

Biological observations and taxonomic notes on *Actias isabellae* (GRAELLS) (Lepidoptera, Saturniidae)

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Summary

1. Proof is given to support the correct original spelling of the specific epithet : i.e. *isabellae* (with two "l"). The alternative spelling with only one "l" is incorrect according to the International Code of Zoological Nomenclature.
2. The traditional placement of this species in a genus of its own (*Graellsia*) must be considered incorrect, based on phylogenetic reasoning. Such a classification leaves the remaining species in the genus *Actias* as a paraphyletic group.
3. Tests were conducted on foodplant acceptance by the larvae of *Actias isabellae* ; L₁ to L₅ freely accepted all species of *Pinus* offered, and several other species of Pinaceae were accepted with increasing reluctance. Outside the plant family Pinaceae no suitable foodplant was found. *Liquidambar* (Hamamelidaceae), a standard foodplant for other species of *Actias* in captivity, was not accepted, probably due to the texture of the broad leaf. Apparently, larvae of *A. isabellae* require the form of a needle in addition to chemical cues to commence feeding.
4. When a pine needle is eaten down to its sheath, the older larvae (L_{4/5}) of *A. isabellae* seal the resin canals of the stub with silk. This remarkable behaviour is probably due to the danger of becoming entangled by the very sticky resin of *Pinus* at the feeding site.

Zusammenfassung

1. Es wird gezeigt, daß die korrekte ursprüngliche Schreibweise des Artnamens der Art *isabellae* (mit zwei „l“) lautet ; die sekundäre Schreibweise mit nur einem „l“ ist falsch im Sinne der Nomenklaturregeln.
2. Der Verbleib der Art im traditionellen monotypischen Genus *Graellsia* muß auf der Basis phylogenetischer Überlegungen als unrichtig interpretiert werden ;

(1) 22nd contribution to the knowledge of the Saturniidae.

in diesem Fall ist nämlich die Gattung *Actias* als paraphyletische Restgruppe anzusehen. Deshalb muß *isabellae* in die Gattung *Actias* einbezogen werden.

3. Es wurden Versuche zur Futterakzeptanz der Raupen von *Actias isabellae* durchgeführt; L₁ bis L₅ akzeptierten sämtliche *Pinus*-Arten, die ihnen angeboten wurden, sowie einige weitere Pinaceenarten mit zunehmender Abneigung. Außerhalb der Pinaceae wurde keine weitere taugliche Futterpflanze gefunden. *Liquidambar* (Hamamelidaceae), eine wichtige Futterpflanze zur Zucht fast aller anderen *Actias*-Arten, wurde nicht gefressen, wahrscheinlich wegen der Blattstruktur (breites Laubblatt); die Raupen von *A. isabellae* benötigen offenbar zusätzlich zu chemischen Reizen noch eine bestimmte Laubtextur (Nadeln) zum Auslösen des Freßaktes.

4. Wenn eine ältere Raupe (L_{4/5}) von *A. isabellae* eine Kiefernnadel bis zur Basis heruntergefressen hat, „versiegelt“ sie die Schnittstelle innerhalb des Kurztriebs mit Spinnfäden, vermutlich um das Austreten größerer klebriger Harzmengen zu vermeiden, in dem sie festkleben könnte.

Résumen

1. Se prueba que la grafía original del nombre de la especie es *isabellae*, con dos «b», y que la modificación subsiguiente con una «b» es incorrecta, de acuerdo con el Código Internacional de Nomenclatura Zoológica.

2. La consideración de esta especie en un género monotípico, *Graellsia*, no puede mantenerse en función de razonamientos filogenéticos; en dicho caso, el género *Actias* devendría un grupo parafilético. Por ello, parece más razonable situar a *isabellae* en el género *Actias*.

3. Se han llevado a cabo ensayos sobre la aceptación de diferentes plantas nutricias por las orugas de *Actias isabellae*. Las larvas de L₁ hasta L₅ aceptan tanto diferentes especies de *Pinus* como otras Pináceas, con síntomas de rechazo mayores a medida que disminuye el parentesco taxonómico de éstas con respecto al *Pinus*. Ninguna planta no Pinácea ha sido tomada por las orugas. El vegetal hospedador por excelencia de las larvas de la mayoría de las otras especies de *Actias*, *Liquidambar* (Hamamelidaceae), no fue consumido, probablemente a causa del limbo ancho de su hoja (como corresponde a una frondosa); al parecer, para que se desencadene en ellas el acto de comer, las orugas de *A. isabellae* requieren, aparte del estímulo químico, una determinada estructura de hoja, en este caso acicular.

