DIVERSE EVIDENCE THAT *ANTHERAEA PERNYI* (LEPIDOPTERA: SATURNIIDAE) IS ENTIRELY OF SERICULTURAL ORIGIN

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Abstract - There is a preponderance of evidence that the tussah silkmoth *Antheraea pernyi* was derived thousands of years ago from the wild *A. roylei*. Historical, sericultural, morphological, cytogenetic, and taxonomic data are cited in support of this hypothesis. This explains why *A. pernyi* is very easy to mass rear, produces copious quantities of silk in its cocoons, and the oak tasar "hybrid"crosses between *A. pernyi* and *A. roylei* reared in India were fully fertile through numerous generations. The case is made that it is critical to conserve populations and habitats of the wild progenitor as a genetic resource for this economically important silkmoth.

Key words: China, Chinese oak silkmoth, India, sericulture, temperate tasar silk, tussah silk, wild silk

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INTRODUCTION

Numerous examples are known for which domesticated animals or cultivated plants differ dramatically from their wild ancestral species, and frequently the artificially-selected entity carries a separate scientific name from the one in nature. In some cases where the wild and domesticated animals are considered to be the same species, and the latter were named first, Opinion 2027 of the International Commission on Zoological Nomenclature, issued in 2003, ensures that the scientific names of both forms can be used, thus conserving the binomials for 17 species of wild animals. In Lepidoptera, such is the case for *Bombyx mandarina* (Moore), which was eventually identified as the wild ancestor of *Bombyx mori* (Linnaeus), decades after *B. mandarina* was named (see Goldsmith 2010). Citing morphological, cytological, and sericultural evidence, Peigler and Naumann (2003) also demonstrated that the eri silkmoth (*Samia ricini* (Anonymous)) (Saturniidae) is a cultivated form of the Himalayan *Samia canningi* (Hutton).

Since the original description of *Antheraea pernyi* (Figs. 1–2, 7) by Félix Guérin-Méneville in 1855, the standard dogma has been that this insect exists as wild populations in China and perhaps neighboring countries, but that it has also been exploited in eastern Asia for its silk. The moth was named after the French Jesuit missionary Paul Perny, who noted that it was being cultured for silk in Guizhou Province (Perny 1858). Moreover, because *A. pernyi* is easy to rear and maintain in lab cultures, it has long been a favorite study animal for researchers investigating insect physiology (e.g., diapause) and molecular genetics in several countries around the world. In this report, I will provide evidence that this moth is easy to mass rear because it is yet another example of a "species" that was derived by artificial selection, but does not actually occur in nature. Although tussah sericulture has centered around the Bohai Gulf of northeastern China for centuries, the tropical and subtropical *Antheraea roylei* Moore (Figs. 3-4) from central and southern China is apparently the progenitor of *A. pernyi*. The silk of *A. pernyi* has been increasingly used in the western apparel market for more than a century (Figs. 9-10).

THE EVIDENCE

Cytogenetic, physiological, and molecular evidence. Studies investigating the cytogenetics of these moths reported the chromosome numbers for *A. roylei* to be *n*=31 and for *A. pernyi* to be *n*=49, with *n*=31 being the modal (ancestral) number for most saturniids (Belyakova & Lukhtanov 1994, 1996, and references cited therein). The higher number of chromosomes in *A. pernyi* is the result of fragmentation, since there is a lot of homologous pairing when the two species are crossbred. Nagaraju and Jolly (1986) reported that the F1 hybrids showed 18 trivalents and 13 bivalents in the first meiotic prophase and metaphase, and hypothesized that "*A. pernyi* possibly evolved from *A. roylei*." The genome of *A. pernyi* is not highly stable (Sezutsu & Yukuhiro 2000).

