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Description of dendrolimnobiontic larvae of Scatopsidae (Diptera) with a review of our knowledge of the preimaginal stages of the family

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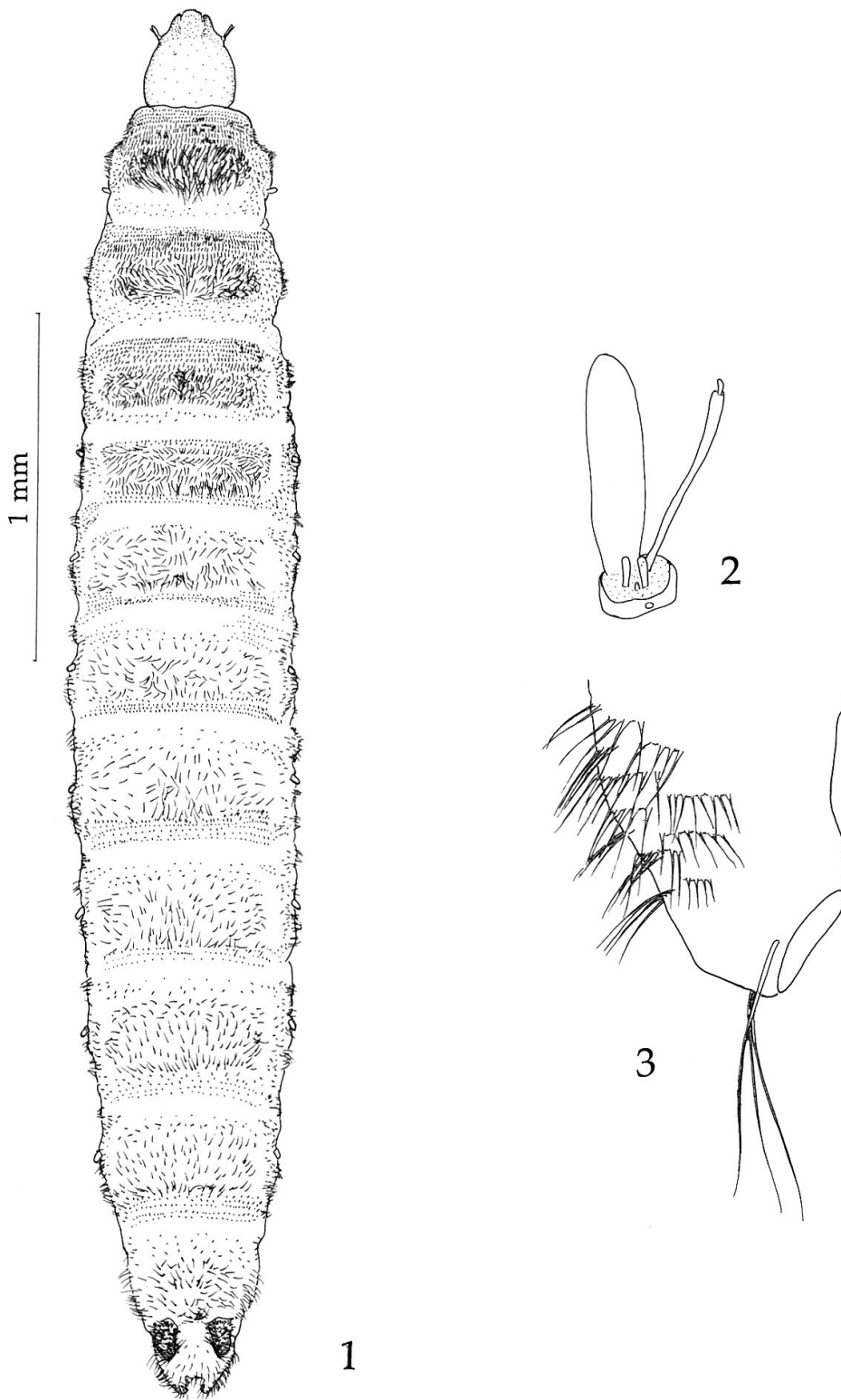
The 4th instar larva of the Scatopsid *Holoplagia richardsi* (EDWARDS, 1934) is described and figured. This is the first known larva of genus *Holoplagia* and the first dendrolimnobiontic larva of the family. The species was reared from larvae collected in a maple tree-hole (*Acer pseudoplatanus*) filled with water in the vicinity of Grenoble (France), together with another Scatopsid, *Ectactia platyscelis* (LOEW, 1869). Both species are rare and are recorded for the first time from France, and even from continental Europe for *E. platyscelis*. Two other true aquatic larvae of unknown generic and specific placement that were collected in little permanent springs and subsequent brooklets in forested areas of SE France are described and figured. Our knowledge of Scatopsid larvae is summarized and reviewed in the light of these new data. An annotated bibliography of the world literature concerning the immature stages of Scatopsidae is given.

Keywords: Diptera Scatopsidae, *Holoplagia*, immature stages, dendrolimnobiontic, aquatic, world bibliography

INTRODUCTION

The life-history and immature stages of Scatopsidae remain largely unknown. While about 340 species in some 30 genera have been described so far from all parts of the world, the larvae of only very few of them are known (see further, tab. 2). During his investigations on the dipterological fauna of tree-holes and springs in France, the second author collected on several occasions larvae of Scatopsidae living in aquatic conditions. In some cases, rearing was successfully undertaken by him. This material was generously given to the first author for identification and study, resulting in the present paper in which the first true aquatic larvae of family Scatopsidae are described.

All previously described larvae of the family have terrestrial habitats. Finally, a critical survey of our knowledge of Scatopsid larvae is presented as a preliminary step for a key to the known larvae of this family for the future Manual of Palaearctic Diptera. This is completed by a world review of literature concerning the immature stages of family Scatopsidae.



