COTESIA CAMERON (HYMENOPTERA: BRACONIDAE: MICROGASTRINAE) PARASITOIDS OF HELICONIINAE (LEPIDOPTERA: NYMPHALIDAE) IN EUROPE, WITH DESCRIPTION OF THREE NEW SPECIES

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ABSTRACT

Taxonomic investigation of specimens of *Cotesia* in the National Museums of Scotland (NMS) that are firmly known to have been reared (gregariously in each case) from species of Heliconiinae in Europe has revealed three species. Although in two cases there are literature citations to these taxa, it is shown that the *Cotesia* species had been misidentified in both cases and all three are described here as new species, ***C. selenevora* sp. nov.**, ***C. eunomiae* sp. nov.** and ***C. adippevora* sp. nov**. A key is given for their separation, although they are not believed to be closely related.

INTRODUCTION

Species of *Cotesia* Cameron (Hymenoptera: Braconidae: Microgastrinae), which are koinobiont parasitoids of Lepidoptera larvae and mostly (though not exclusively) attack "macrolepidoptera", are likely to be familiar to anyone rearing wild-collected caterpillars of butterflies in Europe, as *Cotesia* has strongly colonised that group and the genus is one of their principal enemies (Shaw, Stefanescu & Nouhuys, 2009). On the whole, *Cotesia* species tend to have narrow host ranges, often spanning no more than a few closely related host species, and (at least locally) monophagy is not uncommon. In some species-groups of *Cotesia* close aggregates of species, each parasitising one or a few species within a tight host group, may be morphologically virtually indistinguishable. An example is seen in two clades of *Cotesia* species parasitising Melitaeini (Nymphalidae: Nymphalinae) in Eurasia, as revealed by molecular genetic studies (Kankare & Shaw, 2004; Kankare *et al.*, 2005; Kankare, Nouhuys & Hanski, 2005).

Cotesia species may be gregarious or solitary with respect to their host larva. Oviposition is usually into fairly early instar hosts (in some cases well-developed first instar larvae can be attacked even before they leave the egg), and the endoparasitic larvae develop as koinobionts – that is, while the host continues to develop. When fully grown, the parasitoid larvae erupt from the host larva – which may or may not be fully grown – and form their small cocoons on, below or near the stricken host remains. Most often, the host does not die immediately, and in some cases its subsequent behaviour contributes to the wellbeing of the parasitoids, although in others the stricken host is quiescent. Although most *Cotesia* species, and hence their cocoons, are similarly-sized (individual cocoon lengths about 4 mm) the colour, degree of attachment to one another in the case of gregarious species, and sometimes other structural peculiarities of the cocoon, are often highly characteristic for particular species.

Most *Cotesia* species that parasitise European butterflies pass the winter as first instar larvae inside overwintering hosts, but a few do so as prepupae within cocoons that may be structurally toughened to withstand an existence of ten or eleven months. A very few *Cotesia* species are known to be capable of passing the winter in either state, depending on the host they are using, and some *Cotesia* species are able to develop two or even three generations on a single host generation by attacking successively later instar larvae of their host. A small number of *Cotesia* species with particularly wide lepidopteran host ranges use butterfly caterpillars at only certain times of year, or in an only occasional and non-obligatory way, but extreme specialisation is much more usual. If the cocoons emerge in the summer of their formation, development to the adult stage is rapid (in warm weather) and adult emergence within a week of cocoon formation is not unusual.

In this paper three European species of *Cotesia* that parasitise species of Heliconiinae (Nymphalidae) are discussed and described as new. The hosts of two of them occur in the British Isles, but so far none of the three *Cotesia* species has been found here. These *Cotesia* species are probably not closely related to one another.

TAXONOMIC HISTORY AND ORIGIN OF MATERIAL

From 1965 until 1976 G. E. J. Nixon published extensively on Microgastrinae and his revision (Nixon, 1974) of the N.W. European species of the part of the traditional genus *Apanteles* that was later (Mason, 1981) recognised as *Cotesia* provided a good foundation for species recognition in this genus. One great strength of Nixon's work is that it is based on a rich collection of reared material in BMNH initiated by the previous and systematically intensive approach to the traditional *Apanteles* sensu lato by D. S. Wilkinson (up to his untimely death in 1945), and the latter's private employment for fieldwork of R. L. E. Ford to conduct a great deal of targeted rearing. Subsequent revisions of European Microgastrinae by J. Papp included much work on *Cotesia* (e.g. Papp, 1986, 1987, 1990), in which (especially) substantial nomenclatural changes were made and several additional species were incorporated in the keys, including some that had been described by Russian authors. Unfortunately, however, almost no attention to host data was given (notwithstanding Papp's (1990) subsequent and essentially uncritical compilation). Despite Papp's efforts, considerable difficulty remains in that the many species described from the former USSR in the Russian language (e.g. by N. Telenga and V. I. Tobias) are poorly accounted for in works dealing with Western Europe, with the consequence that considerable undetected synonymy might still exist. It is also undoubtedly the case that a substantial number of European species of *Cotesia* remain undescribed, or are incorrectly in synonymy, often because aggregates of closely similar but biologically distinct species remain unresolved, and taking full account of host relations provides the best and by far the most useful means for further progress on the taxonomy of this large and rather difficult genus.

Papp (1990) produced a host list for European *Cotesia* species but, although he made some effort to "authenticate" records based on whether or not determinations were made by a "specialist", the listings overall are little more than an amalgamation of opinion of uncertain origin and low reliability, and unfortunately published rearing records (though included) are not so-indicated. However, the listings leave little out. Apart from *C. callimone* (Nixon) (see below), the only *Cotesia* species listed as having Heliconiinae among their hosts by Papp (1990) are *C. rubripes* (Haliday), *C. spurius* (Wesmael) and *C. vanessae* (Reinhard), all of which have quite different host ranges (cf. Nixon, 1974), and the records of them as parasitoids of Heliconiinae should be dismissed as almost certainly the results of misidentification.