During the 1970s Indian sericulturists developed a strain of oak-feeding silkmoth by crossing *A. roylei* with *A. pernyi*. The sericultural results were very rewarding, and this new silkmoth was called oak tasar or temperate tasar, with a scientific name *A. proylei* Jolly, although in 1902 J. W. Tutt named *pernyi* ♀ × *roylei* ♂ as hybrid *moorei,* and *roylei* ♀ × *pernyi* ♂ as hybrid *kirbyi*. However, the concept of priority is irrelevant in this case since names proposed for hybrids are not treated in the International Code of Zoological Nomenclature (1999). Biologically, these crosses were highly fertile for numerous generations, which appeared to be an exception to the biological species concept that separate species do not produce viable offspring when crossbred. In the 1970s and 1980s, oak tasar was lauded with much fanfare in India, and cultures were established all along the sub-Himalayan belt that is rich in oak forests. Problems persisted with coordinating moth emergences and oak foliation in spring (Singh et al. 2005), and eventually oak tasar sericulture became restricted to the three states where it is still done today, namely Jammu & Kashmir, Uttarakhand, and Manipur. With genetic deterioration of *A. proylei* compared to *A. pernyi*, it was concluded by Srivastav and Thangavelu (2005: 103) that "cytologically, morphologically and physiologically both the stocks appear to be the same." When one considers that *A. pernyi* is nothing more than a cultivated form of *A. roylei*, it becomes clear why the "hybrid that never really was a hybrid" was fertile through multiple generations. The varieties of oak tasar (*A. proylei*) that have been developed and are being maintained in India should be viewed as simply more strains of *A. pernyi*, because they were developed by introducing genes from the ancestral species into stocks of the cultivated form of the same species.

The unusual mechanism of diapause in *A. pernyi* is also evidence that this entity is not a normal species. Many insects in temperate zones have one generation in the north and two or more in the south, but for *A. pernyi* the reverse is true (SRIL 1994). Diapause in *A. pernyi* can be terminated by 60 days of cold treatment, but also by longer daylength, the latter a feature of northern latitudes. Thus, a treatment of pupae to 8 h dark and 16 h light will promptly terminate diapause in *A. pernyi*, but 12 h light and 12 h dark will maintain diapause (Tohno et al. 2000). Cultures of oak tasar ("*proylei*") also do not diapause if larvae are exposed to long daylengths (Singh et al. 2005). The diapause of *A. pernyi* has been investigated by many insect physiologists around the world for decades, but most of those authors probably assumed they were working with a species that exists in nature in its native China.

In summary, *A. pernyi* has an unusual chromosome number, but these are still sufficiently homologous with those of *A. roylei* when the two are crossbred. Additionally, *A. pernyi* has an unusual mechanism for its diapause regarding the longer daylength. These unusual features must have become genetically fixed by artificial selection.

Morphological and taxonomic evidence. Both *A. roylei* and *A. pernyi* display phenotypic variation of the adult wing color and pattern. There are actually no known consistent traits to separate the two, because their variation broadly overlaps. The ground color in both species can be greenish gray, soft beige, reddish tan, or grayish beige, and the color form of *A. pernyi* commonly called *hartii* Moore is dark chocolate brown. However, in some strains, eggs laid by a single female can yield normal beige and dark brown moths. All of these forms were well-illustrated in color in the volume of tussah varieties published by the Sericultural Research Institute of Liaoning (SRIL 1994). Moths of *A. roylei* are more inclined to have smaller eyespots on the wings and more falcate forewing apices in males, as compared to most *A. pernyi*. Dark brown forms are not recorded for any of the wild populations.

