



Bionomics of Bagworms (Lepidoptera: Psychidae)*

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bottom-up effects, flightlessness, mating failure, parthenogeny,
phylogenetic constraint hypothesis, protogyny

Abstract

The bagworm family (Lepidoptera: Psychidae) includes approximately 1000 species, all of which complete larval development within a self-enclosing bag. The family is remarkable in that female aptery occurs in over half of the known species and within 9 of the 10 currently recognized subfamilies. In the more derived subfamilies, several life-history traits are associated with eruptive population dynamics, e.g., neoteny of females, high fecundity, dispersal on silken threads, and high level of polyphagy. Other salient features shared by many species include a short embryonic period, developmental synchrony, sexual segregation of pupation sites, short longevity of adults, male-biased sex ratio, sexual dimorphism, protogyny, parthenogenesis, and oviposition in the pupal case. The unusual mating behavior of bagworms, characterized by an earlier emergence of females than males and a high proportion of females that do not mate as adults, challenges conventional wisdom regarding the evolution of mating systems.

INTRODUCTION

The bagworm family (Lepidoptera: Psychidae) includes approximately 1000 described species and 300 genera distributed worldwide (48, 94), most of which share an unusual life history (30, 39, 63). All existing reviews of bagworms predate the 1970s and are limited in scope, focusing on taxonomic aspects or on species occurring in restricted geographic regions (14, 20, 21, 29, 41, 56, 59, 109). Understanding the biology and ecology of bagworms is important from an applied perspective, because several species are economic pests of cultivated crops, especially in tropical regions (8, 59). From a fundamental perspective, bagworms may serve as model systems for studying the principles of population dynamics (99) and for understanding life-history strategy related to intraspecific variation of reproductive success (85). The Psychidae represent the only lepidopteran family with a large proportion of species with flightless females (94), thereby providing a ground plan for an evolutionary biology of eruptive population dynamics (79). In this article, we review the literature on bagworms, focusing on aspects related to their taxonomy, life history, phenology and population dynamics, and provide a summary of life-history traits for the 18 best-studied species of the Psychidae (**Table 1**).

SYSTEMATIC REVIEW

The Psychidae is one of five families of moths composing the basal superfamily (Tineoidea) within the most successful and recently evolved clade (Ditryisia) of Lepidoptera (28). Adults are small- to medium-sized moths, with forewings ranging from 4 to 28 mm in length. Males are always fully winged; the females are either fully winged, brachypterous, apterous, or vermiform (with all body appendages vestigial or lost). The larvae construct portable cases, as do genera in at least 10 other families of Lepidoptera. The morphology of the larval stage is conservative and exhibits diagnostic features that indicate the monophyly of the family, including (a) four pairs of epipharyngeal setae;

(b) pronotum expanded laterally and fused to the lateral pinnaculum to include the spiracle and all three prespiracular setae; and (c) abdominal crochets on segments 3–6 arranged in a uniordinal, lateral penellipse (23). The pupa is less diagnostic, with major morphological distinctions according to phylogenetic hierarchy, as well as between males and females in derived subfamilies. Particularly noteworthy are pupal specializations involving the dorsal abdominal spines. The plesiomorphic condition present in the more basal subfamilies Naryciinae and Taleporinae consists of an anterior, transverse patch of 3–20 scattered rows of short, stout spines variably present on abdominal terga 3–8 (males) or 3–7 (females). Pupae in derived subfamilies typically possess a single anterior row of short, stout, caudally directed spines variably present on terga 3–8 and a single posterior row of slender, recurved spines variably present on terga 2–8 (22, 24, 73, 96).

Determining the monophyly of the family on the basis of adult morphology is difficult because of a broad range of morphological variation. However, molecular evidence is beginning to emerge that confirms the monophyly of the Psychidae as currently recognized (115). One important synapomorphy for the Psychidae, the presence of fused metathoracic furcal bridges, is shared with the sister group Arrhenophanidae (26, 91). The female psychid has evolved a greater array of morphological specializations, especially involving appendage reductions, than any other family in the Lepidoptera. This is particularly evident when the broad range of these specializations is applied to the subfamily classification of the Psychidae (**Table 1**). Assessing the family relationships of psychid species with fully winged females was a consistent problem for early lepidopterists, who often assigned such taxa to Tineidae or Yponomeutoidea (24). As a result, previous attempts to classify the family have varied from the recognition of as many as 10 families (109) to as few as two subfamilies (59), or a superficial division into two paraphyletic families: Micropsychidae (= Micropsychiniidae) to include tineid-like forms and the “true” Psychidae, or

Psychidae: one of five tineoid families of Lepidoptera, partially characterized by case-bearing larvae (bagworms)

Tineoidea: the most basal superfamily within the Lepidoptera clade Ditryisia

Ditryisia: the largest, most recently derived clade of Lepidoptera characterized primarily by the presence of two female genital openings

