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MIDDLE PLIOCENE DRAGONFLY NYMPHS, RIDGE BASIN, TRANSVERSE RANGES, CALIFORNIA

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ABSTRACT—Previously undescribed dragonfly nymphs occur as impressions in middle Pliocene lacustrine shale beds from Ridge basin, California. One well preserved specimen is similar to a modern nymph of the Family Gomphidae, and another is similar to a modern nymph of the Family Libellulidae. Locally, three thin shale beds with varve like laminations contain numerous nymphs, mostly incomplete, and plant and fish remains. Paleoenvironmental interpretation of the shale beds and consideration of the modern ecology of lake-dwelling nymphs indicate that these shoreline-dwelling nymphs drifted a short distance out into the lake and then were rapidly buried.

INTRODUCTION

ALTHOUGH the earliest remains of true dragonflies (Order Odonata) are from Lower Permian strata (Carpenter, 1930), preservation of adult dragonflies is more common than that for nymphs. Scudder (1890) reported a few fragments of nymphs from the Oligocene Florissant lake beds of Colorado. Five fragmentary specimens of the larvae of *Orthemis*? sp. (Subfamily Libellulinae) from Miocene lake deposits in California were described by Palmer (1957). These specimens occur as silicified remains, and some of the details of the mandibles and rectal gill system are apparent. In addition, numerous fragmentary specimens of nymphs of the Families Libellulidae and Aeshnidae were reported from the early Pleistocene Rita Blanca lake deposits of Texas (Sublette, 1969).

Previously undescribed fossil dragonfly nymphs have been reported from Pliocene lake beds in the Ridge basin of California (Shepard, 1961, 1962). It is the purpose of this paper to describe the locality and some of these nymphs. Unfortunately, most specimens are fragmental. One well preserved specimen is herein tentatively assigned to the Family Gomphidae, and another to the Family Libellulidae.

The nymphs are from the vicinity of a small ridge along the west side of Piru Creek, northwest of Pyramid Lake (California State University, Northridge [CSUN] localities 276 and 277 [Text-fig. 1]). Locality 277 is in the general vicinity of the University of California, Los Angeles locality 4240 which was reported by Shepard (1961) to contain numerous dragonfly nymphs of the Family Libellulidae. When plotted on Crowell's (1954, 1975) maps, all these localities plot within the middle part of the Ridge Basin Group. Axelrod (1950) described middle Pliocene plant remains and David (1945) described middle Pliocene fish remains from the middle part of the Ridge Basin Group.

The nymph-bearing outcrops at CSUN localities 276 and 277 have a very limited areal extent, occurring only in the vicinity of the previously mentioned ridge. Due to extensive slope cover, the nymph-bearing bed in a small cliff exposure at CSUN locality 276 crops out for a distance of only about 10 m, and because of erosion, the nymph-bearing beds at CSUN locality 277 crop out in dipslope exposures just below the ridge top for a distance of only about 20 m. Most of the north slope of the ridge is a talus slope due to the easily erodable nature of the strata. Only one specimen, a nearly complete gomphid?, came from CSUN 276. All the other specimens came from CSUN locality 277. Locality 276 is 67 m stratigraphically below locality 277. The lower 50 m of this 67-m thick section consists mostly of shale with minor interbedded siltstone and fine grained sandstone beds. The upper 17 m consists of siltstone interbedded with silty shale and shale, and three 0.3 m-thick laminated shale beds in the uppermost 2.5 m contain the nymphs of CSUN locality 277. These laminated shale beds appear to be varved. The middle shale bed yielded numerous nymph specimens and associated fish and plant remains, whereas the other two shale beds yielded only a few nymphs and some plant material. The fish are complete specimens of *Empytrichthys* (Shepard, 1961, 1962). Plant