Another species in the Himalayas that is closely related to *A. roylei* is *A. knyvetti* Hampson (Figs. 5-6). Specimens of *A. knyvetti* were illustrated in color under the name *A. roylei* by Allen (1993, figs. 41c, d) and Lampe (2010, pl. 280). The shape of the forewing apices differs between these two species, as well as more black in the eyespots of the hindwings of *A. knyvetti*. In the Chin State of Burma, Stefan Naumann collected specimens of *A. knyvetti* and *A. roylei* in the same localities, with *A. roylei* arriving to lights 200–430 h, and *A. knyvetti* 2230–2300 h. The male genitalia of *A. pernyi* and *A. roylei* are identical, but these differ from the genitalia of *A. knyvetti*. The larvae of *A. pernyi, A. roylei,* and *knyvetti* appear to be alike, but differ significantly from all other known species in the genus, except *A. lampei* Nässig & Holloway from Sumatra and West Malaysia, which is a very close ally of *A. roylei* (see Lampe 2010). Larvae of the four aforementioned species are characterized by their spotted head capsules ("freckle-face"). Because of color variation in *A. roylei*, Lampe (1985) assigned some material from West Malaysia to *A. roylei* and some to *A. pernyi* (see below), but he later changed that interpretation (Lampe 2010). In his recent review of the genus *Antheraea*, d'Abrera (2012) concurred with me that *A. pernyi* is an artificial derivative of *A. roylei*, and demonstrated that *A. francki* Watson from Sichuan is a junior synonym of *A. roylei*. Additionally, d'Abrera considered *A. lampei* to be a synonym *of A. roylei*, and I concur with that assessment.

To summarize this subsection, there are no taxonomic differences between *A. pernyi* and *A. roylei*, but *A. knyvetti* appears to be a valid species that was long confused with *A. roylei*. However, the names *A. francki* and *A. lampei* are here considered to be synonyms of *A. roylei*.

Wild-collected specimens. Authors of numerous published surveys of insects in central and southern China, some of which are cited here (Fang 2003, Fu & Tzuoo 2004, Guo 1989, Li et al. 2011, Lu 1990, L.-Y. Wang 1988, 1992, H.-Y. Wang 1988, Wu & Lin 1995, Wu & Li 1997, Zhang 1986, Zhao & Li 2005), report collected specimens under the name *A. pernyi*, but never list any material under the names *A. roylei* or *A. knyvetti*. In the cited works that provide collection dates, it is significant that the populations are seen to be bivoltine or multivoltine, but most of these surveys were in regions to the south of where *A. pernyi* is bivoltine, as discussed above. Collections at lights of "*A. pernyi*" at several localities of the mountains of western Taiwan cited by H.-Y. Wang (1988) and Fu and Tzuoo (2004) may be referable to *A. roylei,* although cultures of several varieties of *A. pernyi* have been maintained in Taiwan (SRIL 1994), so the specimens cited by Taiwanese authors could have been escapees from silk farms. *Antheraea roylei* ranges widely across central and southern China, with verified records (specimens in S. Naumann collection) from the provinces of Guangdong, Hainan, Guangxi, Sichuan, Hunan, Yunnan, Jiangxi, Fujian, Shaanxi, and also Taiwan.

For Korea, *A. pernyi* is rarely collected. In a detailed treatise on South Korean moths, Park and Tshistjakov (1999) cited only three collections of *A. pernyi*, the rarity of which suggests that these were escapees from sericultural colonies. These were from Seoul in 1938, Cheju-do in 1924, and Geoje-do in 1992, the latter two on islands. No material of *A. pernyi* from North Korea was found in the extensive East European and South Korean collections of moths from North Korea (Park et al. 2001), although cultures of the tussah silkmoth have been maintained there.

Records of *A. pernyi* in far eastern Russia and Mongolia are also dubious. It has been used for sericulture in Russia since at least 1924 (Nikitin 1936, SRIL 1994). Izersky (1999a, b) gave collection data for four specimens of *A. pernyi* from Russia's Far East, but added that it overwinters in the egg stage, proving that he misidentified specimens of *Antheraea yamamai* (Guérin-Méneville). He further stated that it was univoltine, a trait of *A. yamamai*, but not for *A. pernyi* in the North. Rare records for *A. pernyi* from Russia and Mongolia may also be based on escapees from captive colonies or temporarily established feral populations, as those regions are far to the north of known populations of *A. roylei*.

So what about specimens collected in the Himalayan region in countries that share borders with China? In these Himalayan surveys, authors always cite material under the names *A. roylei* and/or *A. knyvetti*, but never under the name *A. pernyi* (Allen 1993, Arora & Gupta 1979, Devi et al. 2011, Lampe 2010, Pinratana & Lampe 1990, Singh & Suryanarayana 2005). Here again, the populations are seen to be bivoltine or even multivoltine in Nepal, Thailand, West Malaysia, and India.