Table 1 Life-history traits of 18 species of bagworms

Species	Distribution	Length of female (mm) ^a	Development time (day) ^b	Family of host plants (number)	Fecundity ^a	Reference(s) ^c
Psychinae						
<i>Psyche viciella</i>	Palaearctic	13	730	7	225	(59)
<i>Psyche casta</i>	Palaearctic	7	365–730	10	115	(11, 59, 109)
Metisinae						
<i>Metisa plana</i>	Paleotropical	12	69–120	7	130	(8, 57, 85–87, 104)
<i>Pteroma pendula</i>	Paleotropical	8	80	19	81	(57, 60, 104)
<i>Pteroma plagiopleps</i>	Paleotropical	6	40–88	22	174	(52, 53, 71)
Oiketinae						
<i>Apterona helix</i>	Palaearctic	6	365	24	43	(11, 21, 59, 113)
<i>Canephora unicolor</i>	Palaearctic	23	365–730	8	450	(60)
<i>Pachytelia villosella</i>	Palaearctic	18	365–730	10	375	(44, 109)
<i>Sterrobapteryx fusca</i>	Palaearctic	13	365–730	9	180	(59)
<i>Thyridopteryx ephemeraeformis</i>	Nearctic	24	365	50	792	(4, 7, 21, 56, 58, 99, 112, 114)
<i>Eumeta variegata</i>	Paleotropical	20	365	32	3000	(35, 57, 76, 108, 116)
<i>Eumeta crameri</i>	Paleotropical	14	84–365	31	628	(1, 3, 62, 67, 106)
<i>Eumeta moddermanni</i>	Paleotropical	20	365	9	3270	(42, 59)
<i>Chaliopsis junodi</i>	Paleotropical	20	110–365	16	1228	(29, 41)
<i>Hyalarcta buebneri</i>	Paleotropical	18	303	16	1200	(45, 49)
<i>Mahasena corbetti</i>	Paleotropical	31	124	25	2009	(57, 104)
<i>Cryptotbelea surinamensis</i>	Neotropical	13	168	8	875	(11, 21, 22)
<i>Oiketicus kirbyi</i>	Neotropical	34	212–288	40	5752	(20, 21, 31, 86, 102)

^aValues were averaged across different studies.

^bRange of values observed in different studies.

^cIn addition to the references cited above, the HOSTS web database was used to assess the family of host plants of the different species of bagworms (92). Families of host plants for different species of bagworms are listed in **Supplemental Table 1** (follow the **Supplemental Material link** from the Annual Reviews home page at <http://www.annualreviews.org>).

Bombyx-like forms (33, 34). Although the first modern character analysis of psychid genera involved only the Palaearctic fauna (96), it represented an improvement over previous classifications and provided a basis for hypothesizing suprageneric relationships. Utilizing 29 almost exclusively morphological characters, these authors group 77 Palaearctic genera phylogenetically, without any formal cladistic analysis, into

17 tribes and eight subfamilies. Other subfamilies currently recognized include the Pseudarbelinae (*new status*; 28, 91) and the Scoriodytinae (**Table 2**) (40). The 10 subfamilies currently recognized within the Psychidae may be characterized in part by the broad range of morphological and behavioral plasticity present in the adult female (**Table 2**). Significant behavioral modifications appear within the

Table 2 Summary of the subfamilies of Psychidae and their major morphological/behavioral characteristics as typified by the adult female and male pupa

Subfamily	Adult female						Male pupa
	Wings	Legs	Labial palpi: segments	Ocelli	Female emergence behavior ^a	Location for copulation (to bag)	Rows of abdominal spines
Naryciinae	+ or –	+	3, R, –	+ or –	Type 1	Distant or on bag	Anterior: multiple Posterior: 0
Taleporiinae	+ or –	+	3, R, –	+ or –	Type 1	Distant or on bag	Anterior: multiple Posterior: 0
Pseudarbelinae	+	+	3	+	?	?	Anterior: ? Posterior: ?
Scoriodytinae	–	R	1 (males have 3)	–	Type 1	On bag	Anterior: multiple Posterior: 0
Placodominae	+ or –	+	3, R	–	?	Distant or on bag	Anterior: ? Posterior: ?
Typhoniinae	+, R, –	+	3, R, –	–	Type 2	Distant	Anterior: 1 Posterior: 1
Psychinae	–	+	R or –	–	Type 3	On bag	Anterior: 1 Posterior: 1
Epichnopteriginae	–	+, R, –	–	–	Type 4	Within bag	Anterior: 1 Posterior: 1
Metisinae	–	R or –	–	–	Type 4	Within bag	Anterior: 1 Posterior: 1
Oiketiciinae	–	R or –	–	–	Type 5	Within bag and/or in pupal case	Anterior: 1 Posterior: 1

^aType 1: female emerges from bag with pupal exuviae extruded; Type 2: female emerges without exuviae extruded and usually leaves bag; Type 3: female emerges without exuviae but remains on bag; Type 4: female emerges only partially from bag; Type 5: female remains inside bag.

Table modified from Reference 96.

Abbreviations: +, present; –, absent; R, reduced.

family as morphological specializations have evolved.

