomere I; two long trichoid sensilla situated in apical third, one long and one shorter trichoid sensilla situated at antennal apex. Sensorium well developed, ca.  $0.15 \times$  as long as antennomere II, inserted in shallow groove on inner surface of antennomere.

Mandibles (Figs. 20-21) symmetrical, rather wide and short. Each mandible with one pore and two long hair-like setae dorsally on outer margin. Area bearing setae with numerous cuticular tubercles. Apex divided into two lobes, each with six denticles mesally; basal lobe slightly projecting mesad, largely covering ventral membranous fold (pseudomola sensu BEUTEL (1998)) with numerous microtrichia arranged in transverse series. Basal part of mandible with large, strongly sclerotized mola. Mandibular acetabulum (mandibular part of secondary joint) situated laterally; ventral condyle (mandibular part of primary joint) shifted anteromesally.

Maxilla (Figs. 15-16). Cardo as wide as basal portion of stipes, ca.  $0.4\times$  as long as remaining part of maxilla, slightly wider than long, bearing one hair-like seta. Stipes not separated from mala, largely opened dorsally to interior of head capsule; ventral surface bearing two short setae in basal half, one short mesally directed seta on inner surface and one short seta on apical third of outer face; dorsal surface with few cuticular spines near seta on inner face. Apical part of mala with five teeth and two long setae; lateral tooth fixed, remaining teeth represented by stout setae. Palpus situated laterally, small, consisting of two palpomeres; palpomere I short, ring-like, bearing one pore ventrally; palpomere II ca.  $2.7\times$  as long as palpomere I, slightly membranous apically, bearing numerous oval sensilla.

Labium (Fig. 22). Submentum fused with gula. Mentum short, slightly wider than long, lateral margins nearly parallel-sided; anterior part with two pairs of long, hair-like setae. Prementum short and wide, with one pair of short setae situated in posterolateral corners and another pair between insertions of labial palpi. Apical part (ligular area) membranous, with numerous minute sensilla. Labial palpus with two palpomeres; palpomere I ca.  $2.5 \times$  as long as palpomere II, bearing one pore mesally and one short seta laterally; palpomere II very short, ring-like, with apical membranous field bearing three sensilla.

Thorax as long as abdomen. Dorsal surface dark, strongly sclerotized. Pronotum  $3.1 \times$  as wide as long, narrowing anteriad, anterolateral corners slightly projecting anteriad. Mesonotum shorter but slightly broader than pronotum,  $4.8 \times$  as wide as long. Metanotum widest, ca. as long as mesonotum,  $5.0 \times$  as wide as long. Lateral margins of all thoracic segments with fringe of alternating long and shorter hair-like setae. Chaetotaxy of pronotum consists of sparsely distributed, minute hair-like setae; chaetotaxy of meso- and metanotum with only a few minute hair-like setae. Ventral parts membranous, insertions of right and left coxae well separated from each other.

Legs (Figs. 23-25) pentamerous, moderately long, prothoracic legs shorter than meso- and metathoracic legs. Coxa elongate, bearing 13 short, hair-like setae. Trochanter elongate-triangular, with a row of pores on both anterior and posterior surface; in addition with four setae and one pore on anterior surface and two setae on posterior surface. Femur  $1.2 \times$  as long as trochanter ( $1.1 \times$  so in prothoracic leg), bearing five setae and one pore on anterior surface and three setae on posterior surface. Tibiotarsus

 $1.3 \times$  as long as femur (as long as femur in prothoracic leg), bearing three setae on anterior and four setae and one pore on posterior surface; apical part with six fine and long setae and two pairs of cuticular spines. Seta situated on basal third of anterior surface of tibiotarsus different in morphology among leg pairs: scale-like and palmate on prothoracic leg, simple on mesothoracic leg, and bifid or rarely simple on metathoracic leg. Claw ca.  $0.3 \times$  as long as tibiotarsus, with distinct sharp basal tooth and one long hair-like seta.



Figs. 20-25. Larva of *Satonius stysi* sp. nov., penultimate instar. 20 – left mandible, dorsal view; 21 – left mandible, ventral view; 22 – labium, ventral view; 23 – left metathoracic leg, anterior view; 24 – palmate tibiotarsal seta of prothoracic leg; 25 – left metathoracic leg, posterior view.



Figs. 26-31. Larvae of *Satonius* Endrödy-Younga, 1997. 26, 28, 30 – *S. stysi* sp. nov., penultimate instar; 27, 29, 31 – *S. kurosawai* (Satô, 1982), ultimate instar. 26-27 – abdominal segments VII-X, setae of urogomphi omitted; 28-29 – shape of setae of lateral lobes of abdominal segments I-VIII; 30-31 – right urogomphus, ventral view.