4. Una vez que la oruga ya crecida ha comido la acícula del pino hasta la base, «sella» el punto por donde ha cortado ésta con hilos de seda, presumiblemente con objeto de evitar la salida de mayores cantidades de resina, en la cual podría quedar pegada.

Introduction

Actias isabellae GRAELLS, 1849, the only European representative of the “moon moths” with tailed hindwings, is one of the most famous and most beautiful Lepidoptera species in Europe. It is in great demand among amateur lepidopterologists, and many papers have been published on the species. For a review of older literature see TESTOUT (1940). Descriptions of the behaviour of the imagines, notes on artificial pairing and recommendations for rearing, observations on larval morphology, distribution data, etc., were published by CEBALLOS & AGENJO ([1944]), MARTEN (1955), BALCELLS R. & DICENTA (1963), MASÓ I PLANAS & YLLA I ULLASTRE (1989), SANETRA & PEUKER (1991) and others (see below). Nevertheless, some questions remain on the systematics and biology of the species.

In the present paper some biological observations on foodplant acceptance and behaviour of the larvae of the species are given, together with notes on taxonomy. The observations were made during rearing experiments between 1985 and 1988.

Taxonomic and general notes

In 1849 GRAELLS described a new European species of Saturniidae, naming it in honour of the Spanish queen Isabel II (French spelling: Isabelle). His text was translated from Spanish into French by M. L. FAIRMAIRE (TESTOUT, 1940). The editor of the journal used the French spelling on which to base the name *isabellae*. Whether this was the intention or not of GRAELLS, the resulting publication of spelling *Saturnia Isabellae* (with two “l”) must be accepted as *correct original spelling* (see Article 32(b) of the International Code of Zoological Nomenclature, ICZN 1985). There is regrettably a long tradition of using the incorrect spelling (i.e. “*isabelae*”), especially in the Spanish literature on the species. Examples of this *incorrect subsequent spelling* as defined by the Code are seen in all Spanish authors cited here (except GRAELLS himself!), DE PRINS (1978), DEMOULIN (1978), and DE FREINA & WITT (1987 [the spelling was corrected into “ll” during press with two small notes in the main text and in the “Synopsis”]).

Periodically there has been some controversy regarding how GRAELLS intended to spell the name (e.g., AGENJO in CEBALLOS & AGENJO, [1944]; DE PRINS, 1978; DEMOULIN, 1978), but Article 32(c)(ii) of the ICZN clearly restricts what may be regarded as an incorrect original spelling: “An original spelling is an ‘incorrect original spelling’ if ...

there is *in the original publication itself, without recourse to any external source of information*, clear evidence of an inadvertent error ..." (italics mine). In GRAELLS (1849), the original description of the taxon, the name is spelled consistently with the double "l". Therefore, since the Code is clear about this original spelling being mandatory, an application to the International Commission on Zoological Nomenclature, as suggested by DE PRINS (1978), is not necessary.

AGENJO (in CEBALLOS & AGENJO, [1944]) is incorrect when he states (p. 340, bottom): "GRAELLS, in his original description of *isabellae*, wrote *Saturnia Isabelae* GRLLS.", because neither the painted plates nor the manuscript — which is lost, according to AGENJO! — but only the published version, by definition of the Code, constitutes the original description. Even a "copyist's or printer's error", as defined by the Code, Art. 32(c)(ii), is not to be assumed, because GRAELLS in later publications again consistently used *isabellae* with two "l": 1850, in a more detailed and illustrated redescription of the new taxon in French, as well as [1851] (according to TESTOUT, 1940, but [1852] according to CEBALLOS & AGENJO, [1944], and DE PRINS, 1978), in his redescription of the taxon in the Spanish language with a dedication to the Spanish queen Isabel II. AGENJO's interpretation (in CEBALLOS & AGENJO [1944]) is not in accordance with the ruling of the 3rd edition of the Code. There is no valid source for the misspelling "*isabellae*".