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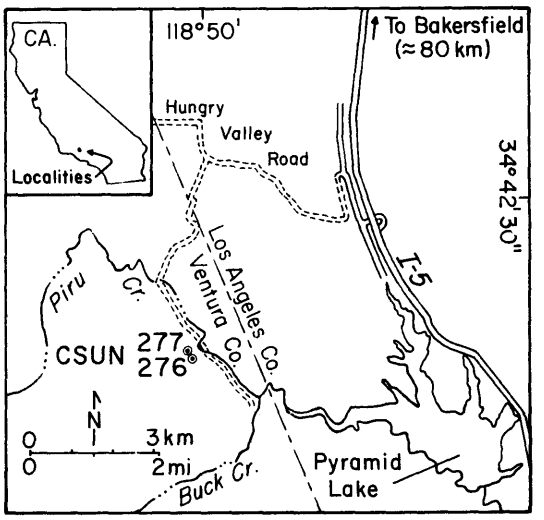
remains include stems of reedlike (aquatic) plants, nodules of presumably seed pod origin, and leaves of various terrestrial plants. Based on comparison with Axelrod's (1950) figured specimens, I was able to identify the following types of leaves: *Acer, Populus*?, *Quercus*? and *Salix*.

A total of 73 dragonfly nymphs were collected at CSUN locality 277. Sixty-six specimens are fragmental and consist only of the abdomen area. No family or generic determinations could be made from any of these specimens. Many occur in clusters, with as many as six specimens on a single bedding plane of a 36 sq. mm slab of rock. Seven specimens, however, are complete, and one is preserved well enough to allow tentative family identification.



TEXT-FIG. 1—California State University, Northridge (CSUN) collecting localities for dragonfly nymphs.