Nixon (1974) included only one species (*Cotesia callimone* (Nixon), as *Apanteles*) for which he gave a host record from a heliconiine, on the basis of the holotype (and some of the paratypes, i.e., those from the same brood) of that species stated as being reared from "Arctiid or Argynid" from Ireland and further paratypes from a separate brood labelled as reared from *Argynnis* sp. [but see comment on the meaning of this name below] from Finland. Examination of this material (in BMNH) reveals that the two broods belong to different species and that the host remains accompanying the brood from which the holotype was chosen (whose labelling does not suggest any host at all) are certainly not of a heliconiine nymphalid but rather, in my opinion, belong to a lithosiine arctiid. The Finnish series labelled as from *Argynnis* sp. is conspecific with material described below as ***Cotesia selenevora* sp. nov**. from two broods reared by C. Turlure and J. Choutt from *Clossiana selene* (Denis & Schiffermüller) at different sites in Belgium, and the Finnish specimens misidentified by Nixon (1974) as his new species *Cotesia callimone* (as *Apanteles*) are included as paratypes of the new species described below.

A study on parasitism of the heliconiine *Proclossiana eunomia* (Esper) in Belgium (Waeyenbergh & Baguette, 1996) revealed an abundance of a gregarious *Cotesia* species that was identified in that publication as *Cotesia vestalis* (Haliday), at the time suggested (erroneously) as a senior synonym of *Cotesia cynthiae* (Nixon), a parasitoid known from the high-alpine melitaeine nymphalid *Euphydryas cynthia* (Denis & Schiffermüller) with which the parasitoid reared from *P. eunomia* was incorrectly believed to be conspecific. [Although that tentative synonymy offered by a taxonomist as a pers. comm. to those authors was never formally proposed, another parasitoid of Melitaeini, *C. melitaearum* (Wilkinson), was formally (but erroneously) treated as a junior synonym of *C. vestalis* subsequently (van Achterberg, 1997). The identity of *C. vestalis* (a solitary species and not conspecific with any parasitoid of Melitaeini) was eventually clarified by Shaw (2003)]. There are many clear differences that separate *Cotesia cynthiae* from the *Cotesia* parasitoid of *Proclossiana eunomia* and the latter is described below as ***Cotesia eunomiae* sp. nov**. from material reared by J. Choutt and by P. J. C. Russell from four sites in Belgium (including the one sampled by Waeyenbergh & Baguette).

A gregarious *Cotesia* species reared by me from *Argynnis adippe* (Denis & Schiffermüller) in alpine N. Italy is also apparently undescribed. In Nixon's (1974) key it runs closest to *Cotesia setebis* (Nixon) (as *Apanteles*), but it does not agree with the holotype (from arctic Sweden) of that species, and (as with the previously discussed species) no better fit results from running it in keys given by Papp (1986, 1987, 1990) and Tobias & Kotenko (1986). As far as I can ascertain no *Cotesia* parasitoid has been recorded from this host, and accordingly it is here described as ***Cotesia adippevora* sp. nov**. A further series (in less good condition) previously reared by M. Kuussaari and J. Paukkunen from *A. adippe* in Finland is included as paratypes but a series reared from *Argynnis aglaja* (Linnaeus) from the same site in Finland is excluded from the type series, although it is morphologically similar and probably conspecific, mainly because of its poor condition but partly also in recognition of the sometimes extreme host specificity of *Cotesia* species parasitising even very closely related hosts.