Figs. 1-3. *Holoplagia richardsi* (EDW.), last instar larva. 1: dorsal view; 2: antenna; 3: detail of vestiture of posterior spiracle (side view).

DESCRIPTION OF NEW LARVAE

Holoplugia richardsi (EDWARDS, 1934) (Figs 1-3)*4th instar larvae*

3.9-4.3 mm long; body cylindrical, somewhat flattened and curved dorsoventrally, creamy-white in colour, with light fuscous head capsule and posterior spiracles; respiration peripneustic; surface of body covered with various types of microtrichia; this vestiture is more developed on ventrum and especially on dorsum of segments, where it often retains small organic or inorganic particles during life. Head scarcely longer than wide, well sclerotized; cephalic capsule disjuncted medially on ventral side; antennae (fig. 2) with digitiform appendix of second segment practically as long as third segment; mouth-parts as in other known genera of Scatopsidae, with four-toothed mandibles and premandibular sclerite developed. Thorax. A pair of lateral prominent spiracles on first segment; tergal vestiture well-developed, composed of close-set rows of long fine, somewhat wavy, microtrichia giving the segments a fur-like appearance with no distinct pattern (fig. 1); front margin of segments covered with close-set rows of shorter and finer microtrichia.

Abdomen composed of 8 segments, the last one formed by the fusion of 2 segments; a pair of prominent spiracles are present on each segment: these are short and lateral on segments 1 to 7, large and dorsal on segment 8 where they are placed at the tip of a pair of sclerotized cylindrical projections; these projections are nearly entirely covered with regular rows of microtrichia and crowned by a circle of fine long setae at apex (fig.3); pygidial plate of last segment unsclerotized, scarcely bilobed above anus, with a pair of very short ill-defined projections bearing longer microtrichia; pattern of tergal pilosity of abdominal segments rather confuse: vestiture shorter than on thoracic segments, composed of a mixture of microtrichia of different length, irregularly arranged on dorsal surface of segments.

Material studied

Several larvae were collected by the second author near Prémol, 3.5 km SE of Grenoble (department Isère, France), 1095 m elevation in a hole of a maple (*Acer pseudoplatanus*), on Mai 15th, 1991. They were successfully reared in laboratory and adults emerged during the summer of 1991. The following material is present in the collection of the first author in Musée d'histoire naturelle of Neuchâtel (MHNN): 5 larvae (4th instar), 11 imagines (4 males, 7 females). Numerous similar larvae that have been collected in a hole of an ash-tree (*Fraxinus excelsior*) between Gresse-en-Vercors and Col du Serpaton, some 30 km S of Grenoble (department Isère, France), 1200 m elevation, on June 3rd, 1991. Although their rearing failed, they clearly belong to the same species that the larvae of *Holoplugia richardsi* from Prémol. 15 larvae (4th instar) are present in the collection of the first author in MHNN (all material leg. F. VAILLANT).

Habitat

In Prémol, the larvae of *H. richardsi* were collected in a dendrolimnic habitat as defined by VAILLANT (1990). The larvae lived in a tree-hole filled with water

under true aquatic conditions together with the typical dendrolimnobiotic Psychodidae *Telmatoscopus havelkai* (WAGNER). One larva of another Scatopsid, *Ectaetia platyscelis* (LOEW) was found in the same microhabitat. The larvae of *H. richardsi* and *E. platyscelis* were reared in very wet conditions during 2 months and were observed swimming at the surface of water by the second author. In Gresse-en-Vercors, the larvae of *H. richardsi* were found in the damp pulverulent wood in the bottom of the tree-hole. Although this appears to be a less aquatic condition, they however lived there in company with larvae of Stratiomyiidae of typical dendrolimnic habitats. The very dry summer was probably responsible for the considerable drying out of the cavity.

Both species are rarely collected and are recorded from the first time from France. *H. richardsi* was described from England, from rotting *Fagus* (EDWARDS, 1934). It has been recorded since from a few localities there, also from rotten *Ulmus* (FREEMAN, 1985). This is the first record of this little known species from continental Europe. *E. platyscelis* is known from 6 localities in England where the species has been obtained from rotting wood of *Fagus*, *Ulmus* and *Tilia* (FREEMAN, 1985). There are 4 other known localities in Austria, Denmark, Sweden and Finland. The larva was described by LAURENCE (1953a), living in apparently less aquatic conditions than the present record since it was reared "...from a deep deposit of wet orange coloured detritus lying in a tree hole inside a lime [*Tilia*] trunk...". Evidently this species seems to be dependent on rotting wood in more or less damp or even aquatic conditions for its development.

Larvae of 2 different species of Scatopsidae living in little springs and brooklets have been collected on several occasions by the second author. These are the first known larvae of this family to be recorded living under freshwater conditions (HAENNI & VAILLANT, 1990). They were successfully reared by the second author but unfortunately imagines could no longer be found again in his collection. Nevertheless, they will be provisionally described below, until new rearings can clarify their identity.

Scatopsini⁺ *gen. sp. 1* and *sp. 2* (Figs 4-7)

