

THE ADULT STAGES OF *PROSOPISTOMA* LATREILLE
(EPHEMEROPTERA), WITH DESCRIPTIONS OF TWO NEW SPECIES
FROM AFRICA.

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Manuscript received 3rd March, 1954.

(Read 5th May, 1954.)

With 22 Text-figures.

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1. INTRODUCTION AND ACKNOWLEDGMENTS.

NEARLY two centuries have elapsed since Geoffroy (1762) described and figured an insect, found in streams near Paris, as *Binoculus haemisphericus*, *cauda foliacea*, *capitis puncto triplici fusco*, "le binocle à queue en plumet". His figures, exact in all important details excepting only the number of caudal appendages, constitute the first remote but recognisable description of this unique aquatic insect. Fourcroy (1785), in listing and applying the binomial system to Geoffroy's species, designated it as *Binoculus foliaceus*. Latreille (1833) separated *foliaceus* from the other Crustacea with which it had previously been aligned, but still regarded it as a branchiopod and created the genus *Prosopistoma* to include both *foliaceum* (as *punctifrons*) and a newly discovered species from Madagascar. Little was seen of *foliaceum* throughout the century that followed Geoffroy's description. In 1868 it was re-discovered by E. Joly, a military surgeon in the French Army who, it is related, found time to collect insects in many rivers of France before and during "the disastrous war" of 1870-71. Joly (1871) and Joly and Joly (1872) were the first to recognise the true nature of Geoffroy's "binocle" as the immature stage of an insect, and correctly assigned it to the Ephemeridae.

The adult remained unknown. In the years that followed, the suggestion was made that reproduction was accomplished in the aquatic phase, and Vayssière (1881a, b) recounted how this prompted him to study the living insect in the laboratory and how this led to the breeding out of the two unique female subimagos in the early summer of 1880. It seems that Vayssière's confidence in announcing the discovery of "l'état parfait" was not fully shared by his contemporaries. Eaton (1884), in his section on *Prosopistoma*, remarked

rather primly that "in accordance with my usual custom, I refrain from passing criticisms upon the work of previous authors", and most subsequent writers have concluded that the real adult, the imago, had not been obtained.

From that date onwards, despite the relative abundance of *foliaceum* in certain rivers of France and its discovery in Sweden, Germany and Czechoslovakia, and despite the finding of other species in Africa and the East Indian Archipelago, no imagoes have been seen. Only after another 45 years could Vayssière (1925) again report the capture of an ill-preserved female trapped in the shuck of a mature nymph bred in his laboratory. The nymph of *Prosopistoma* is set apart from all other Ephemeroptera except *Baetisca* by the limpet-like development of the mesonotum in the form of a carapace, and it differs from this latter insect in several important respects. It has been described in detail by Vayssière (1882, 1890a), Eaton (1884), Lestage (1921) and Lieftinck (1932) and discussed by many other authors, among them Trägårdh (1911), Alm (1918) and Lestage (1925). The female subimago also, even though figured by Vayssière "under very disadvantageous circumstances", as Eaton put it, was shown to differ strikingly from all other Ephemeroptera, and this, coupled with the continued elusiveness of the imago and the male, has helped to create an aura almost of mystery around it.

At the present time, some five or six closely allied species of *Prosopistoma* have been recognised in the nymphal state, distributed as follows :

- P. foliaceum* (Fourcroy), 1785, Continental Europe.
- P. variegatum* Latreille, 1833, Madagascar.
- P. de guernei* Vayssière, 1893, Senegal.
- P. species* Vayssière, 1936 (as *de guernei*), Kenya.
- P. species* Paulian, 1947, Belgian Congo.
- P. woutherae* Lieftinck, 1932, Java ; Sumatra (Ulmer, 1939).

Elsewhere in Africa, nymphs are found in the Kenya Highlands "in nearly all rivers flowing eastwards from Mount Kenya and the Aberdares, at altitudes between 5000 and 6500 feet" (information kindly supplied by Dr. V. D. Van Someren), and in Natal in South Africa (R. S. Crass, *in litt.*). In 1951, nymphs were found by the present writer in the Sigi River in the Eastern Usambara Mountains of Tanganyika. In subsequent years, after attempted rearing in the laboratory had failed, adults of both sexes were bred out in a concrete tank constructed by the riverside, and the evidence this afforded of the emergence season of the adults led to the capture of many others on the wing in nature.

The material obtained in this way forms the basis of the long delayed description of the adult stages of *Prosopistoma* given here. It is hoped that this account may answer some of the questions raised by earlier writers, whose speculations during the three-quarters of a century following Vayssière's discovery have added much to the interest and pleasure of the present studies. In addition, Mr. R. S. Crass has generously asked me to describe the South African nymph discovered by him. He has already bred out a female of this species, and it is to be hoped that further adult material will be obtained in the future.

Reference should be made to the selection of the type species of *Prosopistoma*. Latreille did not indicate which of the two species he considered as

representative of the genus; but it could well be argued either that *variegatum* should be the type as being the insect he had before him at the time, or that *foliaceum* should be chosen on the grounds that Latreille referred to Geoffroy's species as "le prototype de mon crustacé", as well as being the better known and more readily available of the two. Eaton (1884) was the first author to designate a type, and chose *variegatum*. Eaton therefore was free to select either species, and by application of Article 30 of the International Rules this subsequent designation of *variegatum* is not subject to change. Lieftinck's objection that *variegatum* is an undescribed species and therefore invalidated as a type cannot be upheld. This conclusion was apparently based on the specific diagnosis given by Eaton (1884) and ignores the fact that Latreille described it as different from *foliaceum* in terms that, at the time, seemed adequate to him. In addition, Westwood (1877) gave figures of *variegatum* that show the characteristic short antennae, and later Vayssière (1890b, 1893), on the basis of further material, defined the species sufficiently to separate it from both *foliaceum* and *de guernei*. It might be remarked, however, that Eaton's choice was in some ways unfortunate, as *variegatum* differs from three at least of the other species (*foliaceum*, *wouterae* and *africanum*) by possessing the remnant of a sixth gill.

Mention should also be made of the fossil insects described by Brodie (1845) from secondary deposits in England, that were considered by him as having very much the appearance of *Prosopistoma* and by Joly (1871) as "perfectly recognisable" as this insect. There is, however, little to suggest in Brodie's figures that they are other than imperfectly preserved Coleoptera.

