REMARKABLE SYMPATRY IN THE WINTER STONEFLIES *ALLOCAPNIA INDIANAE* AND *A. OHIOENSIS*, A PAIR OF SISTER SPECIES[1, 2]

HERBERT H. ROSS

Illinois Natural History Survey, Urbana, Ill.

AND

PAUL H. FREYTAG[3]

The Ohio State University, Columbus, Ohio

ABSTRACT

Two extremely closely related species of stone flies, *Allocapnia indianae* Ricker and *A. ohioensis* Ross and Ricker, have almost perfectly sympatric ranges extending from south-central Kentucky to southeastern Ohio, with isolated areas of distribution in south-central Indiana and in New York. Both species appear to be restricted to small streams having cave or spring origins. A comparison of their distribution with features of Wisconsin glaciation suggests that (1) the Wisconsin glacial lobes separated the area of occurrence of the ancestral species of these two living stone flies into two isolated geographic units, (2) these isolates evolved into distinctive species, and (3) since then the two resulting species have achieved rigid genetic isolation and dispersed throughout each others' range. It is suggested that the original isolation of the pre-*indianae* and pre-*ohioensis* populations occurred just prior to the Wisconsin glaciation.

The two winter stoneflies under discussion belong to the *Allocapnia nivicola* complex, a group of species inhabiting small, clear, rapid streams that remain cool in summer. The species were recently differentiated taxonomically from *A. nivicola* Fitch, *A. indianae* having been described by Ricker in 1952, *A. ohioensis* by Ross and Ricker in 1964. At the time that the latter species was described, it was noted that both species often occurred in the same stream. It was further noted that occasional specimens appeared to combine characteristics of the two species, and this suggested the possibility that *A. indianae* and *A. ohioensis* hybridized to at least some extent.

In an effort to investigate further the possibility of interspecific hybridization between these two species, collections of winter stoneflies were solicited from colleagues in the eastern half of the continent, several of whom made extensive collecting trips on behalf of the project. To these cooperators (who will be listed in a later publication) we owe our deep gratitude. In examining these collections, it was discovered that in specimens even slightly contracted, the exact shape of the diagnostic parts was difficult to ascertain with certainty; only after the abdomens of such contracted specimens were eviscerated with a warm, 20 percent, caustic potash solution were the parts readily seen.

TAXONOMIC CONSIDERATIONS

Allocapnia indianae and *A. ohioensis* form a monophyletic pair of species arising from the *A. nivicola* complex, characterized by the possession of a relatively large dorsal process on the seventh tergite of the male, in addition to the usual large process on the eighth tergite. Males of *A. indianae* and *A. ohioensis* differ principally in characteristics of the terminal segments. In *A. indianae*, the three points of the dorsal process of the eighth tergite are the same height and the end of the lower supra-anal process is markedly constricted to form a narrow finger-like apex. In *A. ohioensis*, the middle point of the eighth tergal process is much

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[2]Manuscript received June 22, 1966.

[3]Present address: Division of Biological Sciences, Arkansas State College, State College, Arkansas.

lower than the lateral ones, and the end of the lower supra-anal process tapers almost evenly and forms a somewhat triangular apex. Females of the two species are readily identified by the apical margin of the eighth sternite. In *A. ohioensis* this margin forms a short, wide, infolding flange; in *A. indianae* the margin has no flange and may be incised.

The two species were collected in four states at localities listed below and illustrated in Fig. 1.