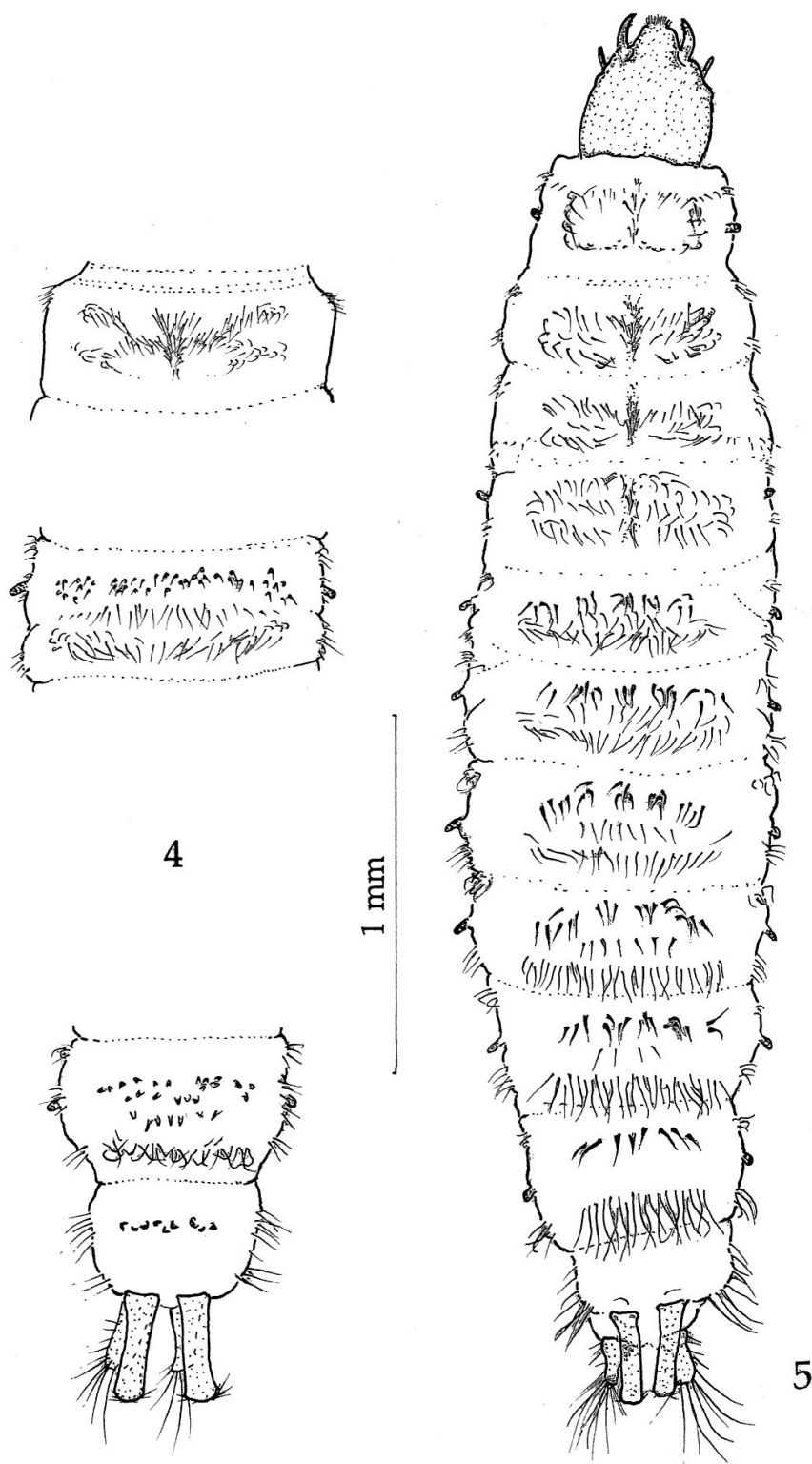
4th instar larvae

About 4 mm long, somewhat flattened dorso-ventrally, light brownish in colour; last abdominal spiracles placed at the tip of a pair of prominent tubular projections that are brownish due to sclerotization; an additional pair of shorter post-stigmatic projections on the last abdominal segment bearing a fan of long microtrichia; spiracles of abdominal segment 8 bordered by a row of short setae; spiracles of prothoracic segment and abdominal segments 1 to 7 prominent.

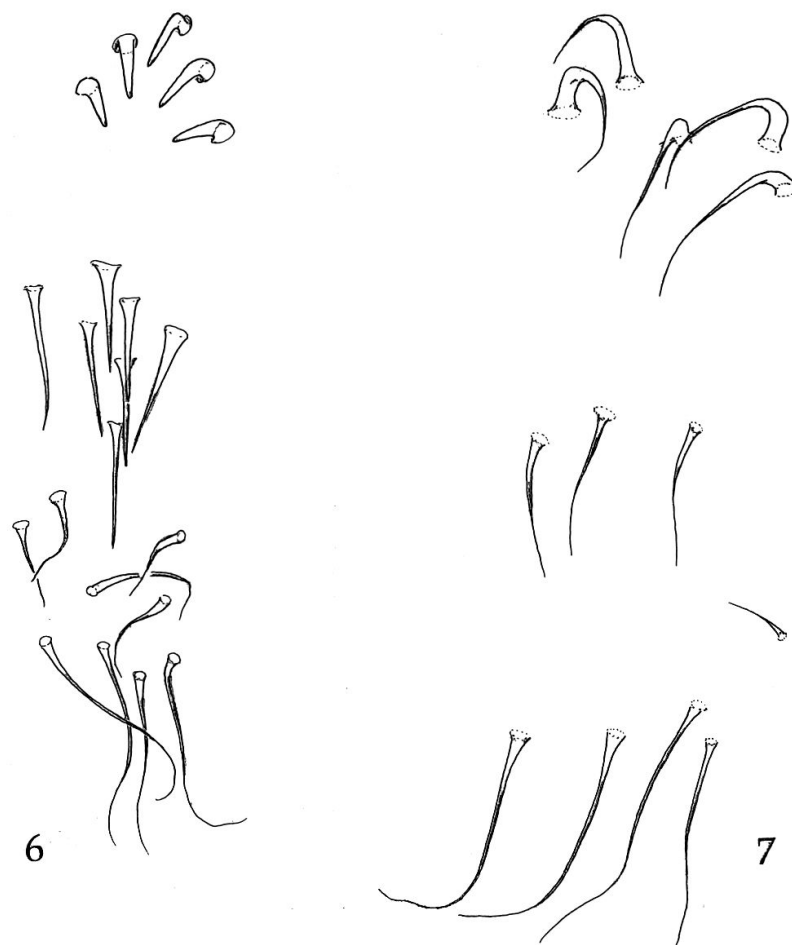
During life, larvae are covered with small organic and mineral particles that obscure the pattern of vestiture of tergites.