Abdomen (Figs. 26) with 10 segments. Segment I slightly narrower than metanotum, each following segment slightly narrower than the previous one. Segments I-VIII short and transverse, projecting into lateral processes; tergum and sternum sclerotized and equally wide; dorsal chaetotaxy consisting of two minute hair-like setae situated along anterior margin, and 8 similar setae situated along posterior margin. Lateral processes bearing long, two segmented tracheal gills; first gill segment very short on abdominal segments I-V, slightly longer on abdominal segment VI and moderately long on segment VII-VIII; second gill segment often with secondary subapical constrictions; trachea opened at base of second gills (Table 1), all setae simple (Fig. 28). Abdominal segment IX bearing pair of fixed urogomphi; each urogomphus with numerous long and thin hair-like seta, one fine short subbasal seta and one short but very

Table 2. Chaetotaxy of lateral lobes of abdominal segments (AS) and urogomphi (UR). For each species, the first column shows the number of setae according to their position (anterior / posterior to the insertion of tracheal gill) and the second column the total number of setae on the respective lobe; the apical spiniform seta of urogomphi is not counted. The numbers are equal in the mature and premature larvae of *S. kurosawai* (Satô, 1982).

	Satonius stysi		Satonius kurosawai	
	position	sum	position	sum
AS I	1 / 4-7	5-8	1 / 2-5	3-6
AS II	1 / 4-6	5-7	1 / 3-4	3-5
AS III	1/3-5	4-6	1/2-4	3-5
AS IV	1/3-5	4-6	1 / 2-4	3-5
AS V	1/3-5	4-6	1 / 2-3	3-4
AS VI	1 / 2-4	3-5	1 / 2-4	3-5
AS VII	2-3 / 0-1	3-4	1 / 0-1	1-2
AS VIII	2-3 / 0-1	2-4	1-2 / 0-1	1-2
UR	_	14-16	-	9-11

Table 3. Characters separating the larvae of Satonius stysi sp. nov. and S. kurosawai (Satô, 1982).

	Satonius stysi	Satonius kurosawai
Body length / body width (penultimate instar, in mm)	1.50-1.80 / 1.20-1.32	1.12-1.25 / 0.72-0.76
Head width (mm) (ultimate / penultimate instar)	- / 0.52	0.43 / 0.37
Setae on apex of mala (Figs. 17-18) (stout spiniform / long trichoid)	4 / 2	3 / 4
Number of maxillary palpomeres (Figs. 15, 19)	2	3
Outer face of maxilla, anterior of insertion of palpus (Figs. 15, 19)	with few cuticular tubercles	with numerous sharp cuticular spines
Setae on lateral lobe of abdominal segment VII (anterior / posterior to gill insertion)	2-3 / 0-1	1 / 0-1
Number of setae on urogomphus (without apical spiniform seta)	14-16	9-11

wide apical seta. Ventral part of abdominal segment IX developed as subpentagonal plate bearing two pairs of fine hair-like setae, the plate ca.  $2 \times$  as wide as long. Abdominal segment X developed as pair of membranous ventral flaps posteriorly to sternite IX.

**Note.** All larvae collected together with the adults represent the same larval instar based on their body measurements. In order to identify the instar, we have compared the ratio of length of larvae and adults (LAR) in *S. stysi* sp. nov. (LAR = 0.85) and *S. kurosawai* (ultimate instar LAR = 0.95, penultimate instar LAR = 0.80). These measurements therefore suggest that the examined larvae of *S. stysi* sp. nov. probably represent the penultimate instar. This is corroborated by the simple shape of the setae of lateral abdominal lobes (i.e. lacking bifid apices), as only simple setae are found in the penultimate instar of *S. kurosawai* (part of these setae is bifid in the ultimate instar, see below, Fig. 29). Number or larval instars is not known for most torridincolids except for *Ytu zeus* and *Delevea namibiensis*, which have four instars (REICHARDT (1973) and ENDRÖDY-YOUNGA (1997), respectively).

#### Satonius kurosawai (Satô, 1982)

(Figs. 18-19, 27, 29, 31)

Material examined. 10 larvae of ultimate instar, 6 larvae of penultimate instar (NMPC): JAPAN: HONSHŪ: Aichi Pref., Houraji-ko, 4.v.1997, M. Satô leg.

**Diagnosis.** Generally similar to larva of *S. stysi* sp. nov. in most external characters, except for measurements, chaetotaxic characters mentioned below, and morphological characters summarized in Table 3.

Measurements. Head width: 0.37 mm (penultimate instar), 0.43 mm (ultimate instar); body length: 1.12-1.25 mm (penultimate instar), 1.42-1.55 mm (ultimate instar); maximum body width: 0.72-0.76 mm (penultimate instar), 0.95-1.02 mm (ultimate instar).