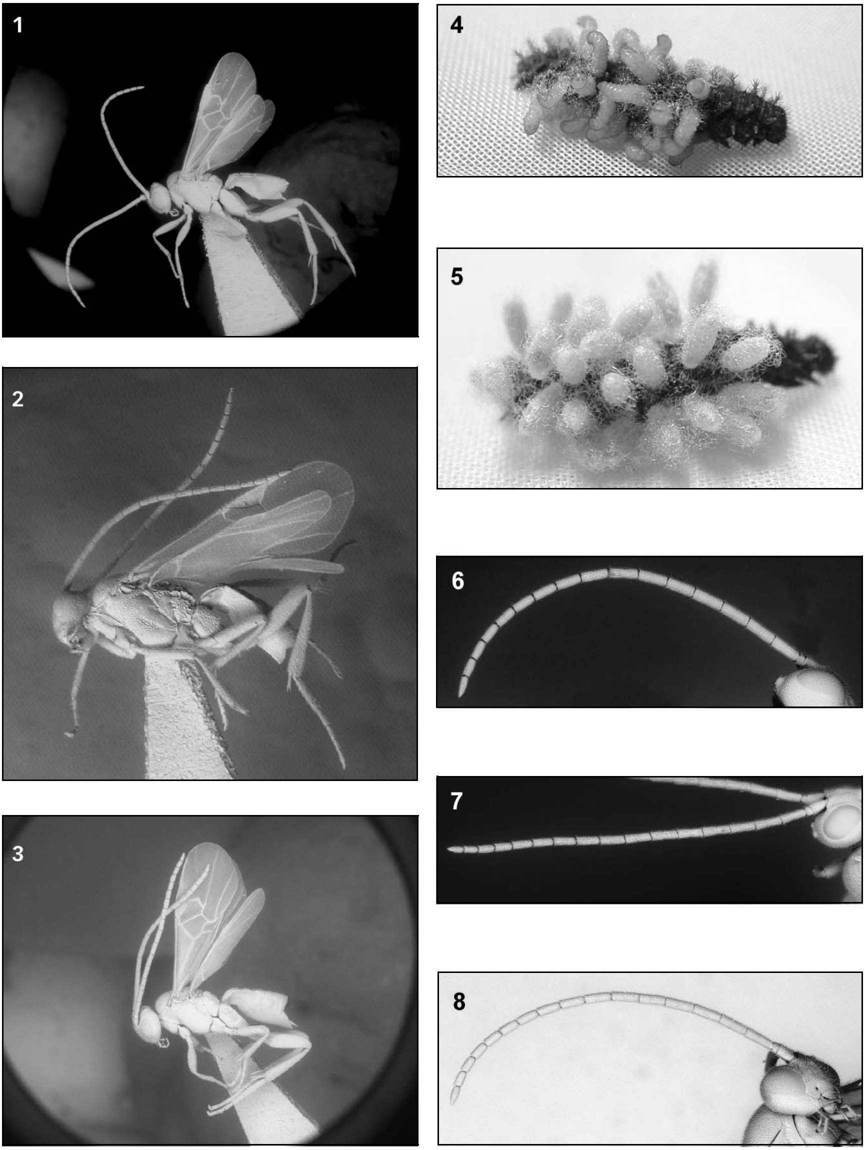
DESCRIPTIONS OF NEW SPECIES AND BIOLOGICAL NOTES

To facilitate integration with his work, terminology follows Nixon (1965,1974) except that pterostigma is used in place of stigma and metasoma is used in place of gaster; see also Mason (1981) and Shaw (2007) who include notes on recognition of the genus. In the first description (only) further notation of wing venation and cells according to van Achterberg (1993) have been added in normal brackets, and according to Shaw & Huddleston (1991) in square brackets. The distal end of the pterostigma is taken as the projection of its lower outer boundary to the wing margin; veins are measured to the midpoint of vein junctions; and the height of the discal cell is measured from the junction of the first and second abscissae of the discoideus. POL refers to the distance between the posterior ocelli and OOL to the distance between a posterior ocellus and the adjacent compound eye.

Scanning electron micrographs were taken on a CamScan MX 2500 (15 kV; spot size 2). NB: some of the images give deceptive impressions of dimensions, as out-of-plane parts remain in good focus; e.g. compare Figs 18 and 19.

Cotesia selenevora **sp. nov. (Figs 1, 6, 9, 13, 16, 20 & 24)**

Holotype, ♀. Length, 2.6 mm. Head in dorsal view (Fig. 24) 1.8 times as wide as long, abruptly roundly narrowing behind eye and clearly widest at eyes, temple 0.8 times as long as eye; face (excluding clypeus) 1.3 times as wide as high, rugulose to weakly rugose-punctate; frons with very weak microsculpture; vertex centrally broadly shiny, rugulose to weakly rugose-punctate at sides; ocelli in a low triangle (Fig. 24), imaginary tangent to posterior pair just touching anterior ocellus, POL 2.3 times diameter of posterior ocellus, distance between anterior and posterior ocellus 0.9 times diameter of posterior ocellus, OOL 2.5 times diameter of posterior ocellus; eyes just extending to level of upper margin of clypeus, weakly convergent; malar space 1.4 times basal width of mandible; antenna (Fig. 6) longer than body, fourth segment about 3.0 and penultimate segment about 2.1 times as long as wide. Mesoscutum dull, strongly rugose-punctate, this sculpture strongest posteriorly where the notaulic courses coalesce and the punctures are fairly distinct, but punctures also distinct anteriorly, extreme hind margin rather smooth and shiny; prescutellar sulcus wide with about 6–8 large fovea, scutellum thereby rendered rather small, a little less dull than mesoscutum, more or less rugose and even anteriorly with a shallow punctate element scarcely evident, phragma of scutellum concealed (Fig. 16); mesopleuron strongly punctate anteriorly where matt, precoxal sulcus depressed and rather strongly crenulate, below this rugulose-punctate, moderately shiny; mesosternum more weakly rugulose-punctate, more shiny. Fore wing (Fig. 9) with pterostigma 2.9 times as long as high, emitting radius (*r*) [2*r*–*rs*] well distal to middle (0.7), metacarp (1–R1) [R] as long as pterostigma and 2.5 times as long as its distance from the apex of the radial cell ([marginal cell]); junction of first abscissa of radius and transverse cubitus (2–SR) [1Rs] externally a (quite abrupt) curve, with neither a sharp angle nor a stub; first abscissa of discoideus (1–CU1) [1Cu] 0.95 times as long as second (2–CU1) [1m–cu], discal cell ([1st discal cell)] 1.25 times as wide as high; setae of median cell ([basal cell]) hardly reduced near medius (M + CU1) [M + Cu]. Hind wing with cubitellan cell 2.2 times as long as wide, and vanal lobe (plical lobe) with a distinct and moderately long hair fringe. Hind coxa dull, rugulose to rugose-punctate below and apically striate above, with large shallow punctures on outer face; hind femur 3.8 times as long as wide; inner hind tibial spur only a little longer than outer and obviously reaching beyond middle of hind basitarsus (Fig. 13). Apical segment of fore tarsus without a preapical curved spine below. Propodeum (Fig. 16) coarsely rugose but the median carina distinct in most specimens. Metasoma (Fig. 16) with first tergite widening towards apex, slightly incurving at extreme apex, about 0.9 times as long as wide; basal field practically co-extensive with second tergite, 2.4 times as wide as long, lateral sulci almost obliterated, sculpture of apical part of first tergite and second tergite similar, coarsely rugose with very little longitudinal element; part of tergites 2 + 3 posterior to



Figs 1–8, *Cotesia* species. 1–3, habitus. 4, 5 host larva with (4) erupting parasitoids and (5) ensuing cocoons. 6–8, antenna (7 with head orientated to show malar space). 1, 6 ♀ *C. selenevora* sp. nov.; 2, 4, 5, 7 ♀ *C. eunomiae* sp. nov.; 3, 8 ♀ *C. adippevora* sp. nov.

foveolate margin of basal field mostly matt, rugulose in anterior half becoming granular then narrowly shiny at apex and about 1.2 times as long as basal field; third tergite moderately densely and evenly setose except anteromedially; hypopygium (Fig. 20) rather roundly becoming right-angled apically, not protruding beyond apex of metasoma, 0.43 times as long as hind tibia, the ovipositor sheaths somewhat protruding.