As can be seen (figs 4-5), two different species are present in this material. They can easily be separated by the vestiture of tergites, which is characteristic for every known genus of Scatopsidae. Shape of microtrichia is also different in both species (figs 6-7).

The precise systematic position of these larvae remains unclear: the projecting spiracles are characteristic of subfamily Scatopsinae to which both species clearly belong. The last pair of spiracles on long paired tubular processes and the



Figs. 4-5. Scatopsini+ *gen. sp. 1* and *gen. sp. 2*, last instar larvae (dorsal view). 4: *gen. sp. 1*, 2nd thoracic segment, 2nd abdominal segment and last abdominal segments; 5: *gen. sp. 2*, general view.



Figs. 6-7. Scatopsini+ *gen. sp. 1* and *gen. sp. 2*, last instar larvae, shape and arrangement of microtrichia on dorsum of 2nd abdominal segment. 6: *gen. sp. 1*; 7: *gen. sp. 2*.

pair of long conical postspiracular processes on last segment crowned at apex by a row of long spread out microtrichia suggest a placement in the Scatopsini or the Swammerdamellini. Larvae of the 2 tribes cannot be separated given the present state of knowledge (see further). Accordingly, these larvae are provisorily placed in Scatopsini+, following the group+ artifact of AMORIM (1982a) for unnamed inclusive taxa in sequenced classifications.

Material studied

Aquatic larvae of Scatopsidae have been collected in three stations, two of which are situated in the French Alps while the third lies at the margin of the mountainous area of Massif Central. *Gen. sp. 1*: Le Sappey (department Isère), 1000 m elevation: 18.VIII.1972, 2 larvae; 22.IV.1973, 1 larva; Revel (department Isère), 700 m elevation, 8.V.1969, 1 larva; 20.III.1979, 5 larvae; 23.IX.1979, 3 larvae; Marcols-les-Eaux, (department Ardèche), 800 m elevation, 30.III.1976, 1 larva. *Gen. sp. 2*: Le Sappey (department Isère), 800 m elevation, 18.III.1972, 3 larvae; 28.III.1973, 2 larvae; 29.III.1973, 1 larva; 16.IV.1984, 1 larva (all material leg. F. VAILLANT in coll. J.-P. HAENNI, MHNN).

Habitat

In the three cases, the larvae lived under rather similar conditions: they were found in little permanent springs and subsequent brooklets in forested areas. The substratum is sandstone with limestone main constitute, in Le Sappey, acid liassic schists in Revel and granite and basalt in Marcols-les-Eaux.

All three springs are in entirely shaded situations in mixed beech (*Fagus*) and ash-tree (*Fraxinus*) forest in Le Sappey, beech and chestnut-tree (*Castanea*) forest in Revel and pure chestnut-tree stand in Marcols-les-Eaux.

Water flows very slowly (much less than 1cm/ second) over fine gravel partly covered with mosses and dead tree leaves.

Scatopsid larvae have been collected among waterlogged dead leaves in the three stations. They were closely attached on leaves, just below the surface of water. They were never observed deeper in water than 1 or 2 mm. Both species have been collected in Le Sappey, while the 2 other stations hold only *sp. 1*.

In the three stations they lived in company with larvae of Ephemeroptera and Trichoptera, and Psychodidae larvae occurred in exactly similar conditions on wet tree-leaves. These larvae are considered by the second author as true madicolous elements, that is living under a very thin, not exceeding 1 or 2 mm, flowing water film, as defined by VAILLANT (1955).

DISCUSSION

Scatopsid with aquatic larvae have been discovered only very recently (HAENNI & VAILLANT, 1990). Noteworthy, however, is the record of larvae found "...under the loose decaying bark of spruce logs floating in a mill pond..." and described by JOHANNSEN (1934) who considered them as living in a semi-aquatic situation. In his redescription of these larvae, BEEKEY (1938) writes that "They occurred just above the water line where they were kept moist by capillary action".

Compared with those of terrestrial Scatopsidae, the aquatic larvae apparently do not display any peculiar adaptation to aquatic life. The respiratory system is apparently peripneustic in the last instar as in all other known genera of the family and there is no unusual regression either of the tracheal system or of the spiracles.

However this is not really surprising since larvae of this family, that are all saprophagous, live in a wide variety of organic matter in all degrees of decomposition and consequently often in semi-liquid or liquid media (e. g. larvae of *Cookella albitarsis* in fresh cow-dung, LAURENCE, in litt.). Mouthpieces of Scatopsid larvae have retained functional toothed mandibles but have also developed a pharyngeal filter retaining the organic particles suspended in water and eliminating water in excess. Posterior spiracles situated at apex of tubular more or less elongated processes can also be considered as a preadaptation to passage to life under aquatic conditions. The experiment by BOVIEN (1935) with non aquatic larvae of *Coboldia fuscipes* (MEIG.) is interesting in this respect. This species is known to develop in a great variety of decaying media of vegetal and animal origin, dung, etc. BOVIEN noted that there is an evident functional preeminence of the last pair of spiracles and that these larvae may well be regarded as "metapneustic (from a physiological point of view)". Furthermore he noted that the larvae of this species, when placed in water, are able to hang down under the surface of the water by means of the setae bordering the posterior spiracles. He even succeeded in rearing this species "in very moist surroundings (partly in water) where they had been forced to spend a good deal of their life hanging under the surface". This appears to be rather surprising

since the crown of setae bordering the posterior spiracles are very short in this species, comparable in size to those of aquatic species described here. This appears to be in contradiction with the observation made by the second author when processing waterlogged leaf litter through modified Berlese apparatus with a jar containing water for collecting the extracted fauna. The Scatopsid larvae fall down to the bottom of the jar and were not able to hang down under the surface of water.