To summarize the main points here, it is illogical to assume that the national borders between China and its neighbors to the south could represent a line separating the natural distributions of *Antheraea roylei* from *A. pernyi*. It is more reasonable to assume that all of the populations existing in nature belong under *A. roylei* and *A. knyvetti*. Some confusion has resulted in rare cases when specimens of *A. pernyi* that escaped from captive colonies were collected and preserved in taxonomic collections, and thus believed to represent wild populations.

Sericultural and historical evidence. Chou (1988, 1990) consulted some of the ancient and classical literature of China, and provided evidence from those sources that *A. pernyi* has been exploited for its silk for at least 3000 years, and began to be mass-reared as early as the Han Dynasty (206 BC–220 AD). During this period, a lot of artificial selection must have taken place, which explains why tussah cocoons contain up to four times as much silk as those of *A. roylei*. The filament length for cocoons was given as 175–210 m for *A. roylei* and 750–810 m for *A. pernyi* by Devi et al. (2011). Pliska (2012) stated the length of filaments in *A. pernyi* cocoons averages 500 m, but can be as long as 1500 m. Cocoons of *A. pernyi* and the American *Antheraea polyphemus* (Cramer) are similar in size and shape, but when they are degummed and spun or reeled, those of *A. pernyi* are found to contain much more silk than those of *A. polyphemus* (Michael Cook, personal communication). Development and maintenance of an artificial strain having cocoons with abundant silk that is now called *A. pernyi* would have been easier to carry out in areas to the north of the natural range of *A. roylei*, since gene flow from wild populations (having cocoons with less silk) would interfere with the artificial selection process. This latter point could explain why the Bohai Gulf region has been the center of tussah culture, since it is beyond the range of the wild populations, yet has a rich oak flora and climate well-suited for mass-rearing the silkworms.

Cocoons of *Antheraea* invited exploitation by people in ancient times, because they are reelable like those of *Bombyx mori*. In India today, *Antheraea paphia* (Linnaeus) is the source of tropical tasar silk, whilst cocoons of *A. assamensis* (Helfer) yield the famous gold-colored muga silk. Archaeological evidence indicates that both of these Indian species have been exploited for possibly 4000 years, because Good et al. (2009) identified their silks from excavations at Harappa, in what is now the Punjab of Pakistan. Although cultured outdoors on trees from which cocoons are harvested, these two Indian species also differ from their wild counterparts.

Comparison of cocoons of *A. pernyi*, *A. roylei*, and the so-called hybrid *A. proylei* supports the earlier hypothesis that the latter simply represents another strain of *A. pernyi*. Cocoons of *A. pernyi* are ovoid, single-layered, and have little or no peduncles. Those of *A. roylei* are irregular in shape, double-layered, with well-developed peduncles (Fig. 8). Cocoons of *A. proylei* look like those of *A. pernyi* in size and form. Loss of the peduncle is also a trait of cocoons of *Bombyx mori* and *Samia ricini*. However, natural colored tussah textiles made in China from silk of *A. pernyi* are pinkish beige or cream, whereas temperate tasar textiles made in India from silk of *A. proylei* are dark grayish brown. I do not know whether the color difference between these textiles is due to genetic differences in the silkmoths or the methods used to process the silk, but I have studied many samples of oak tasar fabrics (from Manipur and Uttarakhand) and tussah fabrics (from several sources in China), and the difference is consistent.

I visited a tussah silk farm in Fengcheng, Liaoning Province, in June 2008, where the details of the rearing operations were described to me in detail. Matings occur indoors in captivity and the eggs or young larvae are then set out onto pruned oak trees on hillsides. Significant technological advances have been made to protect larvae from parasitoids, predators, and pathogens. Some weeks later, mature larvae are collected by hand before they spin cocoons, and the life-cycle again becomes an indoor operation. No wild populations of the moth occur in the oak forests of that area. Scientists and technicians at the Sericultural Research Institute of Liaoning and similar facilities in northeastern China maintain over 130 named varieties of *A. pernyi*, but most of those are maintained in Fengcheng. The majority has green larvae, but some varieties have blue (Fig. 7), yellow, or reddish-orange larvae. Most produce beige silk, but some yield white silk. All of these varieties, including ones from Taiwan and some extinct ones, were described in detail in their treatise on tussah varieties (SRIL 1994).