Black; mouthparts dark brown, palpi yellowish; all legs except coxae and most of trochanter (but including trochantellus) orange-brown, the hind femur somewhat and gradually below and at apical 0.4, hind tibia slightly at apex and hind tarsus more strongly infuscate; venter and side of metasoma basally extensively yellow-orange. Tegula dark brown, wing membrane slightly brownish, pterostigma rather light brown, venation yellowish to light brown.

Male: like female except for sexual differences. Legs a little darker.

Material examined: Holotype ♀ "BELGIUM: Luxembourg, Pisserotte. Ex Clossiana selene [coll.]12.6.[20]05, 7 ♀ 8 ♂ em. 25.6.05 C. Turlure" (in National Museums of Scotland, Edinburgh). Paratypes: 6 ♀ 8 ♂ (with cocoons and host remains), same data as holotype (in NMS except 1 ♀ 1 ♂ in BMNH, London, 1 ♀ 1 ♂ in Nationaal Naruurhistorich Museum, Leiden and 1 ♀ 1 ♂ in Hungarian Natural History Museum, Budapest); 3 ♀ (from one brood of unknown size), Belgium, Luxembourg, Libin, ex *Clossiana selene*, coll. 19.v.2008, cocoons 26.v.2008, em. 16.vi.2008 (*C. Turlure & J. Choutt*) (in NMS); 1 ♀ 2 ♂ (with cocoons) [Finland] "Kärret Wom, Tvarminne by, Ur Argynnis sp. larv (in coll Luther) p. 13.vi–20.vi.1333// Alex Luther// Apanteles callimone Nixon Paratypes, 1974//Not conspecific with type of A. callimone Nix. det. M. R. Shaw, 2006" (seen in BMNH, but 1 ♀ 3 [sic] ♂ stated by Nixon (1974) to be in Helsinki Museum).

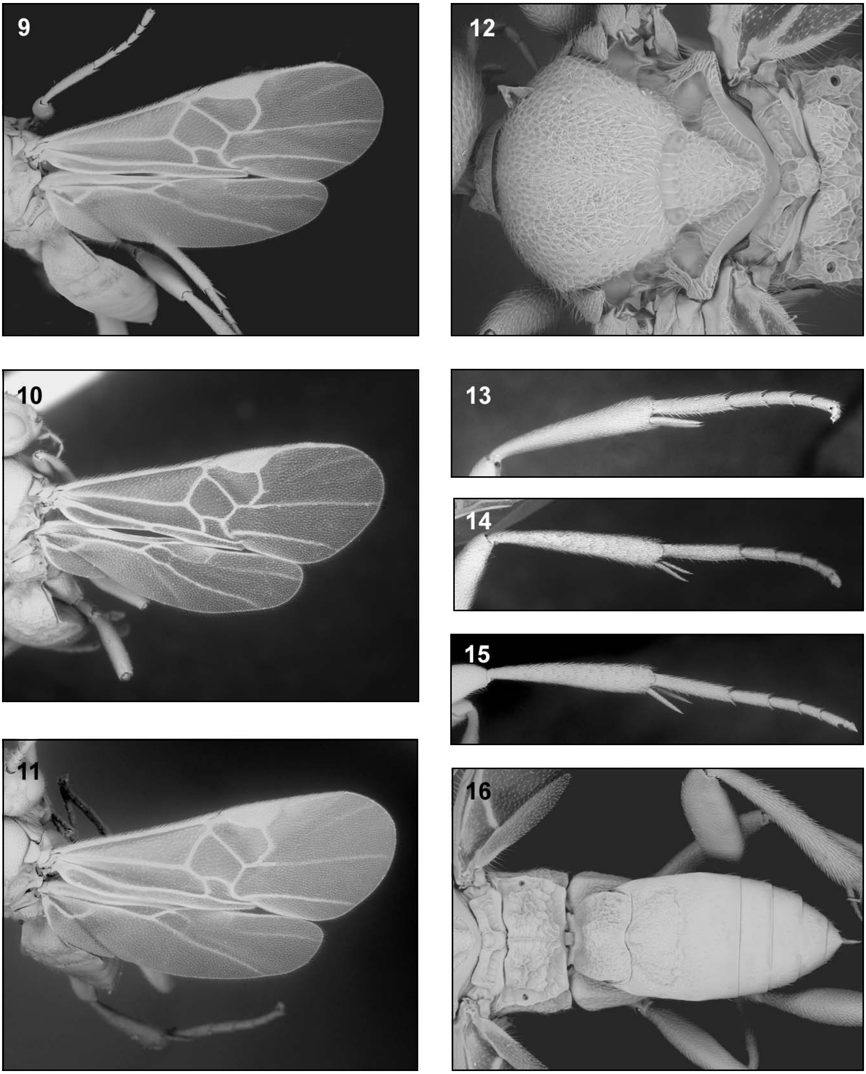
Variation. In the paratypes from Finland the median carina on the propodeum is obscured.