It is quite surprising that so few Scatopsidae have occupied such niches. Maybe the discovery of immature stages of the numerous genera for which they are still unknown will help in answering this question.

REVIEW OF THE KNOWN LARVAE OF SCATOPSIDAE

Our knowledge of immature stages of Scatopsidae is very poor. Including that of *Holoplagia* described in the present paper, larvae of only 8 genera have been described, representing only about 1/4 of the number of genera in the family. Furthermore no larvae are known for the 2 subfamilies Aspistinae and Psectrosciarinae (Tab. 1).

Tab. 1. Number of described larvae and adults of Scatopsidae by subfamilies and tribes (genera / species). Systematic arrangement according to AMORIM (in press).

	larvae	adults
ASPISTINAE	–	2 / 9
ECTAETIINAE	1 / 1	1 / 7
PSECTROSCIARINAE	–	2 / 59
SCATOPSINAE	7(+1?) / 13	26 / 268
Rhegmoclematini	1(+1?) / 1(+1?)	8 / 80
Scatopsini	2 / 2	4 / 29
Colobostematini	1 / 1	6 / 82
Swammerdamellini	3 / 3(+1)	8 / 66
Incertae sedis	? / 4	? / 11

Scatopsid larvae can be easily recognized by the following characters: head capsule complete, not retractable, no hypostomal bridge; antennae well developed, three-segmented; mouthparts with a premandibular sclerite; respiration peripneustic, with 9 pairs of spiracles present.

Characters of the subfamilies and tribes

It should be stressed that due to the small number of described forms, and also due to the absence of any indication for 2 subfamilies, the characters given below

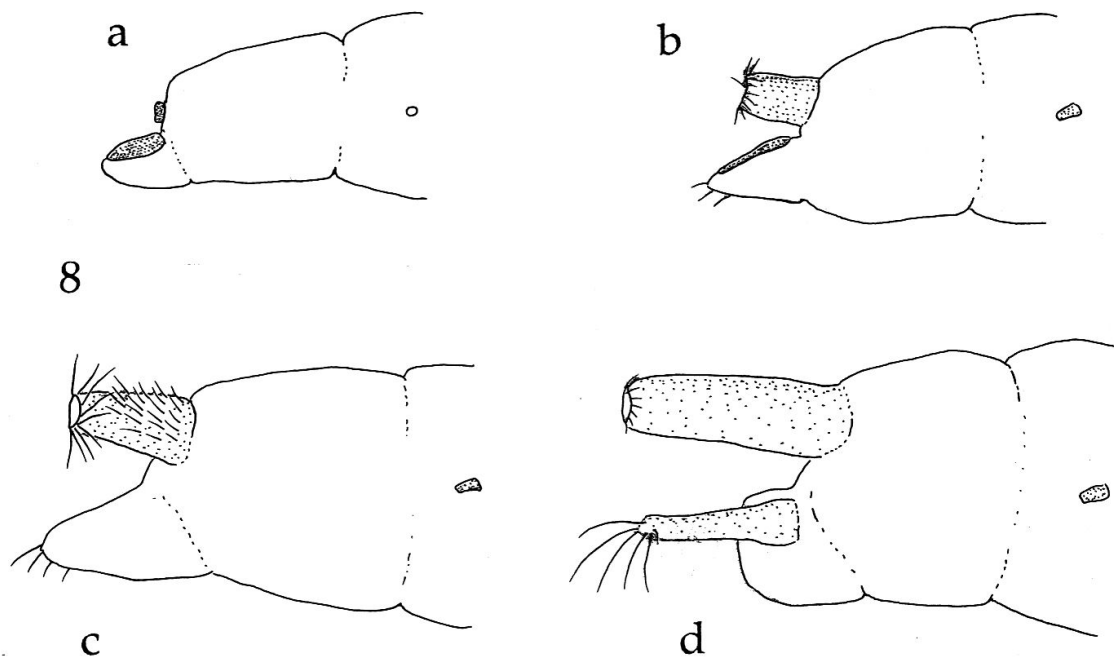


Fig. 8. Last abdominal segment of larvae of Scatopsidae (diagrammatic side view; sclerotized parts are stippled).

a: Ectaeiinae (*Ectaeitia*); b: Scatopsinae Rhegmoclematini (*Parascatopse*); c: Scatopsinae Colobostematini (*Holoplagia*); d: Scatopsinae Scatopsini and Swammerdamellini (*Apiloscatopse*). (a: after LAURENCE, 1953a, modified; b: after SZADZIEWSKI, 1979; c: original; d: after HAENNI, 1981).

should only be considered as tentative until more numerous forms are known. Accordingly, no attempt of phylogenetic interpretation of state of characters has been made. Diagrammatic views of characters are given on fig. 8.

Ectaeiinae: spiracles sessile except for the last pair which is very shortly pedunculate; no paired processes on well developed sclerotized pygidial plate (fig. 8a) (*Ectaeitia*, LAURENCE, 1953).

Scatopsinae: all spiracles projecting, especially the posterior pair which is situated at the tip of long tubular or conical processes (figs. 8b-d). Subfamily Scatopsinae was currently divided into 3 tribes according to COOK (for example 1981). However recent phylogenetic analysis of the family as a whole largely based upon adult morphology, especially genital structures, has conduced AMORIM (in press) to recognize 4 tribes, with partly different limits. It is interesting in this respect to see that the larva of *Holoplagia* described in the present paper possesses several unique characters that could be apomorphies and support erection of tribe Colobostematini.

Rhegmoclematini: in the only satisfactorily described larva of this tribe (*Parascatopse*, SZADZIEWSKI, 1979), the pygidial plate is simple, sclerotized and there are no postspiracular projections (fig. 8b). The larva figured by PETERSON (1951) under the generic name *Rhegmoclema* possibly also belongs in this tribe.