A systematic account of the genus and of the two new species from Tanganyika and Natal follows, and the opportunity is taken to re-define the generic characters of the nymph in the light of the greater number of species now known. I must record my indebtedness to Mr. D. E. Kimmins of the British Museum (Natural History) for helpful discussion of several points and to Mrs. C. A. O'Brien for her drawings, reproduced here as figures 1-4.

2. SYSTEMATIC ACCOUNT OF THE GENUS *Prosopistoma*.

Prosopistomatidae Lestage, 1917.

Containing a single genus, *Prosopistoma*, known from the Palearctic, Oriental and Ethiopian regions and Madagascar.

Prosopistoma Latreille, 1833.

Very small mayflies of fugitive adult existence showing marked sexual dimorphism, suppression of the final ecdysis in the female, reduction in wing venation and partial atrophy of the legs; the nymph an inhabitant of lotic environments, with great enlargement of the mesonotum in the form of a carapace, the tails very short and retractile within the abdomen.

Head in male rather wide; antennae exceptionally well developed, their bases approximating to the mid-line and the second segments separated only by as much as their own width; basal segment small, wider than long and mounted on a prominent sub-median pedestal; second segment enormously enlarged and bottle-shaped, its long axis only slightly shorter than diameter of oculus; filament fine, twice length of second segment. Ocelli

large, widely spaced; oculi simple, rather small but nevertheless prominent owing to their origin from stalked lateral projections of the head. Posterior margin of head everted to form a narrow vertical lip extending between the bases of the oculi. Clypeus well formed and prominent from below, in shape rounded and disc-like and projecting forwards ventral to, and appearing between, basal antennal segments.

Head in female lacking posterior marginal lip. Antennae small, widely separated and on basal pedestals; first segment small, second segment shaped as in male but much smaller. Eyes small.

Male thorax.—Pronotum short, considerably broader than long, saddle-shaped; prosternum very wide. Mesonotum squat, ratio of length: breadth 1.3:1; scutellum prominent, forming a well-developed median projection. Fore legs short; coxite prominent and rotated outwards; trochanter elongate and projecting laterally; femur flexed at trochanteric joint so as to emerge on the dorso-lateral aspect of the thorax, tibia held in reversed flexion at femoral joint so that the tibia and tarsus are directed backwards, above and lateral to the notum; proportions of femur: tibia: tarsus 3:2:1; tarsus with two segments, the first completely fused with the tibia and discernible only as a constriction; claws apparently fused to form a single functioning structure. Mid and hind legs partly atrophied, hind legs slightly the longer; femora attenuated and sharply bent distally; effective length of femora about equal to tibiae and three times that of tarsi, these with two segments and poorly differentiated claws. Wings four, membrane slightly opalescent and reinforced with a system of longitudinal creases associated with the main veins; wing margin fringed with fine hairs. Fore wing relatively wide and evenly rounded, ratio of length to maximum breadth 1.8:1; venation greatly reduced, forks of all long veins detached at wing root except main fork of R_1 ; distal portion of R_2 weak and detached, main trunk of R_2 being transferred apparently to another vein from the R_1 complex; all remaining eight veins simple, with regular alternation of high and low veins; cross veins entirely absent but in stigmatic area a feeble longitudinal thickening of the membrane visible. Hind wing small, obovate and with prominent right angled costal spur; main veins ill developed, simple and interspersed with fine creases; wing fringe extending on to distal one-third of anterior border, i.e., as far as termination of R_1 .

Female thorax.—Pronotum relatively large; mesonotum broad, ratio of length: breadth 1.1:1, this broadness accentuated by the enlarged lateral processes of the pronotum; notum in lateral view humped, the mesonotum with a distinct median keel broadening out anteriorly into a sharp beak that overlaps the pronotum. Legs partly atrophied; femora normal, tibiae and tarsi fused to form an indefinite remnant. Fore wing narrower than in male, basal third of posterior margin being parallel to anterior margin and ratio of length to maximum breadth 2.2:1; longitudinal veins more strongly developed and wing membrane entirely without creases; distal portion of R_2 not detached (as in male) but failing to reach apex of wing and less strongly developed than the lower branch which extends right up to wing margin. Hind wing narrower and costal spur less prominent than in male; longitudinal veins distinct, forming three main series with moderately deep forks.

Abdomen in male elongate, tapering and feebly chitinised; first segment inapparent, postero-lateral margins of seventh to ninth segments produced backwards as spines; ninth segment wider in antero-posterior diameter than preceding segments, the genital forceps arising from a small protuberance on its ventral aspect; these rather stout in dorso-ventral aspect, thin and attenuated in lateral view; with three segments, basal segment broad, second segment twice as long as first and swollen at apex, third segment broad and pyriform and arising from inner aspect of second segment below the apex so as to leave a broad notch between the tips of the two segments. Penes simple, fused except at tip and arising somewhat posterior to forceps base, so that, although appreciably shorter than the forceps, yet appearing to extend almost to distal forceps segments. Tails three, the median subequal, about half body length and covered with relatively long, coarse setae.

Abdomen in female extremely short and stumpy; first segment inapparent, sixth segment rather deeper than the rest, seventh and eighth tergites with acute postero-lateral spines;

ninth sternite extending backwards to form a broad, entire subanal plate, overlapping tenth segment. Tails three, the median subequal, only equalling about one-tenth of body length and lacking coarse marginal setae.

Male subimago much as imago. All legs apparently functional; fore coxite on ventral aspect of sternum and not rotated outwards, mid and hind femora straight. Wing venation and membrane creases as in imago. Abdomen much shorter, tergal spurs shorter and blunter; genitalia well differentiated but stumpy. Tails equalling about one-tenth of body length.

Head of nymph flattened and narrow; antennae with five segments, second segment the longest. Mouthparts bounded below by the mentum, which is enormously enlarged and plate-like, bearing a deep median notch in front below the labium; labrum small; mandibles tapering to a heavily chitinised, narrow, tri-dentate outer canine, inner canine¹ rather smaller, cylindrical and bi-dentate, bearing at its base a number of long fine setae; molar region of mandible absent; lacinia of maxilla heavily chitinised and terminating in four very strong curved spines, from the base of which a number of long, finely serrated hairs arise; inner border of lacinia with a single very small seta; maxillary palp slender and with three segments, the second segment the longest; labium a simple fused plate, narrower at its base and chiselled out along the lateral margins so as to fit snugly into the median notch of the mentum; labial palp slender with three segments, basal segment the longest or subequal to second segment; hypopharynx absent.