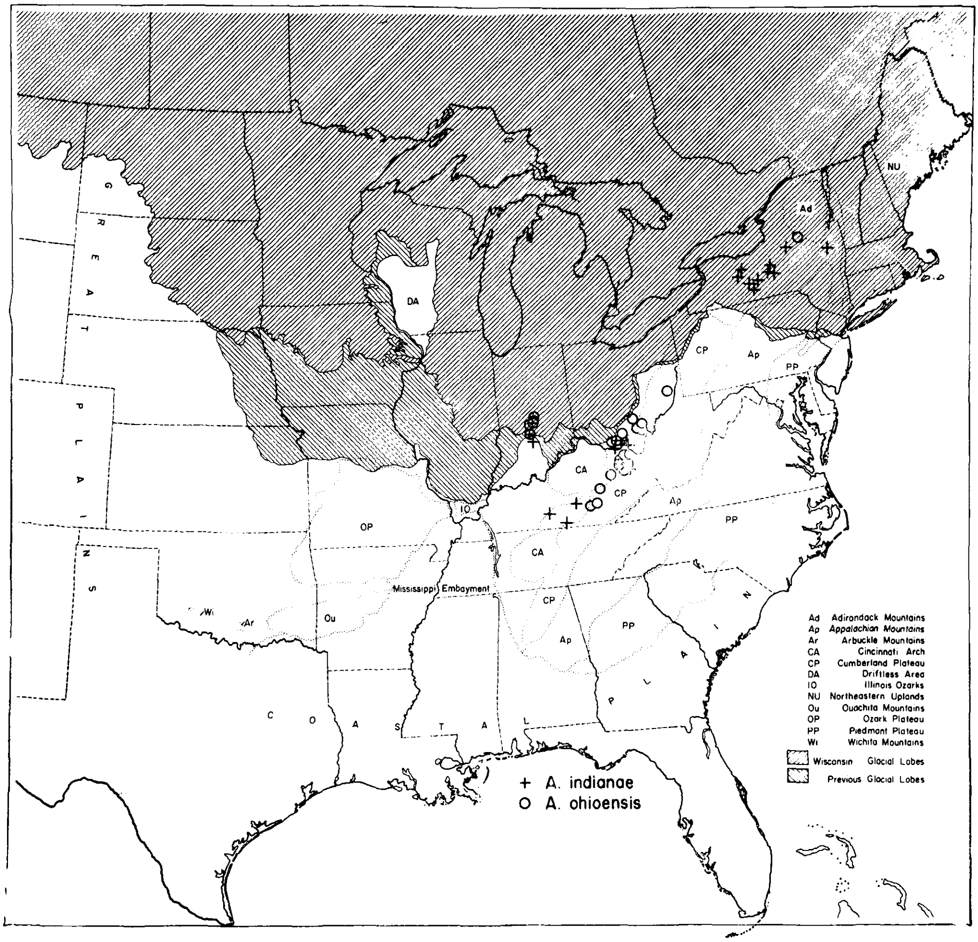

FIGURE 1. Locality records for *Allocapnia indiane* and *A. ohioensis.* The cross-hatching indicates the known extent of Pleistocene glaciation in eastern North America.

A. indianae Ricker. INDIANA—*Brown County*: E. of Nashville (Clay Lick Creek); *Jackson County*: NW of Medora (Creek); *Lawrence County*: 1 mi N of Oolitic (Gullis Creek); *Monroe County*: 10 mi N of Bloomington, 4 mi N of Bloomington (10-dead Creek), 4 mi N of Bloomington (Bean Blossom Creek), 10 mi N of Bloomington; *Morgan County*: 2 mi S of Brooklyn, 2 mi S of Brooklyn (Center Creek), N of Martinsville (Creek and White River), 6 mi S of Martinsville. KENTUCKY—*Barren County*: 4 mi SE of Glasco; *Carter County*: W of Globe, SW of Carter, W of Globe, S of Olive Hill (Tysart's Creek); *Cumberland County*: Bow

(Cash Creek); *Greenup County*: S of Fullerton (trib. of Tysart's Creek); *Lewis County*: NW of Olive Hill. NEW YORK—*Cayuga County*: Aurora (brook at edge of Wells College campus), Aurora (Paines Creek at Rt. 90), Aurora (Glen Creek at Gully Rd. and Rt. 90), Aurora (Little Creek at Rt. 90), Locke Rd., Tompkins Co. line (Hemlock Creek); *Ontario County*: Canandaigua (Barnes Gully and Menteth Gully), South Bristol (Seneca Pt. Gully); *Schenectady County*: 3 mi S of Jct. 30 and 159 (small stream); *Schuyler County*: $\frac{1}{10}$ mi S of Mecklenburg (trib. Taughannock Creek), Montour Falls (diversion channel, Catherine Creek), near Watkins Glen (big Hollow Run at Lover's Lane and Route 14); *Thompkins County*: Ithaca (6-mile Creek). OHIO—*Adams County*: 9 mi E of Blue Creek (road 25); *Scioto County*: W of Portsmouth (Odle Creek, road 25), W of Portsmouth (Turkey Creek). Total specimens—326.

A. ohioensis Ross and Ricker. INDIANA—*Jackson County*: NW of Medora (creek); *Monroe County*: 4 mi N of Bloomington (10-dead Creek); *Morgan County*: 2 mi S of Brooklyn (creek), 2 mi S of Brooklyn (Center Creek), 6 mi S of Martinsville, 6 mi S of Martinsville (Bryant's Creek), S of Martinsville (small trib. of Bryant Creek, above the lake, Morgan-Monroe State Forest). KENTUCKY—*Boyd County*: Catlettsburg; *Elliott County*: Sandy Hook (Middle Fork Creek); *Estill County*: W of Globe, Ravenna (Campbells Fork); *Greenup County*: near Lynn (Tysart's Creek), near Warnock (Leatherwood Creek); *Lewis County*: NW of Olive Hill (stream); *Rockcastle County*: Boone, S of Conway (Roundstone Creek); *Rowan County*: Morehead. NEW YORK—*Herkimer County:* NW Starkville. OHIO—*Adams County*: 5 mi E of Blue Creek, 9 mi E of Blue Creek; *Athens County*: Athens (Margaret Creek), Carbondale, Coolville (trib. Hocking River); *Hocking County*: Ash Cave; *Jefferson County*: Mt. Pleasant; *Pike County*: below Pike Lake (Sun Fish Creek); *Scioto County*: W of Portsmouth (Turkey Creek). Total specimens—149.