Cotesia selenevora sp. nov. would key in Nixon (1974) to his new species [*Apanteles*] *callimone*, which was described from two reared series: one of 4 ♀ (including the holotype) and 1 ♂ from Glenageary [not Glengeary as in Nixon, 1974], Ireland, reared "ex Arctiid or Argynid" according to Nixon (1974), and a further series of 1 ♀ 3 ♂ from Finland labelled as reared ex *Argynnis* sp. The holotype of *Apanteles callimone* is mounted with an adpressed cocoon mass of (estimated) 5 or 6 white cocoons within a frail host cocoon incorporating many long hairs, on top of which are the (? extracted and replaced) host remains, which are very clearly not those of a nymphalid but rather appear to belong to a lithosiine arctiid. The labelling (entirely in Nixon's hand apart from standard BMNH labelling) is "Ireland, Co. Dublin, Glenageary, E. Baynes//BM.TYPE HYM 3c 1896//Apanteles callimone Nix. Type ♀". The remainder of this reared series (3 ♀ 1 ♂) is mounted on a single card (from which the card carrying the holotype appears to have been cut) with similar (but paratype) labelling. Nothing in the labelling relates to the host's identity; the suggestion that it might have been a heliconiine nymphalid – i.e. "[Arctiid or] Argynid" – evidently came from Nixon rather than the rearer. The paratypes of *Apanteles callimone* Nixon from Finland, of which 1 ♀ 2 ♂ are present in BMNH at the time of writing (*pace* Nixon, 1974), labelled as reared from *Argynnis* sp. (but lacking host remains) are not conspecific with the holotype, but rather belong to *Cotesia selenevora* sp. nov. and are here treated as paratypes of that. It should be borne in mind that at the time the material was reared "*Argynnis*" was used in a broad sense that would encompass *Clossiana*. There are numerous differences between *C. selenevora* sp. nov. and *C. callimone*, which has the head much less strongly narrowed behind the eyes, the scutellum more sharply punctate and shiny, the first abscissa of the radius sharply angled externally at its junction with the transverse cubitus and with an evident stub (of 3–SR) [2Rs], a shorter first abscissa of the discoideus in relation to the second (about 0.65:1), and the third tergite more strongly sculptured. In addition the hind tibial spurs of *C. callimone* are even (slightly) longer and more strongly unequal, but this difference is less easy to appreciate.

Cocoons bright yellow (presumably faded in the Finnish material which are pale yellowish-buff), formed in small loosely connected groups and tending to become scattered in the wake of the still actively walking host (C. Turlure, pers. comm.).

Cotesia eunomiae **sp. nov. (Figs 2, 4, 5, 7, 10, 12, 14, 17, 21 & 23)**

Holotype, ♀. Length 2.4 mm. Head in dorsal view (Fig. 23) 1.7 times as wide as long, roundly narrowing behind eye, temple 0.8 times as long as eye; face (excluding clypeus) 1.4 times as wide as high, centrally largely matt, rugulose to weakly rugose-punctate, less sculptured and more shiny towards eyes, boundary between face and clypeus well marked; frons and vertex more or less rugulose and greasy looking; ocelli rather large, in a high triangle (Fig. 23), imaginary tangent to posterior pair clearly not touching anterior ocellus, POL 1.4 times diameter of posterior ocellus, distance between anterior and posterior ocellus 0.8 times diameter of posterior ocellus, OOL 2.0 times diameter of posterior ocellus; eyes not quite extending to level of upper margin of clypeus, divergent below middle of face; malar space 1.4 times basal width of mandible; antenna (Fig. 7) slender, longer than body, fourth segment about 3.2 times and penultimate segment about 2.2 times as long as wide. Mesonotum (Fig. 12) with mesoscutum dull, strongly rugose-punctate, the punctures clearest anteriorly and tending to become overwhelmed by rugosity where the notaulic courses coalesce posteriorly, hind margin becoming smoother and more shiny; prescutellar sulcus (Fig. 12) wide with about 6–8 large fovea, scutellum thereby rendered small, also dull, strongly rugose with punctate element weak, phragma of scutellum more or less concealed (Figs 12, 17); mesopleuron rugose anteriorly and especially so below the wide and shallow precoxal sulcus, often rendering it indistinct; mesosternum rugulose-punctate and similarly dull. Fore wing (Fig. 10) with pterostigma 2.8 times as long as high, emitting radius distal to middle (0.65); metacarp as long as pterostigma and 2.4 times as long as its distance from apex of radial cell; junction of first abscissa of radius and transverse cubitus externally weakly angled; first abscissa of discoideus 0.95 times as long as second, discal cell 1.18 times as wide as high; setae of median cell hardly reduced near medius. Hind wing with cubitellan cell 2.1 times as long as wide, and vanal lobe with a distinct and moderately long hair fringe. Legs rather slender, hind coxa dull, coarsely rugose to rugose-punctate above and at sides, more weakly below; hind femur 3.9 times as long as wide; hind tibial spurs short, subequal and clearly not reaching middle of hind basitarsus (Fig. 14). Apical segment of fore tarsus without a preapical curved spine below. Propodeum (Fig. 17) very coarsely rugose but the median carina distinct in most specimens. Metasoma (Fig. 17) with first tergite roundly widening towards apex, incurving at extreme apex, about 0.9 times as long as wide; second tergite about 2.7 times as wide as long, densely sculptured all over but with wide sunken foveolate sulci more or less defining a smaller basal field in some individuals; first and second tergites with similar very coarsely rugose sculpture lacking a clear longitudinal element; posterior part of tergites 2 + 3 posterior to foveolation behind basal field about 1.2 times as long as basal field and more or less coriaceous and dull, often across the whole surface or becoming weakly shiny



Figs 9–16. *Cotesia* species. 9–11, wings. 12, mesosoma, dorsal view. 13–15, hind tibia and tarsus. 16, part of mesosoma and metasoma with tergites 2–3 in plane. 9, 13, 16 ♀ *C. selenevora* sp. nov.; 10, 12, 14 ♀ *C. eunomiae* sp. nov.; 11, 15 ♀ *C. adippevora* sp. nov.

posteriorly; third tergite with setae more or less restricted to a band across the posterior half, sometimes with setae forward of that at sides; subsequent tergites smooth and shiny; hypopygium (Fig. 21) short, its ventral profile often slightly concave, subtruncate at apex where about right angled, hardly or not protruding beyond apex of metasoma, about 0.5 times as long as hind tibia but its base often partly concealed by the enlarged laterotergites, ovipositor and sheath usually fully concealed.