Chaetotaxy. Identical in both species on most body parts with the following exceptions. Maxilla: apex of mala with one fixed lateral tooth and three stout spiniform setae and four thinner and longer trichoid setae mesally (Fig. 18). Legs: coxa with one additional short hairlike seta basally. Abdomen: lateral lobes of abdominal nodes generally with lower number of setae (see Table 2); at least some setae on these lobes bifid at apex in ultimate instar (Fig. 29), all setae simple in penultimate instar. Urogomphi (Fig. 31): bearing 8-10 long trichoid setae, one fine and short basal seta, and one spiniform seta at apex. For detailed description see BEUTEL (1998).

## Discussion

#### **Phylogenetic implications**

The phylogeny of the Myxophaga was analysed in detail by BEUTEL et al. (1999) and BEUTEL (1999) on the basis of both larval and adult characters. The analyses resolved the phylogenetic relationships of the myxophagan families and genera but the taxon sampling did not allow to define autapomorphies of the particular genera. Our study reveals two generic apomorphies in *Satonius*: (1) metaventrite with a sharp margin projecting into a spine along the mesocoxal cavity (see ENDRÖDY-YOUNGA 1997, Fig. 5D) (without spine in other Torridincolidae); and (2) number of apical setae on parameres increased to 3-6 (two in other Torridincolidae). ENDRÖDY-YOUNGA (1997) suggested two additional characters as apomorphic but we cannot confirm his interpretation: apical tergite of females with large discal emargination (emargination of different shape on tergite VIII is present in both sexes of all Torridincolidae except for *Delevea*) and reduced hind wings (size of wings varies highly between *Satonius* species, see below). In contrast, the adult characters used by BEUTEL (1999) showed to be constant in all *Satonius* species examined.

KUKALOVÁ-PECK & LAWRENCE (1993) studied and illustrated the hind wings of representatives of the Lepiceridae (*Lepicerus* Motschulsky, 1855), Sphaeriusidae (*Sphaerius* Waltl, 1838), Hydroscaphidae (*Hydroscapha* LeConte, 1847), and Torridincolidae (*Claudiella, Iapir, Ytu* and an undescribed genus), revealing numerous differences between the families and even the torridincolid genera. In addition, hind wings of two *Torridincola* species were illustrated by STEFFAN (1964, 1973). In comparison to these taxa, the metathoracic wing of *Satonius*, when fully developed, bears a rather complete venation standing close to the Myxophaga groundplan as suggested by KUKALOVÁ-PECK & LAWRENCE (2004). Moreover, the vein AA<sub>3+4</sub> forks into AA<sub>3</sub> and a short and weak AA<sub>4</sub>, which seems to update the myxophagan venation groundplan; KUKALOVÁ-PECK & LAWRENCE (2004) considered that the bifurcation of AA<sub>3+4</sub> is absent in the Myxophaga. The presence of AA<sub>4</sub> in *Satonius* and its absence in the Lepiceridae, Hydroscaphidae, Sphaeriusidae and Torridincolinae suggests that the hind wing venation (or at least the venation of median, cubital and anal areas) was reduced independently in the Lepiceridae and the Sphaeriusidae + Hydroscaphidae clade, in the latter case most likely due to miniaturization. An alternative explanation, i.e. the loss of  $AA_4$  in an ancestral myxophagan and its 'regain' in basal Torridincolidae, appears improbable. According to J. Kukalová-Peck (pers. comm. 2008), this branch is present in the coleopteran groundplan and did not re-evolve once it was lost in any recent coleopteran families up to the present knowledge.

Larvae of Satonius have a very wide, distinctly flattened, disc-shaped body, with the thorax as long as the abdomen (this character is considered as a synapomorphy of *Satonius* and the Torridincolinae according to BEUTEL et al. (1999)). In addition, the larvae of Satonius are characterised by laterally expanded thoracic and abdominal tergites covering the legs, presence of long setae on the lateral margins of the thoracic tergites, a modified chaetotaxy of the legs (with the anterior tibiotarsal setae flattened and palmate), and tarsal claws with a large basal tooth. All these characters distinguish the larvae of *Satonius* from all remaining Torridincolidae including *Delevea* but are shared with the larvae of *Ytu* (in which the palmate seta is present on the metathoracic leg and absent from the mesothoracic leg; the prothoracic leg was missing in the only larva studied). Based on the presence of three stemmata and the fringed setae on the labrum of larva, Ytu belongs to the Torridincolinae (BEUTEL et al. 1999). This position of Ytu was confirmed also on the base of adult characters by BEUTEL (1999) and the genus seems to stand as a sister-group of the *Iapir* + *Claudiella* clade. Modifications of the body shape and chaetotaxy mentioned above should therefore be considered as a result of parallel evolution in larval Satonius and Ytu, and probably represent analogous adaptations to the larval environment. While the extremely flattened body of both genera could be regarded as an adaptation to the habitats with thin film of water (see below), at present we cannot explain their unusual characteristics of legs. Because of the laterally expanded thoracic and abdominal tergites completely covering the legs, the orientation of legs seems to be modified both in *Satonius* and *Ytu* in contrast to all other Torridincolidae (the meso- and metathoracic legs are directed posteriad, with the anterior face exposed ventrally; all legs are directed ventrad in other Torridincolidae). This unusual leg morphology together with the extremely flattened body and modified leg orientation in both genera may perhaps improve the adhesion of the larva to the substrate. However, as the flattened body and lateral fringes of setae seem to give sufficient adhesion (R. G. Beutel, pers. comm. 2008), further studies are needed to explain the leg adaptations of both genera.