The publication of FAIRMAIRE (1849) is not a valid description; the name proposed therein ("*Saturnia Diana*") must be considered a nomen nudum, because the new species was not described.

The autochthonous existence of the species in France was repeatedly questioned (e.g., BOLLOW, 1932; SCHÜSSLER, 1936; ALVAREZ & TEMPLADO, 1977), but was demonstrated beyond doubt by CLEU (1939), WARNECKE (1943), MARTEN (1955), and most recently by MASO I PLANAS & WILLIEN (1989) and MASO I PLANAS & YLLA I ULLASTRE (1989). There can be no doubt that the French populations are naturally occurring relicts of a formerly much wider distribution. These northernmost populations are still treated as a subspecies, *A. isabellae galliaegloria* OBERTHÜR, 1922 (see DE FREINA & WITT, 1987), but the differences between the Spanish and French populations are very small, and *Actias isabellae* may probably best be interpreted as a monotypic species.

For the sole European species of the "moon moths", GROTE (1896: 3) proposed a new genus *Graellsia* in honour of GRAELLS, within his "table for determination" of saturniid genera. As was usual for his time, this was done from a purely typological and eurocentric viewpoint

instead of on the grounds of a phylogenetic hypothesis, based on studies of all species world-wide. The European moth is a close relative of those Asiatic and North American species which are currently all treated as congeneric under the name *Actias* LEACH, 1815 (see NÄSSIG & PEIGLER 1984, PEIGLER 1986, HOLLOWAY 1987; in these two latter publications the African species traditionally placed in *Argema* WALLENGREN, 1858, are also included under *Actias*). One Asiatic species, *Actias dubernardi* (OBERTHÜR, 1897), is known (MELL, 1950) to also feed on *Pinus*; this is surely a parallel development, which does not necessarily indicate a close relationship of *dubernardi* and *isabellae*.

The wing colouration of *A. isabellae* with pronounced brownish veins is interpreted as an independent autapomorphy of the taxon *isabellae* — an adaptation to the striate environment of pine needles in treetops (HOLLOWAY, 1987), a common resting place of the imagines during the daytime (MARTEN, 1955); it may also be an adequate camouflage for freshly emerged moths in the vegetation near the ground. Also, these patterns and the dark body may be helpful to warm up better during basking behaviour at cold spring evenings. Pronounced venation patterns are rare in Saturniidae, but can be found in several unrelated groups: e.g., in *Bunaeini* (*Bunaeopsis* BOUVIER, 1929), in several groups of Hemileucinae (see HENKE, 1936), in the saturniine genus *Pararhodia* COCKERELL, 1914, or in *Antheraea helferi* MOORE, 1858, where such a pattern is part of the individual variation and may or may not be present (NÄSSIG, unpubl.). There is no reason to interpret the brownish venation of *A. isabellae* as a plesiomorphic pattern. On the contrary, species like *Actias maenas* (DOUBLEDAY, 1847), the African species, and even *A. isabellae* exhibit the typical saturniine wing pattern with submarginal, postdiscal and basal fasciae, etc., and these patterns suggest that the plesiomorphic condition within the *Actias* group was the normal saturniine pattern. Pronounced venation patterns in saturniid moths are always restricted to small species groups and represent apomorphic characters of small monophyletic units, usually below the level of genus.

The short tails of the hindwing, interpreted by several authors as a plesiomorphic condition (e.g., PACKARD, 1914), apparently are adaptations towards the northern temperate climate; in any case the northernmost members of a species group in *Actias* have shorter tails than their closest relatives further south (*A. luna* LINNAEUS, 1758, versus *truncatipennis* SONTTHONNAX, 1899; *artemis* BREMER & GREY, 1853, and *gnoma* BUTLER, 1877, versus *selene* HÜBNER, 1806). The

family in general is a tropical family, and especially the *Actias* group of species is of palaeotropical origin ; short tails are best interpreted as secondary reductions.