Our current knowledge of psychid systematics is based largely on the better-studied Holarctic fauna. Because a greater proportion of pantropical taxa than taxa in temperate regions exhibit generalized, plesiomorphic morphology (e.g., less reduced mouthparts, fully winged females), the Psychidae most likely arose first in tropical regions. Ongoing investigations on the American Psychidae (25) reveal that approximately 55% of Neotropical Psychidae possesses generalized females with no wing reduction, 80% of which represent new taxa. The psychid fauna over much of the paleotropics appears similarly unstudied. In contrast, females in over

90% of the Palearctic species exhibit wing reduction. Genera with females exhibiting little or no wing reduction occur within the five basal subfamilies (Naryciinae, Taleporiinae, Pseudarbelinae, and possibly Placodominae and Typhoniinae). Because genera with brachypterous or apterous females occur in four of these subfamilies, as well as in Scoriodytinae (Table 2) (28, 95), wing reduction may have evolved independently several times within the family, as is confirmed by the molecular phylogeny of 30 psychid species (115). Female brachyptery may have evolved within each subfamily as a result of biological traits (e.g., heavy abdomen and high fecundity) that favored or facilitated flightlessness of females (101).

LIFE HISTORY

Egg Stage

Eggs are cylindrical, smooth, and relatively large compared with the size of females and are smaller in primitive subfamilies (11, 59, 109). Embryonic development is usually completed within one month (2, 8, 11, 13, 29, 50, 67, 104, 113), with the exception of temperate species that overwinter in the egg stage (70, 74). Eggs laid by mated females are generally fertile (8, 50, 87, 102).

Larval Stage

Larvae emerge synchronously, usually within their maternal bag, where they sometimes feed on the remains of their dead mother (3, 11, 89), ova shells (13, 44), or sibling eggs (87). Following a residence time of up to 5 days, neonates exit the maternal bag by a silk thread from its posterior opening (**Figure 1e**) (16, 29, 58, 102, 106), although some individuals die before leaving the bag (8, 11). Stimuli that induce departure from the maternal bag include suitable weather, sunlight, and disturbance caused by wind (11, 16, 20, 29, 41). Larval progeny exit the maternal bag either simultaneously (56, 67) or in small groups over a delayed period (16). Early instars either remain on the plant where they emerged or disperse by ballooning (**Figure 1e**) (16, 29, 41, 42, 52, 56, 68, 83, 86, 89, 102).

Factors associated with an enhanced rate of dispersal by neonates include high density of conspecifics (81, 83), severe defoliation (16), poor quality of the plant on which larvae emerge (68), and strong wind currents (32, 47, 102). Neonates engage in ballooning before or after constructing their primary bag, which may affect their survival or the range attained during wind dispersal (16, 32, 41, 42). Although ballooning larvae sometimes disperse over great distances, most settle within a few meters from their point of origin (16, 32, 66, 83, 86). Neonates enhance their dispersal range by climbing to the top of plants before balloon-

ing (20, 29, 42, 102). The rate of ballooning declines with the age of larvae and is low after first instars start to feed (16, 32, 68), although larvae have the capacity to silk through development (83). The reproductive output of females relative to the carrying capacity of host plant influences the incidence of dispersal among neonates: In species with small females and low fecundity, the larval progeny commonly remain on their natal host, where they initiate feeding and development. In species with large and highly fecund females, in contrast, neonatal larvae often disperse by ballooning irrespective of the quality of the food plant, because the offspring of a few females have the capacity to overexploit their host (32, 41, 42, 86).

First instars construct a self-enclosing bag before they start to feed (11, 24, 30, 44, 59, 109), and the availability of suitable material for bag construction sometimes has priority over the palatability of plants as food as the determinant of host choice (8, 29). The primary bag to which foundation larvae incorporate various materials (such as plant tissue and organic and inorganic debris), consists of a 1- to 2-mm-long conical structure with two openings and is made of silk spun from labial glands (11, 13, 30, 37, 50, 58, 113).

The head and thoracic legs protrude from the anterior opening of the bag, allowing the larva to feed and move over the plant; the small posterior opening serves to expel feces and cast skins (**Figure 1a**) (30, 41, 56). Larvae maintain the interior of their bag clean and dry throughout development. Prolonged wet conditions are detrimental to the maintenance of a suitable microclimate within the bag and allow for the development of entomopathogenic fungi (41, 59). Larvae are capable of repairing damaged bags, but the ability to construct a bag *de novo* is restricted mostly to first instars (12, 30, 58). To accommodate their increasing size, larvae continually enlarge their bag in length and diameter by adding pieces of plant and other material interspersed with silk (12, 13, 21, 37, 78). Bags of first instars are relatively uniform in the Psychidae, but bags of mature larvae vary considerably

Ballooning: mode of dispersal by which larvae drop on a silk thread to become windborne