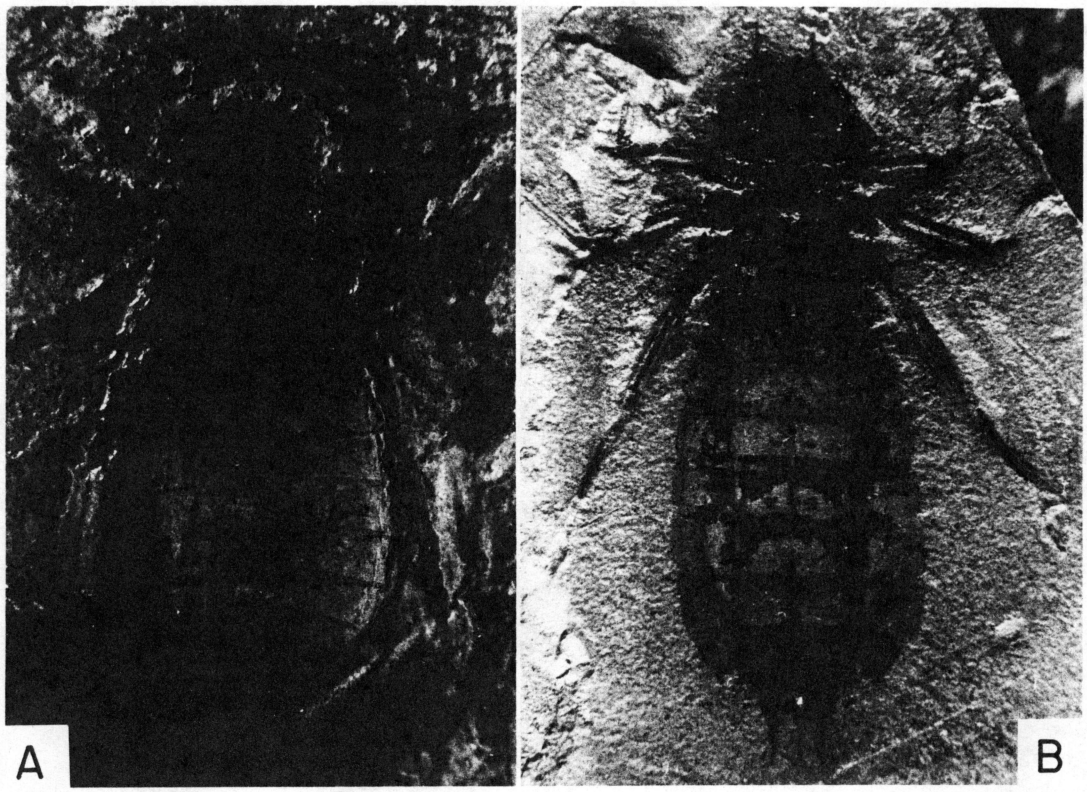
SYSTEMATIC PALEONTOLOGY

Class INSECTA
Order ODONATA Fabricius, 1792
Suborder ANISOPTERA Selys, 1840
Family GOMPHIDAE? Selys, 1850
Text-figs. 2A, 3A

Description.—Elliptical head not markedly wider than thorax. Prothorax distinct, with mesothorax and metathorax consolidated into synthorax. Procoxae closer together at base than equidistant syncoxae; moderately short wing pads; wide subcircular abdomen.

Preservation.—Carbonized impression of ventral? surface of a single specimen in a fine grained, pale greenish gray shale. Total length, 21 mm; head length, 2.5 mm; head width, 4.5 mm; abdomen length, 13 mm; maximum abdomen width, 11 mm. No antennae preserved. Prominent straight lines near front margin of head form an inverted V-shaped feature. Coxa observed on each leg. Procoxae closer together (4 mm) at base than syncoxae which are the same distance apart (5 mm) at their bases. Trochanter observed on each leg. Femur and tibia observed on prothorax legs, right mesothorax leg, and left metathorax leg. Right metathorax leg poorly preserved. Inner margin of lower tibia region of left metathorax leg covered by a row of short spines or hairs. Four wing pads present with longest pair extending to anterior of fourth abdominal segment. Ten overlapping abdominal segments observed with abdomen faintly triquetral and with no lateral hooks preserved. Anal appendages not preserved.

Remarks.—Positive family identification of this specimen could not be made by the use of keys (Wright & Peterson, 1944; Needham & Westfall, 1955; Smith & Pritchard, 1956) for modern dragonfly nymphs. Such keys are based on the nature of the antennae and the mouth parts, but such features are not preserved in this specimen. P. Turner, Jr. examined the specimen and believed that it has enough in common with *Hagenius,* of the Family Gomphidae, to be tentatively identified as such. M. J. Westfall, Jr. concluded that the specimen belongs to the Suborder Anisoptera and that it seems to have the great width of modern *Hagenius*. Based on actual comparison with a modern specimen of *Hagenius,* I observed the following similarities: the wide abdomen, the procoxae closer together than the syncoxae, the presence of a synthorax, and the relatively short wing pads which extend only to the anterior of the fourth abdominal segment (Text-fig. 3A, B). I also believe, based on the lack of prominent dorsal hooks, that the fossil specimen is a ventral surface. The head of the fossil specimen also shows details that are more characteristic of the ventral surface than that of the dorsal surface. A comparison was made between the fossil specimen and the modern specimen with and without its labium. It seems that the labium is missing in the fossil specimen, and, as a result, the out-



TEXT-FIG. 2—*A*, ventral? surface of a dragonfly nymph (LACMNH 5717), Family Gomphidae?, CSUN locality 276, total length, 21 mm; *B*, dorsal surface of a dragonfly nymph (LACMNH 5718), Family Libellulidae?, CSUN locality 277, total length, 32 mm. Both specimens from middle part of Ridge Basin Group, Ridge basin, California.

line of the mandibles is preserved as the observable V-shaped feature. The labium, therefore, is not shown in the sketch of modern *Hagenius* (Text-fig. 3B). Although there are two dark circular areas preserved within the head region, these definitely are not the eyes, which, in the modern specimen, occur along the margins of the head. Thus, if the specimen is a ventral surface, the wing pads must have been impressed onto this ventral surface. Modern *Hagenius* is remarkably flat, and it is conceivable that such an impression could occur during compaction.