It seems quite likely that the European species is more closely related to the other Holarctic species than to the African ones. There are no known synapomorphies that would indicate a sister group relationship between *Actias* sensu lato and *Graellsia*, which would be the only phylogenetic justification for maintaining *Graellsia* as a distinct genus. The genus *Actias* is well proven to be monophyletic by many derived characters, e.g. the presence of a “tail” on the hindwings, incorporating the anal and cubital veins and vein M3, the unique greenish colouration, and several aspects of larval and genitalia morphology (HOLLOWAY, 1987 ; KUZNETSOV & STEKOLNIKOV, 1985). Most of these characters are shared by the African species (traditionally placed in *Argema*), which might represent the sister group of *Actias* sensu NÄSSIG & PEIGLER (1984). The taxon *isabellae* also shares most of these apomorphies. It appears that “*Graellsia*” *isabellae* will prove to be the sister species of only *some* of the short tailed Holarctic species of *Actias* like *luna*, *selene*, *artemis*, *gnoma* and/or others. Therefore, on a phylogenetic reasoning, the exclusion of the only European species from *Actias* has to be interpreted as an unnatural grouping, making *Actias* paraphyletic. Hence the taxon *isabellae* must by necessity be included in *Actias*. *Graellsia* thereby becomes a junior subjective synonym of *Actias*. This inclusion is also supported by the results of hybridisation experiments (e.g., COCAULT et al., 1979, 1980). Maintaining the genus *Graellsia* requires division of the homogenous genus *Actias* into many small or monotypic genera to avoid paraphyletic taxa.

The genus *Actias* s.l. is a true member of the subfamily Saturniinae (MICHENER, 1952). Some early authors (e.g., SCHÜSSLER, 1936) included *Actias* s.l. into a “family Syssphingidae, subfamily Rhescyn-tinae” (that is, among a distantly related assemblage of genera, which share only quadripectinate antennae and tailed hindwings).

Observations on foodplant acceptance

During laboratory rearing experiments in 1985-1988 in Germany, caterpillars of *Actias isabellae* of differing ages (L_1 to mature L_5) were offered a variety of different plants. The standard method was to have a small group (2-5) of larvae of the same age within a rearing container and to offer them twigs of several plant species in addition to one small twig of *Pinus sylvestris* L., a plant known to be utilized in the wild. Behaviour of the larvae toward these plants was observed for

1-2 days and tabulated for acceptance or rejection into several categories. When a plant species seemed to be accepted, it was tested as a single available food for a longer time of one week or more. It was not specifically tested whether the surrogates when used as sole food during the full larval development would enable the larvae to pupate successfully (compare MASÓ I PLANAS & YLLA I ULLASTRE, 1989); the larvae were fed with mixtures of *Pinus sylvestris* or *P. mugo* and other food during their life, and a high percentage of them resulted in healthy pupae.

The results of these foodplant acceptance tests (see Table I) demonstrate the clear preference of *Actias isabellae* caterpillars for Pinaceae, especially for plants of the genus *Pinus* itself. All *Pinus* species tested could be used as the sole food during rearing. This is also supported by observations (e.g., MARTEN, 1955; ALVAREZ & TEMPLADO, 1977) that other *Pinus* species besides *P. sylvestris* L. may be the main food resource for some populations in the wild, such as *P. nigra* ARNOLD (= *P. laricio* (POIR.) MAIRE) or *P. uncinata* MILL. (= *P. mugo* TURRA). A wide acceptance of *Pinus* species as food in captivity was shown already by VUATTOUX (1984, 1985). However, it is rather surprising that a high degree of acceptance of other Pinaceae was also found in the present study, and this information may be valuable for those rearing this moth. MASÓ I PLANAS & YLLA I ULLASTRE (1989) found several foodplants to be unsuitable for *A. isabellae*, but their results must be interpreted cautiously, as they also determined a survival rate of only 50% with the most common natural foodplant *Pinus sylvestris*, which is incorrect under laboratory conditions. According to my observations, generally more than 90% of the larvae reared with *P. sylvestris* as sole foodplant reach the pupal stage in captivity, when no infections increase the mortality. Of course, average mortality may be much higher in the wild, and multiple changes of foodplants also increase the mortality in the laboratory.

