ADDITIONS TO THE TAXONOMY, ZOOGEOGRAPHY, AND BIOLOGY OF *ANALETRIS EXIMIA* (ACANTHAMETROPODINAE: SILPHLONURIDAE: EPHEMEROPTERA)[1]

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Abstract

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The previously undescribed adult male and female of *Analetris eximia* Edmunds are treated. Additional features of nymphs are illustrated. In the Saskatchewan River system the species is found in areas unaffected by reservoirs; nymphs develop in May?, June, and July; adults emerge in late July. Nymphs are carnivorous (chironomids were the main food item in field collected specimens), live in backwaters adjacent to the main river current, and are morphologically adapted to life on an unstable silty substrate. Invasion of the Saskatchewan system was apparently via Missouri tributaries from the Colorado system. It occurred in recent times in the latter but apparently not the former. Because of habitat destruction, the species is considered endangered.

Analetris eximia Edmunds (Edmunds and Koss 1972), a recently described but fairly common mayfly in the Saskatchewan River system, is a member of one of the least known subfamilies of Ephemeroptera in the world. The four genera which make up the Acanthametropodinae have a wide distribution in the northern hemisphere (China, Siberia, North America), but they are seldom collected. Edmunds and Koss (1972) point out that at the time of their study only about 55 specimens, seven of which were imagos or subimagos and the balance nymphs, were known in collections for the entire subfamily. Biological information was scarce, but many specimens were associated with larger rivers and on the basis of the nymphal mandibles they were considered carnivorous.

Type material for *A. eximia* consisted of a male subimago and nymphs and originated from Utah, Wyoming, and Saskatchewan. Edmunds and Koss (1972) provided an excellent introduction to the subfamily as well as information on *A. eximia*. Adult stages and additional biological information are now available and are the subject of this paper. The following descriptions contain both specific and generic characters.

The general features of *A. eximia* are shown in Figs. 1, 2, and 9. Wing venation is shown in Figs. 3 and 4 and is labelled according to the family Siphlonuridae in Tschernova (1964). This system, which is different from that in most North American texts, was used by Edmunds in the description of *Analetris*.

Adult Male (Figs. 2–8). Body length 18 mm, front wing 13 mm.

MATERIAL EXAMINED. One reared adult male in alcohol, Saskatchewan, North Saskatchewan River at Battleford, reared 11 July 1974, D. M. Lehmkuhl; two reared males in alcohol, Saskatchewan, North Saskatchewan River, Borden Bridge at Hwy. 5, 20 July 1974, R. Demaray.

DESCRIPTION. Color markings as in subimago (Edmunds and Koss 1972); dorsal abdominal pattern of same basic elements as nymph (Fig. 9) but more diffuse (Fig. 2); small but distinct white projection between fore-coxae, a smaller projection between mid-coxae, and a distinct semi-membranous spine on each side postero-dorsally to the front coxae; front to hind wing length ratio 7.5:4; longitudinal veins slightly pigmented with black, darker in stigmatic area; crossveins and wing membrane colorless; legs and antenna as in Figs. 5, 6, and 8; forceps small in relation to body size, penes fused (Figs. 2, 7); upper portion of compound eye white, lower part grey.

Adult Female. Body length 19 mm, front wing 15 mm (Fig. 1).

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MATERIAL EXAMINED. Two adult females collected floating on river surface, 3:00 P.M., cloudy cool day, no eggs in abdomen. Saskatchewan, North Saskatchewan River, Lloydminster Ferry, 18 July 1973, D. M. Lehmkuhl.

DESCRIPTION. Color pattern similar to male; dark sclerotized area present at opening of oviducts (base of abdominal segment 8); sternite 9 produced posteriorly as a blunt triangle the posterior apex of which is truncate and very slightly concave; eyes blue-black in alcohol, ocelli large, white, 1/3 diameter of compound eyes; small but distinct mid-ventral white spines between fore- and mid-coxae, and a semi-membranous spine on each side postero-dorsally to front coxae as in male.

Nymph (Figs. 9, 10). Length of mature specimens 17–18 mm, cerci 4–5 mm.

Edmunds and Koss (1972) provide extensive descriptions of the nymph, but the following is added: dorsal abdomen covered with scale-like hairs as in Figs. 12–14; legs beyond the trochanter consist of what appear as three articles, presumably the femur, a fused tibia and tarsus, and a long sharp tarsal claw (Figs. 20–22); as in adults there are small mid-ventral projections between the coxae (Fig. 15) and also posterior and dorsal to the prothoracic coxae (Fig. 9); mouthparts as in Figs. 17–19; cerci fringed as in Fig. 16.