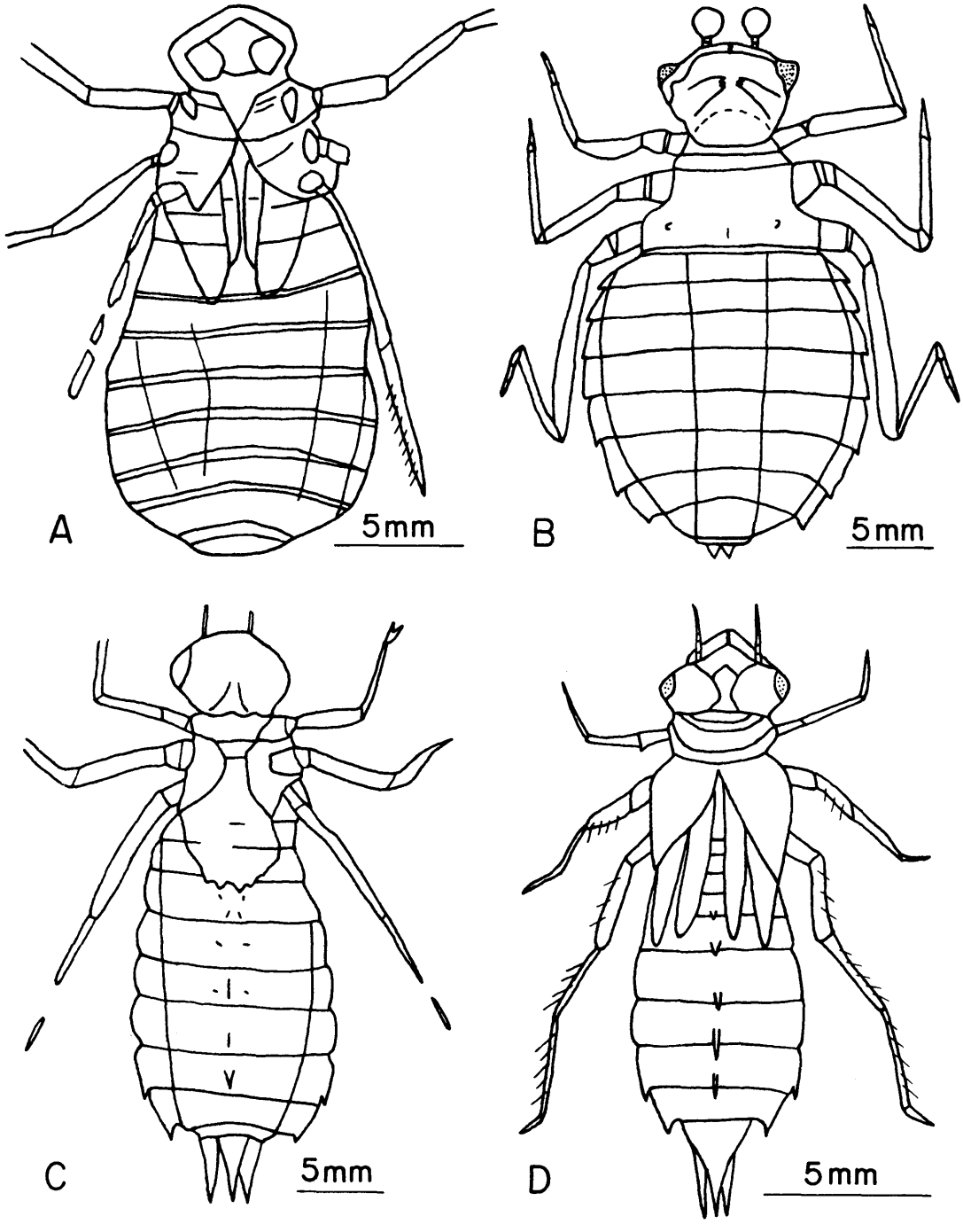
According to Needham & Westfall (1955), the maximum total length of modern *Hagenius* is between 36 and 41 mm. Because the fossil specimen is much shorter and because the wing pads are relatively short, it is apparent that it must be an instar of the middle stages of molting. Also according to Needham & Westfall (1955), there is only one living species of *Hagenius* in North America, *H. brevistylus*. It is widely distributed throughout the eastern half of the United States but does not range any further west than Oklahoma and Texas.