Colobostematini: pygidial plate unsclerotized, vestigial in the only known larva (*Holoplagia*); no paired tubular sclerotized poststigmatic projections but a pair of short lobes with longer microtrichia at apex; tubular sclerotized processes bearing the posterior spiracles largely covered with regular rows of long microtrichia and circled at apex by a row of very long fine setae (figs 3, 8c).

Tab. 2. Descriptions of immature stages of Scatopsidae (partly compiled after HENNIG, 1948, modified and completed). Systematic arrangement follows AMORIM (in press). (Abbreviations. L₁₋₄: larval instars, P: pupa).

Species	Instar	Author	Reference
ECTAETIINAE <i>Ectaetia platyscelis</i> (Lw.)	L ₄	LAURENCE, 1953a FREEMAN, 1985	p. 205, figs. 1-6 p. 24, fig. 54
SCATOPSINAE Rhegmoclematini <i>Parascatopse litorea</i> (Edw.) <i>Rhegmoclema</i> sp. [?]	L ₃ or L ₄ L ₄	SZADZIEWSKI, 1979 PETERSON, 1951	p. 388, figs. 6-11 p. 274, fig. D6(J)
Colobostematini <i>Holoplagia richardsi</i> (Edw.)	L ₄	HAENNI & VAILLANT, present paper	pp. 44-46, figs. 1-3
Scatopsini <i>Scatopse notata</i> (L.) « <i>Scatopse</i> » sp. [<i>Apiloscatopse</i> sp.] (<i>Apiloscatopse flavicollis</i> (Mg.) <i>A. scutellata</i> (Lw.) (<i>Reichertella pulicaria</i> (Lw.)	P L ₄ L ₄ , P L ₁₋₄ L ₁₋₃ L ₄ L ₄ , P L ₄ L ₄ L ₄ , P L ₄ L ₄	DE MEIJERE, 1902 DE MEIJERE, 1916 MORRIS, 1918 BOVIEN, 1935 KEILIN, 1944 KRIVOSHEINA & MAMAEV, 1967 FREEMAN, 1985 BRAUNS, 1954a GOETGHEBUER, 1925 HAENNI, 1981 SEDDON, 1985 BISCHOFF, 1992 WEHRMEISTER, 1924	p. 669, figs. pp. 180-183, pl. 4 figs. 1-4 pp. 103-111, figs. 1-7, pl. 10 figs. 1-8 p. 38 pp. 23, 26-28, figs. 21-22 pp. 115-117, fig. 42 (6-8) pp. 23-24, figs. 49-53, 55 p. 43, fig. 9 p. 149, fig. 4 pp. 263-265, figs. 8-11 pp. 50-52, figs. 2-3 fig. Pl. 2 fig. 17
Swammerdamellini <i>Rhexoza subnitens</i> (Verr.) <i>Rhexoza s.l. similis</i> (Beekey) <i>Rhexoza s.l. sp.</i> <i>Coboldia fuscipes</i> (Mg.) « <i>Rhegmoclema atrata</i> » [? <i>fuscipes</i>]	L ₄ , P L ₄ L ₄ , P L ₄ , P L ₄ , P L ₄ , P L ₄ L ₁₋₄ L ₁₋₂ , L ₄ L ₄ , P L ₄ , P L ₄ , P L ₄ L ₄ L ₄ , P	TONNOIR, 1927 KRIVOSHEINA & MAMAEV, 1967 JOHANSSEN, 1934 BEEKEY, 1938 COOK, 1981 LYALL, 1929 BURAKOVA, 1931 BOVIEN, 1935 FLACHS, 1943 HENNIG, 1948 RABELLO & FORATTINI, 1962 COOK, 1963 KRIVOSHEINA & MAMAEV, 1967 FREEMAN, 1985 MALLOCH, 1917	pp. 353-356, figs. 1-2 p. 115, fig. 42 (1-5) p. 50 pp. 151-153, pl. 4 figs. 1-3, 6-7 p. 316, figs. 24-26 pp. 631-635, figs. 1-14 pp. 115-117, figs. pp. 35-42, figs. 1-3 pp. 182-186, figs. p. 88, figs. 21-23, pl. 2 figs. 2, 4-5 pp. 304-307, fig. 4 p. 4, pl. 1 figs. 1-2 pp. 113-115, figs. 40-41 p. 24 pp. 301-302, pl. 45 figs. 1-5, 8
Scatopsinae incertae sedis « <i>Scatopse</i> » sp. [unknown genus] gen. sp. « <i>Scatopse</i> » sp. [unknown genus] gen. sp. 1 gen. sp. 2	L ₄ P L ₄ L ₄ L ₄	PETERSON, 1951 BRAUNS, 1954b KRIVOSHEINA & MAMAEV, 1967 HAENNI & VAILLANT, present paper HAENNI & VAILLANT, present paper	p. 274, fig. D6 (K) p. 42, fig. 6 pp. 117-119, fig. 43 pp. 46-49, figs. 4, 6 pp. 46-49, figs. 5, 7

Scatopsini and Swammerdamellini: tubular sclerotized processes bearing posterior spiracles bare, with a circle of short microtrichia at apex; an additional pair of long tubular postspiracular processes on the last abdominal segment, crowned at apex by a fan of long spread-out microtrichia (fig. 8d). No larval characters could be found so far to separate larvae of these 2 tribes. On the other hand, there are good characters in the dorsal pattern of vestiture of microtrichia of thoracic and abdominal segments as well as in proportions of antennal segments that allow recognition of genera not only of these tribes but of all Scatopsinae.