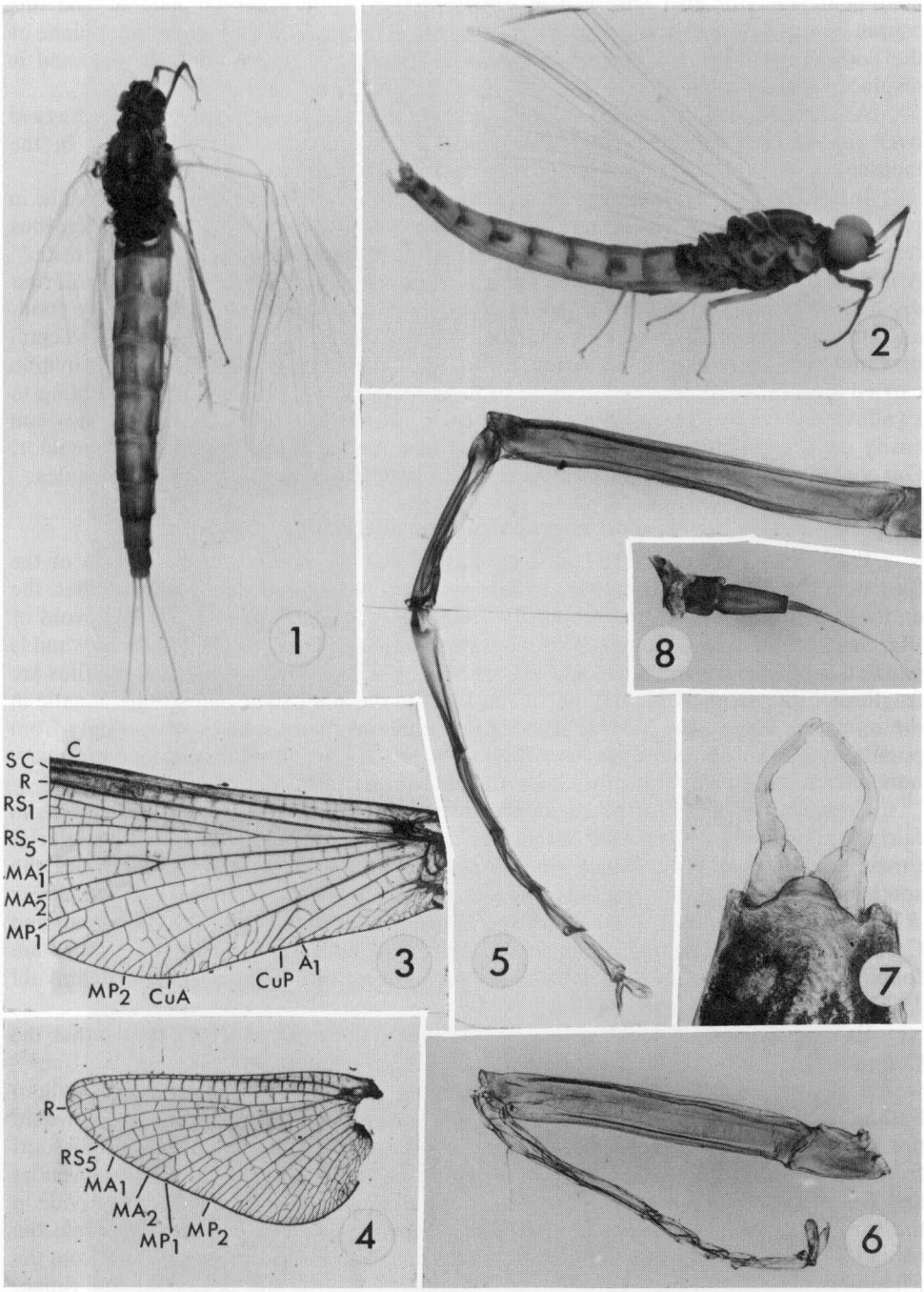
Biology and Distribution

The known distribution of *A. eximia* is summarized (Fig. 23). I have collected the species in the Saskatchewan River in the Province of Saskatchewan only. With further collecting it undoubtedly will be found in the same river system in Alberta and Manitoba, and it is known from Wyoming and Utah (Edmunds and Koss 1972). In the South Saskatchewan River it is abundant at Lemsford Ferry near the Alberta border, but it has not been collected at Saskatoon or other points downstream from Gardiner Dam. It was present at a number of localities in the North Saskatchewan River (Lloydminster Ferry near Alberta border, Battleford, Borden Bridge at Hwy. 5, and Cecil Ferry about 10 miles east of Prince Albert) but was not found downstream from Tobin Lake, a mainstream impoundment about 100 miles east of Prince Albert. For a discussion of the relationship between reservoirs and mayfly distribution, see Lehmkuhl (1972*a*).