Black; mouthparts, all legs except coxa and most of trochanter (but including trochantellus) more or less honey-brown but hind femur darker, often except for a central and basal flush dark brown or blackish; venter and side of base of metasoma only a little lightened. Tegula dark brown, wing membrane slightly brown, venation including pterostigma pale yellowish brown.

Male: like female except for sexual differences. Hind femur often not as dark.

Material examined: Holotype ♀ "BELGIUM: Luxembourg, Pisserotte. [Ex] Proclossiana eunomia [coll.] 26.5.05, cocs 30.5.05, em 22.6.2005 [brood of] 42 (22 ♀ 15 ♂ [emerged]) J. Choutt" (in National Museums of Scotland, Edinburgh). Paratypes: 21 ♀ 15 ♂ (with cocoons and host remains), same data as holotype (in NMS except 1 ♀ 1 ♂ in BMNH, London, 1 ♀ 1 ♂ in Nationaal Naruurhistorich Museum, Leiden and 1 ♀ 1 ♂ in Hungarian Natural History Museum, Budapest); 21 ♀ 2 ♂ (with cocoons), data as above except coll. v.05, cocs 31.v.05, em. vi.2005, 34 (21 ♀ 2 ♂ em.); 16 ♀ 7 ♂ (with cocoons and host remains), data as above except coll.19.v.05, cocs 29.v.05, em. 23.vi.2005, 41 (16 ♀ 7 ♂ em.); 12 ♀ 3 ♂ (with cocoons), data as above except cocs coll. 7.vi.05, em. vi.2005, 32 (12 ♀ 3 ♂ em.); 13 ♀ 3 ♂ (with several cocoon clusters), data as above except [coll. and] em. vi.2004, [parts of] several gregarious broods; 2 ♂, data as above except coll. and em. 2008; 27 ♀ 3 ♂ (with cocoons and host remains), Belgium, Liege, Prés de la Lienne, ex *Proclossiana eunomia* coll. 25.v.05, cocs 29.v.05, em. vi.2005, 50 (27 ♀ 3 ♂ em.) (*J. Choutt*); 2 ♀, Belgium, Luxembourg, Tailsus, ex *Proclossiana eunomia* coll. and em. 2008 (*J. Choutt & C. Turlure*); 4 ♀ 1 ♂ (extracted from cocoons; with cocoons and host remains), Belgium, Luxembourg, Cetturu, ex *Proclossiana eunomia* coll. v.1997, cocs v.97, brood of 33 failed to em. (*P. J. C. Russell*) (the foregoing all in NMS).

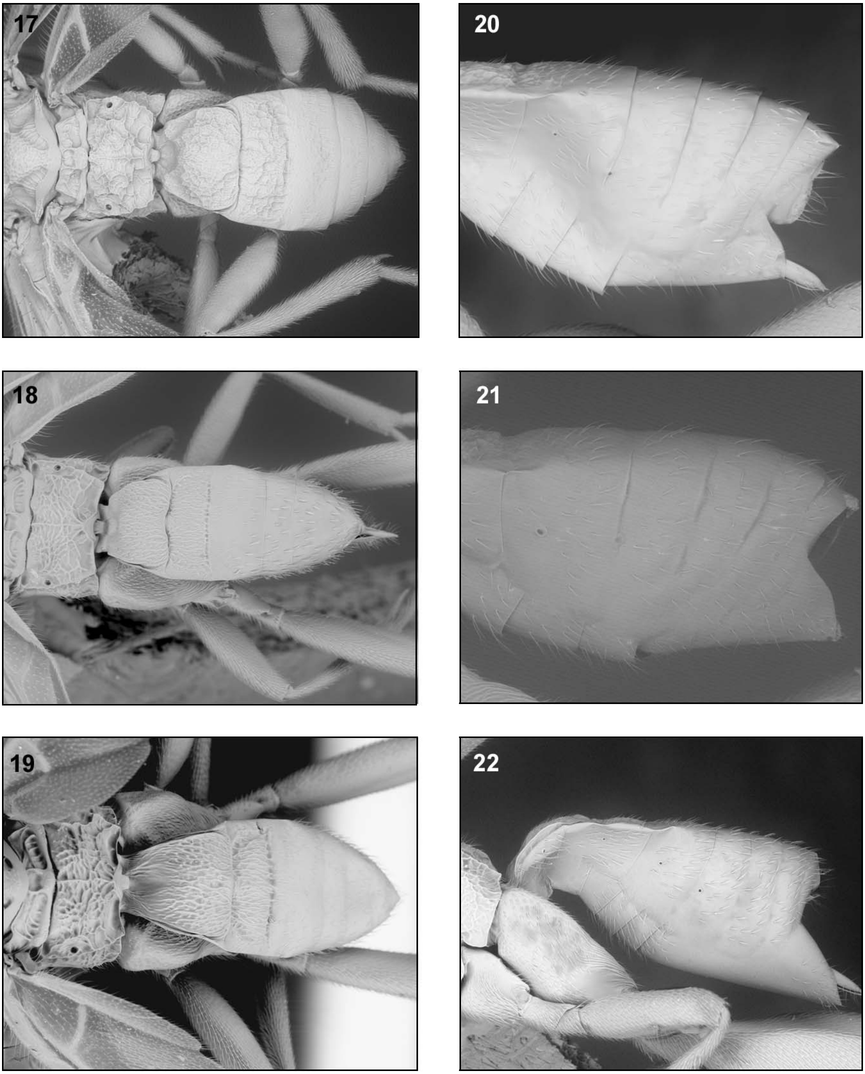
Variation. The hind femur varies from almost black to honey-brown more or less infuscate above and below. The position of the radius on the pterostigma is sometimes less distal (down to about 0.58). Third tergite sometimes with setae more widely distributed, and its sculpture varies from weakly coriaceous only in the anterior half to strongly so and matt over the whole tergite.