Available modern descriptions and figures of immature stages of the family are summarised in tab. 2. The only key to the identification of larvae of Scatopsidae is that by KRIVOSHEINA & MAMAEV (1967) (timber-dwelling species) in Russian which deals with only 4 species, one of which being an unidentified "*Scatopse*" species. Comparative notes are also given by LYALL (1929) and by HAENNI (1981) for respectively 4 and 6 species. On the other hand HENNIG (1948) thoroughly reviews the published descriptions and figures while SMITH (1989) gathers published figures of 6 described species.

More or less precise indications concerning the biology and development medium exist for some 35-40 species. The published data are summarized in tab. 3 (see "Appendix" further). However, most of the literature records concern the 2 cosmopolitan and anthropophilous species *Scatopse notata* and *Coboldia fuscipes*, the larvae of which develop in a wide variety of decaying organic matter of both vegetal and animal origin, and these will only appear later in the annotated bibliography.

Biology of the early stages of other genera is rather diverse, but all known larvae appear to be saprophagous. MÜLLER (1919) reports however the emergence of 2 species, assumed by him to be parasitic, from pupae of *Phora*. This is quite surprising and we agree with EDWARDS (1925) opinion that "... the pupae may well have been dead when attacked."

Decaying vegetal material (especially rotten plants and fruits) is generally favoured, particularly by Scatopsini and Swammerdamellini. Ectaeiinae larvae seem restricted to rotten wood while several Swammerdamellini (*Rhexoza* s. l.) have been found under decaying bark of dead trees and the species of *Holoplagia* (Colobostematini) described in this paper in water-filled tree-holes. Some genera are tericolous: *Parascatopse* in saltings, *Aspistes* in sandy soils, *Apiloscatopse* in leaf litter. Larvae of some Psectrosciarinae and Rhegmoclematini possibly develop in wet or even marshy soils. Aquatic species of unknown generic placement described in this paper probably feed upon the waterlogged dead leaves among which they were collected. Myrmecophilous genera are present in Colobostematini (*Colobostema*, *Holoplagia*) and possibly in Swammerdamellini (*Swammerdamella*). There are indications that their larvae live upon wood and other debris in ants' nests. A large number of species of fungi have been recorded as medium for larvae of *Coboldia fuscipes*, and there are few other records of *Apiloscatopse* species. Dung is mainly exploited by Scatopsini (*Scatopse*, *Reichertella*) but also by Colobostematini (*Cookella*), Swammerdamellini (*Coboldia*) and Psectrosciarinae (*Anapausis*, one record). Finally, one should stress the fact that nearly all the available data concern species of the temperate climatic zones. Practically nothing is known of the immature stages or life-histories of genera and species from the tropical and sub-tropical regions.

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RÉSUMÉ

La larve L₄ de *Holoplugia richardsi* (EDWARDS, 1934) est décrite et figurée. Il s'agit de la première larve connue du genre *Holoplugia* et de la première larve dendrolimnobile de la famille des Scatopsidae. L'espèce a été élevée à partir de larves vivant dans un trou rempli d'eau d'un Erable sycomore dans la région de Grenoble en compagnie de celle d'un autre Scatopsidé, *Ectactia platyscelis* (LOEW, 1869). Les 2 espèces sont rares et nouvelles pour la faune de France, et même pour la faune d'Europe continentale pour *E. platyscelis*. Deux autres larves franchement aquatiques de Scatopsidae de genres inconnus sont décrites provisoirement et figurées. Elles proviennent de sources et de ruisselets forestiers du Sud-Est de la France. Toutes les autres larves de Scatopsidae connues sont terrestres. Nos connaissances des stades pré-imaginaux de cette famille sont revues à la lumière de ces nouvelles découvertes. Une bibliographie annotée des stades préimaginaux des Scatopsidae du monde est finalement présentée.

ANNOTATED BIBLIOGRAPHY OF THE IMMATURE STAGES OF SCATOPSIDAE

All the references dealing with the immature stages of Scatopsidae that are known to the first author are included. However only a selection is given of the numerous papers merely mentioning the occurrence of larval development of *C. fuscipes* and *S. notata* in various media like fungi, fruits, foods, dung, carrion and other decaying material. Additional notes and comments are in square brackets. References quoted in the main text but dealing with other topics are grouped separately at the end of the list.

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Appendix (pp. 58-59)

Tab. 3. Biology and ecology of immature stages of Scatopsidae (compiled after FREEMAN, 1985 and SMITH, 1989, modified and completed). Systematic arrangement according to AMORIM (in press). Species with described larvae are marked with *.