Of approximately 25 collections totalling about 200 specimens, collection dates range from 2 June to 31 July. Young nymphs (5–10 mm in length) were taken on 2 June '71, 12 July '70, and 14 July '71, and it could be assumed that hatching took place at least a month prior to these dates. Adults or nymphs with black wing pads (17–20 mm) were taken on 18 July '73 and 31 July '74. Thus, there appears to be an extended period of hatching and extended period of emergence but the rate of development is rapid. All takes place in mid-summer. It is hypothesized that the balance of the year (September to April) is passed as a diapausing egg or embryo.

Nymphs were never collected in strong current but always in slow moving eddies, backwaters sheltered from the main current by ferry ramps (Fig. 11), or among boulders artificially placed along the river bank to prevent erosion. On one occasion at Battleford (30 June 1974) as the June floods were subsiding, nearly 100 nymphs were collected in a matter of minutes among the boulders along the river shore. Ten days later, only two nymphs were collected in the same area and these with great difficulty. Migration to new habitats probably accounts for the decline and the prior abundance was probably due to concentration by dropping water levels.

Laboratory observations (using a shallow white pan, river sand, and air stone) were made in June 1971. Nymphs are excellent swimmers and can rival small fish. After sudden swimming activity caused by a longitudinal–vertical (as opposed to lateral) whipping of the body, nymphs settle to the bottom and anchor themselves with their legs in the position indicated in Fig. 9. All legs have long, sharp claws (Figs. 20–22), but the legs are short in comparison to *Pseudiron centralis* McDunnough, a psammophilous



FIGS. 1–8. *A. eximia* Edmunds. 1, adult female; 2, adult male; 3, front wing of male; 4, hind wing of male; 5–6, front and mesothoracic legs of male; 7, genitalia and forceps of male; 8, antenna of male.

species found in the same river but in a different habitat. In both, the legs work in opposition, gripping the friable substrate like ice tongs. *A. eximia* are able to walk over sandy substrate with ease and they frequently make single whipping movements of the abdomen, behavior also observed in *Ametropus* sp. from a similar habitat, and this causes water to flow over the gills which are held at an angle to the longitudinal plane of the body (Figs. 9, 9a). *A. eximia* also make a longitudinal "shiver" so that sand is displaced and the nymph sinks below the general level of the substrate.

As nymphs walk over the substrate the long maxillary palps (Fig. 18) are dragged over the surface and probably have a sensory function for locating prey. In the laboratory, annelids and chironomid larvae were readily taken from forceps.