Cotesia eunomiae sp. nov. runs smoothly in Nixon's (1974) key to couplet 9, but then founders, and it is profoundly different from all species with which it might be compared. It has been confused in the past (Waeyenbergh & Baguette, 1996; and see above) with the species correctly known as *Cotesia cynthiae* (Nixon) but among many differences that species has the ocelli in a low triangle, the prescutellar groove narrower with more fovea, the mesoscutum and larger scutellum more coarsely sculptured (reticulate-punctate), a considerably longer hypopygium, and the metasoma laterally compressed apically. It is similar to *Cotesia villanus* (Reinhard) in the arrangement of the ocelli, but among many characters that species differs in its less transverse head with smaller eyes, shorter and stouter antennae, shorter metacarp, longer and more acute hypopygium, and larger and more distinctly punctate scutellum.

Cocoons identical in all material examined: bright strong yellow, usually in broods of about 30–50 ex final instar larvae, weakly adhering to one another and remaining aggregated. The whole brood of larvae erupts in concert (Fig. 4), and initially the cocoons are constructed around the yet mobile host (Fig. 5), which normally subsequently frees itself from the cocoons and moves away before dying (Waeyenbergh & Baguette, 1996). These authors, as also J. Choutt (pers. comm.) working at the same site a decade later, record very high levels of parasitism in final instar host larvae found exposed, but it is not clear whether this is a result of altered host behaviour and/or retardation of parasitised individuals, or a true reflection of the level of parasitism in the population. It is also unknown whether the parasitoid may have two annual generations on the single host generation; a trait seen in several *Cotesia* species whose hosts overwinter as larvae that can contribute to high levels of parasitism in the final instar. Poor emergence rates in the captive broods seen is almost certainly an artefact resulting from the use of small airtight containers.

Cotesia adippevora sp. nov. (Figs 3, 8, 11, 15, 18, 19, 22 & 25)

Holotype, ♀. Length 2.4 mm. Head in dorsal view (Fig. 25) 1.7 times as wide as long, initially slightly produced but then gradually roundly narrowing behind eye, temple 0.7 times as long as eye; face (excluding clypeus) 1.3 times as wide as high, rugulose; frons rather smooth and shining; vertex feebly sculptured, subshiny; ocelli in a low triangle (Fig. 25), anterior ocellus almost touched by imaginary tangent to posterior pair, POL 2.3 times diameter of posterior ocellus, distance between anterior and posterior ocellus 1.0 times diameter of posterior ocellus, OOL 2.2 times diameter of posterior ocellus; eyes extending to level of upper margin of clypeus, moderately convergent; malar space 1.0 times basal width of mandible (Fig. 8); antenna (Fig. 8) slender, longer than body, fourth segment about 2.9 times and penultimate segment about 2.0 times as long as wide. Mesoscutum rather dull, distinctly but shallowly rugose-punctate, most strongly along notaulic courses, more coarsely so posteriorly except at extreme hind margin where becoming smooth and dull; prescutellar sulcus moderately narrow, with at least 10–12 fovea, scutellum not reduced in size, less clearly punctured and more shiny than mesoscutum, phragma of scutellum concealed (Fig. 19); mesopleuron clearly punctate anteriorly, precoxal sulcus depressed and weakly foveolate, below this matt and coriaceous; mesosternum rather shiny. Fore wing (Fig. 11) with pterostigma 2.5 times as long as high, emitting radius a little distal to middle (0.55); metacarp 0.9 times as long as pterostigma and 1.8 times as long as its distance from apex of radial cell; junction of first abscissa of radius and transverse cubitus externally sharply angled; first abscissa of discoideus 0.85 times as long as second, discal cell 1.17 times as wide as high; setae of median cell only slightly reduced near medius. Hind wing with cubitellan cell 2.2 times as long as wide, and vanal lobe with a distinct but centrally rather short hair fringe. Hind coxa rather smooth and matt at side, more (sub)shiny below with weak sculpture, striate apically and basally weakly rugose-punctate above; hind femur 3.5 times as long as wide; inner hind tibial spur longer than outer and reaching to middle of basitarsus. Apical segment of fore tarsus without a preapical curved spine below. Propodeum (Figs 18, 19) moderately coarsely rugose but with median carina distinct in most specimens (only anteriorly in some). Metasoma (Figs 18, 19) with first tergite widening towards apex, as long as wide; second tergite with basal field not co-extensive, transverse, 2.4 times as wide as long, lateral sulci distinct, curved; sculpture of both apical part of first tergite and basal field rather finely rugose with a strong longitudinal element; part of tergites 2 + 3 posterior to foveolation behind basal field almost smooth (dull but scarcely sculptured anteriorly), mostly shiny and ca. 1.4 times as long as basal field; third tergite almost evenly (except medially) but rather sparsely setose; hypopygium (Fig. 22) wedge shaped, acute, angled at about 60°, extending beyond



Figs 17–22. *Cotesia* species. 17, 18, part of mesosoma, and metasoma with tergites 2–3 in plane. 19, the same, tergite 1 in plane. 20–22, metasoma, lateral view. 17, 21 ♀ *C. eunomiae* sp. nov.; 18, 19, 22 ♀ *C. adippevora* sp. nov.; 20 ♀ *C. selenevora* sp. nov.

apex of metasoma and about 0.75 times as long as hind tibia, the ovipositor sheaths slightly protruding.

Black; mouthparts dark brown, palpi basally brownish becoming yellowish apically; all legs except coxa and most of trochanter (but including trochantellus) honey-brown, the mid and hind femur gradually but extensively much darker above, below and towards apex; hind tibia and tarsus obscurely infuscate apically; hind tibial spurs and venter and side of metasoma basally yellowish. Tegula dark brown; wing membrane weakly brownish; venation including pterostigma brown but costa basally markedly yellow grading to brown at its apex.