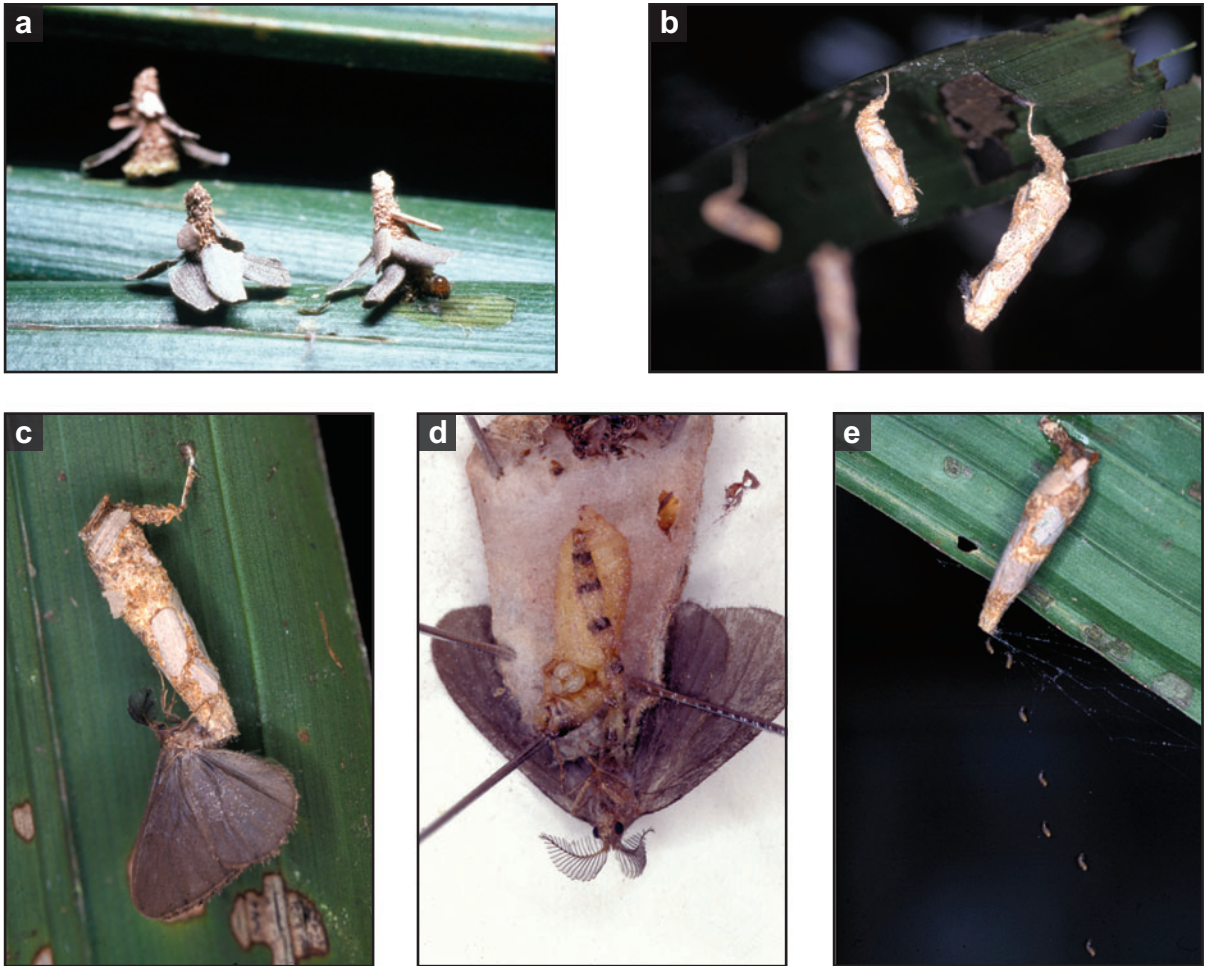


Figure 1

Photographs illustrating the life history of *Metisa plana* Walker. (a) Bag of early instars. (b) Pupal bag of male (right) and female (left). (c) Male mating with a female by intruding his abdomen into the lower section of the female's bag. (d) Male mating with a receptive female; the female bag has been opened and the pupal case removed to illustrate how the extensible abdomen of the male reaches the female's genitalia. (e) Neonates emerging from their maternal bag suspended from a silken thread. Photographs are reproduced with permission of *Applied Entomology and Zoology* (see Reference 87).

between species in both shape and dimension (20, 21, 28, 42, 56, 109).

The possession of a self-enclosing bag generates microclimatic conditions (e.g., elevated temperatures) that may accelerate development (6, 100) and favor the survival of overwintering eggs (90). Larvae close the anterior part of their bag before molting or when disturbed, and as such the bags physically protect them against natural enemies (3, 37, 58, 62, 67, 102). The

cryptic appearance of bags (3, 41, 42, 75, 109) also serve as camouflage.

The duration of the larval stage is extended in temperate bagworms because mature larvae are the most common overwintering stage (59, 109). In tropical and subtropical species, the duration of larval development varies between 32 days in *Pteroma pendula* Joannis to more than 200 days in *Oiketiscus kirbyi* Guilding (60, 102). Females have a longer larval development

and greater feeding requirements than males do, which in some species involves a supernumerary feeding instar (2, 8, 24, 41, 71, 104, 106).

Larval Performance

Bagworms in the more basal subfamilies are omnivorous scavengers with a diet similar to that of some Tineidae, feeding on lower plant forms such as lichens and mosses, as well as on small insects and organic debris (21, 27, 59, 109). Although omnivory is observed in Oiketicinae (21, 50, 110), most species are polyphagous defoliators with a broad range of hosts (Table 1). A high midgut pH may allow larvae to effectively extract leaf nutrients while detoxifying secondary metabolites from several families of plants (15). Larvae can tolerate long periods of starvation lasting a few weeks to several months (21, 44, 58, 59), especially late during development (41).