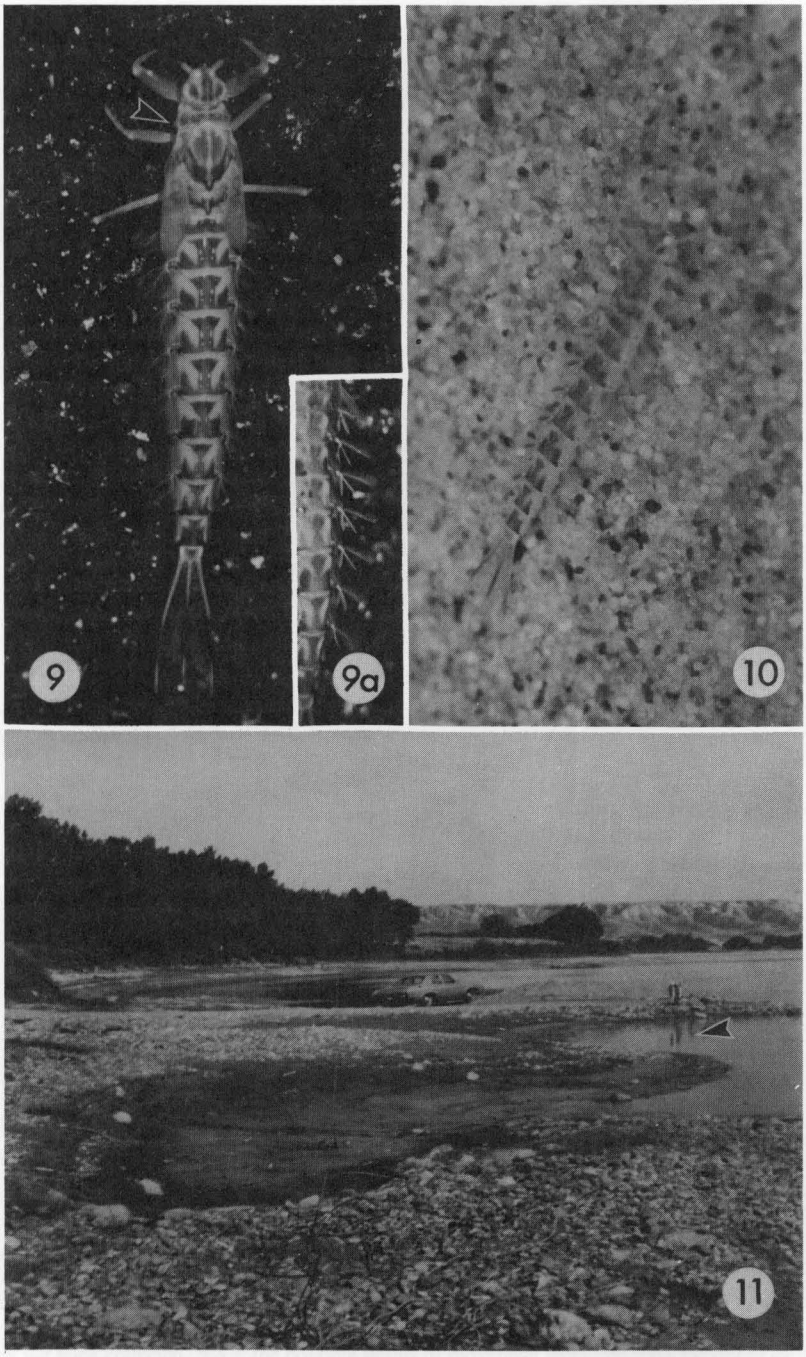
In preliminary experiments, it was not possible to determine the role of sight in prey detection. A small wriggling chironomid larva held 1 cm distant elicited a vigorous response from an *A. eximia* nymph, but the response could have been through "taste." Attack of prey is vigorous. Nymphs, upon detecting prey beneath the substrate, will first dig and probe with their front legs and mouthparts in an attempt to dislodge the food, and after the forward dive will dig in with the posterior legs, curl the abdomen and cerci upward, and continue the backward effort until the prey is dislodged. One nymph carried a 1/4-in. section of chironomid in its mandibles for 15 min while attempting to swallow it. The structure of the digestive tract has not been investigated but they can easily eat several chironomids which in total length exceed the length of the predator. Gut contents of field collected nymphs contained numerous chironomid head capsules.