The acceptance of a food in captivity does not necessarily mean that this plant will also be used by populations in the wild. Female Lepidoptera generally exhibit a very narrow range of accepted substrates for oviposition in nature. I doubt that a wild population of *A. isabellae* will be found to live on plants other than *Pinus*. From a practical standpoint for the rearer, species of pine having two needles per bundle may be more preferable than those having five per bundle, because the latter dessicate faster in water.

A remarkable result is the acceptance of the petiole of a leaf of *Liquidambar* by one larva. The related *Actias* species of North America

Table 1 : Acceptance of different plant species as food for caterpillars of *Actias isabellae*. Tested were Spanish *A. i. isabellae* (sensu DE FREINA & WITT 1987) in 1985-1988 and French *A. i. galliaegloria* in 1987 ; no significant difference between the two subspecies was observed.

Plant species	Acceptance	Remarks
Categories of acceptance :		
	++	= fully accepted as food for extended periods
	+	= accepted as food, but with some reluctance
	*	= only nibbled (i.e., small parts eaten), but not really accepted
	-	= not eaten at all, but sometimes tested by the larva
Pinaceae :		
<i>Pinus sylvestris</i> L.	++	Main foodplant in the wild ; fully accepted
<i>P. nigra</i> ARNOLD	++	Rarely some problems for L ₁ larvae ; for older caterpillars fully acceptable
<i>P. mugo</i> TURRA	++	Fully accepted in all instars
<i>P. strobus</i> L.	++	Fully accepted in all instars ; not a good food in captivity because needles of cut twigs desiccate quickly
<i>P. wallichiana</i> A. B. JACKS.	++	As <i>P. strobus</i>
<i>Abies alba</i> MILL.	+	Accepted in all instars, but with some reluctance
<i>A. nordmanniana</i> (STEV.) SPACH	++	Accepted in all instars
<i>Picea abies</i> (L.) KARST	++	Accepted in all instars
<i>P. pungens</i> ENGELM.	++	Tried only in L ₁ ; accepted
<i>P. omorika</i> (PANCIC) PURKYNE	++	Accepted in all instars
<i>P. glauca</i> (MOENCH) VOSS	+	Accepted in older instars, but with some reluctance
<i>Pseudotsuga menziesii</i> (MIRB.) FRANCO	*/+	1986 : only nibbled and then refused ; 1987 : <i>A. i. galliaegloria</i> accepted it in L _{1/2} , but with some reluctance
<i>Larix decidua</i> MILL.	+ / ++	Sometimes only with reluctance, probably caused by the softness and fast desiccation of the needles ; otherwise accepted
<i>Cedrus atlantica</i> (ENDL.) MANETTI	+ / ++	Sometimes only with reluctance
Taxaceae :		
<i>Taxus baccata</i> L.	-	Rarely tested by larvae, but never really eaten
Cupressaceae :		
<i>Juniperus communis</i> L.	*	Last instar caterpillars ate a little, but with great reluctance
<i>J. sp. near virginiana</i> L.	*	Repeatedly nibbled, not really eaten
<i>Chamaecyparis lawsoniana</i> (A. MURR.) PARL.	-	Rarely tested by larvae, never eaten
<i>Ch. sp.</i>	-	Rarely tested by larvae, never eaten
<i>Thuja occidentalis</i> L.	-	Rarely tested by larvae, never eaten
Taxodiaceae :		
<i>Metasequoia glyptostroboides</i> HU & CHENG	-	Rarely tested by larvae, never eaten
Myrtaceae :		
<i>Eucalyptus globulus</i>	-	No nibbling observed
Hamamelidaceae :		
<i>Liquidambar styraciflua</i> L.	- / *	L _{1/2} refused ; L ₅ once ate the petiole, but not the leaf ; leaf sometimes tested by larvae