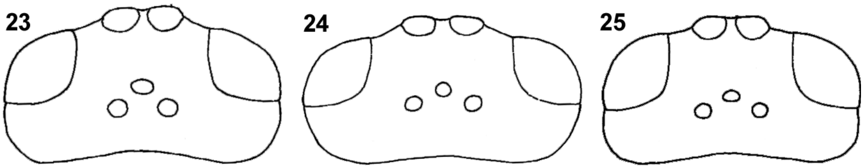
Male: like female except for sexual differences. Legs a little darker.

Material examined: Holotype ♀ "ITALY: S. Tyrol. W of Burgeis 1450 m [ex] Argynnis adippe 11.7, P[arasitoid] L[arvae] E[Erupted] 12–14.7.04, em. 21–23.7.[20]04 brood [of] 36 (25 ♀ 9 ♂ em) M. R. Shaw" (in National Museums of Scotland, Edinburgh). Paratypes: 22 ♀ 8 ♂ (with cocoons and host remains), same data as holotype (in NMS except 1 ♀ 1 ♂ in BMNH, London, 1 ♀ 1 ♂ in Nationaal Naruurhistorich Museum, Leiden and 1 ♀ 1 ♂ in Hungarian Natural History Museum, Budapest); 10 ♀ 4 ♂ (all in poor condition, with cocoons) Finland (S.), Lapinjärvi, ex *Argynnis adippe* coll. 8.vi.1996, brood of ca. 15 (*M. Kuussaari & J. Paukkunen*). Non-paratype material: 15 ♀ 28 ♂ (all in poor condition, with cocoons) Finland, same data but ex *Argynnis aglaja* and brood of ca. 50.

Variation. The paratypes from Finland are slightly more heavily sculptured, the metacarp is 2.5 times as long as its distance from the apex of the radial cell, and the preapical antennal segment is a little shorter. In the non-paratype series ex *A. aglaja* the hind femur tends to be more strongly darkened (almost black except centrally towards the base) and the mesopleuron tends to be shiny below the precoxal suture. In this brood there is considerable size variation.

Cotesia adippevora sp. nov. could be run either way in the sometimes difficult couplet 2 of Nixon's (1974) key. If run through couplet 3 it comes closest to *Cotesia* (as *Apanteles*) *setebis* (Nixon), a little-known species described from non-reared material collected on mountains in arctic Sweden and at high altitude in Switzerland. The type material of *C. setebis* (examined) is rather variable, but the holotype differs from *C. adippevora* sp. nov. in several respects; *C. setebis* is a more heavily built species, with a less transverse head (i.e. longer temple), stouter antenna (especially towards the base), the mesopleuron and hind coxa more strongly sculptured and less shiny, legs more robust, hind tibial spurs stouter and a little longer, fore wing with pterostigma slightly more elongate with *r* issuing more distally, the discal cell wider and the costal vein entirely brown. If it is taken the other way through Nixon's (1974) couplet 2 to couplet 18 it will run – on account of its similarly produced hypopygium – to *C.* (as *A.*) *cajae* (Bouché), an often abundant parasitoid of *Arctia* spp (Arctiidae), and indeed it bears rather a strong likeness to that species. However, *C. cajae* is a somewhat more robust, heavily sculptured and pubescent species, having a longer hypopygium (0.95 times as long as hind tibia), the antenna more robust and shorter, the tibial spurs shorter, and the first metasomal tergite shorter and tending to be more strongly widened apically. The cocoons of the similarly gregarious *C. cajae* are also often scattered singly, as a result of the parasitoid larvae erupting over a period and the host not becoming quiescent initially, but they are generally white to pale pink in colour.

Cocoons identical in all three broods examined: pale lemon yellow, constructed individually and (in the brood from Italy for which it was observed) tending to become scattered in the wake of the actively walking host, the parasitoid larvae erupting singly over a period of at least two days.



Figs 23–25. *Cotesia* species, heads in dorsal view. 23 ♀ *C. eunomiae* sp. nov.; 24 ♀ *C. selenevora* sp. nov.; 25 ♀ *C. adippevora* sp. nov.

Key to females of *Cotesia* species reared from European Heliconiinae

This key is obviously not applicable to specimens of different origin.

1. Hind tibial spurs short, clearly not reaching to middle of hind basitarsus (Fig. 14); ocelli in a higher triangle, imaginary tangent to posterior pair clearly not touching anterior ocellus (Fig. 23) . . . . *eunomiae* sp. nov.

– Hind tibial spurs long, the inner one reaching to middle of hind basitarsus or beyond (Figs 13, 15); ocelli in a lower triangle, imaginary tangent to posterior pair touching anterior one (Fig. 24) or nearly so (Fig. 25) 2

2. Hypopygium (Fig. 22) wedge shaped, acute, angled at about 60° and about three quarters as long as hind tibia; head in dorsal view not narrowing immediately behind eyes (Fig. 25); in fore wing junction of first abscissa of radius with transverse cubitus externally sharply angled (Fig. 11) . . . . *adippevora* sp. nov.

– Hypopygium (Fig. 20) roundly becoming right angled apically and less than half as long as hind tibia; head immediately behind eyes strongly narrowing (Fig. 24); junction of first abscissa of radius with transverse cubitus rounded on outer side (Fig. 9) . . . . *selenevora* sp. nov.

ACKNOWLEDGEMENTS

I am grateful to Julie Choutt, Atte Komonen, Mikko Kuussaari, J. Paukkunen, Peter Russell and Camille Turlure for donation of reared specimens, to Camille Turlure for permission to publish her photographs of parasitised *Proclossiana* caterpillars bearing erupting *Cotesia* larvae and subsequently cocoons, to Diane Mitchell, Richard Lyszkowski and Daniella Watson for help with SEM image capture and manipulation, and to Gavin Broad for arranging loans of types from the BMNH and for his comments on a draft of the MS (some of which was kindly typed by Jennifer Felton).

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