Zoogeographical Considerations

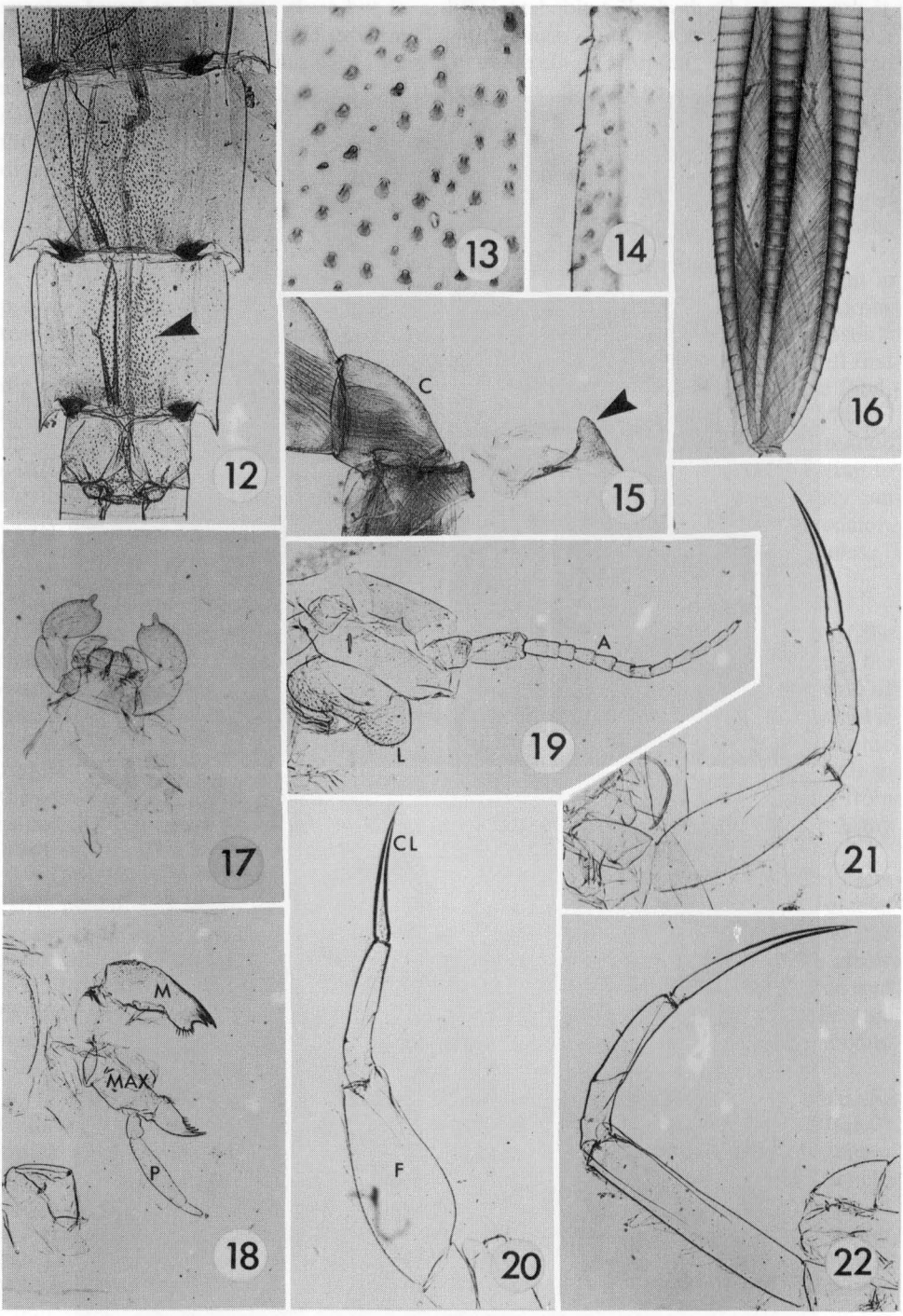
Previously (Lehmkuhl 1972*b*) I have broached the problem of the origin of the Saskatchewan River mayfly fauna, an intriguing problem for several reasons. First, the entire system was ice-covered perhaps 15,000 years ago and was obviously devoid of life. Second, the river system at present drains north ultimately into Hudsons Bay and is isolated from Pleistocene refugia to the south (Fig. 23). Third, while most mayflies are fragile-bodied, short-lived, and inefficient fliers in the adult stage and strictly aquatic in the immature stages, the Saskatchewan River contains many species known only from populations in other river systems which flow in the opposite direction and are many hundreds of miles away, i.e., the Colorado and Mississippi systems.

Connections between the Saskatchewan and Missouri–Mississippi systems seem fairly straightforward as pointed out for *Baetisca* (Lehmkuhl 1972*b*). During late glacial times, the Saskatchewan River flowed south into the Mississippi system and the southeastern mayfly elements thus had a direct aquatic invasion route (Fig. 23, arrow #1). It is not so clear in the case of the connections between the Saskatchewan and Colorado systems. *A. eximia* along with about a dozen other species of mayflies are found in both, but as far as is known, not between in the Missouri system (Lehmkuhl 1970; Edmunds and Musser 1960).

Examination of a map (Fig. 23 shows major drainage patterns) shows that the Colorado, Missouri (Mississippi), and Saskatchewan systems can be viewed as "fans" which slightly overlap or are at least contiguous covering the area from southern Saskatchewan and Alberta to Wyoming and Utah. While a direct aquatic route would not have existed, it is possible that even weak-flying insects could invade the Missouri from the Colorado system, probably in Wyoming (lower +++, Fig. 23). Van Devender and Tessman (1975) hypothesized that snapping turtles crossed the continental divide in the same area in the late Pleistocene. The insects could then gradually infiltrate the tributaries of the Missouri system, and perhaps enter the Saskatchewan system from the Missouri tributaries which flow through southern Alberta and Saskatchewan (upper +++, Fig. 23). This scenario makes two assumptions—that the Missouri system once provided a suitable habitat for the mayfly community under consideration and that



FIGS. 9–11. *A. eximia* Edmunds. 9, nymph on black substrate emphasizing color pattern; 9a, detail of gills; 10, nymph on river sand showing camouflage; 11, habitat (arrow) exposed by low water levels.