Occurrence.—Middle Pliocene, middle part of the undifferentiated part of the Ridge Basin Group, Ridge basin, California; CSUN locality 276.

Repository.—The specimen (LACMNH 5717) is deposited in the Los Angeles County Museum of Natural History invertebrate paleontology collection.

Family LIBELLULIDAE? Selys, 1850
Text-figs. 2B, 3C

Description.—Broadly rounded head not markedly wider than thorax or abdomen, narrow antennae, uniform width throughout, small eyes more frontal than lateral. Prothorax distinct, apparent consolidation of mesothorax



TEXT-FIG. *3*—Comparative drawings of fossil dragonfly nymphs and similar modern genera. *A,* ventral? view, LACMNH 5717, Family Gomphidae?; *B,* ventral view, labium removed, *Hagenius brevistylus,* Family Gomphidae, Florida; *C,* dorsal view, LACMNH 5718, Family Libellulidae?; *D,* dorsal view, *Ladona deplanata,* Family Libellulidae, Florida.

and metathorax into synthorax. Procoxae approximately same distance apart as syncoxae; short wing pads. Long, triquetral abdomen not markedly wider than thorax and not markedly tapered; lateral hooks on abdominal segments 8 and 9, dorsal hooks on abdominal segments 4?, 5, 6, 7 and 8?; inferior and superior anal appendages same length.

Preservation.—Carbonized impression of dorsal surface of a single specimen in a fine grained, pale greenish gray shale. Total length, 32 mm; antennae length, 2 mm; head length, 4 mm; head width, 6 mm; abdomen length (excluding anal appendages), 16.5 mm; maximum abdomen width, 11 mm; superior anal appendage length, 4 mm. Socket areas of antennae obscured; right eye poorly preserved. Coxa and trochanter observed on prothorax and mesothorax legs. Trochanter regions poorly preserved on metathorax legs. Femur and tibia observed on all legs; claw observed on right side of body on prothorax leg. Poorly preserved, incomplete wing pads extend to anterior margin of fourth abdominal segment. Ten distinct abdominal segments observed with indented margins between segments. Lateral anal appendages not preserved.

Remarks.—As previously mentioned, a positive family identification of a dragonfly nymph is largely dependent upon the nature of the mouth parts. Although the labium is not visible in this specimen, P. Turner, Jr. examined the fossil and believed it has enough in common with *Ladona,* of the Family Libellulidae, to be tentatively identified as such. M. J. Westfall, Jr. concluded that the specimen belongs to the Suborder Anisoptera and that it must be a dorsal view. He thought that the fossil specimen might possibly be related to *Ladona* although he noted that the fossil is larger, has a wider abdomen, and is less tapered than modern *Ladona.* Based on actual comparison with a modern specimen of *Ladona,* I observed the following similarities: the shape of the head, the size and position of the eyes, the size and position of the antennae, the nature of the prothorax and synthorax, the presence of dorsal hooks on segments 4 through 8, the size of the lateral hooks on segments 8 and 9, and the equal lengths of the interior and superior anal appendages (Text-fig. 3C, D). In my opinion, therefore, the fossil specimen is similar to *Ladona.* As pointed out by Westfall, it is uncertain whether the size of nymphs has remained stable through geologic time, thus the larger size of the nymph is not that much of a problem. The wider abdomen of the fossil specimen may be due to compression during preservation. The less tapered nature of the abdomen may be due to contraction of the tenth abdominal segment up into the abdominal cavity just prior to the death of the nymph.