Thorax.—Mesonotum enormously enlarged to form a rounded carapace, convex above with a narrow median ridge and flattened lateral flanges; anterior margin excised to fit closely with head, posterior margin straight or concave and overlapping abdomen as far as base of seventh tergite, its mid point shallowly excised to mark the exhalant aperture of the branchial chamber. Wing buds enclosed within carapace. Underside flattened, prosternal suture well marked, suture between meso- and metasternum absent; coxites arising from shallow depressions which extend backwards and receive the femora when folded. Hind leg rather the longest; fore femur bearing a few very small spines, fore tibia with an armature of serrated spines on the distal half, or rather more, of the inner surface; other legs lacking spines, claws simple and slender.

Abdomen overlapped anteriorly by notal carapace; first segment not distinguishable, second to sixth tergites forming floor of branchial chamber, posterior margin of sixth tergite raised up to form a ridge fitting closely with the posterior margin of the carapace; second to sixth sternites fused with, and completing, the flattened undersurface of the carapace, two inhalant slits present at the junction of the notal flanges with the lateral borders of fourth and fifth sternites. Gills five in number (six in *P. variegatum*), overlapped above by hind wing buds; first gill narrow and ribbon-like, inner border intersected by long digitate processes, second gill a large rectangular lamella overlying third to fifth gills, which are small and each composed of 6–10 fine digitations. Lateral margins of seventh and eighth segments produced backwards as broadish flattened spines; ninth segment narrow and tubular above, broad, flattened and projecting backwards below, with lateral margins flattened and projecting but fused behind with the sternite; tenth segment very small, sternite split almost completely down the mid-line, retractable within the ninth segment. Tails three, equalling about one-seventh to one-eighth of body length and heavily fringed with long hairs on inner and outer borders.

Type species: *P. variegatum* Latreille.

***Prosopistoma africanum* sp. n. (figs. 1–3, 5–16, 18, 20, 22).**

Male imago (fresh). A delicate, mainly white insect. Head sooty; basal half of second antennal segment amber, distal half reddish-brown; eyes black. Pronotum sooty, meso-

¹ Considered by some authors to be the prostheca or lacinia mobilis.

notum and sternites sandy brown; in front and slightly below anterior wing root is a small, sharp horizontal projection made conspicuous by its dark brown colour; recurrent membrane of wing extending as a fine, filamentous projection from the tip of the scutellum as far as the base of the fifth tergite. Fore leg purplish-brown throughout, anterior border of femur marked by a line of 18-22 delicate, recurved hairs; anterior margin of tibia rugose. Wings generally opalescent, this more marked and tinged with purplish-brown in costal and subcostal areas and basally; main veins pale; costal process of hind wing tinged with brown. Abdomen white and distended with air; terminal segments in life tinged with pink, apparently imparted by the contents of the seminal vesicles. Forceps white; penes simple, strongly tapered, particularly in the antero-posterior plane, terminating in a narrow bifid apex; penis tips separated by a median notch extending to about one-third length of penes ventrally but dorsally to only half this distance. Tails white.

Female adult (subimago). A short, squat, sombrely-coloured insect. Head and thorax dark purplish brown; antennal segments brown, filament colourless. Wings generally milky, anterior and basal areas tinged with brown; veins dark brown. Recurrent membrane projecting beyond scutellum as in male. Abdomen and tails dark brown, the former tinged with yellow from the enclosed eggs.

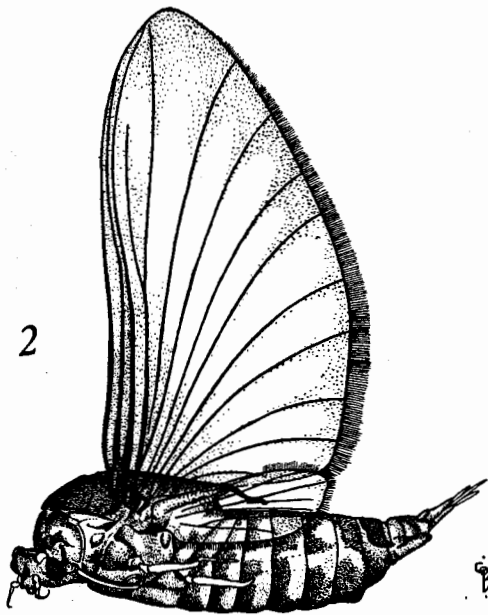
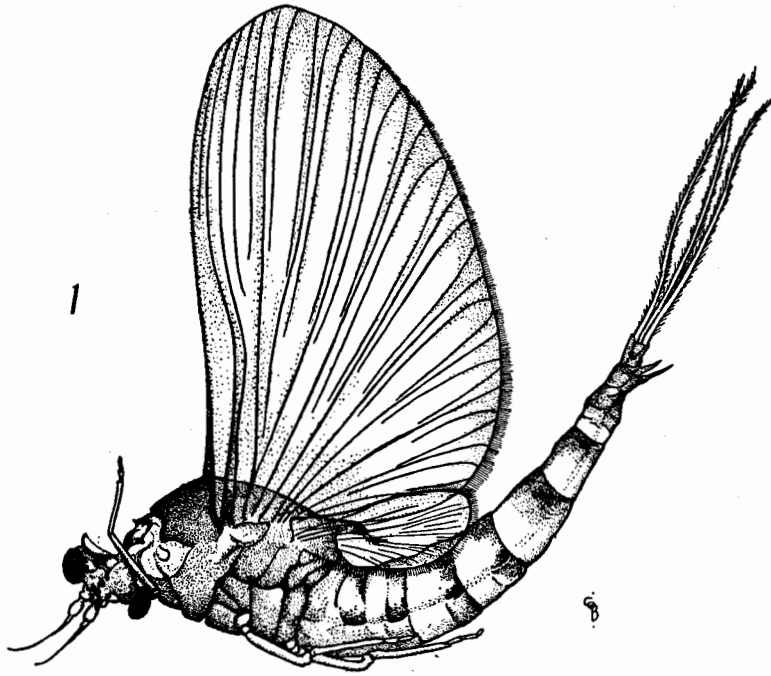
Male subimago.—Colouring much as in imago. Fore leg brownish mauve, the femur lacking marginal fringe of hairs and the tibia not rugose; other legs colourless. Wings slightly more cloudy than in imago, borders rather more heavily fringed. Abdomen and tails white.