Species	Location of immature stages	Country	Author	Remarks
ASPISTINAE <i>Aspistes berlinensis</i> (Mg.)	sandy places coastal dunes	Czechoslovakia Sweden	VIMMER, 1935 ARDØ, 1957	sifted litter
ECTAETIINAE * <i>Ectaetia platyscelis</i> (Lw.) <i>E. clavipes</i> (Mg.) <i>E. lignicola</i> Edw.	rotting <i>Fagus</i> , <i>Ulmus</i> , <i>Tilia</i> tree hole tree hole filled with water (<i>Acer</i>) rotting wood rotting trees, wood debris	Great Britain Great Britain France Great Britain Great Britain	EDWARDS, 1925 LAURENCE, 1953 HAENNI & VAILLANT, present paper FREEMAN, 1985 EDWARDS, 1925	
PSECTROSCIARINAE <i>Anapausis aratrix</i> H. & B. <i>A. baueri</i> Fritz <i>A. soluta</i> (Lw.)	soil in peat-bog (pH 4.7-5.9) reed-beds (temporarily flooded) cow dung	France Germany Great Britain	BRUNHES & HAENNI, 1982 FRITZ, 1983a SKIDMORE, 1978	emergence trap emergence trap
SCATOPSIINAE Rhegmoclematini * <i>Parascatopse litorea</i> (Edw.) * <i>Rhegmoclema</i> sp. [?] <i>Rhegmoclema edwardsi</i> (Coll.) <i>Rh. halteratum</i> (Mg.) <i>Rh. verralli</i> (Edw.)	soil in saltings in rotten vegetation, under bark of dead tree soil in peat-bog (pH 4.9 - 5.7) soil in peat-bog (pH 4.9 - 5.7) dry reed-beds (temporarily flooded), marshy meadows	Poland U.S.A. France France Germany	SZADZIEWSKI, 1979 PETERSON, 1951 BRUNHES & HAENNI, 1982 BRUNHES & HAENNI, 1982 FRITZ, 1983b	emergence trap emergence trap emergence trap
Colobostematini <i>Holoplagia transversalis</i> (Lw.) * <i>H. richardsi</i> (Edw.) <i>Colobostema infumatum</i> (Hal.) <i>C. nigripenne</i> (Mg.) <i>Cookella albitarsis</i> (Zett.)	ant's nest (<i>Lasius fuliginosus</i>) around ant's nest (<i>Formica</i> 3 spp., <i>L. fuliginosus</i>) rotting <i>Fagus</i> tree hole filled with water (<i>Acer</i>), damp tree hole (<i>Fraxinus</i>) in ant's nests (<i>L. fuliginosus</i> , <i>F. rufa</i>) in ant's nests (<i>L. fuliginosus</i> , <i>F. rufa</i>) cow dung burrows of voles cow & small rodent dung	Great Britain Sweden Great Britain France Great Britain Sweden Great Britain Finland Great Britain	DONISTHORPE, 1927 ANDERSSON, 1982 EDWARDS, 1934 HAENNI & VAILLANT, present paper DONISTHORPE, 1927 ANDERSSON, 1982 LAURENCE, 1953b, 1954 HACKMAN, 1963 SKIDMORE, 1978	

<p>Scatopsini * <i>Scatopse notata</i> (L.) * « <i>Scatopse</i> » sp. [<i>Apiloscatopse</i> sp.] <i>Apiloscatopse flavicollis</i> (Mg.) * <i>A. scutellata</i> (Lw.) <i>Reichertella nigra</i> (Mg.) <i>R. pulicaria</i> (Lw.)</p>	<p>all kinds of decaying vegetal & animal matters, mushrooms, etc. terricolous mushroom (<i>Tricholoma</i>) mushroom (<i>Bjerkendera</i>) leaf litter in deciduous forests soil in deciduous woodland emerged from pupa of <i>Phora</i> wet forests, marshy meadows, dry reed-beds dung (privies)</p>	<p>Cosmopolitan ? Germany Great Britain Great Britain Switzerland Great Britain Germany Germany Great Britain</p>	<p>various authors BRAUNS, 1954a CHANDLER, 1978 CHANDLER, 1978 HAENNI, 1981 SEDDON, 1985 MÜLLER, 1919 FRITZ, 1983a SKIDMORE, 1978</p>	<p>assumed to be parasitic [?] emergence trap</p>
<p>Swammerdamellini * <i>Rhexoza subnitens</i> (Verr.) <i>Rh. incisa</i> Cook <i>Rh. (s.l.) aterrima</i> (Mel.) <i>Rh. (s.l.) teskeyi</i> Cook <i>Rh. (s.l.) amaryllis</i> Cook <i>Rh. (s.l.) ryckmani</i> Cook * <i>Rh. (s.l.) similis</i> (Beek.) * <i>Coboldia fuscipes</i> (Mg.) <i>Quateiella quatei</i> (Cook) <i>Q. miniscula</i> (Cook) <i>Swammerdamella brevicornis</i> (Mg.) <i>S. acuta</i> Cook <i>S. adercotris</i> Cook <i>Sw. [?] cryptica</i> Cook</p>	<p>under bark of cut down <i>Populus</i> under bark of cut down <i>Quercus</i> under bark of <i>Ulmus</i>, <i>Acer</i>, <i>Populus</i> log of <i>Pinus</i> twigs of <i>Pinus</i> rotting bulbs <i>Echinocactus</i> beneath bark of floating spruce logs (above water) all kinds of decaying vegetal & animal matter, mushrooms, dung, etc. <i>Echinocactus</i> cucumber stems, melon roots emerged from pupa of <i>Phora</i> marshy soil (pH 6.5-7.2) peat-bog soil (pH 4.9-5.7) peat-bog soil (pH 4.9-5.7) debris in tree crotch</p>	<p>Belgium Russia, Ukraine U.S.A. U.S.A. Canada Canada U.S.A. U.S.A. Cosmopolitan U.S.A. U.S.A. Germany France France France U.S.A.</p>	<p>TONNOIR, 1927 KRIVOSHEINA & MAMAEV, 1967 COOK, 1956 COOK, 1956 COOK, 1975 COOK, 1975 COOK, 1975 COOK, 1975 JOHANSEN, 1934, BEEKEY, 1938 various authors COOK, 1975 COOK, 1956 MÜLLER, 1919 BRUNHES & HAENNI, 1982 BRUNHES & HAENNI, 1982 BRUNHES & HAENNI, 1982 COOK, 1956</p>	<p>assumed to be parasitic [?] emergence trap emergence trap emergence trap</p>
<p>Incertae sedis (Scatopsinae) * « <i>Scatopse</i> » sp. [unknown genus] * gen. sp. * « <i>Scatopse</i> » sp. [unknown genus] * gen. sp. 1 * gen. sp. 2</p>	<p>decayed tomatoes on the ground terricolous under rotten bark waterlogged leaves in springs and forest brooklets waterlogged leaves in springs and forest brooklets</p>	<p>U.S.A. ? Germany Ukraine, Kirghizistan France France</p>	<p>PETERSON, 1951 BRAUNS, 1954b KRIVOSHEINA & MAMAEV, 1967 HAENNI & VAILLANT, present paper HAENNI & VAILLANT, present paper</p>	<p></p>