GENERAL NOTES

Journal of the Lepidopterists' Society
50(3), 1996, 261–268

LIFE HISTORIES OF THREE *TAENARIS* SPECIES (NYMPHALIDAE: AMATHUSIINAE) IN PAPUA NEW GUINEA

Additional key words: *Musa*, *Pandanus*, mimicry, parasitism, natural enemies.

Papua New Guinea, Irian Jaya and their satellite islands support a number of species in the butterfly genus *Taenaris* Fruhstorfer. *Taenaris artemis* Vollenhoven, *T. catops* Westwood and *T. myops* Felder closely resemble each other, occur sympatrically and are members of a Müllerian mimetic complex (along with *Hyantis hodeva* Hewitson; Vane-Wright 1971, Parsons 1991). Adults of these *Taenaris* species have striking, possibly aposematic color patterns, with large bright yellow or orange eye-spots on a dark or white background. Although the recorded larval foodplants of these species are not known to be toxic, adult *T. catops* appear to indulge in pharmacophagy of cycad juice (Parsons 1984, Merrett 1993), which contains a toxic MAM-glycoside (cycasin) possibly making them unpalatable to predators (analysis of dried specimens of *Taenaris* has revealed the presence of cycasin in *T. catops* but not in *T. myops*; Nash et al. 1991).

The purpose of this paper is to provide new life history data for the subspecies *Taenaris artemis staudingeri* Honrath, *T. catops westwoodi* Staudinger and *T. myops kirschi* Staudinger. *Taenaris artemis staudingeri* and *T. myops kirschi* occur in eastern Papua New Guinea, and *T. catops westwoodi* occurs from Geelvink Bay in Irian Jaya to the Herzog and Rawlinson Mountains in Papua New Guinea (D'Abrera 1977).

Searches for larvae and ovipositing females of *Taenaris* were made at the National Botanic Gardens in Lae, Morobe Province; at the Papua New Guinea University of Technology; and villages in the Boana District, Morobe Province. Wild butterflies were netted in flight, or trapped at fermenting banana bait. Females were sleeved in net bags over cut leaves or whole plants in pots to induce oviposition. Voucher specimens of *Taenaris* larvae and pupae have been deposited in the Natural History Museum, London.

Taenaris artemis staudingeri

Table 1; specimen voucher numbers BMNH ES 3233-3237.

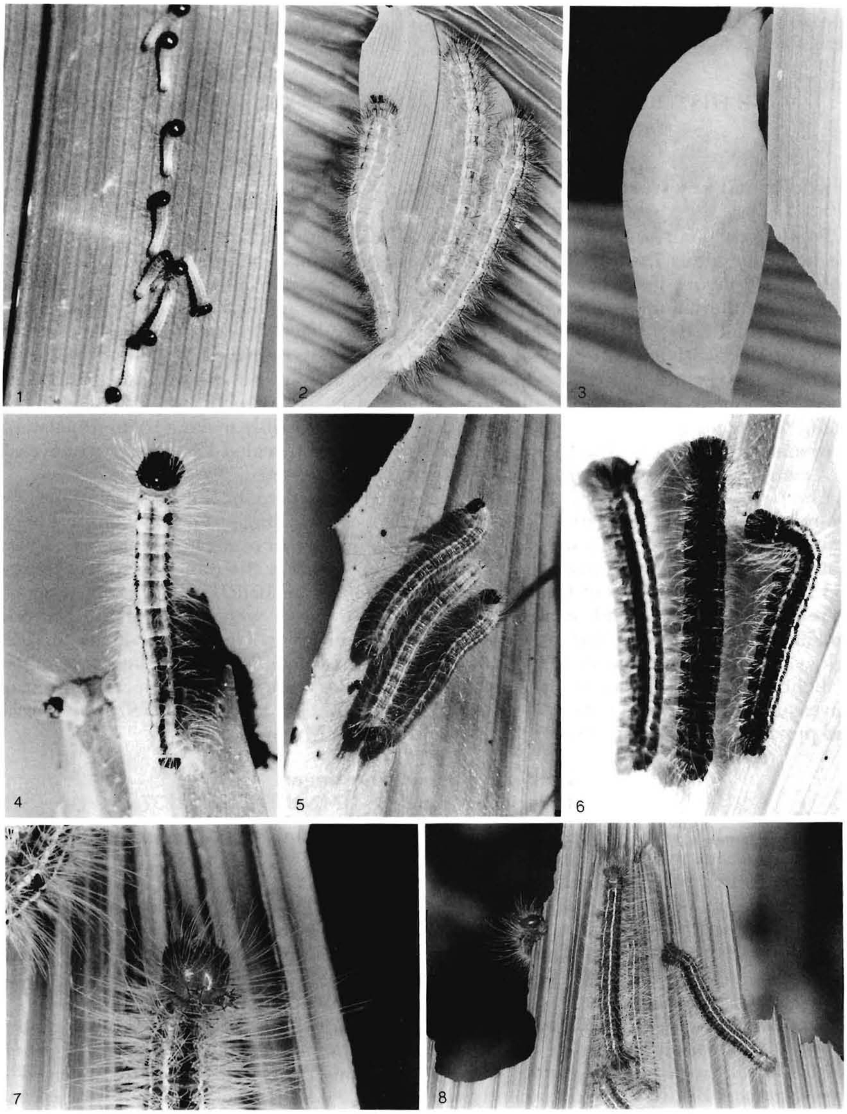
Egg (n=271). Roughly spherical, greenish, becoming pinkish; laid in batches on underside of *Pandanus* spp. fronds; diameter circa 1.5 mm.

First instar (n=264). Head shiny dark brown with white 2 mm hairs (Fig. 1); dorsolaterally, prothorax bears two blackish tubercles; meso- and metathorax bear two orange tubercles; anal segment bears dark dorsal plate; body pale orange becoming greenish with age (prothorax and posterior abdominal segments developing brighter orange), covered with white hairs; mid-dorsal line slightly darker orange; spiracles orange; head capsule width slightly less than 1 mm; larva grows to 4-8 mm in length.

Second instar (n=136). Head brown or black with two dorsolateral, forward-pointing brown horns bearing six translucent spines each, central longest; body light green, orange tint to dorsal thorax and segments A10–A11 (Parsons [1984] recorded the larvae of *T. artemis jamesi* Butler as predominantly yellow marked with black); prothorax bears two dorsolateral dark green welts; mesothorax and metathorax bear pairs of dorsolateral, orange tubercles; tubercles decrease in size caudally; head and body clothed with short and long white hairs, 3 mm on thorax; dark green mid-dorsal line; lateral coloration green with broken, creamy white line joining brown spiracles; head capsule width 1.5 mm; larva grows to 10 mm in length.

Third instar (n=120). Spines on horns from short pedicels marked with brown rings; dorsolateral tubercles of prothorax less pronounced; intersegmental membranes and underside lighter green than rest of body; segments A8-A10 brighter orange than in second instar; dorsal line outlined with darker green; creamy white dorsolateral lines; head capsule width 2 mm; body hairs 3 mm; larva grows to 20 mm in length.

Fourth instar (n=173). Dorsolateral, orange tubercles on each body segment become



FIGS. 1–8. Immature stages of *Taenaris* species. 1-3: *Taenaris artemis staudingeri* Honrath. **1**, first instar larvae; **2**, fifth instar larvae; **3**, pupa. 4–6: *Taenaris catops westwoodi* Staudinger. **4**, fourth instar larva; **5** and **6**, fifth instar larvae. 7–8: *Taenaris myops wahnesi* Heller. **7**, fifth instar larva (showing horns); **8**, fifth instar larvae.

TABLE 1. Duration in days of immatures of *Taenaris artemis staudingeri* reared at circa 27°C: means, ranges and sample sizes (n). Rearing batches: 1, wild-collected fourth instar larvae, 12 November 1986; 2, wild-collected second instar larvae, 4 February 1987; 3, from eggs laid by female, September 1987; 4, from eggs laid by female, May 1988; 5, from eggs laid by female, August 1988; 6, from eggs laid by female, September 1988.

		Life Stage								
Brood		Egg	L1	L2	L3	L4	L5	L6	Pupa	Total
1	mean	—	—	—	—	—	10	—	10.5	—
	range	—	—	—	—	—	8–11	—	9–12	—
	n	—	—	—	—	—	33	—	25	—
2	mean	—	—	—	6	6	12	14.5	11	—
	range	—	—	—	6	6	7–16	14–15	9–14	—
	n	—	—	—	46	43	38	4	28	—
3	mean	11	7	12	7	5	5.5	—	11	40
	range	5–14	7	7–12	7	5	4–9	—	10–11	39–42
	n	88	30	24	17	14	4	—	3	3
4	mean	9	8	8	5	—	—	—	—	—
	range	9	8	8	5	—	—	—	—	—
	n	17	17	17	17	—	—	—	—	—
5	mean	11.5	—	—	—	—	—	—	10.5	76
	range	10–12	—	—	—	—	—	—	9–12	67–81
	n	51	—	—	—	—	—	—	7	15
6	mean	12	5	4	6.5	—	—	—	12	53
	range	12	5	3–4	5–7	—	—	—	10–14	48–58
	n	74	44	49	40	—	—	—	7	9

continuous welts, with white hairs (5 mm) and shorter darker hairs, surrounded by orange cuticle; segments A8-A10 entirely orange; spiracles orange, outlined black, ringed by orange; above spiracles are two lateral, creamy white lines; head capsule width 3 mm; larva grows to 28 mm in length.

Fifth instar (n=75). Head capsule shiny, light brown, mottled black (Fig. 2); mean width 4.6 ± 0.2 mm (n=23); horns and lateral ocelli black; up to two extra spines may be present on horns; mouthparts strongly sclerotized; orange dorsal prominences on each segment continue laterally to spiracles, ringed by greenish orange cuticle; each thoracic segment has dorsolateral prominence; each abdominal segment has two dorsolateral welts, two creamy white, transverse lines between, and one anterior transverse line; dorsally grey hairs tipped with black, 6 mm, on thorax; lateral hairs shorter, denser; segments A5–A10 flushed orange; first six intersegmental membranes creamy yellow; dorsal line alternately black, from anterior of segment through orange prominences, and lighter green, from prominences to posterior; dorsolateral and super-spiracular lines creamy yellow; larva grows to 30-56 mm in length.

Sixth instar (n=6). Presumed supernumerary (two larvae died and four emerged as females); head capsule width 5 mm, shiny light brown with black horns, ocelli and mouthparts; coloration as in fifth instar; thoracic hairs up to 6 mm; larva grows to 41 mm in length.

Pupa (n=70). Light green with two pale yellowish points on head (Fig. 3); dorsolaterally, prothorax has two yellow spots set in yellowish green patch; more dorsally, mesothorax bears two shiny grey spots; wing cases translucent; abdomen paler green; cremaster and its supports black with dark green ovoid between roots of supports; length 30 mm, width 10 mm; similar in appearance to pupae of *T. myops* and *T. catops*.

Foodplants and biological notes. In 1987 and 1988, six wild-collected females were sleeved in net bags over cut leaves of *Pandanus* sp. or whole plants of *Pandanus odorus* Ridl. (Pandanaceae). These six females laid 230 eggs in four batches (Table 1). A seventh female was sleeved over both *P. odorus* and *Curculigo erecta* Lang (Amaryllidaceae), and she laid 41 eggs on *C. erecta*; 34 larvae hatched and fed but died during the next moult. Two wild larval batches were collected from *Pandanus* in 1986 and 1987 (Table 1). In a feeding experiment, six fifth instar larvae from the 1986 batch were offered *Cocos nucifera* L. (Palmae) leaves, upon which they successfully completed development.

Larvae fed on the undersides of tough, spiny fronds of *Pandanus*, consuming the frond from the tip down to the base before moving on. Larvae were gregarious during instars one through four, and tended to feed and molt synchronously. Fifth instar larvae became more solitary. Although the gregarious habit may be linked to unpalatability in *Taenaris artemis* (Vane-Wright 1971), as is certainly the case in *T. onolaus* (Parsons 1984), leaves of *Pandanus* are not known to be toxic, and the fruit of some *Pandanus* is prized as food in Papua New Guinea (species eaten include *P. conoideus*, *P. jiulianetii* Mart. and *P. brosimos* Merr. & Perry; May 1984).

Parsons (1984) recorded the foodplant of *Taenaris artemis* as coconut, *Cocos nucifera*, and that of *T. artemis jamesi* from the Western Province of southern Papua New Guinea as *Pandanus* sp.

Over 50% of the wild-collected larvae from batch 1 were parasitised by *Apanteles* sp. (Hymenoptera: Braconidae). No larvae from batch 2 were parasitised. Two of nine pupae in batch 6 were attacked by *Brachymeria* sp. (Hymenoptera: Chalcididae), with 19 individuals emerging from one larva. Many of the larvae bred *ex ovis* were killed by immature sucking bugs, *Montrouzierellus melacanthus* (Boisduval) (Heteroptera: Pentatomidae: Asopinae). Larvae of *T. artemis staudingeri* may be protected to some extent from parasites by dense pubescence. When provoked, fifth instar larvae tuck their heads under the prothorax and present their horns.

Taenaris catops westwoodi

Table 2; specimen voucher numbers BMNH 3229-3232.

Egg (n=94). Greenish, becoming greyish from the center before hatching; diameter circa 1.5 mm; laid in batches.

First instar (n=69). Head capsule shiny dark brown to black; body whitish green, 3 mm white hairs on meso- and metathorax, slightly shorter on A5 and A6; head and body clothed with short white hairs arising from tubercles; anal segment has short black hairs; larva grows to 4-8 mm in length; head capsule width slightly less than 1 mm.

Second instar (n=39). Head bears two short black dorsolateral horns with seven spines each, and white hairs; body greenish with two dorsolateral creamy white lines, between lines two rows of dorsolateral tubercles bearing white hairs; sides of thorax and segments A1-A6 and prolegs greenish with black spiracles, connected by faint creamy line; Segments A7-A8 have orange patch around spiracles; segments A9–A10 flushed with orange, including anal prolegs; body clothed in white hairs, longest (up to 3 mm) on prothoracic and anal segments; larva grows to 5–11 mm in length; head capsule width just over 1 mm.

Third instar (n=27). Prothorax to A8 dark or greyish green; orange patches around each spiracle; from segments A7–A10 arise two broken black lines either side of midline, terminating in black anal plate bearing two short brown papillae with short brown hairs; on segments A7-A8 black marks between dorsolateral line and spiracles; apart from these black marks, larva matches description by Parsons (1984); white hairs on thorax up to 4 mm; larva grows to 9-16 mm in length; head capsule width 1.5–2 mm.

Fourth instar (n=15). Eight with continuous black dorsal and dorsolateral stripes as in Parsons (1984), one with a broken black line (Fig. 4) and two with a dark green line; between dorsal and dorsolateral lines are green and then white lines; dark green to black

TABLE 2. Duration in days of immatures of *Taenaris catops westwoodi* reared at circa 27°C: means, ranges and sample sizes (n). Rearing batches: 1, from eggs laid by female, August 1987; 2, from eggs laid by female, September 1987; 3, from eggs laid by female, July 1988.

Brood		Life Stage							
		Egg	L1	L2	L3	L4	L5	Pupa	Total
1	mean	8	—	—	—	—	—	—	—
	range	8	—	—	—	—	—	—	—
	n	14	—	—	—	—	—	—	—
2	mean	10	7	6	7	14	13	—	—
	range	10	7	6	5–12	13–14	13	—	—
	n	14	14	12	12	3	1	—	—
3	mean	10	11	9	—	—	10.5	13	85
	range	9–10	10–11	8–11	—	—	10–11	13	85
	n	38	26	15	—	—	2	1	1

dorsolateral lines extend to segment A8, where these terminate in orange patch around last spiracle; legs and prolegs flushed with orange; prothorax has dark brown collar; black anal plate surrounded by black hairs; 6–7 mm white hairs on thorax and segments A8-A9; larva grows to 15-35 mm in length; head capsule width 3 mm.

Fifth instar (n=7). Color variable (see Figs. 5–6), ranging from nearly black (as in Parsons 1984) through dark brown to greenish grey; brown specimens have yellowish brown dorsolateral lines, black larvae have faint white lines; black dorsal and dorsolateral lines complete; black spiracles ringed with orange patches, connected by light orange to creamy line, reduced to orange spots in black larvae; prolegs light orange or pink, with black basal spot in black specimens; extra spine may be present on horns; prothorax greyish without lines; larva grows to 25-37 mm in length; head capsule width 4–4.5 mm; 8 mm hairs on thorax and segments A8-A9.

Pupa (n=2). Light apple green with two short yellow horns on head; thorax slightly humped and 10 mm at widest; cremaster yellow basally and black apically; length circa 32 mm.

Foodplants and biological notes. Parsons (1984) listed *Cordyline terminalis* (Liliaceae) and *Phaius tancarvilleae* (Banks in L'Herit) Bl. (Orchidaceae) as larval foodplants of *Taenaris catops westwoodi*. D'Abrera (1977) listed *Caryota rumphiana* Mart. (Palmae), *Areca catechu* L. (Palmae), *Musa acuminata* Colla, and *M. balbisiana* Colla (Musaceae), and the Insect Farming and Trading Agency (Ipou, pers. comm.) added the ground orchid *Spathoglottis* (Orchidaceae).

In the present study, three batches of eggs were obtained by sleeving five females over potted *Caryota rumphiana* (Table 2). All the aforementioned foodplants were available for testing except the two recorded by Parsons. The larvae from batch 1 refused to eat any of the foods offered, and died. Larvae from batch 2 fed on *C. rumphiana*, but died before pupation. Three larvae from batch 3 (which was begun on *C. rumphiana*) switched to a neighboring *Pandanus* plant, and pupated on it. The later instar larvae reared in this study appeared sick, and this may have contributed to increased mortality and/or protracted larval periods.

Taenaris catops westwoodi is a potential economic pest of *A. catechu* (which is widely used as a mild stimulant in Papua New Guinea) and of *C. rumphiana* (which is used as an ornamental, a famine food and for making bows).

Taenaris myops wahnesi

Table 3; specimen voucher numbers BMNH (E) 1994-109, tube nos. 4007–4008.

Egg (n=105). Roughly spherical, pale green becoming pinkish red in 1–2 days; laid in batches on the underside of leaves.

First instar (n=105). Shiny, light brown head capusle, width slightly less than 1 mm, bearing short white hairs and two small bumps; greenish body 4 mm, bearing longer white hairs; posterior abdominal segments become pinkish or orange with age; two dark tubercles on orange prothorax, spiracles dark.

Second instar (n=85). Head bears two short horns, each with crown of five translucent spines surrounding central knob; body pinkish with two paler dorsolateral lines and two paler lateral lines, interrupted by pinkish patches around each spiracle; segments A8-A10 pinkish or yellowish orange; head capsule width just over 1 mm; body 7 mm in length, with 3 mm white hairs arising from dorsolateral tubercles on thorax.

Third instar (n=58). Head brownish orange with black spines and stemmata; horns darker brown; body orange to pinkish or wine red, darker from mesothorax to segment A7 (cf. Parsons' [1984] report of steady darkening in brownish black second to fourth instar *T. myops kirschi*); thoracic segments each bear transverse ridge dorsally; spiracles brown, ringed with black, surrounded by orange patch; posterior abdominal segments and underside orange; head capsule width 1.5 mm; hairs 7 mm; larva grows to 11-18 mm in length.

Fourth instar (n=46). Body brownish red from orange prothorax to segment A7; dark brown dorsal stripe, two white dorsolateral lines and two white lateral lines; body hairs 10 mm, arising from white tubercles; two white transverse lines on side of segment A9; underside reddish orange; head capsule width 2 mm; larva grows to 20–32 mm.

Fifth instar (n=14). Head reddish orange, body dark wine red (Figs. 7–8), contrasting with descriptions for *T. myops kirschi* Staudinger (dirty greyish yellow, Szent-Ivany & Barrett 1956; black and unlined, Parsons 1984); segments A6-A8 orange; body bears 9 mm white hairs and shorter black ones; mean head capsule width 4.4 ± 0.2 mm (n=14) across; larva grows to 25-45 mm in length.

Pupa (n=10). Light green, with two yellowish horns on head; external sex distinguishing marks brownish; cremaster yellowish green marked with black, 2.5 mm; two whitish wavy dorsolateral lines; length 26-29 mm, width 9-10 mm at first abdominal segment.

Foodplants and biological notes. Females of *Taenaris myops wahnesi* were confined on *Musa acuminata* Colla and *M. balbisiana* (Musaceae) (n=5), *Ptychosperma robusta* (Palmae) (n=3), and *Curculigo erecta* (n=1). The females confined on *P. robusta* and *C. erecta* oviposited readily, but no eggs were laid by the females confined on *Musa* (a foodplant reported by Szent-Ivany & Barrett 1956).

Three egg batches were obtained and rearded from these females (Table 3). Larvae from batch 2 refused to eat *Ptychosperma robusta* leaves. When they were offered cut leaves of banana, *Costus* sp. (Costaceae), *Cocos nucifera* and *Areca catechu* instead, they fed until the third instar on *Costus* sp. and then on banana leaves. Larvae from batch 3 fed successfully on *P. robusta*. Fifteen of these larvae were forced at the third instar onto *C. nucifera* (a foodplant recorded for *T. myops kirschi* [Anon 1969] and *T. myops* [Szent-Ivany, pers comm.]), *Areca catechu* and banana. Only four of the larvae held on banana survived to pupation. Larvae from batch 4 were fed solely on *C. erecta*, and only one adult was produced.

Five wild *Taenaris myops wahnesi* larvae were found on a hybrid *Ptychosperma robusta* in August 1986, and two others were found on cultivated banana in May 1987 (Table 3). Parsons (1984) collected larvae of *T. myops kirschi* on *Tapenochilus* sp. (Costaceae) in the Port Moresby District of southeastern Papua New Guinea, and the Insect Farming and Trading Agency (Ipou, pers. comm.) has recorded larvae of *T. myops wahnesi* feeding on *Costus* sp. near Bulolo, in northern Papua New Guinea. *Taenaris myops* is known as a pest of banana, *Musa acuminata* and *M. balbisiana* (Szent-Ivany & Barrett 1956), coconut, *Cocos nucifera* (Anon 1969 and Szent-Ivany, pers. comm.) and oil palm, *Elaeis guineensis* Jacq. (Palmae) (Prior, pers. comm.).

One pupa from a wild larva taken on *Ptychosperma* sp. yielded a tachinid parasite (Diptera). It is possible that the wine red larvae of *T. myops wahnesi* are aposematic, like

TABLE 3. Duration in days of immatures of *Taenaris myops wahnesi* reared at circa 27°C: means, ranges and sample sizes (n). Rearing batches: 1, wild-collected fourth instar larvae, August 1986; 2, from eggs laid by female, 2 October 1986; 3, from eggs laid by female, 9 October 1986; 4, from eggs laid by female, September 1988.

		Life Stage							
Brood		Egg	L1	L2	L3	L4	L5	Pupa	Total
1	mean	—	—	—	—	—	7	14	—
	range	—	—	—	—	—	7–11	14	—
	n	—	—	—	—	—	3	1	—
2	mean	11	5.4	7	4	5	14	12	64
	range	11	5–7	7–10	4	5	14	11–15	60–68
	n	27	27	9	5	4	1	2	2
3	mean	10	7	5	5	7	10	11.5	57
	range	10	7	5	5	8–13	9–11	10–13	55–59
	n	59	59	57	34	24	8	4	4
4	mean	11	6	6	6	6.5	14	13	65
	range	11	6	6	6–8	6–7	9–17	13	65
	n	19	19	19	19	18	3	2	1

the similarly colored larvae of the *Cycas*-feeding *Taenaris onolaus* and *T. butleri* Oberthur (Nash et al. 1992).

I thank the staff of the Botanic Gardens in Lae and the Forestry Department of the Papua New Guinea University of Technology for plant identifications and providing potted foodplants; M. S. K. Ghauri and G. M. Stonedahl (International Institute of Entomology, London) for identifying the larval predators and parasitoids; Peter Clark (Insect Farming and Trading Agency, Bulolo, Papua New Guinea) for confirming adult identifications and helpful suggestions; Ava Kila (Papua New Guinea University of Technology) for help with rearing; and my wife, Joy, for much encouragement and help.

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Received for publication 25 January 1993; revised and accepted 7 January 1996.

Journal of the Lepidopterists' Society
50(3), 1996, 268–270

CHARLES REMINGTON'S CONTRIBUTIONS TO THE SPECIES CONCEPT

Additional key words: speciation, hybridization, hybrid zones.

The following remarks were written with the encouragement of the Editor in order to supplement issue 49(4) of the *Journal*, which commemorated the career of Charles Remington. I first met Charles Remington in 1971 at the Pacific Slope meeting of our Society, at which he gave a talk on the special aspects of genetic divergence and speciation on islands. His presentation, as in his writing, was authoritative, detailed, liberally spiced with interesting non-lepidopteran examples, and delivered with conviction. Charles Remington has long held a special interest in speciation. No topic is more central to evolutionary theory, nor more controversial, and those with strong conviction soon themselves become controversial.

Remington was an early proponent and remains a strong advocate for the "Biological Species Concept" (BSC), wherein species are thought to arise by genetic divergence in isolated populations, and are defined by presumed (the usual case) or by demonstrated (less often) reproductive isolation from closely related taxa. Traits serving this isolation function are assumed to have evolved through, or were perfected by, selection favoring the reduction of wasteful interspecific hybridization. Early criticism of the BSC stressed the difficulty in demonstrating reproduction isolation, especially between allopatric populations of organisms not amenable to experimental hybridization. Indeed, the great majority of lepidopteran species and subspecies are based on comparisons of wing pattern and genitalia, not on demonstrated mating barriers or measured hybrid fitness. More recently, the "Recognition Concept" proposes that reproductive isolation is only an incidental byproduct of adaptations increasing reproductive success through the evolution of species-specific mate recognition systems. Hybrid zones would seem a likely setting to observe the perfection of incipient reproductive isolation, yet few convincing examples have been found among many detailed studies. The apparent long-term stability of hybrid zones conflicts with Remington's view that they should be ephemeral, quickly evolving toward either fusion or toward speciation and a cessation of hybridization (see Collins 1991 and Coyne 1994 for reviews of these controversies).

The divergence in allopatry tenet of the BSC has endured, partly because biogeographic patterns of variation support it, and also because population genetics theory shows that even low rates of gene flow can prevent divergence between adjacent populations. Remington's early papers cited intriguing patterns of phenotypic variation, and advocated the active pursuit of studies in geographic variation and speciation by lepidopterists (Remington 1951, 1958). The work of his graduate student Charles Oliver was a product of this period, in which Oliver hybridized intra- and interspecific populations to reveal geo-