Antheraea pernyi has been introduced to several places around the world since the mid-1800s, but the populations never persist, and eventually go extinct. The silkmoth was introduced at some localities in northern Spain in the 1850s, including the provinces of Navarra and Gipuzkoa in the Basque region, as well as Barcelona, Castellón de la Plana, and on the Balearic Islands off the east coast of Spain (Gómez and Fernández 1976). In a recent field guide to European moths, Leraut (2006) stated "Survival in Europe restricted to the Balearic Islands and around Barcelona" with the status given as "Quite local." Although most Spanish authors have conceded that *A. pernyi* is extinct on Spain's mainland, some maintain the belief that it continues to live on the Balearic Islands, but I believe it is also extinct there.

The tussah silkmoth was also brought to Japan in 1875, where it was first reared experimentally around Sapporo and Tokyo, and then widely throughout Japan. However, by 1880 tussah sericulture was mainly in Nagano Prefecture in central Japan, and this continued well into the 20th century (Honda 1909). *Antheraea pernyi* is kept in a few places around Japan even today, but has never established feral populations. In 1951, this silkmoth was brought to the town of Polisie in the Ukraine, and tussah culture spread to 14 regions of the Ukraine. Today, the Polesskiy Tussah variety is only maintained at the National University of Life & Environmental Sciences of Ukraine (Pliska 2012). Introduced populations of *Antheraea pernyi* apparently

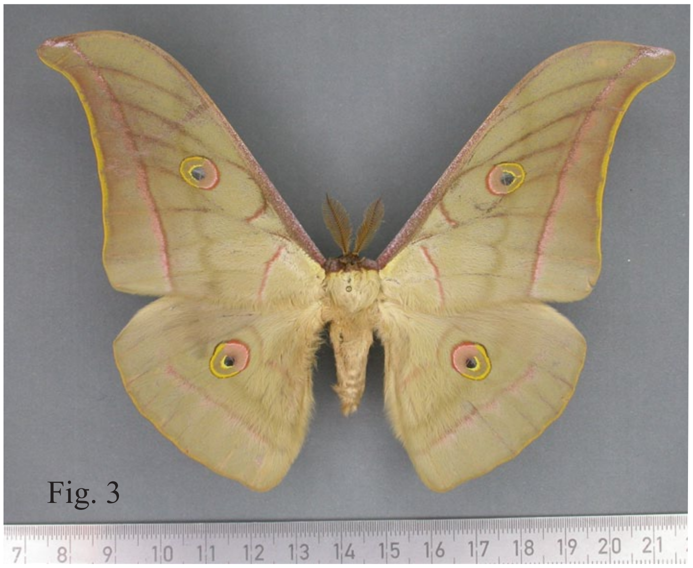

Fig. 1. *Antheraea pernyi*, sibling males. The form with more falcate forewings also exists in some males of *A. roylei*. **Fig. 2.** *A. pernyi*, female. **Fig. 3.** *Antheraea roylei*, male, 5 km N Paro, Dochu Valley, 2350 m, Bhutan, 28 July 2005, leg. S. Naumann et al. **Fig. 4.** *Antheraea roylei*, female, Kanphant, 1642 m, Kachin State, Burma, 29 May 2006, leg. S. Naumann et al. **Fig. 5.** *Antheraea knyvetti*, male, Nagaland, 1900 m, India, April 2008, leg. E. Grigorev & V. Sinyaev. **Fig. 6.** *Antheraea knyvetti*, female, Dexin (=Deqen), Mount Baimaxue, Yunnan, China, June 1999. Specimens in figs. 3-6 are in the collection of Stefan Naumann (Berlin).