In these collections, every male specimen but one possessed the set of two characteristics considered as diagnostic of the species. The single exception was a male that combined a lower supra-anal process typical for *A. ohioensis* with a dorsal process of the seventh tergite typical for *A. indianae*. We take this as evidence that the two species are reproductively isolated to a high degree, with the possibility of an occasional hybrid being produced. The discovery of only one such specimen in a large number of completely typical specimens would further suggest that such hybrids produce no offspring as either strictly hybrid progeny or backcrosses. This distinctness is especially emphasized by the fact that both species were taken together in 15 different streams in two separate areas, one area in Indiana, the other including parts of both Ohio and Kentucky.

ECOLOGY AND DISTRIBUTION PATTERNS

Compared with the more widely ranging species of *Allocapnia*, *A. indianae* and *A. ohioensis* have a relatively restricted range (fig. 1). This includes an isolated area in south-central Indiana, a series of records from south-central Kentucky to southeastern Ohio, and a cluster of records in New York. Neither species has been found in typical mountainous country, but rather in broken or hilly country. Neither species has been found east of the Appalachian Mountain system.

Except for the records in New York, the two species appear to be restricted to small streams having cave or spring origin. This probably accounts for the association of the Indiana, Kentucky, and Ohio collections with faults or erosional features that have exposed or cut into limestone strata bearing subterranean water. The two stoneflies are not confined to the headwater spring sources of their respective streams, but are abundant in these streams for several miles from their source, and presumably at such distances that any special ecological features superimposed on the stream by the underground nature of the source water would have been dissipated. The one feature of the underground environment persisting for some distance, especially in the shaded valleys through which these streams pass, would be the underground temperature of the source water. In winter this temperature is considerably higher than in streams of the area made up chiefly of surface run-off water, and in summer it is considerably lower.

The extent of the temperature differences in summer between surface-water streams and subsurface-water streams has been demonstrated by measurements taken during hot weather in July in Union County, southern Illinois. Streams fed only or chiefly by surface water had mid-afternoon temperatures exceeding 80°F., whereas streams containing only artesian water had temperatures of 58°F to 60°F, measured between the source and a distance of a mile downstream. Stream temperatures of 65°F were twice found five miles from the source. In one case where a spring flowed directly into an otherwise surface-water stream, the water temperature on the spring side of the stream was 58°F for a hundred yards downstream, where it gradually became mixed with the main current and depressed the temperature of the entire stream. The measured streams were in hilly, wooded terrain similar to that in which *Allocapnia indianae* and *A. ohioensis* are found, and within the latitudinal range of these species, though no specimens of these stoneflies were collected from these streams.

The occurrence of both species in New York would seem to indicate that the higher stream temperatures in winter are not a necessity for the survival of the species in the southern part of its range. By elimination, the cool temperatures maintained in summer are probably the limiting factor, permitting the persistence of these species in the spring-fed streams of Indiana, Kentucky, and Ohio.

ORIGIN AND DISPERSAL

If *A. ohioensis* and *A. indianae* were allopatric species, it might be a simple matter to postulate past events that would explain logically the distributional pattern existing at present. Because the two species now occupy the same range, however, it is most difficult to deduce circumstances that would have produced the present, and only the present, distribution pattern. Because the ecological tolerances of the two species have a wide overlap, it seems certain that (1) the two species originated by the geographic division of their parent species; that (2) these isolated portions evolved into distinct, genetically isolated sister species; and that (3) subsequently the ranges of the two species expanded or changed, resulting in an almost complete overlap of the two. Furthermore, the two species are so similar morphologically that their evolution would seem to have been relatively recent, possibly during or just before the Wisconsin glaciation. It is obvious that, since this last glaciation, both species have dispersed in a northeasterly direction into glaciated areas of New York from which the ice had only recently disappeared.

Perhaps the most reasonable and simplest possibility is that the parent species was a pre-Wisconsin one that became isolated into a northeastern segment, possibly occurring in the northeastern uplands, and a more southwestern segment isolated in the cave and spring area of southern Ohio and northeastern Kentucky. If the pre-Wisconsin climate had been a little warmer than that of the present, the known records of the species would support such an idea. If such had been the case, the southern movement of the Wisconsin glaciers presumably created conditions between the northeastern uplands and the Cincinnati Arch area (Flint, 1957), that would have allowed the dispersal of the northeastern segment (by then a distinct species) southwestward and brought it into contact with that of the southwestern segment (by then also a distinct species). With present information, it is impossible to tell which of these isolated segments might have been *A. ohioensis* and which one *A. indianae*.

There is a second possibility with sufficient merit to bear consideration. Local populations of the *indianae-ohioensis* ancestor may have been isolated in two areas in or near the present more southerly segment of the species' ranges, perhaps in or around the Cincinnati Arch or in the Cumberland Plateau area. Exactly this same situation gives the best explanation for the evolution of cave beetles in this same geographic area. If this did happen, with these two winter stoneflies, then their respective isolated populations would have been separated at a time when small streams, fed only by surface-runoff, were about as warm as or warmer than they are now. The two newly formed species would have become sympatric when the surface-runoff streams became at least as cool in summer as those in New York now occupied by the species.

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