Because the wing pads of the fossil nymph appear to be broken, it is difficult to determine whether or not the specimen is representative of a late instar. If the wing pads are not broken, then the fossil is less than fully grown, as pointed out by Westfall. According to Needham & Westfall (1955), there are only five living species of *Ladona.* Three of these occur in North America and the other two in Europe. One of the North American species, *L. julia,* occurs as far west as Washington, whereas the other two species are confined to the eastern and southern states. According to Smith & Pritchard (1956), *L. julia* does not occur in California.

Occurrence.—Middle Pliocene, middle part of the undifferentiated part of the Ridge Basin Group, Ridge basin, California; CSUN locality 277.

Repository.—The specimen (LACMNH 5718) is deposited in the Los Angeles County Museum of Natural History invertebrate paleontology collection.

BURIAL ENVIRONMENT

According to Crowell (1954, 1975), the middle part of the Ridge Basin Group, in which the nymph-bearing shale beds occur, is nonmarine. Furthermore, Crowell (1975) reported that most of these nonmarine beds were apparently deposited as ". . . broad alluvial fans extending basinward into an intermittent freshwater lake." Such a gradation from lacustrine shale into alluvial fan deposits is readily seen in exposures near locality 277. All of the above is in keeping with known habitats of present-day dragonfly nymphs. Most living species of the Family Libellulidae occur in ponds and swamps (Borror, Delong & Triplehorn, 1976). According to Needham & Westfall (1955), most Libellulidae are sprawlers that live on mud that settles in embayments of streams or lakes. They also reported that *Hagenius* is another sprawler that usually lives among plant debris that collects in the

eddies of woodland streams. *Hagenius,* furthermore, is the only sprawler among the normally burrowing forms of Gomphidae. The occurrence of *Hagenius* in the lacustrine beds of the Ridge Basin Group might be explained by the fact that according to Corbet (1963) many modern species which are normally riverine forms can occur in nearly equivalent habitats along straight margins of large lakes. The nymphs at localities 276 and 277, however, do not occur in beds that were deposited in a shoreline environment. Instead, the nymphs were deposited in quiet water as indicated by the fine grained, laminated shale. The associated plant fragments, which consist of stems of reed like plants and various leaves of terrestrial plants, are definitely transported. The fish, all of which are complete specimens, may or may not be *in situ*. It is also important to mention the noticeable absence of benthic organisms, especially trace fossils, at the localities. If the nymphs were *in situ,* one would expect to find associated lake-dwelling invertebrates or, at least, signs of their activities. It is interpreted, therefore, that the nymphs are transported. Only a short distance of transportation could have taken place in order to account for those few nymph carapaces that are complete. The fragmentary aspect of most of the nymphs cannot be used to prove or disprove the possibility of post molting or postmortem transport because they may be the discarded abdomens of disarticulated larval exuvia. Burial of the nymphs must have been rapid, otherwise scavengers most likely would have obliterated the remains. Because the nymphs at locality 277 occur in several thin bedded, laminated shale beds that seem to be varved, it is possible that the entombing of the nymphs in the lake beds most likely occurred at regular intervals. It is feasible that during runoff from the nearby alluvial fans, the nymphs and plants drifted short distances out into the lake and subsequently were buried rapidly.

LOCALITIES

California State University, Northridge (CSUN) locality numbers.

276—214 m (700 ft) west and 274 m (900 ft) south of NE corner sec. 5, T7N, R19W, Black Mountain quadrangle, 7.5 series, 1958, revised 1974. = LACMIP 16245

277—427 m (1400 ft) west and 198 m (650 ft) south of NE corner sec. 5, T7N, R19W, Black Mountain quadrangle, 7.5 series, 1958, revised 1974. = LACMIP 16246

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