REICHARDT (1973) noted that species of *Ytu* live in hygropetric habitats, mainly on the seepages along roads which are usually exposed, with rather thin film of water and often fluctuating water regime. In this respect, larvae of *Ytu* differ from the remaining Neotropical Torridincolidae, which are usually found at sides of streams and rivers (REICHARDT 1973, VANIN & COSTA 2001). Similar habitats at sides of streams and rivers are known for *Torridincola* (STEFFAN 1964, 1973) and *Delevea* (ENDRÖDY-YOUNGA 1997). Morphological modifications of the larva of *Ytu* can be therefore regarded as an adaptation to a very thin film of water on the seepages. Specimens of *Satonius* were mostly found at sides of streams. Because the larva of *Satonius* shows analogous adaptations as *Ytu*, we suppose that the larvae of *Satonius* are adapted to inhabit the hygropetric habitats at sides of watercourses with a very thin layer of water. This seems to be supported by the microhabitats on which the specimens of *S. stysis* sp. nov. were collected (see bionomics under this species) as well as by habitat preferences of Japanese *S. kurosawai* (SATÔ 1982).

## Distribution and wing polymorphism

The present findings of *Satonius* suggest that the genus is widely distributed in the subtropical border area between the Palaearctic and Oriental regions. In contrast to the Japanese species *S. kurosawai*, members of the genus were only rarely collected in China so far and each Chinese species is currently known only from a single locality (see Fig. 32). This may be due to insufficient sampling effort, collecting bias (the beetles may be easily overlooked due to their small length and specific habitats), and/or their sensitivity to regulation of streams and their eutrophication. The latter reason seems to be supported by the fragmented distribution of Chinese *Satonius* in isolated patches with undisturbed streams, predominantly in mountain areas.

All Chinese species of *Satonius* are macropterous or brachypterous (with reduced but still membranous wing lacking venation) but so far known from a single locality. In the widely distributed S. kurosawai, only micropterous specimens are known so far. Both the interspecific variability of hind wing size in Satonius and the surprisingly wide distribution of S. kurosawai are interesting features with parallels in semiaquatic and aquatic bugs (Heteroptera: Gerromorpha and Nepomorpha). Both heteropteran groups inhabit aquatic and hygropetric habitats and exhibit a wide spectrum of wing polymorphism both between and within species (e.g., ANDERSEN 1982, POLHEMUS & POLHEMUS 2008). In most of the usually micropterous or apterous species, the macropterous morph occurs in low numbers, in some cases representing less than 1 % of the specimens, and is in some species induced by environmental factors (ANDERSEN 1982; P. Kment, pers. comm. 2008). These rare macropterous specimens presumably allow for sufficient dispersal and gene flow between local population of a predominately flightless species, resulting in a wide geographical distribution and limiting allopatric speciation (ANDERSEN 1982, DAMGAARD 2008). A similar scenario could explain the interspecific wing polymorphism of Satonius and the wide distribution of S. kurosawai (assuming that macropterous specimens of the latter species do occur but have not been discovered so far). Within aquatic beetles, similar inter- and intraspecific wing polymorphism is known also in the Elmidae (KODADA & JACH 2005), for example in the Palaearctic representatives of the genera *Esolus* Mulsant & Rey, 1872, Grouvellinus Champion, 1923, Normandia Pic, 1900, Optioservus Sanderson, 1954, and Riolus Mulsant & Rev, 1872 (M. A. Jäch, pers. comm. 2008).

The extent of flight activity in the Torrindicolidae is unknown, although they presumably fly rarely at most. Even the winged species of *Satonius* were never observed or collected at flight, and ENDRÖDY-YOUNGA (1997) mentioned that the winged African species *Delevea namibiensis* was never found at light even at sites where they had been collected from the water.

In spite of the fragmentary knowledge on the distribution and bionomics of the *Satonius* species, we assume that most of the species are highly threatened by destruction of natural habitats, and may get easily extinct.

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Fig. 32. Known distribution of the genus Satonius Endrödy-Younga, 1997.

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