Nymph.—General colour in life chestnut brown with paler markings; carapace marked with a pair of pale lateral spots at the junction of mid and posterior thirds and usually with an additional pair of pale dashes on either side of the mid-line between the outer spots; integument finely pitted. Antennae moderately long and extending beyond anterior margin of head; second segment cylindrical and shorter than third to fifth segments together. Outer canine of mandible slender with 4 or 5 fine teeth on inner margin below apex, inner canine with 4 fine teeth below apex; 3 hairs arising from base of inner canine, the two distal hairs with the finest possible serrations, third hair apparently simple, and a single long hair arising from the middle of the outer border of mandible; sub-apical area of lacinia of maxilla with 3 simple hairs, none serrated; anterior lip of labium without hairs but very finely corrugated in median area, basal segment of labial palp about twice length of second segment; anterior margin of mentum finely corrugated, except in median notch, and clothed in extremely fine hairs. Thoracic carapace relatively narrow and lateral flange reduced, length along median ridge 1.1 times maximum breadth. Legs: anterior margin of fore femur with a line of short hairs with the finest possible serrations; fore tibial armature composed of 6-7, occasionally 5 or 8, spines each bearing 9-10 fine teeth on inner margin, the most distal spine being one-and-a-quarter to one-and-a-half length of preceding spine; fore tarsus occasionally with one or two simple spines.

Body length: male, 4.8 mm., female, 3.6 mm., male subimago, 4.2 mm. *Wings:* male, 3 mm., female, 4.5 mm. *Tails:* male 2.4 mm., female 0.3 mm.; male subimago, 0.4 mm. *Nymph,* total length, mature male, 2.8-3 mm., female, 3.5-4 mm.

EAST AFRICA, TANGANYIKA: Sigi river, Amani (5° 5' S., 38° 40' E.), iv.1951 to vi.1953. The material comprises 46 male imagines, 1 male subimago, 6 females and about 70 nymphs. The holotype (nymph) and a series of adults and nymphs have been presented to the British Museum (Natural History).

This species differs from *crassi* and *de guernei* by the carapace length being equal to or greater than its maximum width, and from *variegatum* by the greater length of the antennae. It is closest to *Prosopistoma* sp. Paulian, from which it differs by the second antennal segment being shorter than segments 3-5 together, by the character of the fore tibial armature, the proportions of the segments of the labial palps and by the unserrated hairs in the maxillae. The

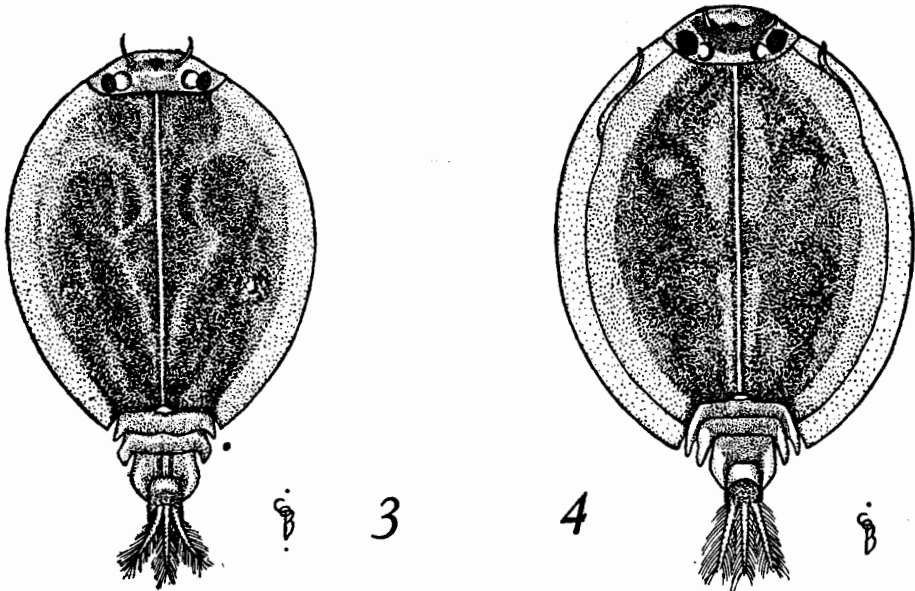


FIGS. 1-2.—Adults of *Prosopistoma africanum* sp. n. (1) ♂ imago ; (2) ♀ subimago.

female adult apparently differs from that of *foliaceum* by the extension of the recurrent wing membrane some way beyond the tip of the scutellum.

***Prosopistoma crassi* sp. n. (figs. 4, 17, 19 and 21).**

Nymph.—A moderately large species, pale greenish-brown when preserved in spirit; carapace marked with a pale lateral margin round inner side of flange, rest of area dark except for one or two indefinite pale areas along median suture, the posterior such area being much the smaller; integument finely pitted. Antennae short, not quite reaching anterior margin of head; second segment cylindrical and about as long as third to fifth segments together. Canine region of mandible strongly developed, 2 small heavily chiti-