Even though most species have a broad host range, larvae often die when they are transferred to a new plant species during development, suggesting that host preference is induced through larval experience (21, 56, 111). Both the level of polyphagy (20, 29, 47, 59, 112) and the rate of feeding (8, 58) increase with the age of larvae. In a highly polyphagous species such as *Thyridopteryx ephemeraeformis*, larvae are thought to adapt to different plant species, leading to the evolution of sympatric races based on distinctive host plant exploitation (43, 56). However, the performance of larvae is only weakly influenced by the host of origin in the parental generation, indicating a lack of specialized adaptations to different plant species (75, 112). Polyphagy may be maintained at the species level by inherent variation among neonates in their tendency to disperse, for example, some larvae disperse irrespective of the quality of the host plant on which they emerge (68). The dispersal behavior of larvae may also affect the exploitation of different plants regardless of their nutritional quality, for example, tall or exposed trees are more likely to intercept ballooning larvae (32, 75).

Pupation

Upon completion of feeding, larvae tightly attach the anterior portion of their bag onto a substrate (Figure 1b) and reverse their position within the bag, with the head oriented downward (21, 59); larvae that do not reverse their position usually fail to emerge as functional adults (55, 56, 58). The larva of one species, *Brachygyna incae* Davis, does not invert its position prior to pupation, with the adult consequently emerging from a subapical opening in the bag (25). Male larvae in some species undergo a nonfeeding instar before pupation (45, 50, 59, 109). Larvae either pupate on the same host plant where they fed or disperse before pupation (14, 42, 109). Larvae that seek pupation sites are often gregarious (41, 42, 43, 56, 59). Sexual segregation of pupation sites has been recorded in several species: Compared with males, female larvae are more likely to pupate away from the host where they fed or in higher locations (19, 20, 55, 59, 102, 109). This behavior likely results from sex-specific selective pressures. Female larvae enhance their fitness as sessile adults by pupating in locations most suitable for mate attraction or for the performance of their progeny; male larvae are not subjected to these constraints because winged adults are capable of dispersal (17, 38, 80, 82, 83, 86).

Female pupae are larger and differ morphologically from male pupae. In the more derived subfamilies, the female often does not exhibit well-defined appendage sheaths. The elongate, obrect pupa of the male is typical of moths, exhibiting enclosed structures readily identifiable as wings, legs, eyes, or antennae; the abdomen characteristically possesses an anterior row(s) of tergal spines that aid the male in moving downward in its bag before emerging (22, 59, 73). The pupal stage is shorter for females than for males (2, 8, 20, 29, 41, 45, 102, 106).

Adult Stage

Shortly before emergence, the male pupa pushes itself partway outside of the caudal end

Sexual segregation of pupation sites:

distinctive dispersal behavior of male and female larvae, which results in different positions of male and female pupae on a plant

of the bag; a terminal cremaster, sometimes assisted by a posterior row of recurved spines on abdominal tergites 2–8, prevents the male from falling to the ground (73). The male emerges after rupturing the anterior segments of its pupal case and takes flight on the same day (69). The male is a typical winged moth, often with well-developed bipectinate antennae, relatively long legs, and reduced mouthparts. Males are capable of sustained flight and are active a few hours each day, either during daytime or at night depending on the species (21, 29, 41, 50, 56, 59, 109).

Females in most primitive species are fully winged and undergo the same process as males during emergence, yet they are less active as adults (21, 94). Females in about half the species are apterous, possibly due to an inhibition of cell proliferation in wing disks caused by hemopoietic organs among late instars (76). Apterous females with fully developed legs leave their pupal case upon emergence and spend their adult life clinging on the exterior surface of the bag (21, 41, 59, 61, 109) (**Table 2**). In many species, neotenic females lack functional appendages; their emergence is indicated by a dehiscence of the anterior segments of the pupal case. The head and thoracic segments are fused and poorly developed, and most of the body consists of a weakly sclerotized abdomen tightly packed with ova (2, 21, 39, 59, 89, 109). The length of females varies between 6 and 34 mm depending on the species (**Table 1**). Adults with vestigial appendages remain in their pupal case and protective bag until shortly before death.

Neither male nor female bagworms feed as adults. The longevity is longer for females (up to two weeks) than for males (usually one or two days) (3, 8, 29, 41, 50, 52, 56, 58, 59, 61, 62, 67, 71, 102, 105, 106, 108, 109). Sex ratios of laboratory-reared bagworms are often male biased (3, 8, 45, 52, 67; but see 69). In field populations, males are either more abundant than females (4, 17, 47, 55, 108), less abundant than females (13, 18, 38, 85), or equally abundant (41). A high population density of bagworms is often correlated with a male-biased sex ratio (17, 31, 51, 55), possibly because female larvae

have greater feeding requirements than males and are more susceptible to intraspecific competition for food (85). The sex ratio of adult bagworms is also influenced by the higher level of mortality among male pupae than female pupae (19, 85, 99).

Mating Behavior

Females attract conspecific males over large distances by releasing sex pheromones that consist of chiral esters (35, 63, 84, 103). In the more basal subfamilies, females clinging to their bag exhibit a calling behavior characterized by periodic pulsations of the abdomen (61). In some Oiketicinae, the pheromone is synthesized in glands located on thoracic segments and on the first abdominal segment (10, 35, 64, 103). The pheromone is sometimes released from deciduous thoracic setae shed by females outside of the pupal case into the lower portion of the bag (2, 10, 42, 63, 64, 84). In the subfamily Metisinae, females periodically protrude their thorax outside of the lower section of the bag, possibly to further the dissemination of pheromone (**Table 2**). Females eventually drop onto the ground to die if they fail to attract a mate (8, 13, 29, 30, 41–43, 55, 58, 62, 102), and the sexual attractiveness of females declines with age (105).