Fig. 7

Fig. 8

Fig. 7. Mature larva of *A. pernyi*, blue form, photographed at tussah silk farm in Fengcheng, Liaoning Province, in June 2008. **Fig. 8.** *A. roylei*, cocoons, which are double-layered, with a papery and inflated outer layer. An inner cocoon has been removed (top). Cocoons in Denver Museum of Nature & Science, and photographed by Rick Wicker. **Fig. 9.** Suit of natural-colored 100% tussah silk, tailored in Hong Kong in 2008. **Fig. 10.** Knit shirt of 70% tussah silk and 30% cotton, dyed a greenish gray, made in China.

Fig. 9

Fig. 10

never become firmly established, but possibly persist longer on islands like Taiwan and those of Spain and South Korea cited above; perhaps the most instructive comment was offered by Székely (2010), who wrote that liberated or escaped cultures could be found in nature for five to seven years in Romania, "but these small and isolated populations disappeared shortly after." The observations that *Antheraea pernyi* introductions fail to establish and exist without human assistance enhance my belief that it is not a wild species in China. This information should also provide solace to agricultural and forestry officials who might fear that its intentional or accidental introduction could lead to a newly established pest. By contrast, the Japanese oak silkmoth (*Antheraea yamamai*) was introduced from Japan (where it is mass reared for tensan silk) to Austria in the 1860s, and it subsequently spread to Hungary, northern Italy, Switzerland, Slovenia, and Croatia (Leraut 2006), and has now reached the Passau area around the Danuvian Valley in southeastern Bavaria of Germany (S. Naumann, personal communication). There is even a small possibility that *A. yamamai* was introduced to Japan from China millennia ago for sericultural purposes, but DNA studies would be necessary to test this hypothesis.

To summarize the important points of this subsection, features of *A. pernyi* such as being easy to mass rear, having cocoons with ample silk and with little or no peduncles, and the inability to establish and maintain feral populations, all point to the conclusion that it was derived and perpetuated by artificial selection long ago.

CONSERVATION OF THE WILD GENETIC RESOURCES

As discussed above, several of the *Antheraea* (*pernyi, paphia, assamensis,* and *yamamai*) are the basis for wild silk industries that earn a lot of money every year in exports to western countries and domestic consumption in the Asian countries. China now exports more than 90% of its tussah silk to India to be used as a substitute for the over-exploited tasar silk. *Samia canningi* remains an important genetic resource for its cultivated strains known as *S. ricini*, and this eri silk is second only to mulberry silk in world production and consumption of silk. Indian authors (e.g., Srivastav & Thangavelu 2005, Singh & Suryanarayana 2005, Devi et al. 2011, and many others) have noted the importance of conserving the natural populations and habitats of these wild silkmoths.

It is well documented that tropical and subtropical biomes of Southeast Asia are increasingly suffering from the effects of deforestation, acid rain, climate change, and pollution. Critical to the *Antheraea*, the old oak forests are being exploited at a rapid rate by an expanding human population in Nepal and northern India. Local people in the mountains and foothills who engage in subsistence living, have long used oaks for firewood and fodder for livestock, and acorns are used for human food (Singh & Rawat 2012). Oaks are sometimes clear cut to make way for grazing land. Some montane ecosystems depend on snowmelt from glaciers in the Himalayas, so climate change is a direct threat to these areas.

Sericulture based on oaks has been identified by the World Bank and other agencies as a vehicle to allow the local people to benefit more from the oak forests by keeping them, than by destroying them. Oaks regenerate better in disturbed and open areas, rather than in dense forests. However, in their assessment of oak tasar sericulture in Uttarakhand, Lal et al. (2010) wrote that "sericulture farmers gradually are showing less interest towards sericulture activities due to continuous failure of their crop or low crop yield" in spite of efforts to promote the industry by state and national governments. (I suspect part of the problem is that they are trying to culture a silkmoth in northern India that was developed in, and is better adapted to, northeastern China.) In any case, it is my hope that by identifying the wild progenitors of the tussah silkmoth and eri silkmoth, this paper will be used in efforts to promote conservation programs of wild populations of *A. roylei* and *S. canningi*, which are a valuable genetic resource for the two most important silk producers in the world after the mulberry silkmoth.

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