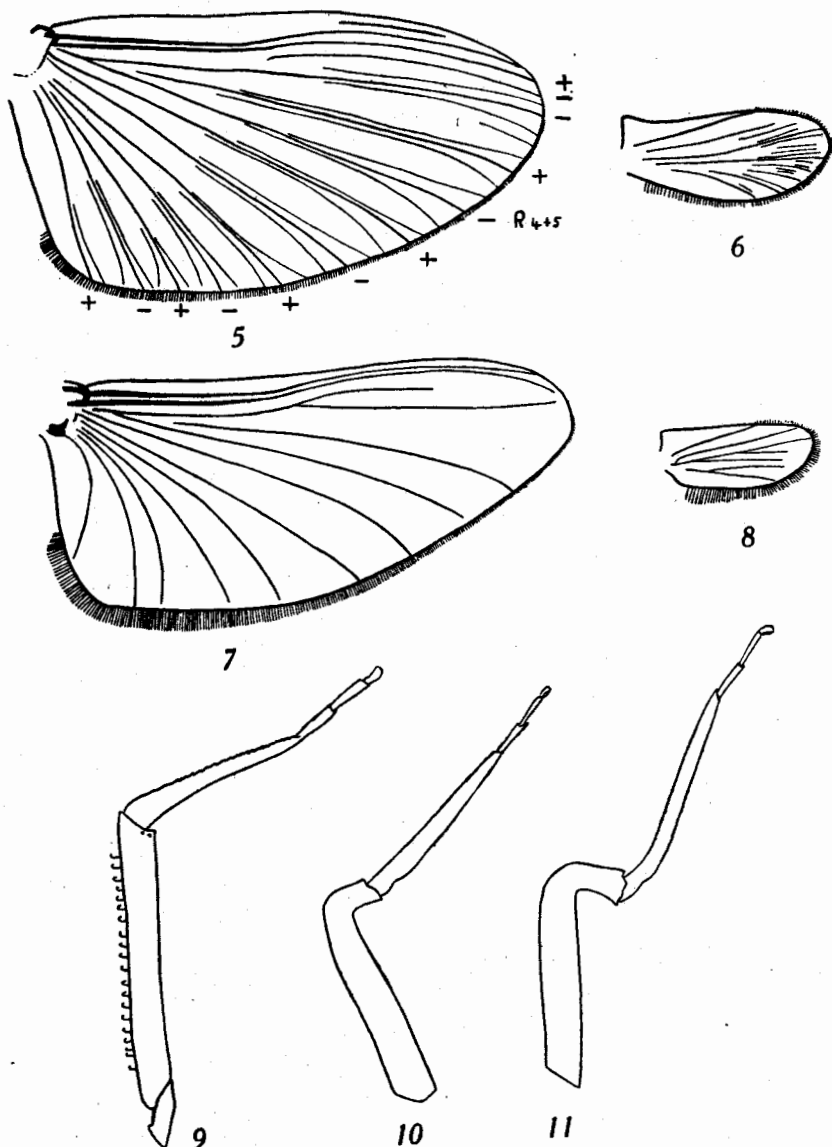
FIGS. 3-4.—Nymphs of *Prosopistoma*. (3) *P. africanum* sp. n.; (4) *P. crassi* sp. n.

nised teeth on outer margin immediately below apex of outer canine, inner margins of both canines with 1-2 fine sub-apical teeth, 2 long and 1 short hair arising from base of inner canine, all coarsely serrated, and a single long hair arising from outer margin of mandible; lacinia of maxilla with 3 slender hairs, none serrated (or so finely serrated as not to be detectable); anterior lip of labium without hairs or corrugations, basal segment of labial palp about twice length of second segment; anterior margin of mentum finely corrugated, except in median notch, and clothed with extremely fine hairs. Thoracic carapace broad and lateral flange well developed, length along median ridge 0.8-0.9 times maximum breadth. *Legs*: anterior margin of fore femur with very fine unserrated hairs; fore tibial armature composed of 8-10 spines each bearing 7-9 teeth on inner margin only, the most distal spine not longer than preceding spines. Abdominal tergites sparsely covered with very fine hairs, lateral processes of seventh and eighth segments rather long and posterior margins of these processes coarsely corrugated.

Total length (mature nymph, probably female) 5.5 mm.; maximum width 3.5 mm.

Holotype nymph, 2 paratypes, SOUTH AFRICA, NATAL: Umgeni river (29° 30' S., 30° 30' E.), 1200 feet, xii.1953, (*R. S. Crass*). 1 nymph, Tugela ferry (28° 75' S., 30° 30' E.), 12.xi.1953 (*W. D. Oliff*). Holotype in British Museum (Natural History).

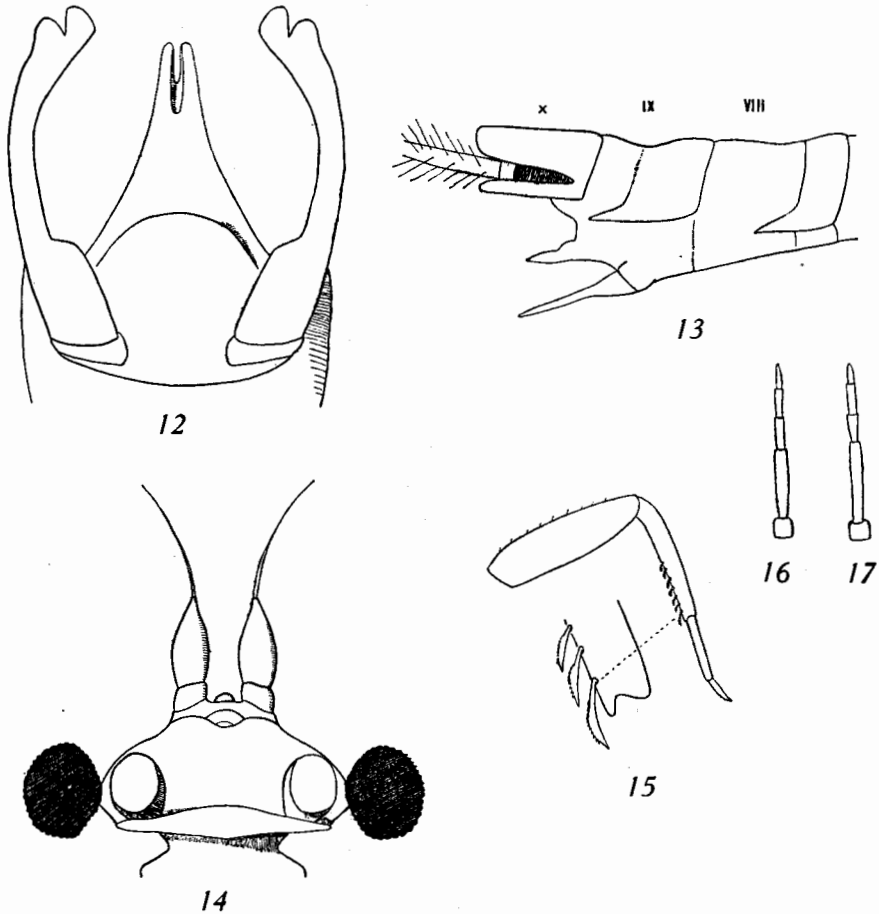
This species differs from all other *Prosopistoma* except *de guernei* by the width of the carapace exceeding that of its length. From *de guernei*, which



FIGS. 5-11.—Details of *P. africanum* adults. (5) ♂ fore wing; (6) ♂ hind wing; (7) ♀ fore wing; (8) ♀ hind wing; (9) ♂ fore leg; (10) ♂ mid leg; (11) ♂ hind leg.

was described from a single immature nymph, it should be distinguishable by the much shorter antennae. It was discovered some years ago by Mr. R. S. Crass, for whom I have pleasure in naming it.