In the more basal genera with winged females, or with females that cling outside of their bag upon emergence, the mating procedure is similar to that of typical moths (21, 50, 59). Species with vermiform females that remain within their bag exhibit a highly modified mating behavior. Upon being attracted by the pheromone plume of a virgin female and landing on her bag, the male pneumatically inserts his extensible abdomen through the posterior opening of the female's bag all along her body inside her pupal case to reach the caudal genitalia (**Figure 1c,d**) (39, 43, 55, 63, 105). Males of Oiketicinae typically possess paired sclerotized apophyses, arising from the male eighth sternum, that assist in the considerable extension of the abdomen (up to three times its original length) during copulation (21, 59). Males

sometimes die with their abdomen inserted into the female's bag after unsuccessful mating attempts (41, 58, 105). The abdomen of males is retractable, and they are capable of multiple copulations (21, 55, 109), although their mating capacity is limited by their brief life span (14, 41, 50, 52, 61, 105, 109). The fertility of females declines when they copulate with previously mated males (61).

Females mate only once and cease being attractive shortly thereafter (29, 41, 55, 59, 109). A high proportion (up to 30%) of unmated females (hereafter called mating failure) has been reported in several species (7, 42, 52, 62, 80, 82, 85, 99, 105), which may be attributed to the complex mating procedure, limited mating capacity of males, short longevity of adults, or late emergence of males; alternatively, flightlessness of female bagworms per se may constrain their mating success (85). Male-biased sex ratios may have evolved as a strategy to compensate for the low mobility of females (8, 45, 108). The high incidence of mating failures likely selected for behavioral adaptations of females to enhance mating success, e.g., pupation in locations most suitable for mate attraction (82). Because large female bagworms effectively attract mates independently of their location, the fitness impact of pupation site in terms of enhanced mating success is most pronounced for small females (80).

Although rare in Lepidoptera, parthenogenesis has evolved independently in many genera of the Psychidae (46, 61, 65, 72). Studies on the genetics of *Dablica triquetrella* Hübner reveal the existence of sexual and parthenogenetic (diploid and tetraploid) races whose distributions closely match recent geological history and biotic changes (97, 98). Facultative parthenogenesis has not been demonstrated for any sexual species.

Oviposition Behavior

Winged females use their long ovipositor to lay eggs in crevices, usually some distance from the pupation site (59, 94, 109). In the predatory bagworm *Perisceptis carnivora* Davis, females

wrap their eggs individually inside cocoon-like cases made from abdominal setae, a behavior that appears unique in insects and may have evolved to protect the eggs from carnivorous siblings (27). Apterous females with functional legs stay on their bag upon mating and insert their telescopic abdomen into the lower opening of the bag to oviposit in their pupal case (21, 59, 61, 109). In species with vermiform females that remain inside their pupal case, peristaltic contractions of the abdomen allow females to discharge their eggs intermixed with abdominal setae inside the upper section of their pupal case, progressively shrinking in the process (14, 21, 59, 109); oviposition is initiated immediately after copulation and completed within two days (21, 39, 55, 56, 89, 102, 104). Mated females lay a high proportion of their eggs (67, 87, 102), and more than two thirds of larval-derived resources are allocated to egg production (87, 88). Large female *T. ephemeraeformis* are more effective than small females at converting adult biomass into eggs (88). The high rate of conversion of adult biomass into reproductive tissue in bagworms may be related to the neoteny of short-lived females that invests little in somative tissue (88). Females usually depart their bag upon completing oviposition to perish on the ground (2, 13, 29, 52, 55, 58, 102, 104), but occasionally they remain in their bag (8, 14, 30, 39, 109). The presence of a dead female inside the bag may provide neonates with a food source (3, 11, 89), or with material for constructing the primary bag (14, 30, 42), while potentially obstructing the lower segment of the bag through which neonates emerge (11).

Fecundity

The reproductive success of females in field populations of insects is inherently difficult to quantify owing to the small size and high mobility of adults. Apterous female bagworms complete all reproductive activity within their bag, and as such provide a model system to estimate realized fitness in natural conditions (85). For example, the reproductive output of females that fail to mate as adult is null. The

Mating failure: an adult female fails to attract a male for mating during her lifetime and consequently dies as virgin

Parthenogenesis: production of offspring by a female with no genetic contribution from a male

Neoteny: preservation in reproductively mature adults of traits usually associated with immature stages

Protogyny: early emergence of females relative to males

lifetime fecundity of mated females can be assessed by counting the number of eggs laid in pupal cases, which is a good estimate of fitness because eggs laid by mated females are generally fertile.

The distinctive reproductive strategies of bagworms (neoteny to apterous to winged, sexual and asexual reproduction) affect the realized fecundity of females. The number of eggs laid by females in different species varies by two orders of magnitude (**Table 1**), with overall trends of enhanced fecundity with increasing body size, both within (19, 20, 31, 85, 87, 88, 102) and among species (**Table 1**). The fecundity tends to be higher for tropical species than for temperate species (**Table 1**), and for species with vermiform females than those with winged females (41). The latter trend possibly reflects the metabolic cost associated with the production of wing structures (93). Similar fecundity of coexisting parthenogenetic and sexual species suggests no direct cost related to sexual reproduction (61), although a high incidence of unmated females in sexually reproducing species may indirectly reduce the reproductive output of females.