FIGS. 12–22. *A. eximia* Edmunds. 12, cleared cast skin of nymph showing distribution of scale-like hairs; 13–14, enlarged scale-hairs in surface view and profile; 15, projection between coxae; 16, terminal filaments of nymph; 17, labium; 18, mandible, maxilla, and palp; 19, antenna and labrum; 20–22, front, middle, and hind legs, respectively, of nymph.

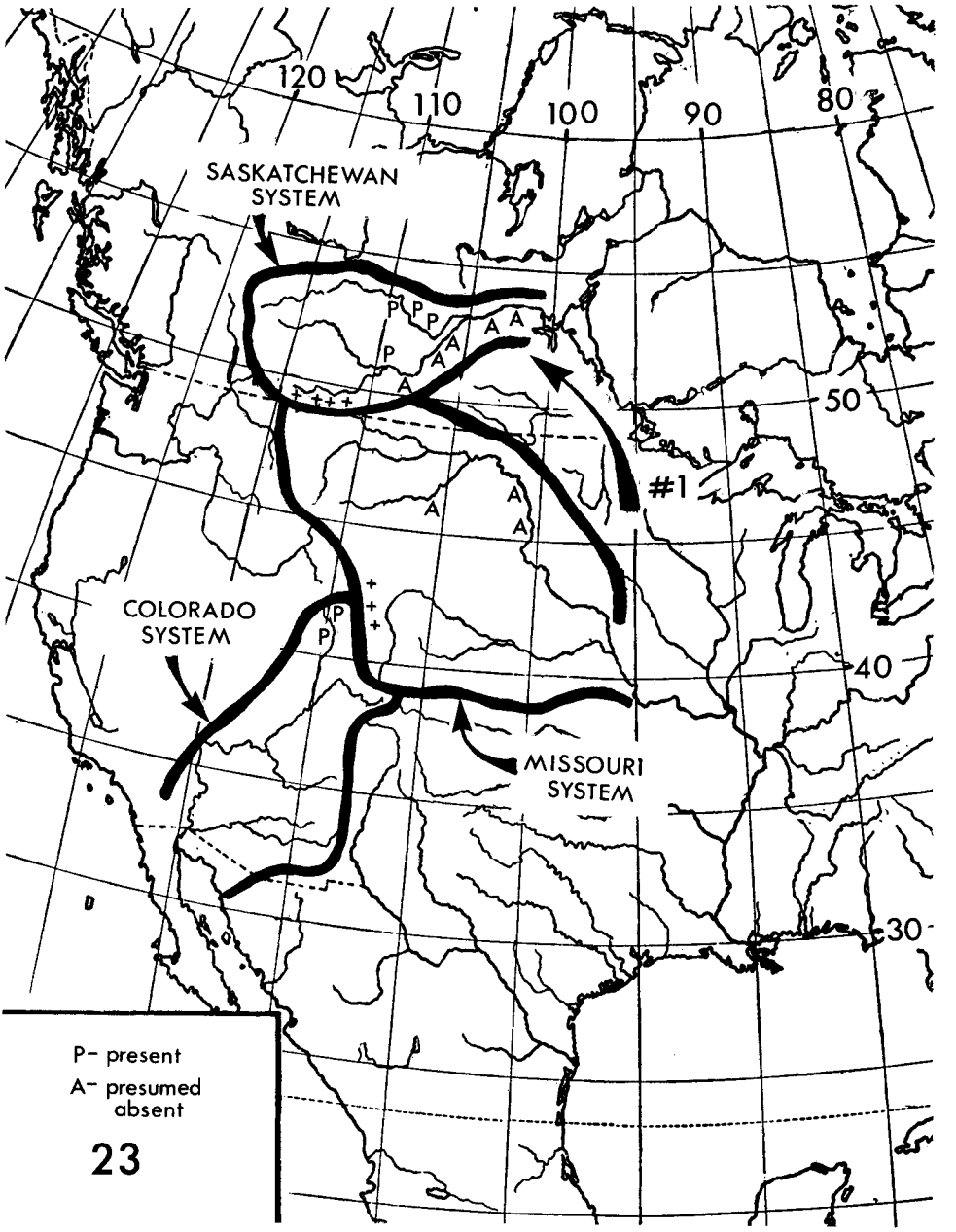


FIG. 23. Known distribution of *A. eximia*. "P" indicates that specimens were collected, "A" that samples were taken but none collected, +++ the possible points of movement from one river system to another, and arrow #1 indicates the late Pleistocene route of Mississippi elements to the Saskatchewan System via drainage patterns which have since altered.

adults could cross distances of 50 or more miles to make the crossing from one system to another. I have made a number of collections from Missouri tributaries (Yellowstone in Montana and Grande, Cheyenne, and other small rivers in South Dakota; "A"s in Missouri System, Fig. 23) and the species under consideration were not taken. It is my opinion that they are absent from the Missouri system at the present time. (The mainstream of the Missouri has been entirely destroyed in the present context by dams for reasons proposed by Lehmkuhl, 1972*a*.) For the second assumption, documentation is available in that *Lachlania saskatchewanensis* Ide is known to be strictly a river form but the type specimen was a female taken floating on a lake, near Humbolt, Sask., over 50 miles from the river which must have been the source of the specimen.

The discussion above assumes that movement was from the southwest to the northeast, but this may not have been the case. Under earlier climatic regimes the insects may have been widespread in the rivers south of the glacial ice and recent warming and drying may have exterminated the community of mayfly species so that relict communities now remain in two widely separated river systems. Information is not available to make a judgment on these questions but it is at least possible to pinpoint the general areas of movement from one system to another even though the direction and time of movement is uncertain.

Discussion

Owing to their excellent swimming abilities, *A. eximia* nymphs are seldom taken by ordinary collecting methods such as hand-picking, grab, or stationary net samplers, or by trapping on artificial substrates. Edmunds and Koss (1972) also found drift nets unsuitable. This probably accounts for the late discovery of the species. In my experience, the main factor is to find suitable habitat for the species and they can then be collected with fairly energetic sweeping with a standard aquatic net. It was also found that after the first few successful attempts in a given backwater or eddy, further effort is wasted, again owing to the swimming ability of the nymphs.