and East Asia are known to feed on resiniferous deciduous trees (PEIGLER, 1986) or, in the case of *A. dubernardi*, on *Pinus* (MELL, 1950) [M. OWADA, Tokyo, pers. comm., suspects that the Taiwanese *Actias neidhoeferi* ONG & YU, 1968 might possibly also feed on *Pinus*]. *Liquidambar* is a well-known standard foodplant for practically all *Actias* species (VUATTOUX, 1985); but the pine feeding *A. isabellae* was not known thus far to accept it. Only hybrid larvae of *A. isabellae* and other species of the genus are known to accept *Liquidambar* (e.g., COCAULT et al., 1979, 1980). One interpretation of this may be that feeding on pine needles instead of broad leaves requires a different behaviour of the larvae. Therefore a pine feeding larva rarely accepts a normal leaf (the only exceptions are polyphagous larvae). The texture of a petiole, however, is very similar to that of a strong pine needle. The chemical composition of *Liquidambar* leaves did not seem to be repellent; by contrast, hungry larvae of *Actias isabellae* repeatedly tested the leaf, but then refused to feed. It may therefore be expected that the larvae would probably be able to accept the chemical composition of *Liquidambar* leaves, but cannot cope with the structure of a broad, soft leaf, evidently needing a stiff, thin, elongate needle to feed on.

Observations on the behaviour of the larvae : Sealing the resin canals of pine needles

During the rearing, the feeding behaviour of the *Actias isabellae* larvae was observed in more detail. The caterpillars always begin to feed on the tip of a *Pinus* needle. In early L₁ they cut triangular parts out of the needle, so that after some time the tip of the needle looks like the serrate blade of a saw (SANETRA & PEUKER, 1991 : fig. 10). Later the larva consumes the needle completely from tip to base, then the next needle of the same shoot, and so on. Especially the older larvae (L₄ and L₅) often eat one needle after the other in one feeding period. The older larva always sits on the twig and reaches for a needle with the thoracic legs, then “walks up” with these legs to the tip of the needle, thereby bending the needle. The feeding starts only at the tip.

In all cases when a needle is eaten down to the sheath of the shoot, the larva tries to feed into the sheath, that is, to remove as much of the finished needle as possible. Then the larva repeatedly moves over the fresh cut with the ventral part of its mouthparts (not with the mandibles); observation from the side clearly shows that the older caterpillar (thus far observed in L₄ and L₅ only) uses its spinneret when it moves its head over the base of the needle. The larva obviously

spins silk in the typical oscillating movement of spinning behaviour. This silk can be seen on the SEM photograph (Fig. 1).

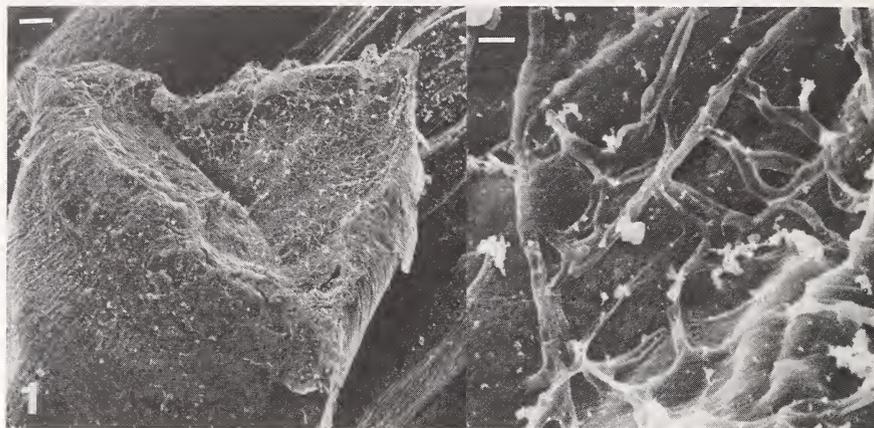


Fig. 1 : Scanning electron microphotographs of the sheath of a shoot of *Pinus mugo* eaten by a larva of *Actias isabellae*. Some silken strands can be seen on the surface. Older larvae clearly seal the resin canals after feeding. Scale, left : 100 μm ; right : 5 μm . Photographs M. RUPPEL, Frankfurt am Main.

The ecological reason for this very unusual behaviour is probably the fact that living pines are very resiniferous and would exude sticky resin through the wound of the remnants of the eaten foliage. Therefore any manipulation which decreases the amount of resin exuded is advantageous for the larva. It may be speculated whether it is not only the silk itself, but some other substance(s) contained within it which reduces the exudation of resin. A chemical analysis of the silk of mature larvae of *A. isabellae* (but not of the cocoon silk, of course ; cocoon silk is generally quite viscous and most likely different from the “sealing silk”) may be interesting.

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