With the list of species of *Prosopistoma* described from the nymph now amounting to seven, it is possible to assess the value of some of the taxonomic



FIGS. 12-16.—*P. africanum*. (12) ♂ genitalia from below; (13) ditto, lateral view; (14) Head, ♂ imago; (15) Nymph, fore leg; (16) Nymph, antenna; (17) *P. crassi* nymph, antenna.

characters used. The relative proportions of the carapace are clear cut and easily measured, and it has been observed in *P. africanum* that the ratio of length to breadth is remarkably constant even in the smallest nymphs (1-1.5 mm.) measured. For this reason, Vayssière's conclusion (1936) that the breadth of the carapace in the type specimen of *de guernei* from Senegal was simply the result of its immaturity, and that the specimens with quite different dimensions from Mount Elgon in Kenya were attributable to the same species, cannot be accepted. The Kenya species must be considered distinct and as yet inadequately described.

The markings on the carapace are also important and will probably be found to be distinctive once a sufficiently large series of each species is available. In over 50 *P. africanum* examined, the two lateral pale areas were nearly always present, and it was only in completely mature specimens that these markings were occasionally obscured by the dark colour of the adult within. On the head, the total length and proportions of individual segments of the antennae form another easily determined character, although in *africanum* occasional apparently malformed specimens are seen with only four segments. Similarly, the character of the fore tibial spines—"armature" seems an appropriate term—is also very valuable. In all except the very smallest specimens of *africanum* their number was constant at 6-7 or occasionally 5 or 8 spines, and within certain limits their number alone may be a useful guide. In addition, the presence of teeth on one or both sides of the spines, the number of teeth on each spine and the relative length of the ultimate spine all seem to vary between species. In the mouthparts, useful characters may be found in the number of teeth on the stalks of the canines, the number and serrated nature of the accessory hairs on the mandibles and maxillae and the proportions of the different segments of the maxillary and labial palps.

It is clear that many characters are available for the separation of the nymphs of this genus, while the ease with which the adults may be separated is still to be discovered. For this reason, the nymph has been designated as the holotype of *africanum* and no hesitation was felt in describing and naming *crassi* from nymphal material alone. The following key has been prepared and may be of value as a provisional guide to the African fauna as known at present.

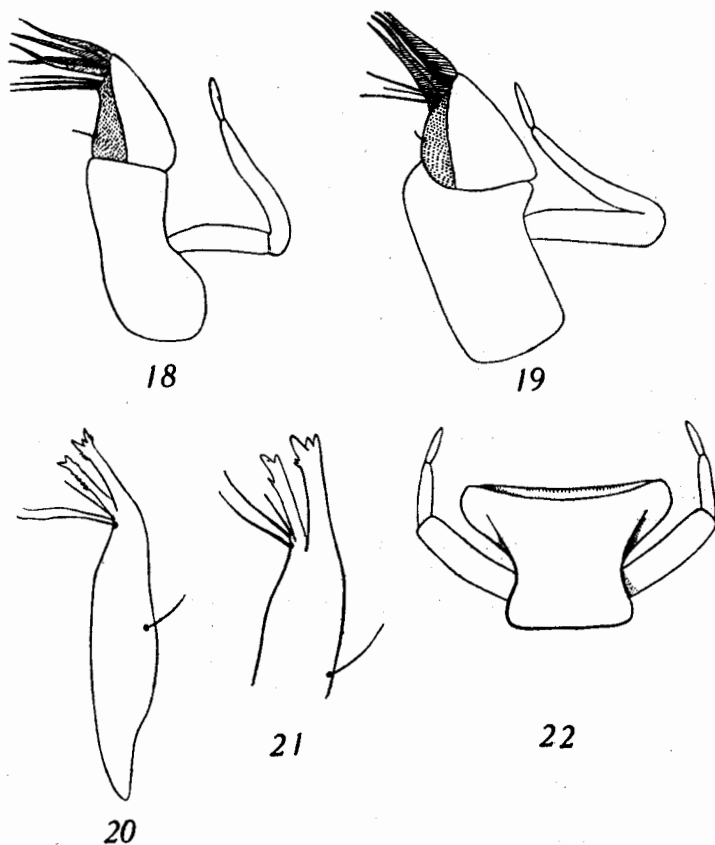
- 1. Carapace length along median suture equal to, or greater than, maximum width 2
- Carapace length less than maximum width 4
- 2. Antennae longer than distance between base of antenna and anterior margin of head 3
- Antennae shorter than distance to anterior margin of head (Madagascar) **P. variegatum**
- 3. Second antennal segment shorter than segments 3-5 together, fore tibial armature composed of 5-8 spines **P. africanum**
- Second antennal segment longer than segments 3-5 together, fore tibial armature composed of 10-12 spines **Prosopistoma** sp. Paulian
- 4. Antennae longer than distance between base of antenna and anterior margin of head **P. de guernei**
- Antennae not longer than distance to anterior margin of head **P. crassi**

3. TAXONOMIC FEATURES OF THE ADULT *Prosopistoma*.

Many unusual taxonomic features are displayed by the adults of *Prosopistoma*. It may be convenient to discuss some of these in greater detail.

Sexual dimorphism.—While the suppression of the final ecdysis in the female undoubtedly accentuates the differences between the sexes, *Prosopistoma* shows a far greater degree of dimorphism than has hitherto been recognised within the order. Differences in the eyes, legs and abdominal appendages are usual amongst the Ephemeroptera, but only in *Tortopus*, Traver (1950), and to a lesser extent *Campylocia*, Ulmer (1942) and Spieth (1943), do these extend

to the wing venation. But in *Prosopistoma*, the wings are quite different in both shape and venation in the two sexes. In the forking of the R_s complex in the fore wing, R_2 is detached but complete in the male, intact but incomplete in the female, and the strongly formed veins of the female contrast with the feebler venation of the male, a weakness apparently compensated for in the male by the development of "creases" parallel to the main veins. The shape and venation of the hind wings are even more divergent. No less striking



FIGS. 18-22.—Mouthparts of nymphs. (18) *P. africanum*, maxilla; (19) *P. crassi*, maxilla; (20) *P. africanum*, mandible; (21) *P. crassi*, mandible; (22) *P. africanum*, labium.

is the short, plump body of the female, four-fifths or less the length of each wing, and the long relatively insubstantial body of the male, which is more than one and a half times the length of the wings.

Antennae.—The extraordinarily large and bottle-shaped second antennal segment in the male is almost without parallel in the order. The same organ in the female, well figured by Vayssière (1881*a, b*), is of similar shape, but much smaller and the antennae have not converged towards the mid line.

Legs.—As far as can be made out, the peculiar conformation of the fore legs of the male imago has resulted from the following structural modifications: (i) prominence and outwards rotation of the fore coxite; (ii) slight elongation and lateral projection of the trochanter; (iii) fixed flexion of the femur at the trochantero-femoral joint, and (iv) reversal of the femoro-tibial joint. In this way, the legs project onto the dorso-lateral aspect of the thorax and are apparently incapable of extension in any other direction. This is presumably an adaptation for mating. In most Ephemeroptera in which the male seizes the female from below, the legs are elongated and curve backwards over the head, Needham, Traver and Hsu (1935, fig. 13); but the male of *Prosopistoma* appears to achieve the same power of grappling with quite short legs by bringing them up on either side of the thorax, surely a unique type of specialisation! Observation of the actual mating position assumed would be valuable.

Wings.—The wings are characterised by the elimination of all cross veins and the deepening and detachment of all forks beyond R_s , so that all veins behind this are simple and a very perfect system of fluting has developed. Thus interpretation of the homologies of the main veins posterior to the sector fork is difficult. The simple alternation of high and low veins makes clear that this pattern has not simply resulted from the disappearance of intercalary veins to leave the main branches of MA and MP intact. It is suggested tentatively that IMA and MA_2 (using the system of nomenclature outlined by Tillyard, 1932) may have been lost and that the veins represented posterior to R_{4-5} are respectively MA_1 (+), MP_1 (—), IMP (+), MP_2 (—), CuA (+), CuP (—) and A_1 (+). In the hind wings there is also great reduction in venation, but less so in the female than in the male, in which the intermingling of fine veins with creases in the membrane makes interpretation almost impossible.

The wing membrane in the male is unique for the development of a system of longitudinal thickenings or "creases" in association with the main veins. Their distribution is very constant, but their precise structure or origin for the moment remains obscure. It is possible that they are similar to the creases observed in certain Diptera, for example Blepharoceridae or Deuterophlebiidae. On the other hand, the rather broader longitudinal band of thickening in the stigmatic area in the male may perhaps have been derived from anastomosis and fusion of marginal veinlets.

Abdomen.—The final ecdysis in the male is accompanied by lengthening of the abdomen. The distension of the gut with air and the extreme thinness and delicacy of the integument suggest that some degree of extension and thinning of the segments occurs at this stage. The first abdominal segment cannot be distinguished for certainty in either sex, but the possibility of its existing as a narrow basal ridge cannot be excluded. The forceps appear quite stout when seen from below but in lateral view it is seen that the terminal segments are thin and flattened. The penes are apparently fused except at the extreme apex.

Comparison of the female of *P. africanum* with Vayssière's description of *foliaceum* shows that there is close similarity between the two forms and that his figures and description of all organs, with the notable exception of the wings, must be accepted as accurate and adequate. As suggested by him, and confirmed in the present work, there is every reason to believe that the subimago is the ultimate stage in the female, and he was therefore perfectly correct in his claim to have discovered the "perfect state" of that particular sex.

4. SYSTEMATIC POSITION OF *Prosopistoma*.

Prosopistoma is a specialised mayfly, long separated from the main stem of development of the Ephemeroptera. As specialised features one may mention the antennae in the male, partial atrophy of the legs with reduction in the number of tarsal segments to two, the extreme simplification of the wing venation and the complete elimination of all cross veins, the fused penes and reduction in the length of the tails. The structure of the nymph is well known and one need only mention the mesonotal carapace, branchial chamber and retractile tails as evidence of its specialised character.

Apart from a superficial resemblance of the adults to *Caenis*—a resemblance which is not confirmed by close examination of any individual structure—*Prosopistoma* is quite remote from the adults of all other Ephemeroptera. It only remains to consider how far the undoubted similarity of the nymphs of *Baetisca* and *Prosopistoma* is paralleled in the adults and whether these affinities reflect genuine phylogenetic kinship. Lestage (1917), on the basis of nymphal characters, placed both these insects in the same group of Cryptobranches, and Lameere (1917), a few months later, was also so impressed by the similarities between them that he placed them together in the same family, Prosopistomidae. Apart from nymphal structures, he considered that certain characters in the wings of the adults indicate their common origin. He mentioned, in particular, the shape of the wing with long posterior border and basal position of the anal angle, the closely parallel course of CuA, CuP and A_1 before their termination *distal* to the anal angle and the fact that this last character is found in no other recent Ephemeroptera. These arguments cannot, however, be fully accepted now. The male wing resembles in shape that of *Caenis* as much as *Baetisca*, and, in interpreting the homologies of the veins of *Prosopistoma*, Lameere was misled by the indefinite nature of Vayssière's figure of the wing to locate the veins posterior to R_2 too far forward, so that the last vein called by him fourth anal was, in fact, the third anal (= A_1); this terminates, in the female, posterior to the anal angle and thus differs from *Baetisca* and resembles other Ephemeroptera. But it is true, nevertheless, that CuA and CuP run a more or less parallel course in both these insects and in no other mayflies except the fossil *Hexagenites*, figured by Eaton (1871) and Handlirsch (1908). In other respects the wings show wide differences and, apart from a superficial similarity between the genitalia of the two genera, the adult stages of *Baetisca* and *Prosopistoma* show few signs of close relationship.

The nymphs on the other hand have many structural features in common, notably a mesonotal carapace, branchial chamber and the cephalisation of the central nervous system, and these have been regarded as evidence of the close relationship of the two forms. The relationship does not, it should be noted, extend to at least one important taxonomic character—the mouthparts. The general facies of the adults suggests to the present writer that the relationship between the two forms is remote. Nevertheless, it is hard to see how the simultaneous development of similar structures in the nymphs and in the wings of the adults, as shown by the unique arrangement of the cubital veins, could result from the parallel development of two distinct stocks under the influence of similar environmental pressures. For this reason, it must be concluded that

both forms are derived from a common stock of great antiquity, but that since then evolution and specialisation have proceeded independently.

5. BIOLOGY OF *Prosopistoma africanum*.

P. africanum is relatively abundant in streams belonging to the Sigi River system of the Eastern Usambaras. These mountains form a narrow range of ancient crystalline rocks, bounded by steep escarpments, some 20–30 miles inland from the East African coast at Tanga; they rise to a maximum height of between 4000 and 5000 feet. They are noted for the luxuriance of the rain forest that covers much of the uncleared areas and for the presence of relict and endemic elements in the fauna and flora (Moreau, 1935, 1952). *Prosopistoma* nymphs occur in some of the smallest streams as little as one or two feet across, as well as in the main Sigi river, and have been found at all altitudes between 700 and 2800 feet; the former figure, it may be noted, is now near the lower limit of the forest. They were found in greatest numbers in the 1500–2200 feet zone of the main river, but they also occurred not uncommonly in an overgrown forest stream at the lower altitude limit in water in which hot season temperatures of 80–84° F. were regularly recorded.

The nymphs harbour on the underside of rocks or under quite small stones at depths varying from 2 inches to 3 feet, in reaches where the current is rapid or moderate and where sand and silt are not deposited. As a rule they are not found in the most torrential stretches, but their presence at greater depths or under rocks too big to move cannot be excluded. The catching of 10–12 nymphs in the course of an hour's searching was considered to indicate local abundance, but it was not unusual to turn over many rocks without result and then to find several nymphs close together under the same stone. Other insects associated with them included *Euthraulius* (an undescribed species), undetermined Baëtidae, Psephenid larvae, *Helicopsyche* and *Neoperla*. *Prosopistoma* nymphs were found at all times of the year and it is possible that the emergence season varies with altitude. Mature nymphs were, however, found in June at 900 and 1500 feet and in January at 700 and 2200 feet. Their tolerance to static water in the laboratory is surprising; specimens can often be kept alive in corked specimen tubes overnight with only few deaths, and one nymph survived for two weeks under these conditions without even the water being changed. No evidence was obtained about their feeding habits, but, as Lestage (1925) pointed out, their carnivorous potentialities must still be considered unproven. Doubts might also be raised over the frequently repeated statement that *Prosopistoma* is an active and efficient swimmer. It is true that in captivity the nymphs swim with elegance and rapidity, and it is a pleasure to watch their active gyrations when first captured and placed in still water. But anyone who has watched their helplessness when placed in a gauze cage in running water must be struck by the ill adapted nature of such a flattened bodily form to free swimming in a current, and it seems unlikely in nature much use is made of this form of progression.

The capture of the first adults was facilitated by the fortunate chance that the first serious attempt at breeding out from nymphs coincided with the emergence season at the 2000 feet level (water temperatures from a few observations 70–75° F.), where a natural swimming pool in the Sigi river at the base

of a waterfall provided a convenient and attractive site for collecting nymphs. These were transferred to a gauze breeding-out cage maintained in a small concrete tank constructed by the side of a stream at Amani (2900 feet) and fed with water direct from it. The first adult emerged within a week, and during the course of a month three females and a male were bred out in this tank and another male (a subimago) obtained in the laboratory. During the months of January and February ten visits were made to the river in the vicinity of the swimming pool, at and soon after dawn, and on seven mornings adult *Proso-pistoma*, mostly males, were caught on the wing over the river. Adults were only seen during the 45 minutes immediately following daybreak, between 06.15 and 07.00 hours (East African Standard Time), and it seems likely that emergence is at dawn and that their entire adult existence is encompassed within this short period of time. Females obtained from the emergence cage showed no inclination to shed the subimaginal pellicle and were identical in appearance with those caught on the wing in nature. These wild caught females fluttered without intermission after capture until water was introduced into the tubes that confined them; this led to the instant deposition of eggs. Thus it is practically certain that the subimago represents the final adult female and that they are precluded by atrophy of the legs from ever settling again or from indulging in any other activity beyond this single nuptial flight. There was, it may be added, no evidence that the pellicle was shed in flight.

The first male to be obtained was found in the emergence cage trapped by its wings in the subimaginal shuck. A second male bred in the laboratory in a specimen tube was unable to escape and died still a subimago, thus establishing the existence in the male of the normal subimaginal and imaginal phases. All males caught in nature were imagines. They fly with a peculiar jerky side-to-side motion, quite unlike the usual graceful dancing of mayfly spinners, and form close-knit little swarms from 6 to 12 feet above the river, that drift slowly down stream and are often hard to see in the early morning light. Occasional individuals are seen at lower levels. After capture, like the females, they continue their efforts to fly, their fore legs held grotesquely above and beside the thorax.

The adults, particularly the males, are extremely delicate insects and their bodies rapidly become dried up and shrivelled. In collecting material, it was found necessary to wait until a number of specimens had been collected in the net at one time before tipping them all without handling direct into 70 per cent. spirit. Similarly, in examining material under the microscope, dense mounting media such as balsam or polyvinyl alcohol cannot be used for examining the abdominal appendages, owing to the crushing and distortion that results.

Eggs were obtained from one or two females caught in nature. These were yellow in colour, not much longer than broad and with a rugose and apparently sticky outer layer of, or secretion from, the chorion. This layer appeared to be detachable and was absent from one pole of the egg in all specimens examined. With this qualification, the general appearance is much as figured by Vayssi re (1881*a, b*). They are laid separately, but tend to stick to the bottom and to each other subsequent to laying and rapidly become covered with detritus. Egg batches were kept in bowls of water in the laboratory for up to two months without hatching of larvae being observed.

This inevitably superficial study of the biology of *P. africanum* has shown that in behaviour it does not differ in any major respect from other Ephemeroptera. It shares with *Palingenia*, Schoenemund (1930), but not apparently *Campsurus*, the suppression of the final ecdysis in the female. Morgan's account (1929) of the mating flight in the latter genus is not quite clear on this point. While the total limits of the flight period for the species as a whole are very restricted, it is possible that the life of an individual *Prosopistoma* is not very much shorter than, for instance, *Caenis*. If this same flight period is common to other species, it might be suggested that adults of *foliaceum* should be sought soon after daybreak in early summer over the rivers of Europe where nymphs have been found. The presence of *africanum* in small streams, and the abundance and relative hardiness of the nymphs, have undoubtedly simplified the study of this species, and this has made it possible, even in the limited time available for this work, for some progress to be made towards a fuller knowledge of this elusive insect.

6. SUMMARY.

An account is given of the hitherto very imperfectly known adult of *Prosopistoma*, based on a collection of adults and nymphs made in Tanganyika. Two new species are described from East and South Africa respectively. The taxonomy and systematic position of the genus are discussed, and some notes are given on the biology and behaviour of the East African species.

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