Because of the rarity or absence of the species in most parts of North America and the difficulties presented by turbidity, currents, deep water, and flood stages (up to 25 ft vertical fluctuation in a matter of weeks) in the Saskatchewan River, many details of the biology of *A. eximia* remain unknown. The overwintering stages, the exact period of hatching, and possible habitats other than eddys along the shore, remain to be investigated. Studies on reactions to current and light intensities and prey selection could be carried out in the laboratory but have not as yet.

The Ephemeroptera are an ancient group of insects and the Siphlonuridae, to which *Analetris eximia* belongs, is considered to be one of the more primitive families. If one accepts continental drift then the worldwide distribution of the subfamily could be expected since the group may have existed before the separation of the major land masses. While the family is widespread in the world, individual species, as far as is known, are not. Existing mayflies, numbering about 2000 species for the world, are considered to be remnants of a once much larger group, and it may be that the Acanthametropodinae were declining even before the influence of man. They require a specialized habitat, they are evolutionarily conservative as indicated by the small number of species, and ecologically they are carnivores which are classically considered to be less numerous than herbivores. Mayflies predate (Pennsylvanian) predatory aquatic insects such as Odonata, Trichoptera, and Plecoptera (Permean) and the predatory mayfly may have once played an important ecological role. With the evolution of more efficient groups the predatory mayfly may have declined to its present non-dominant status. The distribution and abundance of members of the Acanthametropodinae before the influence of man on their habitat will never be known, and thus it is not possible to say if the situation in the Saskatchewan River is anomalous or simply a

matter of good fortune in finding effective collecting techniques. In any case, the example of *A. eximia* in the Saskatchewan River gives insight into the subfamily as a whole since all members seem to be predators which live in large rivers.

The future of the group is not very encouraging. Most remain very rare in nature and it is unfortunate that *A. eximia* must be listed as an endangered species. Its distribution is very local and vulnerable. Much of its probable and known habitat in the U.S.A. has already been altered through dam construction and pollution, and similar developments are a possibility in Canada (Edmunds 1973).

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