SEASONAL HISTORY

The development of temperate bagworms is usually completed in one or two years (**Table 1**). Populations often exhibit developmental synchrony, e.g., individuals overwinter as late instars and emerge as adult in late spring (21, 59, 109). Individuals also overwinter within their maternal bag, either as first instars (*Apterona belicoidella* Vallot) (21, 113) or diapausing eggs (*T. ephemeriformis*) (70, 74). Diapausing eggs of *T. ephemeriformis* that undergo a short period of chilling exhibit asynchronous development and a prolonged interval of adult emergence (69, 74).

The development time of tropical bagworms is variable (**Table 1**). In allopatric species that exploit the same host plant, the duration of development increases with the size of adults (**Table 2**) (8, 29, 41, 42, 86). The abundance or performance of individuals may fluctuate sea-

sonally or along a latitudinal gradient in response to variation in abiotic conditions or availability of host plants (3, 47, 52, 53, 62, 67, 69). The continuous development of bagworms in tropical regions allows for the occurrence of asynchronous development and overlapping generations (all developmental stages simultaneously present) (41, 59), although some populations exhibit synchronous development (8, 82, 85, 108). The level of developmental synchrony affects population dynamics through its effect on natural enemies (9) or on the mating success of females (8, 74, 82, 104).

Temporal pattern of adult emergence is often characterized by protogyny (31, 62, 69, 71, 82, 85, 89, 102, 106), although males may also emerge in synchrony with (8, 41) or before (45, 104) females. Protogyny is not an incidental consequence of sexual dimorphism in the adult stage, because the pupal stage, which is shorter for females than for males, is offset by the longer developmental period of female larvae (2, 8, 41, 106). Protogyny did not evolve to enhance the mating success of emergent adults, at least not in populations with nonoverlapping generations in which early-emerging females and late-emerging males encounter few receptive partners (82, 85). The presumably high level of genetic relatedness within local populations of bagworms (21, 22, 61, 85, 109) suggests that protogyny may have evolved as a strategy to reduce inbreeding depression (82, 85), assuming that the timing of adult emergence varies among different sites and that effective dispersal by males between sites connects local populations of bagworms (88).

POPULATION DYNAMICS

An Evolutionary Hypothesis

Outbreaks, defined as explosive increases in abundance over a short period, have been documented in temperate and tropical bagworms (9, 29, 43, 44, 45, 51, 71, 104, 109). The Psychidae share several life-history traits with other lepidopteran species with flightless or poor-flying females and eruptive population dynamics, such as high fecundity, no adult feeding,

broad host range, exploitation of persistent host plants, eggs laid in clutches, clustering of progeny, and dispersal by ballooning on silken threads (5, 54, 77). These traits are more common within certain families of Lepidoptera than in other taxa (77), suggesting that phylogenetic constraints are associated with flightlessness of females and eruptive population dynamics.

The Psychidae share with other ditrysian Lepidoptera the presence of anal papillae, a pair of caudal sensory lobes that assists in placing the eggs onto a substrate, but not inserting the eggs into plant tissue (36). Information regarding plant quality for larval feeding is therefore superficial for ovipositing females, and substrate specificity relating to larval food quality may decline. A lack of ovipositional preference requires larvae to forage as first instars, which selects for an ability to feed on a range of plant species. Reduced oviposition preference is compensated by high fecundity, achieved through reduced activity, flightlessness, aptery, loss of appendages, and eventually neoteny. With declining mobility of females, selection will promote dispersal among larvae, with ballooning on silken threads a common evolved response. The ecological consequences, or emergent properties, of indiscriminate oviposition as a phylogenetic constraint, and the adaptive syndrome of traits outlined above, will be a high probability of eruptive population dynamics in the taxon (79). Females with low or no mobility, and larvae with limited dispersal, will result in a population rapidly reaching the environmental carrying capacity under favorable ecological conditions (13, 16, 17, 31, 32, 41, 43, 56, 71, 89).

In the ditrysian Lepidoptera, the Psychidae were among the first external folivores (36), with the bags providing essential protection against the elements for the poorly adapted external feeders. This adaptation of the bag became a preadaptation for oviposition within the bag (94). The evolution of aptery and neoteny is widespread in the Psychidae and evolved early in the lineage. This contrasts with other lepidopteran families in which aptery has evolved more at the genus and species levels (54) and no

neoteny occurs. The presumably tropical origin of aptery and neoteny in the Psychidae also contrasts with other groups with wingless females that occur predominantly in temperate regions (5). In the tropics a major selective advantage of aptery and neoteny may have been the shortening of the life cycle as well as increased fecundity, thereby greatly increasing population growth rates and the potential for pest status.

The Relative Influence of Bottom-Up and Top-Down Forces

Bagworms are excellent subjects for population studies, because postmortem dissections of bags reveal several demographic parameters related to population dynamics (99). Even though the relative effect of bottom-up and top-down forces on population regulation has not been investigated for any species of bagworms, the literature reveals consistent trends relative to the effect of plant attributes and natural enemies on the population dynamics of bagworms.

