

A REVIEW OF THE CRABHOLE MOSQUITOES OF THE GENUS *DEINOCERITES*

(Diptera, Culicidae)

BY

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ONE OF THE MOST unique and interesting endemic elements of the mosquito fauna of the New World is the genus *Deinocerites* whose distribution centers in the intercontinental area or the American Mediterranean Region. Zoögeographically this region is most important for it has had a very complex geological history, has served as a filter in the population of the South American continent, and has been a refuge for a number of relicts. In view of this, it is surprising that since the pioneer work of Dyar and Knab (1915: 196-215), no attempt has been made to review the genus *Deinocerites*, to study its distribution, and to determine its affinities. Currently four valid species are recognized, and five additional nominal species have been synonymized with one of these (Edwards, 1931: 222). In the fall of 1956, one of us (J.N.B.), attempting to identify specimens of *Deinocerites* from the west coast of Mexico, examined material of all four recognized species. It became evident that characters currently in use for the separation of species are inadequate, that additional unrecognized forms exist, and that the peculiar distributions attributed to several species are based largely on misidentifications. To clarify this situation we are presenting here a preliminary review of the genus. In spite of the fact that the material available is very fragmentary, it is clear that the genus is rich in species and that with further study it may contribute materially to the understanding not only of the morphology and phylogeny of the Culicidae but of the zoögeography of the American Mediterranean Region as well.

This study is based almost entirely on material in the collections of the U. S. National Museum. A total of 1,562 specimens has been examined, 417 ♂, 793 ♀, 306 larvae, and 46 pupae. We were particularly handicapped by the lack of immature stages definitely associated with adults; only in two species were individual rearings available. Therefore no attempt is made to describe the immature stages in detail, and the keys to the immature stages presented here will be of limited value.

As others before, we have found that all the available stages of species of *Deinocerites* are extremely similar except for details. Therefore we have summarized all the general characteristics under the diagnosis of the genus and have confined the descriptions of groups and individual species to a presentation of diagnostic features or departures from these general characteristics. All the figures (see pp. 449-458) are the work of Charles L. Hogue and in general are intended to show pertinent details only.

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Deinocerites

- Deinocerites* Theobald, 1901, Jour. Trop. Med., 4: 235, July 15, no included species; Monograph Culicidae 2: 215, Nov. 23, one included species only. Type species. *D. cancer* Theobald, 1901, Jamaica, first subsequently included species.
- Brachiosoma* Theobald, 1901, Jour. Trop. Med., 4: 235, July 15, no included species. Type species: *D. cancer* Theobald, 1901, Jamaica, selection of Coquillett (1910: 515).
- Brachiomya* Theobald, 1901, Monograph Culicidae, 2: 343-344, Nov. 23. Type species: *B. magna* Theobald, 1901, St. Lucia, monobasic.
- Deinokerides* Giles, 1902, Handbook Gnats or Mosquitoes, ed. 2, pp. 335, 472, invalid emendation. Type species: automatically *D. cancer* Theobald, 1901, Jamaica.
- Dinocerites* Blanchard, 1905, Les Moustiques, pp. 413-414, invalid emendation. Type species: automatically *D. cancer* Theobald, 1901, Jamaica.
- Dinomimetes* Knab, 1907, Jour. N. Y. Ent. Soc., 15: 120. Type species: *D. epitedeus* Knab, 1907, Port Limon, Costa Rica, monobasic.
- Dinanamesus* Dyar and Knab, 1909, Smithson. Misc. Coll., 52: 259. Type species: *D. spanius* Dyar & Knab, 1909, Corozal, Panama Canal Zone, monobasic.

Female.—Small to medium-sized, light to dark brown mosquitoes without obvious ornamentation on legs or abdomen.

Head: Vertex with narrow curved recumbent scales and with a large number of erect scales, a small patch of small broad scales laterally, no marginal ocular scales, a slight indication of a frontal tuft of elongate scales or scalelike bristles; a continuous row of marginal ocular bristles with a pair developed as frontals; eyes contiguous above antennal bases; clypeus prominent, without scales or bristles; proboscis usually distinctly shorter than abdomen; labium rather uniform in diameter, weakened beyond middle and often curved caudad, dark-scaled and with numerous short bristles; labella small, elongate; palpus about 0.2 of proboscis, dark-scaled, 3-segmented and with an indistinct palpifer, third segment elongate; antenna distinctly longer than proboscis; scape distinct, visible under torus; torus (pedicel) small, with a few short hairs on anterior mesal surface and sometimes with a few small broad scales; flagellar segment 1 always conspicuously elongated, without distinct whorl of bristles but with scattered long and short bristles and always with numerous small broad appressed scales; segments 2 to 13 of variable lengths, without scales except sometimes a few at base of 2, flagellar whorls short, composed usually of 8 bristles, dense vestiture of short hairs.

Thorax: Scutum and scutellum with narrow curved recumbent dark scales, some scales broader, particularly on lateral scutellar lobes; acrostichal bristles always absent on disk, sometimes slightly developed anteriorly, dorsocentrals always present and usually very strongly developed, supra-alars always strongly developed, marginal scutellars strongly developed, postnotals present or absent; paratergite bare; pleuron with rather light integument; *apn* with bristles only; *ppn* with several bristles in dorsocaudal angle and with narrow curved recumbent scales on upper part followed sometimes by some broad scales caudoventrad; lower part of *ppn* always with at least two hairs but without scales; *ppl* with several bristles or hairs and sometimes with a few small translucent scales; *psp* bare; *stp* always with numerous bristles arranged in a continuous curved row along dorsal and caudal margins and with a variable, usually extensive, patch of broad appressed translucent scales, sometimes with scattered hairs in addition; *pra* with several bristles; *ume* with a variable number of bristles, *lme* with one very strong bristle and sometimes with additional short hairs, mesepimeron with or without a patch of broad appressed translucent scales and sometimes hairs; usually 1 or more short hairs below base of haltere; meron small, bare, not in line with base of hind coxa; metameron bare; haltere light and bare on stem, dark-scaled on knob.

Wing: Venation and scaling normal; vein 1A ending well distad of fork of Cu, cell R₂ longer

than its stem; all scales dark; base of R (remigium) usually with 2 or more strong bristles, base of 1A without scales on ventral surface; fringe normal, dark except near base; alula with long marginal narrow scales and broader dorsal scales; upper calypter with a long marginal row of bristles.

Legs: Largely dark-scaled, ventroposterior surfaces of fore- and midfemur and ventral surface of hindfemur lighter; femora subequal in length and not markedly different in length from proboscis, midfemur slightly swollen; foretibia about equal to forefemur, mid and hind slightly longer, subequal; basal tarsal segments shorter than respective tibiae; claws all simple, empodium well developed, padlike but short and with setiform spicules, pulvilli small and with setiform spicules.

Abdomen: Tergite 1 extensively scaled; tergites completely dark-scaled, sternites 2 to 6 lighter.

Genitalia: Not studied in detail (see Gerry, 1932: 43-44); segment 8 partly withdrawn into segment 7, sternite 8 strongly sclerotized in distal part, deeply emarginate and projecting caudad of tergite; cercus large, more or less conical, usually withdrawn completely or with apex showing; spermathecae 3, one larger, the others subequal.

Buccopharyngeal armature: A single series of blunt teeth on the pharyngeal bar; a large, roughly hemispherical, strongly reticulate sclerite dorsally over ventral point of articulation of cibarium and pharynx (hyoid).

Male.—In general similar to female.

Head: Labium slightly longer and with a more or less distinct joint beyond middle; palpal segment 3 slightly longer and thinner; antenna usually distinctly longer but similar, flagellar whorls same and only slightly longer; flagellar segment 1 usually longer, segment 2 usually with small broad scales, segments 2 to 6 or 7 with variable number of shaft bristles of approximately same length as those in whorls, distal segments progressively shorter or subequal, never elongated.

Legs: Claws of fore- or fore- and midlegs enlarged, with or without teeth; claws of hindleg always small, simple as in female; empodium of legs with enlarged claws very strongly developed and with branched processes.

Genitalia (fig. 6): Very uniform throughout genus; short and thick. Segment 8 well developed but normally retracted for half or more of its length into segment 7; without special features except for broad median emargination of caudal border of tergite and development of numerous strong bristles on and near this border, particularly on lateral tergal lobes. Segment 9 very strongly developed; sternite long and with a median longitudinal apodeme, a caudolateral wing-like lobe, and an anterolateral narrow sclerotized bar which extends dorsad on each side and articulates at its dorsal end with tergite; tergite movable on the articulation with lateral dorsal process of sternite, composed largely of a pair of greatly developed lateral lobes which articulate also with a dorsomesal process of sidepiece and the basal piece; median part of tergite largely membranous; tergal lobes variously developed. Proctiger strongly developed, with basal, ventrolateral, and dorsal sclerotizations; apex of each half produced and with an arcuate crown of short, heavy, curved spines basad of which on dorsal surface is a patch of small cercal bristles. Sidepiece conical, very thick, with or without scales; a median mesal lobe projecting dorsad and bearing on its dorsal and lateral surfaces 3 differentiated setae 2 of which are always spiniform (*a* most mesal, and *b*) and the other (*c*) bristlelike or setiform, often a thumb at dorsomesal angle, always a variable patch of short setae on base of lobe on dorsal surface, 3 short specialized setae and a variable number of small hairs on ventromesal surface of lobe; a differentiated seta laterad of median mesal lobe on tergal surface of sidepiece; a membranous area basad of median mesal lobe; a more or less distinct ventromesal apical bristly lobe, dorsad of which the clasper folds at rest against body of sidepiece, this area at least partly membranous. Clasper short, irregular in shape; a dorsal inner postmedian angular shelf-like process, a ventral inner apical tooth, and a dorsal outer apical rounded process; inserted between the two apical projections is a heavy subapical forked spiniform. Phallosome complex, consisting of a ventral aedeagus and a pair each of ventral and dorsal parameres; dorsal paramere articulating ventrolaterally with ventral paramere, latter with aedeagus ventrally and basal piece laterally; dorsal paramere has been called the outer or tergal division of aedeagus but appears to be homologous with complex dorsal part of the paramere of Dixinae; dorsal parameres consisting of a pair of lateral toothed

plates with an apical dorsal spine and ventrolateral teeth, the two sclerotized plates are often more or less connected by an incomplete dorsal sclerotized bridge; aedeagus more or less conical or cylindrical in tergal aspect, with a pair of lateral sclerotized plates, variously developed and connected by a basal sternal sclerotized bar (details not studied).

Pupa.—Quite uniform in structure, in general as in *mcdonaldi* (figs. 38, 39).

Cephalothorax: Hairs 2, 3-C moderately removed from caudal border of sclerite and moderately spaced; 5-C very strongly developed, largest hair on cephalothorax; 8, 9-C placed well caudad of trumpet and moderately close together.

Trumpet: Inserted about halfway between middorsal line and wing base; index variable; inner wall well separated from outer throughout; tracheoid in basal third or more; meatus without slit; pinna short.

Abdomen: Hair 1-I with about 12 to 20 primary branches, fringed, barbed, or secondarily lightly dendritic; 1-II very close together on mid-line, slightly closer than 1-I, and very similar to the latter (appears to form another pair of float hairs); 2-II external to 3-II, long; 10-II ventral in position; 2-III-VII placed well mesad of 1-III-VII; 6-I-VII long, single, as well developed on VII as on other segments; 7-II-VI variable in position; 7-VII removed from caudolateral angle on dorsal surface, mesad of 6-VII; 7-VII long, single, inserted ventrally near caudolateral angle; hairs 1-IX, X not developed.

Female genitalia: Strongly developed cercal lobes.

Male genitalia: Strongly developed, paired 9th tergite lobes ventrad of median lobe.

Paddle: Margins without spicules; midrib strongly developed; external buttress not developed; hair 1 subapical, at least two-thirds as long as paddle; hair 2 not developed.

Larva.—Very uniform in structure, in general as in *mcdonaldi* (fig. 41); hairs strongly pigmented.

Head: Lightly and uniformly pigmented; rather elongate but appearing slightly broader than long owing to development of conspicuous lateral expansion on each side caudad of antenna; a broad deep pouch open cephalad within this expansion; wall of pouch membranous, withdrawn when mandible is abducted and expanded out and inflated when mandible is adducted eliminating pouch; maxillary sutures strongly developed, close together and subparallel to each other to posterior tentorial pit then divergent dorsolaterad; mental plate rudimentary, poorly sclerotized and with a few small denticles or filamentous spicules; mouthbrushes strongly developed, composed of large number of filamentous spicules; labrum broadly and evenly rounded on anterior margin; hair 1-C long, thin, widely spaced, arising on dorsal surface of labrum, not apically; 2-C well developed, mesad of level of 1-C; 3-C apparently represented by rudiment in form of spicule, cephalolaterad of 2-C (possibly homology of 2, 3-C reversed); hairs 4-6-C in a group caudad of level of 7-C; hair 4-C minute, multiple; 5, 6-C strongly developed; 10-C quite close to 9-C; 11-C dorsal, mesad of pouch; 12, 13-C close together; 14-C removed from margin; 15-C in anterior half of submentum; antenna lightly and uniformly pigmented, about half as long as head capsule, unsegmented, slender, gradually tapered apically, a few minute spicules in basal half; hair 1-A near middle, moderately long, branched; hair 2-A subapical, 3-6-A apical; mandible (Howard, Dyar, and Knab, 1912, fig. 524) with curved fingerlike process densely covered with long setiforms (setalike spicules) arising from anterolateral basal angle and projecting into lateral head pouch, and with apical mesal angle below teeth developed into a long curved horn; maxilla (Howard, Dyar, and Knab, 1912, fig. 479) large, normal, palpus short.

Thorax: Without apparent outstanding features; hairs 1-3-P with poorly developed, largely unsclerotized common tubercle; 1, 2-P long, single; 3-P branched; 4-P well developed, branched; 5, 6-P long, single; 7-P long, branched; 8-P well developed, long, single or branched; 9, 12-P long, single; 10-P moderate; 13-P absent; 14-P single; 1, 2-M short; 3, 4-M moderate; 5-7-M long, single, 6-M heaviest; 8-M long, multiple, with heavy tubercle; 9-M long, multiple; 10, 12-M long, single; 14-M short, dendritic; hairs 1-6-T minute to small; 1, 2-T placed far mesad; 1, 5-T always minute; 6-T variously developed; hair 7-T large, multiple, with heavy basal tubercle; 9-T long, multiple; 10-T long, single; 13-T short, multiple.

Abdomen: Hairs 6-I-VI long; 7-I short or long; 7-II-VI always short; 1-I, II distinctly mesad of others, minute; 1-III-V more or less strongly developed; 2-III-V mesad of 1; 5-I-VII

small, branched; 9-II-VI minute, single; 10-II-VI strong, single; 13-III-V strong; 11, 12-II-V laterad of 13; segment I with complete complement of hairs 10-13.

Segment VIII: Comb of numerous scales in large triangular patch, individual scale long, parallel-sided, with expanded, fringed, spatulate apex; hair 1-VIII mesad of 2; hairs 2, 4-VIII strongly developed, single.

Siphon: Moderately to well pigmented; index moderate; acus present; valves moderate, normal; trachea well developed, stirrup-shaped piece without median caudal process; pecten not extending to middle of siphon, individual tooth usually unequally bifurcate or trifurcate from base, rarely with additional denticles, largest branch of pecten tooth with broad lateral bladeliike expansion; 3 pairs of lateral hairs, a large one (1-S) near middle and two small ones (1a-S) beyond middle, one dorsal and one ventral.

Anal segment: Saddle poorly developed, usually represented by poorly defined, unconnected small dorsal and ventral sclerotizations; spicules short, in a patch; acus absent; gills not developed as such, segment ending in a pair of broadly rounded lateral protuberances, each usually more or less distinctly indented in middle, no tracheae; hair 1-X small, not on saddle; 2-X moderately long, multiple; 3-X very long, single; hairs 4-X all on grid, from 6 to 8 pairs, well developed, multiple.

Egg.—Not definitely known and undescribed; apparently laid singly above water surface in crabholes (Dyar and Knab, 1915: 205; Fisk, 1941: 547).

BIONOMICS

Practically all the information available on the bionomics of species of *Deinocerites* is to be found in Dyar and Knab (1915: 196-215). Horsfall (1955: 599-600) adds a few references to more recent observations. Only a brief summary is presented here.

As far as known all species of *Deinocerites* normally utilize for breeding sites, as well as for adult resting places, holes made by land crabs of the families Gecarcinidae and Ocypodidae. Immature stages have been reported also from flooded areas (probably flushed there from crabholes), from water-filled old postholes, and, occasionally, artificial containers such as tin cans (Carpenter and LaCasse, 1955: 327). No information is available on the specificity of the association between the mosquito and the crab. Only in two cases has the species of crab been reported and it is by no means certain that the identifications were correct; Knab collected *pseudus* from holes of *Cardiosoma crassum* Smith (Dyar and Knab, 1915: 212), and Fisk (1941: 543) reported *mathesoni* (as *spanius*) from holes of the fiddler crab, *Uca pugilator* (Bose). Crabholes near the shore, in mangrove swamps, and even on hillsides a considerable distance from shore have been found to harbor *Deinocerites*. The water in these holes may be fresh or brackish; Dyar (Dyar and Knab, 1915: 205) found a few larvae in a crabhole filled artificially with salt water. Dyar and Knab (1915: 200) state that "the larvae feed upon the matter in suspension in the water, of which the excrement of the crab not improbably forms an important part." The peculiar development of the lateral head pouches, the basal and apical lobes of the mandible, and the rudimentary mental plate all would seem to indicate an unusual type of food and a peculiar method of feeding. As in the case of other mosquitoes breeding in confined habitats, the aquatic cycle is prolonged, at least under laboratory conditions; Fisk (1941: 547) reports a larva of *mathesoni* completing development in about two months. Several species of *Culex* (*Culex*) and *Culex* (*Melanocnion*) have been reported either in association with *Deinocerites* species or breeding in similar crabholes: *inflictus*

Theobald, 1901 (as *extricator*); *janitor* Theobald, 1903; *carcinophilus* D. and K., 1906; *latisquama* (Coquillett, 1906); *opisthopus* Komp, 1926. In flooded areas several additional species of various genera may be found together with *Deinocerites* species.

The adults of *Deinocerites* seem to be nocturnal or crepuscular in activity, resting by day in the upper parts of crabholes. It has been suggested that "the remarkably elongate antennae perhaps serve as special sensory organs to warn them of . . . danger . . . when the crustacean host enters" (Dyar, 1928: 261). When disturbed the adults do not fly far and promptly return to the crabholes. Mating swarms have been reported to take place above the holes at dusk and dawn. It seems that *Deinocerites* species have a relatively short flight range and are restricted in their activities largely to the immediate neighborhood of their breeding sites. However, occasional specimens of either sex are collected in light traps up to several miles from the nearest known breeding sites (Fisk, 1941: 544). It has been generally assumed that the females of the majority of species of *Deinocerites* either take no blood or feed on reptiles and amphibians (Dyar and Knab, 1915: 200; Fisk, 1941: 544-545). Reports of at least occasional attacks on man have been made for *cancer* (Carpenter and LaCasse, 1955: 327), *magnus* (Bonne and Bonne-Wepster, 1925: 173), and *spanius* (Dyar, 1928: 261). In addition, four species have been reported to be readily attracted to horses: *epitedeus* and *melanophyllum* in Panama (Carpenter and LaCasse, 1955: 327, both as *cancer*), *epitedeus* and *pseudes* in Costa Rica (Kumm *et al.*, 1940: 392), *pseudes* in El Salvador (Kumm and Zuniga, 1942: 406), and *magnus* in Brazil (Cerqueira, 1938: 291, as *cancer*).

Eggs of *Deinocerites* have not been definitely identified. It seems very probable, however, that the surmise that eggs are laid singly on the sides of the crabhole (Dyar and Knab, 1915: 205) is correct and that the eggs observed by Fisk (1941: 547) were in fact those of *mathesoni*.

TAXONOMY

In the 43 years since the first review of this group of mosquitoes by Dyar and Knab in the classic monograph of Howard, Dyar, and Knab, practically no advance has been made in the systematics of *Deinocerites*. On the contrary, errors in observations, misinterpretations, and misidentifications have been perpetuated and compounded. The treatment by Dyar and Knab (1915: 191, 196-215) was excellent on the whole except that the structure of the male genitalia was completely misinterpreted. All existing figures of male genitalia are either copied from those of Dyar and Knab or drawn from whole mounts without any attempt to interpret the various components. We have seen only two slides of dissections, and apparently the only published figure of a part of the phallosome complex is for *cancer* (Carpenter *et al.*, 1946, fig. 154). Dyar and Knab (1915: 191), impressed by the peculiar structure of these mosquitoes, separated them as a distinct group, the deinoceritines, coördinate with the culicines, megarhinines, and anophelines, and considered the group to have "been long separated from the other Culicini." They retained three genera (*Deinocerites*, *Dinomimetes*, and *Dinana-mesus*) but indicated that these formed a compact group. We recognize six of the

seven species treated by Dyar and Knab as valid taxonomically in the present review; *tetraspathus*, the seventh, is apparently conspecific with *cancer* but may prove to be subspecifically distinct when more material is examined. Dyar and Knab did not particularly stress a relationship between *Deinocerites* and *Culex* although the similarities in male genitalia were noted and *spanius* was said to be the least specialized member of the group showing "a transition toward the culicine forms."

Dyar (1918: 101-102), on the basis of supposed similarity in male genitalia, reduced *Deinocerites* (with *Dinomimetes* and *Dinanamesus* as synonyms) to a subgenus of *Culex* and recognized six species, not mentioning *tetraspathus*. Later, Dyar (1925: 154-156) restored *Deinocerites* to generic status, retained the other generic taxa in synonymy, synonymized *tetraspathus* with *melanophylum*, and described *monospathus*. Bonne and Bonne-Wepster (1925: 168-176), apparently independently, treated *Deinocerites* as a genus with all other proposed generic taxa as synonyms and recognized as valid all the species treated by Dyar and Knab (1915). Dyar (1928: 261-265) continued to recognize *Deinocerites* as a genus, which he believed to have been derived from *Culex* (*Tinolestes*) (1928: 377), and reduced the number of species to five by synonymizing *melanophylum* (together with *tetraspathus*) and *troglydytus* with *cancer*. Edwards (1932: 221-222) followed Dyar (1928) and further reduced the number of valid species by considering *monospathus* as an aberration of *cancer*. Edwards apparently considered *Deinocerites* to be a specialized offshoot of *Culex* for he placed it following the latter in the catalogue. He recognized three groups in the genus, corresponding to *Deinocerites*, *Dinanamesus*, and *Dinomimetes*, but did not use these names in the subgeneric sense. Although Edwards introduced a good new character, the development of spiniforms on the forefemur, he unfortunately mixed the characteristics of the three groups and in addition reported inaccurate distributions for two species, both actions leading to misidentifications by subsequent workers. Finally, Lane (1955: 553-559) followed Edwards in recognizing only four species: *cancer*, *pseudes*, *epitedeus*, and *spanius*.

Although *Deinocerites* is an amazingly compact genus and all the species seem to be very similar, there is a multitude of good but often obscure and minute characters that distinguish species and even groups of species within the genus. Some of these have been used in the past; we have introduced a few in the present review; and many more have not yet been studied in detail. In the adults the following characters are excellent: proportions of flagellar segments in the antenna, presence or absence of spiniforms on forefemur, scaling of the pleuron, presence or absence of genital scales (sidepiece in male, 8th sternite of female). On the other hand, postnotal bristles, formerly believed to be of generic or subgeneric value, are of sporadic occurrence in the genus and even within a species. The male claws are characteristically developed in every species. The male genitalia offer a multitude of characters in the 9th tergite lobe, the median mesal lobe, apicosternal lobe, the phallosome complex, and particularly the dorsal paramere which is again characteristically developed in every species. On the other hand, the features formerly used to distinguish the male genitalia are either nonexistent or based on misinterpretations and artifacts due to mounting and observation of

similar structures from different aspects. We have not studied the female genitalia in detail, but it is evident that differences can be found other than the striking ones we are using here: specialized apical cercal bristles, postgenital lobe, and 8th sternite. The pupae are more or less adequately known for only two easily differentiated species. The larvae offer good diagnostic characters in features most of which are not widely used in other mosquitoes: the mental plate; hair 3, 5, 6-C; antennal spicules; hairs 4-P; 3, 4-M; 6-T; 7-I; 6-II-V; 1-VII, VIII; 1a-S; pecten teeth; and 2-X.

On the basis of the above-mentioned characters we have been able to recognize eleven species in *Deinocerites*; the four currently accepted species (*cancer*, *pseudus*, *epitedeus*, and *spanius*), two species previously synonymized with *cancer* (*magnus* and *melanophylum*), four new species (*mathesoni*, *dyari*, *mcdonaldi*, and *howardi*), and an additional form, species A, known from a single female. There is some evidence of racial differentiation in *cancer* and *melanophylum*.

The genus is so compact that we see no justification for splitting it into subgenera at present. To be consistent we would have to erect at least one additional subgenus and redefine the three already proposed. We recognize instead four groups of species as follows:

SPANIUS GROUP

1. *mathesoni*, n. sp. 2. *spanius* (Dyar and Knab, 1909)

DYARI GROUP

3. *dyari*, n. sp.

CANCER GROUP

4. *magnus* (Theobald, 1901) 5. *cancer* Theobald, 1901
6. *melanophylum* Dyar and Knab, 1907

EPITEDEUS GROUP

7. *mcdonaldi*, n. sp. 8. species A 9. *epitedeus* (Knab, 1907)
10. *pseudus* Dyar and Knab, 1909 11. *howardi*, n. sp.

ZOÖGEOGRAPHY

Deinocerites is nearly but not entirely confined to the American Mediterranean Region, that is, the intercontinental area of Central America and the West Indies and the adjacent parts of the North American and South American continents. The one conspicuous known extension from this region is on the Atlantic seaboard of South America down to the State of Maranhão, Brazil. It is very probable that another extension occurs on the Pacific seaboard of South America.

The American Mediterranean Region has had a complex geological history which is still very imperfectly known (Schuchert, 1935, 1955; Eardley, 1954; Woodring, 1954). Clearly established, however, is the fact that portals have existed on several occasions and at least in two general areas in Central America, connecting the Atlantic and Pacific ocean basins, and that these portals have been instrumental in determining the distribution and the composition of the ter-

restrial, fresh-water, and marine biota throughout the region as well as on the adjoining continents.

The map of the known ranges of *Deinocerites* species (fig. 1), although based on fragmentary material, clearly shows that this genus is an ancient one, and that its distribution, speciation, and evolution have been influenced markedly by former marine portals, land bridges, and island chains. It might even be possible to guess at the geological age when certain of the species in the genus were separated by plotting their present distributions on paleogeographic maps. We believe that it would be premature to draw too many conclusions at this time and that it would be better to wait until more material has been studied and more is known about the bionomics of the genus, particularly ecological requirements and methods of dispersal. However, some observations and even a few speculations might not be out of place now and may serve to stimulate further work on this interesting genus, one which we believe will prove to be of considerable value in elucidating the biogeography of the American Mediterranean Region.

1. All the species of *Deinocerites*, except one, are in general restricted either to the Atlantic or Pacific basins. The major exception, *pseudus*, apparently crossed from the Pacific to the Atlantic basin in the Tehuantepec area either through the portal or possibly through the lowlands of the isthmus after the closure of the portal. As far as we can determine, the two apparently disjunct modern populations are not even subspecifically distinct. In the Panama Canal Zone, at the point of the narrowest present separation of the basins, three species, *pseudus*, *epitedeus*, and *spanius* (possibly a distinct form) have been collected occasionally outside the basin in which the major part of the population of each species occurs. In every case it is not clear at all whether these records are due to mislabeling, to natural distribution, or to recent transport or dispersal through the canal.

2. The *Spanius* group (with the exception noted) and the *Cancer* group are restricted to the Atlantic basin whereas the *Dyari* group and the *Epitedeus* group are Pacific except that *epitedeus* itself is restricted to the Atlantic and *pseudus* crosses over at two points but has its major populations in the Pacific. In general the groups have mutually exclusive ranges except that on the Atlantic seaboard of Panama all but *Dyari* come together.

3. In the *Spanius* and the *Cancer* groups the species within a given group occupy mutually exclusive ranges. In the *Epitedeus* group, *pseudus* has a very wide range which overlaps that of every other known member of the group and even that of the *Dyari* group (one species only) at the two extremes.

4. As a corollary of 2 and 3 above, throughout most of the range of the genus, only one species of *Deinocerites* occurs in any given locality. The three outstanding exceptions are the Atlantic seaboard of Panama where there are major populations of *spanius*, *melanophylum*, and *epitedeus* and a small one of *pseudus*; the Pacific seaboard of Panama where major populations of *pseudus* and *dyari* are found, and in addition *spanius* (or a closely related form) and a small population of *epitedeus* apparently occur; and Bahia de Banderas, Mexico, where three species of the *Epitedeus* group occur. In addition, on the Pacific side of Costa Rica, species A occurs within the range of *pseudus*.

5. The *Spanius* group of two species shows a remarkable disjunct distribution.

D. mathesoni to date is known only from the southwest corner of Texas and *spanius* has not been taken outside of Panama (chiefly on Atlantic seaboard). We believe that this group is the most generalized and ancient segregate in *Deinocerites*.

6. The Dyari group, represented at present by a single species, has been found only in the Bay of Panama, but it may extend south along the Pacific seaboard of South America. In several characters *dyari* seems to be a relict of the original stock which first occupied the Pacific and we believe that it was cut off to the south probably at the same time that the Cancer and Epitedeus groups became isolated in their respective areas and were differentiated.

7. The Cancer group of three species forms a ring around the Caribbean Sea and extends northward into the keys and the southeast coast of Florida and southward to northern Brazil. It appears that *magnus* was cut off first and at a later date *cancer* and *melanophylum* were separated to produce the present complementary allopatric picture.

8. The Epitedeus group of five species occupies Central America, Mexico, and extends into the Cape region of Baja California. *D. pseudus* is the dominant and the only widespread species, occupying almost the entire range of the group on the Pacific side and crossing into the Atlantic at two points. Near the southern end *epitedeus* is largely confined to the Atlantic basin, and species A is known from the Pacific coast of Costa Rica. At the northern end *mcdonaldi* occurs; where its range overlaps with *pseudus* at Bahia de Banderas, Mexico, a third species, *howardi*, is found. We believe that *howardi* arose through hybridization of the *pseudus* and *mcdonaldi* stocks. It seems probable that species A and *epitedeus* are also of hybrid origin.

9. No *Deinocerites* is known from the Gulf coast of the United States east of Corpus Christi to the Florida keys, nor from the Bahamas. The Yucatan peninsula, the Gulf of California, and the Pacific side of Baja California have not been surveyed.

PHYLOGENY

There is nothing in the meager fossil record of the Culicidae that will help us to determine the relationships of *Deinocerites*. However, as pointed out recently by Ross (1957: 87), in insects many lines of evolution have been preserved from their inception to the present, often with very little change. Therefore, by means of thorough and judicious comparative morphological studies of living forms, it is possible to reconstruct the phylogeny of many insect groups much more satisfactorily than a fragmentary record of fossils would allow.

For a group that is often stated to be best known of all insects, the Culicidae are glaringly lacking in basic morphological studies. Most of the work done in the family has been carried only to the point necessary to establish the identity of species and their habitats in connection with the control of economically important forms. The universally accepted classification of the Culicidae (Edwards, 1932) is a synthesis based partly on Edwards' own taxonomic studies, which included relatively little detailed morphological study, and partly on the work of others who likewise did not carry out extensive comparative studies. This classification has

been questioned in small details only, and it is evident that nothing can be done to improve it until the basic morphology of the family is thoroughly understood. No major contributions toward this goal have appeared as yet. This lack of comparative morphological studies has been a great handicap in our attempt to determine the relationships of *Deinocerites*. Unfortunately, it has not been possible for us to undertake such studies or even to make a thorough morphological examination of the genus. Therefore our conclusions can be only tentative.

Opinions regarding the relationships of *Deinocerites* have varied widely, from placing it in a separate subfamily (Mitchell, 1906: 19) to relegating it to a subgeneric or apparently even a lower status (Dyar, 1918: 101; 1928: 337). Edwards (1932: 221) placed it as a separate genus following *Culex*; in his scheme of classification and arrangement this meant that he regarded it as a derivative of *Culex* and the most specialized of all mosquito genera. In our opinion, *Deinocerites* is an ancient specialized and stabilized derivative of the stock that also gave rise to the plastic and dominant genus *Culex* and that has retained some of the most generalized characters in the entire tribe. It seems possible also that *Deinocerites* may have been derived from a primitive segregate of *Culex*, but it is highly improbable that it is related at all to any of the species of the latter which have been proposed as possible intermediates, such as *C. (Melanoconion) latisquama* (Coquillett, 1906). As noted by Dyar and Knab (1915: 191) most of the outstanding features of *Deinocerites* seem to be adaptive specializations. Since these features vary only within narrow limits within the genus we would probably be justified in considering that the habitat specialization (association with crabholes) is an ancient one and occurred at the time of the segregation of the genus. There is nothing even remotely suggesting *Deinocerites* anywhere else in the world. Therefore we believe that it originated in the American Mediterranean Region, was narrowly specialized from the beginning, and never reached the Old World.

Several features relate *Deinocerites* to *Culex*: in the females, the presence of buccopharyngeal teeth; in the male genitalia, the crown of spines on the proctiger lobes (probably modified cerci) and the median mesal lobe (=subapical lobe); in the larva, the general pattern of abdominal chaetotaxy and 3 pairs of hair 1-S on the siphon. Edwards (1932: 65) states that padlike pulvilli are present at the base of the claws in *Deinocerites* as well as in *Culex*, and these occur in no other genus in the Culicini. We do not find these in *Deinocerites*; instead the empodium is greatly developed and what may be pulvilli are represented by slight lobes with simple or branched spicules.

Deinocerites is distinct from *Culex* in a number of unusual characters, some of which seem to be unique in the Culicini. Although the majority of these are adaptive secondary features, some may very well represent generalized features retained exclusively in this genus, and a detailed study of these should be most illuminating in interpreting the more specialized homologs in *Culex* and probably in the whole subfamily. Of particular interest is the phallosome complex, that is, the aedeagus (mesosome) and parameres. Although the aedeagus at least is widely used not only for specific characters but also for characterization of groups, the entire complex is the least understood of all the structures of the male genitalia of mosquitoes. We find in *Deinocerites* a pair of sclerites which we have called the

dorsal parameres. These structures have been interpreted in the past as homologous with the inner or dorsal division (dorsal plate or finger) of the aedeagus of *Culex*. This homology may be entirely correct, but we find that the dorsal parameres are articulated structures and that their articulation is with the ventral parameres (the parameres of the accepted nomenclature) which in turn articulate with the aedeagus. Although it is possible that the dorsal parameres of *Deinocerites* are secondary, they bear at least a superficial resemblance to the dorsal part of the paramere complex in the Dixinae, particularly in *mathesoni* (in our opinion the most generalized species in the genus) where each consists of two incompletely joined parts very much as in some primitive Dixinae. It has been overlooked that the greatly developed 9th tergite lobes of *Deinocerites* are articulated with the long slender dorsolateral processes of the sternite and that apparently they are moved through an arc of 90° and are used as accessory clasping structures in mating. This is not found elsewhere in the Culicinae, to our knowledge. A very uniform and distinctive feature of *Deinocerites* male genitalia is the structure of the clasper and particularly the presence in all species of a forked subapical spiniform. The latter has been consistently confused in part with the ventral apical spine, and this has been the source for many misidentifications. The female genitalia of *Deinocerites* seem to have a number of peculiar and perhaps primitive features (Gerry, 1932: 43-44, 48-51) but unfortunately we have had no time to study them in detail. An unusual, but not entirely unique feature of both sexes of the genus is the great length of the antenna which is due to the elongation of the first flagellar segment always and frequently also of one or more of the succeeding 5 or 6 segments. Again it is quite possible that this elongation is a secondary adaptive feature, and this we believe to be the case with flagellar segments 2 to 6. However, the long first flagellar segment may be a primitive character as most certainly the short apical segments of the male are. Here, too, a superficial resemblance to some Dixinae (*Paradixa*) is suggested.

The immature stages of *Deinocerites* exhibit some unique characters also. In the pupa, for instance, there seem to be two float hairs, since hairs 1-II are inserted slightly closer together on the mid-line than hairs 1-I, are similarly developed, are almost as large, and are held in a similar position. The trumpets are more widely spaced than in any other culicine genus, and the chaetotaxy is quite different from *Culex*. In the larva the outstanding features seem to be adaptive and secondarily developed but some at least may be primitive and generalized. Head hairs 1-C (clypeal spines) are on the dorsal surface of the clypeus and not on the margin nor on anterior processes. We interpret the well-developed hairs caudad of 1-C as 2-C, since laterad and not mesad of them there is a spicule on each side which might be a vestige of hair 3-C; this is a unique feature in the Culicini. The characteristic very small mental plate and the peculiar anal papillae are not necessarily due to reduction as might be assumed at first glance, but the unique lateral head pouches and the basal lobe of the mandibles are undoubtedly secondary. In other features such as the chaetotaxy, siphonal hairs, and anal segment, *Deinocerites* is very similar to *Culex*.

We have attempted to summarize our views on the relationships and the evolution of the known species of *Deinocerites* in figure 2. This has been entirely on the

basis of adult morphology. For the sake of simplicity, only one or two characters are indicated for each line; a fuller diagnosis will be found in the discussion of every group and every species in the following sections. We regard the Spanius group as the most generalized and most ancient line of *Deinocerites* and probably very close to the original stock of the genus which, we suggest, was formed in isolation on some island in the American Mediterranean Region. *D. dyari* is in some characters intermediate between the Spanius group and the Cancer and Epitedeus groups. For the present we suggest that the Dyari, Cancer, and Epitedeus groups arose as a result of a tripartite splitting of a common stock derived from the Spanius group.

It seems to us that evolution in the genus has proceeded by the formation of new types in isolation chiefly on islands in the central, most unstable area. When the new types thus formed came into contact with related stocks on more stable continental margins at later dates new forms of hybrid origin were produced. This has resulted in the accumulation of species along the continental margins of the Central American land bridge, consisting of relicts and hybrids of various ages as well as dominant modern forms.

Each of the three species (*howardi*, *epitedeus*, and species A) which we consider as hybrid in origin might be interpreted instead as an intermediate type from which the two stocks, whose characters it shares, evolved independently. This does not seem to be the case since every one of these species would have had to acquire first both sets of characteristics, lose a different set in the two subsequent lines, and then reacquire them again in apparently an identical condition later in evolution. Furthermore, in every case we are not dealing with one or two characters but whole blocks of characters. In addition there appears to be evidence of hybrid vigor in the intensification of the strongest character in each line, particularly in the case of the development of the antenna.

KEYS TO SPECIES

FEMALES

1. Forefemur with an anteroventral row of short spiniforms 2
Forefemur with an anteroventral row of long thin bristles 4
2. (1) Forefemur with a posterodorsal row of thin bristles to near base..... *epitedeus* (Knab)
Forefemur with posterodorsal row of bristles replaced by short spiniforms near base.. 3
3. (2) Proboscis not extending beyond end of 6th flagellar segment *howardi*, n. sp.
Proboscis extending beyond base of 8th flagellar segment *pseudus* D. and K.
4. (1) Mesopleuron with a patch of broad appressed translucent scales 5
Mesopleuron without scales 6
5. (4) Cercus without specialized bristles *mcdonaldi*, n. sp.
Cercus with 5 specialized subapical bristles species A
6. (4) Cercus with a pair of long apical specialized bristles 7
Cercus without long apical specialized bristles 8
7. (6) Specialized apical bristles of cercus arising distinctly apart; lobes of postgenital plate elongate and with a long apical bristle *magnus* (Theo.)
Specialized apical bristles of cercus arising side by side; lobes of postgenital plate short and without long apical bristle *cancer* Theo.; *melanophyllum* D. and K.
8. (6) Eighth sternite without scales; proboscis not reaching beyond 8th flagellar segment
dyari, n. sp.
Eighth sternite densely covered with scales; proboscis reaching beyond base of 9th flagellar segment *spanius* (D. and K.); *mathesoni*, n. sp.

MALES

1. Antenna short; proboscis extending beyond 9th flagellar segment; sidepiece with numerous scales 2
 Antenna long; proboscis not extending beyond apex of 5th flagellar segment; sidepiece without scales or with an occasional scale 3
2. (1) Both foreclaws simple *mathesoni*, n. sp.
 Anterior foreclaw toothed *spanius* (D. and K.)
3. (1) Forefemur with an anteroventral row of short spiniforms 4
 Forefemur with an anteroventral row of long thin bristles 6
4. (3) Forefemur with a posterodorsal row of thin bristles to near base *epitedeus* (Knab)
 Forefemur with posterodorsal row of bristles replaced by short spiniforms near base.. 5
5. (4) All claws simple *pseudes* D. and K.
 Both foreclaws and anterior midclaw toothed..... *howardi*, n. sp.
6. (3) Mesopleuron with a patch of broad, appressed translucent scales..... *macdonaldi*, n. sp.
 Mesopleuron without scales 7
7. (6) Proboscis extending to about middle of 5th flagellar segment *dyari*, n. sp.
 Proboscis not extending beyond apex of 4th flagellar segment 8
8. (7) Both foreclaws with a tooth at base *magnus* (Theo.)
 Only anterior foreclaw toothed beyond base 9
9. (8) Anterior foreclaw with a large tooth *cancer* Theo.
 Anterior foreclaw with a minute tooth *melanophyllum* D. and K.

MALE GENITALIA

1. Sidepiece with numerous scales dorsally, laterally, and ventrally; apicosternal lobe of sidepiece without a long heavy differentiated bristle 2
 Sidepiece without scales or at most with one or two scales; apicosternal lobe of sidepiece with a long heavy differentiated bristle 3
2. (1) Dorsal paramere in form of a small compact uniformly and heavily sclerotized plate, its dorsoapical spine short; 9th tergite lobe very slender, only slightly widened beyond middle and at apex *spanius* (D. and K.)
 Dorsal paramere with two rather light sclerotizations widely separated, its dorsoapical spine long; 9th tergite lobe broader, distinctly widened beyond middle and at apex
mathesoni, n. sp.
3. (1) Ninth tergite lobe strongly flattened, dorsal in position, not markedly angled laterad at base 4
 Ninth tergite lobe cylindrical, markedly angled laterad at base and more lateral in position distally 6
4. (3) Ninth tergite lobe short, not reaching level of median mesal lobe of sidepiece; apical spine of dorsal paramere thick, not strongly differentiated from body of paramere
magnus (Theo.)
 Ninth tergite lobe long, extending distad of level of median mesal lobe of sidepiece; apical spine of dorsal paramere slender, strongly differentiated from body of paramere 5
5. (4) Dorsal paramere with ventral teeth strongly outstanding, usually arising from distinct distal process or lobe; its dorsal bridge broad and short; its apical spine rather short and only slightly curved *cancer* (Theo.)
 Dorsal paramere with ventral teeth appressed; its dorsal bridge narrower and long; its apical spine long and strongly curved *melanophyllum* D. and K.
6. (3) Ninth tergite lobe short, not reaching level of median mesal lobe of sidepiece, distinctly attenuate apically *dyari*, n. sp.
 Ninth tergite lobe longer, at least reaching level of median mesal lobe of sidepiece, its apex rounded 7
7. (6) Dorsal paramere with a strong dentate process from ventrolateral border, in tergal aspect extending almost as far caudad as apical spine *pseudes* D. and K.

- Dorsal paramere with ventral teeth arising from convex ventrolateral border not from a distinct process 8
8. (7) Ninth tergite lobe extending well beyond median mesal lobe, strongly bent mesad near middle and with this distal part more or less paralleling sidepiece. *epitedeus* (Knab.)
 Ninth tergite lobe not extending beyond median mesal lobe
mcdonaldi, n. sp.; *howardi*, n. sp.

PUPAE

(Pupae of *dyari*, *howardi*, *melanophyllum*, *pseudes*, and *spanius* completely unknown; those of *cancer* and *magnus* insufficiently known to be included in key.)

1. Trumpet index over 6.0 *epitedeus* (Knab)
 Trumpet index under 5.0 2
2. (1) Hair 1-VII shorter than tergite VIII *mcdonaldi*, n. sp.
 Hair 1-VII longer than tergite VIII *mathesoni*, n. sp.

FOUR-INSTAR LARVAE

(The larvae of *dyari*, *howardi*, and *spanius* are completely unknown; that of *melanophyllum* is insufficiently described.)

1. Mental plate broader than long; head hair 6-C similar to 5-C, usually 3- to 5-branched.
mathesoni, n. sp.
 Mental plate longer than broad; head hair 6-C with fewer branches than 5-C and usually longer 2
2. (1) Head hair 5-C with 2 branches *epitedeus* (Knab)
 Head hair 5-C with 3 or more branches 3
3. (2) Antenna with numerous spicules *pseudes* D. and K.
 Antenna with a few minute spicules 4
4. (3) Head hair 6-C always branched, usually 2- or 3-branched *mcdonaldi*, n. sp.
 Head hair 6-C usually single, rarely double 5
5. (4) Head hairs 2-C closer together on mid-line than dorsal distance between 1-C and 2-C on each side; hair 4-P usually 4- or 5-branched *magnus* (Theo.)
 Head hairs 2-C more widely separated on mid-line than dorsal distance between 1-C and 2-C on each side; hair 4-P usually 2- or 3-branched *cancer* Theo.

SPANIUS GROUP

Adults.—Very small in size, wing about 2.0–2.5 mm.; general coloration light brown; antenna short and almost identical in structure as well as length in the two sexes, flagellar segment 1 slightly shorter than the combined lengths of 2 and 3, segments 2 to 13 progressively shorter distad, proboscis extending to at least the middle of segment 9; *ppn* with narrow scales only; mesepimeron without scales; postnotum without bristles; forefemur without spiniforms; claws of fore- and midlegs greatly enlarged, posterior member of a pair slightly smaller than anterior and without teeth.

Female genitalia: Eighth sternite densely covered with scales on sclerotized apical part; cercus without specialized apical setae.

Male genitalia: Ninth tergite lobe with distal part cylindrical, curved mesad apically, and extending distad of median mesal lobe; sidepiece with numerous scales dorsally, laterally, and ventrally; median mesal lobe without thumb, seta *c* a moderately heavy bristle; apicosternal lobe short, without differentiated seta; dorsal parameres widely spaced in tergal aspect, with at most a very slight indication of a sclerotized dorsal bridge.

Pupa and larva.—Known only for *mathesoni*.

This is the most clearly marked and apparently the most generalized of the four groups of *Deinocerites* so that it may be even worthy of recognition as a subgenus (*Dinanamesus*). It consists of two superficially very similar species, *spanius* and

mathesoni, inseparable at present in the females but clearly differentiated by the male claws and genitalia. In *mathesoni* the dorsal paramere consists of two parts narrowly connected and reminds one of the complex paramere of Dixinae. Although this condition could easily have been developed secondarily from the dorsal paramere of *spanius* we regard it as primitive in the group, particularly since a tendency to splitting of the paramere does not occur anywhere else in *Deinocerites*.

The two known species of the group have very restricted, widely disjunct distributions in the Atlantic Basin, *mathesoni* occurring in the southwestern corner of Texas and *spanius* on the Atlantic seaboard of Panama. A few female specimens which we provisionally regard as *spanius* have been collected on the Pacific seaboard of Panama. Since, as mentioned above, we have not been able to differentiate females of known species in this group, we cannot tell if these females, which include the lectotype of *spanius* (selection of Stone and Knight, 1957: 197), are identical with the Atlantic *spanius* (in our present sense) or represent a different species. It is not definitely established that *mathesoni* is indigenous to Texas; it has been suggested that it was introduced by plane from Trinidad. Mosquitoes of this group are very small and inconspicuous and apparently have rather specialized habitats; therefore it is possible that their presence has been overlooked in other areas and that other species actually exist. In addition, it would be very easy to mistake females of this group for species of *Culex* and this is the sex which is most frequently collected.

It seems likely that this group is associated with crabs of the family Ocypodidae since *mathesoni* has been found in the holes of *Uca pugilator*.

1. *Deinocerites mathesoni* Belkin and Hogue, n. sp.

Deinocerites spanius of Fisk (1941: 543-550); Matheson (1944: 253-254); Knight and Chamberlain (1948: 10); Carpenter and LaCasse (1957: 327-329); and all other records from Texas.

Adults.—Antenna, palpus, and proboscis of male and female as illustrated (fig. 16); anterior claw only of the foreleg of male with a long subbasal tooth (fig. 28).

Male genitalia (fig. 3): Ninth tergite lobe slender but strongly widened and flattened beyond basal part and with a constriction subapically; dorsal paramere with two weak sclerotizations connected by a narrow bridge; dorsal sclerotization of dorsal paramere bearing the long slender apical spine which is strongly hooked near apex; ventral sclerotization of dorsal paramere with 2 or 3 large heavy outstanding teeth; aedeagus cylindrical, broad at base, then constricted, lateral plates connected by a basal tergal bridge.

Pupa (Knight and Chamberlain, 1948, fig. 30, as *spanius*).—Cephalothorax undescribed except for metanotum which appears to be similar to that of *mcdonaldi*.

Abdomen: Similar to *mcdonaldi* except for the following: hair 7-III-VI apparently at or very near the posterolateral angle of tergite, and 7-VII on the lateral border; hair 5-VII single; hair 1-VII longer than tergite VIII. Paddle narrower than in *mcdonaldi* and with a distinct apical emargination.

Larva (Carpenter and LaCasse, 1957: 328-329, fig. 288, as *spanius*).—In general very similar to *mcdonaldi* with the following exceptions.

Head: Hairs 5, 6-C subequal in size, both 3- to 5-branched and long plumose; mental plate much broader than long, its marginal teeth frayed apically.

Thorax: Hairs 3, 4-M shorter; 6-T short, double.

Abdomen: Hair 7-I short, inconspicuous; 6-II-VI weak, usually single; hair 13-V single or double. Siphon as figured; hairs 1a-S proportionately stronger; pecten teeth unequally bifid, usually 5 on each side.

Anal segment: Hair 2-X usually 3- to 5-branched; ventral brush with 6 pairs of hairs; anal papillae hardly indicated.

Holotype.—♂, Brownsville, Texas, Feb. 8-9, 1940, reared (F. W. Fisk, U.S.N.M. No. 64, 261).

Material Examined (11 ♂, 22 ♀, 4 larvae).—TEXAS: Corpus Christi, 3 ♀, Nov. 19, 1944 (F. R. du Chanois, U.S.N.M.). Brownsville, 1 adult, on plane from Port of Spain, Trinidad (40-22166, U.S.N.M.); 6 ♀, Dec. 4, 1939, 3 ♂, 2 ♀, 2 larvae, Feb. 8-9, 1940, 2 ♂ (4022-23), Mar. 15, 1940, 1 ♀, Apr. 1940 (F. W. Fisk, U.S.N.M., U.C.L.A., holotype and paratypes); 3 ♂, 7 ♀, Sept., 1942 (T. N. Burns, U.S.N.M., paratypes); 1 ♂, 2 ♀, Nov. 29, Dec. 18, 1939, Jan. 15, 1940 (U.S.N.M., paratypes); 2 larvae, Sept. 27, 1942 (E. S. Ross, U.S.N.M., paratypes). Harlingen, 1 ♂, Mar. 9-10, 1945 (U.S.N.M.). Cameron Co., 1 ♀ (U.S.N.M.).

Fisk (1941: 543-550) gives rather extensive notes on the bionomics of *mathesoni* (as *spanius*). This species utilizes holes made by a fiddler crab, *Uca pugilator* (Bosc). Although the evidence is not conclusive, it seems probable that the eggs observed by Fisk in the laboratory were of this species. They were found attached above the water line in glass jars kept in an observation cage in which adults emerging from field-collected larvae were seen to mate. Four larvae hatched during the course of observations, and one of these completed development in approximately two months. Eggs, larvae, and pupae are all whitish in color; the pupa darkens about a day before emergence of the adult. The larvae will not withstand pollution or an overabundance of food. A pooled sample of water from crabholes showed a soluble chloride content of 8,430 ppm and contained several species of diatoms and Protozoa.

During the day the adults rested in the observation cage just above the water surface inside the jars. When disturbed they tended to crawl or run rather than to take flight. Mating was observed early in the morning. Females fed on a turtle, were somewhat attracted by a frog and horned toad though actual feeding was never noted, and disregarded crab and human hosts. Fisk states that "after dark . . . the mosquitoes have proven to be strong fliers. Both sexes have been taken in light traps several miles from their breeding grounds, though the females were most commonly trapped."

D. mathesoni was first taken in light traps at Brownsville, Texas, on November 29, 1939. Apparently a specimen recovered from a plane from Port of Spain, Trinidad, at the Brownsville municipal airport prompted the speculation by Fisk (1941: 543) that this species could have been introduced. It seems much more probable to us that *mathesoni* is indigenous to Texas and that its presence on the plane was due to entry of the specimen at Brownsville rather than at Port of Spain. However, the possibility still exists that it is an introduction in Texas. We have seen very few specimens of *Deinocerites* (all *magnus*) from Trinidad, and since *mathesoni* does not attack man it is quite possible that its presence has been overlooked there as elsewhere. Only careful search for this species will resolve this problem.

2. *Deinocerites spanius* (Dyar and Knab, 1909)

Dinanamesus spanius Dyar and Knab, 1909, Smithson. Misc. Coll., 52: 259. Lectotype: Female, Corozal, Panama, Dec. 11, 1907, from crabhole, A. H. Jennings, 69; selection of Stone and Knight, 1957: 197 (U.S.N.M. 12052).

Adults.—Antenna, palpus, and proboscis of male and female as illustrated (fig. 17); anterior claw of both fore- and midleg of male with a long subbasal tooth (fig. 29).

Male genitalia (fig. 4): Ninth tergite lobe very slender, slightly widened near middle, then slightly constricted subapically; dorsal paramere a small compact uniformly sclerotized plate; apical spine of dorsal paramere short, broad at base, slightly curved and gradually pointed; ventral teeth of dorsal paramere a group of 4 or 5 outstanding denticles.

Pupa and larva.—Undescribed.

Material examined (38 ♂, 224 ♀).—PANAMA CANAL ZONE: Ft. Randolph, 1 ♂, 2 ♀, June 19, 1920 (J. Zetek, U.S.N.M., U.C.L.A.); 29 ♀, Oct. 18, 1924—May 16, 1925 (D. Baker, U.S.N.M.). France Field, 1 ♂, Oct. 22, 1921 (C. S. Ludlow, U.S.N.M.). Margarita, 6 ♂, 20 ♀, Nov. 5, 1921—July 22, 1922 (J. B. Shropshire, U.S.N.M.). Toro Pt., 6 ♀, Apr. 21, 1922 (J. B. Shropshire, U.S.N.M.). Ft. