

## SYSTEMATICS OF *HYPOCHILUS SHEARI* AND *HYPOCHILUS COYLEI*, TWO SOUTHERN APPALACHIAN LAMPSHADE SPIDERS (ARANEAE, HYPOCHILIDAE)

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**ABSTRACT:** A quantitative analysis of variation of genital characters among 16 population samples supports Platnick's (Forster et al. 1987) hypothesis that *Hypochilus sheari* Platnick and *Hypochilus coylei* Platnick are separate species. Both the width and tip length of the conductor separate these species unambiguously, and an index of spermathecal dimensions distinguishes the otherwise very similar females of each species. A conductor tip synapomorphy indicates that these are probably sister species. Extensive field work indicates that these species are confined to a 35 mile north-south mountain corridor in six counties of western North Carolina and are separated by five miles. It is suggested that subtle deficits in habitat due to a constriction of the mountain corridor and the presence of a watershed divide may have bisected the parent stock and may be maintaining the allopatry of the daughter species. Both species appear to have a two year life cycle and commonly to feed on gryllacridid crickets and cursorial spiders.

In a review of the hypochiloid and austrochiloid spiders (Forster et al. 1987), Platnick described two similar species of Appalachian *Hypochilus* which he separated on the basis of minor differences in genital morphology observed in small samples. *Hypochilus coylei* was described from ten males and nine females from three neighboring sites, and *H. sheari* was described from three males and three females from a single site 27 mi from the *H. coylei* sites. The primary goals of this study are (1) to test more rigorously Platnick's hypothesis that these two morphs are different species and the alternative hypothesis that his samples might simply represent geographic variants of a single species, and (2) to define accurately their geographic ranges. Moreover, we hope this study will foster the kinds of research and management decisions needed to protect the habitat of these unusual (Forster et al. 1987) and geographically restricted spiders.

### METHODS

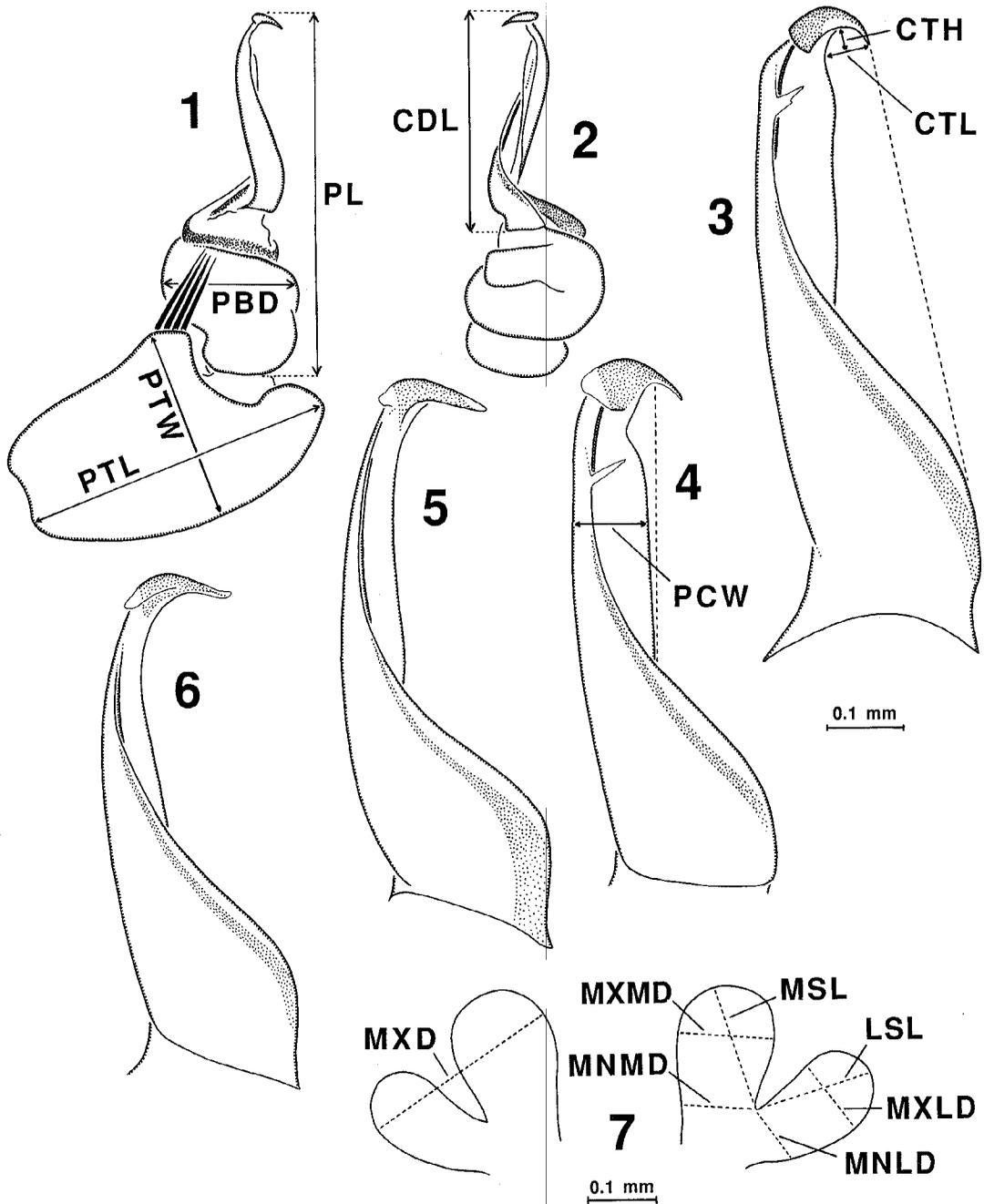
During 1987 (August to November) and 1988 (March to November) we searched for *Hypochilus* in the region around the sites where these species were first collected. When a deme was encountered, we collected only as many adults of each sex as we felt we could without threatening the deme's survival.

**Material Examined.**—Collection data for all specimens used in this study are listed below by species and

county (all in North Carolina). Specimens will be deposited in the AMNH. Each site (deme) is identified on the map (Fig. 12) by its letter/number code. Throughout this report we use the term "deme" for each local population, and the terms "morph" or "species" for all demes (collectively) of each putative species.

*Hypochilus sheari*: **BUNCOMBE CO.**; S1—Long Branch Creek, 0.8 mi N on Long Branch Road from Bee Tree Road, rock outcrop along road on right, elev. 3100 ft, 28 Sept. 1987, 3 males, 5 females; 6 Oct. 1987, 1 male, 1 female; 15 Oct. 1988, 10 males, 13 females, 1 egg sac; **MCDOWELL CO.**; S2—Buck Creek, 9.9 mi N of US 70 on NC 80, dry exposed rock face on right of highway, elev. 3400 ft, 1 Sept. 1987, 10 males, 5 females; S3—Curtis Creek, 5 mi up Curtis Creek road from US 70, rock outcrop on left of road, elev. 2500 ft, 13 Sept. 1987, 3 males, 1 female; 16 July 1988, 1 male, 2 females; 24 Sept. 1988, 1 male, 2 females, 1 egg sac; S4—Mill Creek, 0.2 mi SE of Andrews Geysers, large rock outcrop on left, elev. 3100 ft, 29 Sept. 1987, 1 male, 3 females; 6 Oct. 1987, 12 males, 15 females; 24 Sept. 1988, 3 males, 5 females, 1 egg sac; S5—Newberry Creek, 1.5 mi W on Newberry Creek from Curtis Creek confluence, rock outcrop on either side of road, elev. 2400 ft, 13 Sept. 1987, 7 males, 10 females; 24 Sept. 1988, 3 males, 2 females; **YANCEY CO.**; S6—Upper Crabtree Falls, Blue Ridge Parkway, elev. 3200 ft, 1 Sept. 1987, 6 males, 5 females.

*Hypochilus coylei*: **BUNCOMBE CO.**; C1—Garren Creek, approx. 0.5 mi up Owenby Gap Road from intersection of Eads Gap Road, disturbed rock above stream on left, elev. 3100 ft, 19 Sept. 1987, 1 male, 4 females; C2—Round Mountain, 4 mi NE of NC 9 on Bat Cave Road, rock outcrops on left above road, elev.



Figures 1-7.—*Hypochilus* genitalia: 1-2, *H. sheari* male palpus (traced from Forster et al. 1987) showing measurement characters; 1, retrolateral; 2, prolateral; 3-6, approximately retrolateral views of palpal conductor; 3-4, *H. coylei* showing measurement characters; 3, from C7; 4, from C6; 5-6, *H. sheari*; 5, from S1; 6, from S3; 7, *H. sheari* spermathecae from S4 showing measurement characters.

3200 ft, 9 Oct. 1988, 2 males, 2 females, 1 egg sac; **HENDERSON CO.**; C3—Hickory Creek, 1 mi SE Gerton on US 74, rock outcrop on either side of road, elev. 2575 ft, 13 Aug. 1987, 9 females; 3 Oct. 1987, 1 female; 6 Oct. 1987, 2 females; 14 Oct. 1988, 2 females; C4—Minihaha Falls, 0.8 mi N on NC 9 from US 74,

rock outcrop below road on left, elev. 1600 ft, 13 Aug. 1987, 2 males, 5 females; C5—Reedy Patch Creek, 10.5 mi E of I-26 on US 64, rock face above creek on right, elev. 2000 ft, 21 Aug. 1987, 1 male, 2 females; C6—Turnbreeches Creek, approx. 1 mi SW of US 64, rock outcrop on left, elev. 2400 ft, 3 Oct. 1987, 6 males,

Table 1.—Descriptive statistics for the quantitative characters found most useful in distinguishing *Hypochilus sheari* from *Hypochilus coylei*. Character abbreviations defined in Methods section. Measurements in mm.

Character	<i>Hypochilus sheari</i>				<i>Hypochilus coylei</i>			
	<i>n</i>	Range	Mean	SD	<i>n</i>	Range	Mean	SD
Male								
CTL	56	0.075–0.120	0.093	0.010	43	0.045–0.065	0.057	0.005
PCW	50	0.045–0.068	0.058	0.005	41	0.075–0.113	0.093	0.008
PCW(100)/CTL	50	41.7–83.9	62.5	8.3	41	132–221	164	19.8
Female								
CW	69	2.50–3.75	3.11	0.24	57	2.85–4.40	3.65	0.33
LSL	69	0.110–0.263	0.179	0.032	50	0.160–0.348	0.251	0.040
MXMD	68	0.103–0.170	0.135	0.016	48	0.070–0.128	0.101	0.013
MXMD(100)/LSL	68	57.7–131.8	77.5	14.4	48	28.8–55.6	40.9	7.1
MXMD(100)/CW	66	3.3–6.1	4.4	0.6	48	2.2–3.3	2.8	0.3

3 females; **POLK CO.**; C7—Clifffield Mountain, 2.5 mi W of Mountain View Church, rock faces, elev. 1300 ft, 3 Sept. 1988, 5 males, 8 females; **RUTHERFORD CO.**; C8—Bat Cave Nature Preserve, 1 mi SE of Bat Cave village, cliffs below cave, elev. 1600–1800 ft, 3 Oct. 1987, 2 males, 3 females; C9—Broad River, 1.3 mi E of NC 9 on US 74 (0.3 mi NW of start of Rainbow Falls Trail), disturbed rock on either side of river, elev. 1300 ft, 3 Sept. 1988, 5 males, 4 females; C10—Rainbow Falls Trail, 1.6 mi E of NC 9 on US 74, disturbed rock along trail, elev. 1500–2200 ft, 13 Aug. 1987, 6 males, 8 females; 6 Oct. 1987, 13 males, 3 females; 28 May 1988, 4 females; 1 Nov. 1988, 1 egg sac.

**Characters Examined:**—In order to identify characters that might distinguish one or more demes, we focused on genital characters for two reasons: 1) they tend to evolve rapidly and divergently (Eberhard 1985, 1990), and 2) Platnick (Forster et al. 1987) used genital characters to differentiate *H. coylei* and *H. sheari*. We selected potentially useful genital shape characters, defined measurements which alone or in ratio form would represent these shapes, recorded the values of these characters for every specimen, and, with the Statview II (Abacus Concepts, Inc.) statistics program, generated scatter plots to identify any clusters of individuals and/or demes with distinctive values. Carapace width (CW) was used in some of these bivariate analyses to control for body size; CW measurements are accurate to 0.05 mm. A few other potentially useful non-genital characters (e.g. pigmentation patterns) were also surveyed.

**Male quantitative characters.**—The following eight palpal dimensions were measured after removing the palp: PL = length of palpal organ in retrolateral view (Fig. 1); PBD = diameter of

palpal bulb in retrolateral view (Fig. 1); PTW = width of palpal tarsus perpendicular to PTL at distoventral apophysis in retrolateral view (Fig. 1); PTL = length of palpal tarsus in retrolateral view (Fig. 1); CDL = conductor length in pro-lateral view (Fig. 2); CTL = conductor tip length in approximate retrolateral view (positioned so CTL is maximized), defined as the distance from the conductor tip to the edge of the conductor along the line perpendicular to the line connecting the tip of the conductor to the dorsal edge of conductor (Fig. 3); CTH = conductor tip height in retrolateral view, defined as the maximum distance to lower edge of conductor tip from line defined by CTL and perpendicular to CTL (Fig. 3); PCW = palpal conductor width in retrolateral view, measured along the line originating at the midpoint of, and perpendicular to, a line defined as the maximum distance from point where conductor edges overlap to inside edge of conductor tip (Fig. 4). CTL, CTH, and PCW were measured with the palpal organ in glycerine under a coverslip on a depression slide at 250× using a Wild M-20 compound microscope with an ocular reticle with two perpendicular scales; these measurements are accurate to 0.0025 mm. The other measurements were made at 100× using a Wild M5 stereomicroscope and are accurate to 0.009 mm.

**Female quantitative characters.**—The following seven spermathecal dimensions were measured (Fig. 7): LSL = lateral stalk length, defined as the maximum distance from junction of lateral and median stalk to end of lateral stalk; MXLD = maximum lateral stalk diameter perpendicular to longitudinal axis of stalk; MNLD = minimum lateral stalk diameter perpendicular to longitu-

dinal axis of stalk; MSL = median stalk length; MXMD = maximum median stalk diameter; MNMD = minimum median stalk diameter; MXD = maximum distance from medial edge of median stalk to lateral edge of lateral stalk. The portion of body wall containing spermathecae was removed, cleared, and mounted in lactic acid on a glass slide under a coverslip. Measurements were recorded from the right spermathecae at 100 $\times$  using a Bausch and Lomb compound microscope and are accurate to 0.005 mm.

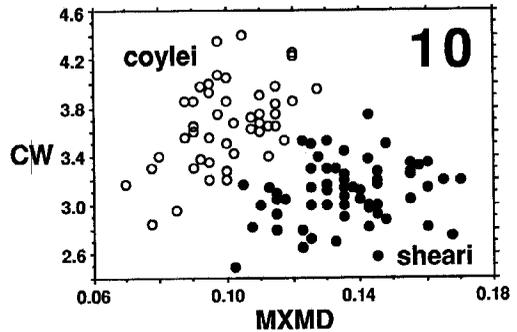
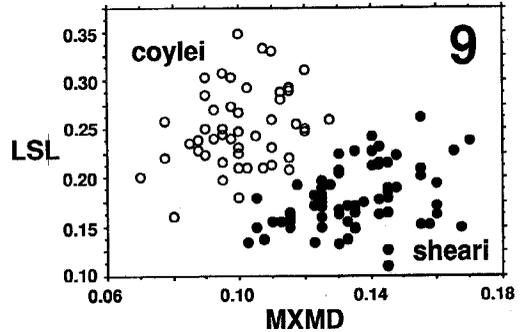
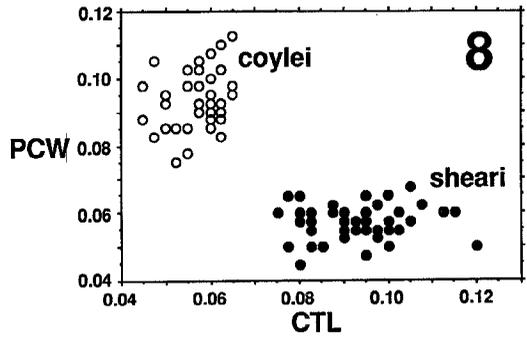
## RESULTS

### Morphological Variation.—Male characters:

T-tests reveal that the two morphs are significantly different ( $P < 0.001$ ) for each of the eight palpal characters. Although six of the eight show broad overlap among demes and between morphs, PCW and CTL clearly distinguish the two species (Table 1, Fig. 8). *Hypochilus coylei* (Figs. 3–4) has a wider conductor (PCW) and a shorter, more sharply bent conductor tip (CTL) than *H. sheari* (Figs. 5–6). When plotted against each other, these characters produce better separation of the morphs (Fig. 8) than do any other pair of characters. Only one of the pigmentation differences described by Platnick (Forster et al. 1987) helps separate the larger samples we have studied; the pigment patches on the edges of the sternum are confluent in *H. coylei* but in *H. sheari* are usually disjunct and seldom appear as a continuous band. The small finger-like apophysis which we discovered extending from the retro-dorsal edge of the conductor near its distal end is usually much longer and easier to see (at 100 $\times$ ) in *H. coylei* (Figs. 3–4) than in *H. sheari*.

**Female characters:** T-tests showed that the two morphs are significantly different ( $P < 0.001$ ) for each spermathecal measurement except MXD. However, for each of these characters, there is broad overlap between the two morphs and among the demes. Nevertheless, highly confident identification of females is possible when the two characters with the least overlap, MXMD and LSL (Table 1), are plotted against each other (Fig. 9) and when MXMD is plotted against CW (Fig. 10). *Hypochilus sheari* has, on average, wider median bulbs, shorter lateral spermathecae, and a smaller carapace than *H. coylei* (Fig. 11). Neither of the pigment differences described by Platnick (Forster et al. 1987) (endite pigmentation, palpal tarsal pigment ring) appear to distinguish any of the demes or separate the morphs.

**Clinal variation:** With one exception (LSL), no



Figures 8–10.—Scattergrams of measurement characters which best distinguish *Hypochilus sheari* from *H. coylei*. Characters defined in Methods section. Measurements in mm. 8, males; 9–10, females.

clinal pattern was found when the mean of each quantitative character for each deme was ranked (low to high) and mapped. LSL means increased from north to south in *H. sheari*, but showed no clinal pattern in *H. coylei*.

**Habitat and Distribution.**—The preferred (most heavily populated) web substrate and habitat for both morphs appears to be the same as that of *Hypochilus pococki* Platnick (Fergusson 1972). Webs are nearly always on vertical or overhanging surfaces of rock outcrops and boulders which are typically beside or near a stream in deciduous or mixed deciduous/conifer forest. With the exception of two demes (S2 and C7), these spiders

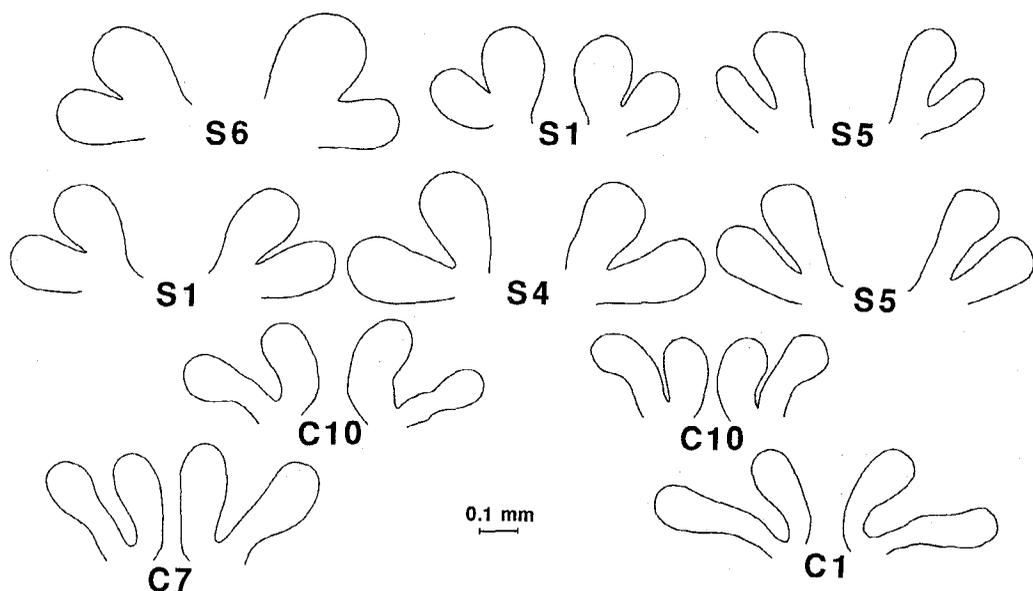


Figure 11.—Spermathecae of *Hypochilus sheari* and *H. coylei* selected to illustrate range of variation; arranged so that MXMD(100)/LSL values decrease from left to right and from top row to bottom row. Codes identify demes (see Methods section).

were seldom found on relatively exposed and dry rock outcrops. Curiously, areas of seemingly favorable habitat but devoid of *Hypochilus* were found within the known geographic range of each species (Fig. 12).

Both *H. sheari* and *H. coylei* are confined to a 35 mile north-south mountain corridor that is bounded on the west by the relatively flat and unforested basin of the French Broad River, on the east by low (below 1400 ft elev.), relatively flat Piedmont terrain, and on the north and south by allopatric populations of *H. pococki* (Fig. 12). The *H. sheari* demes are confined to the northern half of this corridor. The two species are separated by an uninhabited five mile zone that includes the divide between their respective watersheds. All known *H. sheari* demes are in the Catawba River watershed (Atlantic drainage), except for S1, which lies in the French Broad watershed (Gulf drainage). All *H. coylei* demes are in the Broad River and Green River watersheds (Atlantic drainage).

A search in the zone that separates the ranges of *H. sheari* and *H. coylei* revealed no sites with preferred substrate and habitat; and although several sites with suboptimal but apparently suitable substrate and habitat were found, *Hypochilus* was not present. Even such seemingly suitable habitat is rare in this zone because here the

mountain corridor is constricted to a width of only a few miles by convergent lobes of the French Broad basin and Piedmont (Fig. 12) and includes a divide separating the watersheds occupied by the two species.

**Life History and Reproductive Biology.**—Like *H. pococki* (Fergusson 1972, Coyle 1985), these species appear to have a two-year life cycle. Medium to large juveniles (that had overwintered) constructed webs as early as March 15; these individuals appeared to be large enough to reach maturity later in the year. Adult females began to appear in late May and adult males in late July. Adult males disappeared after early October and adult females by the end of October. Juveniles were recorded until late November. New egg sacs were observed from early September until late October. Spiderlings emerged from egg sacs in early May; no occupied egg sacs were recorded later than mid-May.

Adult males were often found just outside the webs of females. On several occasions (both species and only after mid-September) single males were observed motionless in webs of adult females, with the male either directly over the female or with the legs of one side held across her, reminiscent of the post-mating position observed by Fergusson (1972). Three *H. sheari* egg sacs contained 44, 74, and 87 eggs, and two *H. coylei* sacs held 62 and 93 eggs.

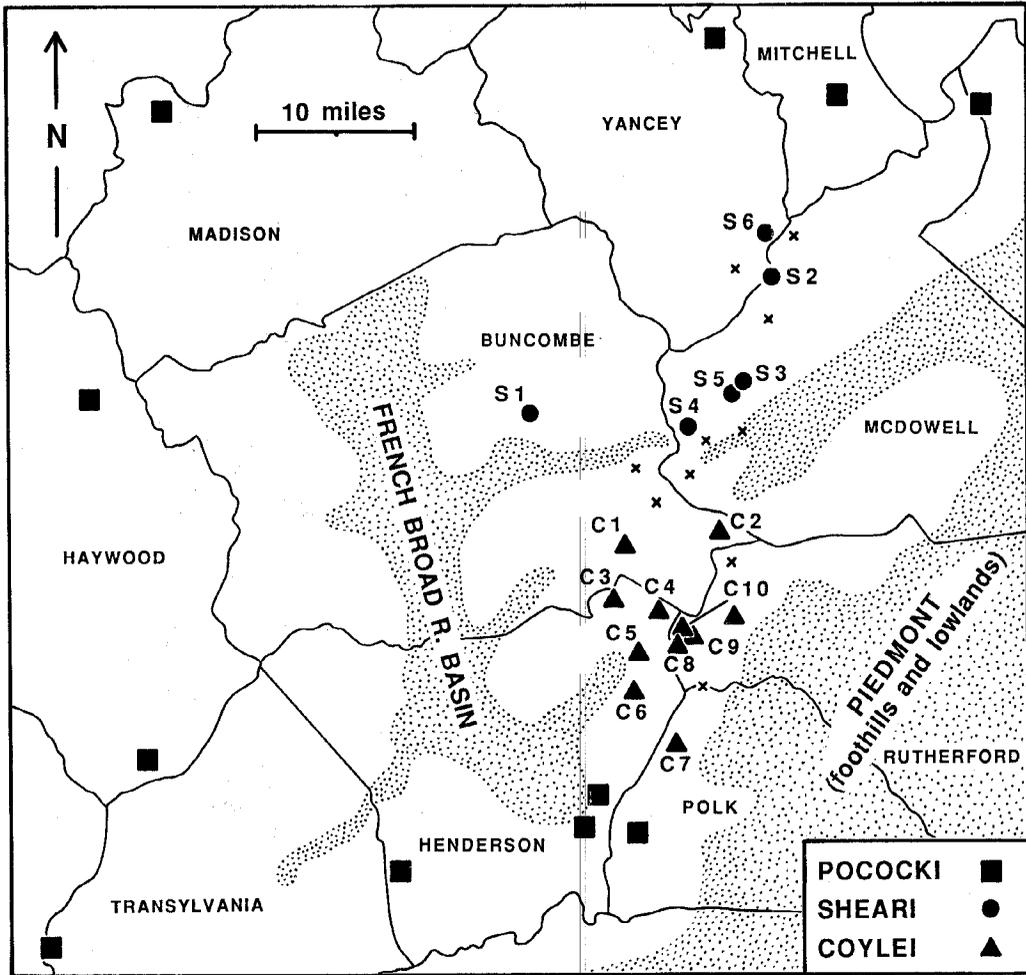


Figure 12.—Map of a ten county region of western North Carolina showing the known distribution of *Hypochilus sheari* and *H. coylei* and neighboring sites where *H. pococki* has been collected. Each sampled deme of *H. sheari* and *H. coylei* is identified with code (see Methods section). X's mark sites with apparently suitable *Hypochilus* habitat but found to be devoid of *Hypochilus*. French Broad River basin (stippled) ranges in elevation from about 2000 to 2400 ft. Boundary between mountains (not stippled) and Piedmont (stippled) roughly follows elevation of 1400 ft.

**Feeding Biology.**—Feeding was observed several times in both morphs (*H. coylei*:  $n = 6$ ; *H. sheari*:  $n = 8$ ) and resembles that of *H. pococki* (Fergusson 1972). The primary prey type was gryllacridid crickets (*H. coylei*:  $n = 3$ ; *H. sheari*:  $n = 5$ ) and cursorial spiders, including lycosids (*H. sheari*:  $n = 2$ ), gnaphosids (*H. coylei*:  $n = 1$ ), and pisaurids (*H. coylei*:  $n = 2$ ; *H. sheari*:  $n = 1$ ). No spiders were observed feeding on tipulid flies even though they were abundant at many demes.

DISCUSSION

The results of this study provide strong support for Platnick's contention that these two *Hy-*

*pochilus* morphs represent distinct species. The distinct genital morphologies of the two population clusters (Table 1, Figs. 3–6, 8–10), the virtual absence of clinal variation in the characters studied (the demes closest to the geographic gap separating the species are as distinct morphologically as those farthest from the gap), and the absence of hybrid populations indicate that there is no gene flow across the small geographic gap separating them. Whether these allopatric morphospecies are also separated by intrinsic reproductive isolating mechanisms, and are therefore biological species *sensu* Mayr (1969), Dobzhansky et al. (1977), and Futuyma (1986), can be determined only by courtship and mating trials

in laboratory situations with appropriate intramorph controls. However, the fact that the diagnostically most useful genital features (conductor width and conductor tip shape) are those which contact the female most intimately during copulation, hints that *H. sheari* and *H. coylei* cannot successfully interbreed. Male genitalic differences probably are not just manifestations of genetic divergence but may be important in influencing the female's acceptance of sperm (Eberhard 1985, 1990) and, consequently, vital parts of the actual mechanism of reproductive isolation.

Among the many shared character states of *H. sheari* and *H. coylei*, there is at least one probable synapomorphy which supports the hypothesis that these are sister species: the conductor tip is abruptly and strongly bent and tapered so that it resembles a beak (Figs. 3–6). We postulate that some event, perhaps divide migration and subsequent drainage capture, a common event in the Southern Blue Ridge during Tertiary times (Hack 1969), divided the parent species into two geographic isolates distributed much like they are today.

It is not obvious why *Hypochilus* demes do not exist in the five mile zone separating these species, but we suggest that, because of the drastic constriction of the mountain corridor and the presence of a watershed divide, this region does not contain enough favorable substrate and habitat to support persistent populations and allow dispersal. *Hypochilus* species have not been observed to balloon, and observations by Shear (1969) and Fergusson (1972) indicate that only adult males are highly likely to walk from one outcrop to another.

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