Bottom-up effects strongly influence population dynamics. The performance of larvae varies on different host plants (19, 53, 62, 75, 111, 112), which influences the fitness of adults (88). Stress factors that negatively affect the growth of plants either enhance or reduce the nutritional quality of plants as a food resource for larvae (47, 71, 107). Plants with a low level of tannins or a high content of nitrogen may be nutritionally superior (8). Defoliation caused by bagworms can reach high levels, sometimes causing the death of plants (13, 16, 31, 32, 41, 43, 56, 71, 89). A high density of conspecifics or defoliation of host plants limits the availability of food and reduces the performance of larvae (8), often resulting in larval death (56, 89), reduced body size (31, 42, 55, 56, 81, 85), and low reproductive output of females (7, 17, 41, 42, 85). Individual variation in fitness caused by a limited availability of food has consequences at the population level: For example, the body size and reproductive output of females are negatively correlated with population density (7, 17, 85, 87), which may influence the size of

Phylogenetic constraints: critical plesiomorphic characters that limit adaptive trajectories in a lineage, and therefore ecology

bagworm populations in offspring generation. Resource partitioning is often mediated by density-dependent dispersal of larvae that emigrate from crowded plants by walking or silking (16, 41, 43, 81, 86, 89), especially late during development when feeding is at its peak (8, 56, 83, 104).

Bagworms often suffer a high level of mortality owing to natural enemies (4, 9, 20, 102), but few studies have evaluated the relation between population density and the incidence of parasitism, predation, or disease. Top-down population regulation is generally believed to arise from an increasing level of mortality caused by natural enemies with an increased population density of herbivores, either on a temporal or spatial scale. The level of pupal mortality caused by natural enemies often decreases with population density (9, 18, 51, 85), which suggests a limited impact of top-down forces in terms of regulation of bagworm populations. The considerably higher level of mortality for male pupae than for female pupae, combined with the low level of mortality among large, mostly fecund females (19, 85), also implies that natural enemies do not significantly reduce the overall reproductive output of females in parental generations. However, the lack of field data documenting the relation be-

tween population density and the rate of larval mortality caused by different natural enemies precludes definitive conclusions with regards to the role of top-down forces on the dynamics of bagworm populations.

CONCLUSION

The unusual biology of bagworms, characterized by the possession of a larval bag and extreme forms of appendage reduction in females, has long attracted the attention of entomologists, leading to a vast accumulation of literature. The existence of broad patterns in the Psychidae, most notably in terms of eruptive population dynamics and mating failures among females, provides excellent yet largely neglected material to further life-history theory. For example, only two reviews on the evolutionary significance of flightlessness have included the Psychidae as prime examples, and in both cases only one temperate species, *T. ephemeraeformis*, was considered (5, 79). We hope this review helps to promote bagworms as a model system to study population dynamics and intraspecific variation of reproductive success, in particular to explore consequences at the population level of traits that influence the fitness of individuals.

SUMMARY POINTS

1. The bagworm family includes approximately 1000 species, all of which complete larval development within a self-enclosing bag. Aptery of females has evolved several times independently in the family and is present in over half the species.
2. In the more basal subfamilies, larvae are omnivorous scavengers and mobile females leave their bag upon emergence. Some species are parthenogenetic.
3. Bagworms in the most derived subfamilies are higher-plant feeders with a broad host range. Larvae disperse suspended from a silk thread to be windborne. Male and female larvae exhibit distinctive dispersal and pupation behavior. Sexual dimorphism at the adult stage is extreme. Neotenic females remain in their bag within their pupal case and release a sex pheromone to attract males. Copulation involves the insertion of the telescopic abdomen of males inside the female bag. Females oviposit within their pupal case upon mating. A high incidence of mating failures among females has been reported in many species.

4. Populations often exhibit developmental synchrony and discrete generations. Females often emerge before males, which may have evolved as a strategy to reducing inbreeding.
5. Life-history traits of bagworms are associated with eruptive population dynamics. Consistent trends observed for several species include strong bottom-up effects and resource partitioning mediated through larval dispersal.

FUTURE ISSUES

1. The biology and systematics of bagworm species with winged females remain poorly understood. Further studies on these taxa, especially in tropical regions, are needed.
2. Species with neotenic females that reproduce within their bags represent model systems for studying the principles of population dynamics or for quantifying intraspecific variation of reproductive success. Future studies need to explore consequences at the population level of traits that influence the fitness of individuals.
3. Species with apterous females are ubiquitous worldwide, providing valuable yet neglected comparative data on temperate and tropical species.
4. Extreme wing reduction in females is generalized in the Psychidae, which appears to lead to eruptive population dynamics. Long-term studies are needed to unravel bottom-up and top-down forces that contribute to the regulation of bagworm populations.
5. The high incidence of mating failures among females challenges conventional wisdom relative to the evolution of mating systems, most notably with respect to the prevalence and significance of protogyny, behavioral adaptations of female larvae to enhance their mating success, and the cost of sexual reproduction.

DISCLOSURE STATEMENT

The authors are not aware of any biases that might be perceived as affecting the objectivity of this review.

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30. An inspired description of the life history of bagworms, with shrewd observations.

38. The first study rigorously documenting sexual segregation of pupation sites and discussing its adaptive significance.

41. Together with Reference 42, a good source of testable hypotheses for contemporary ecologists.

42. Together with Reference 41, a good source of testable hypotheses for contemporary ecologists.

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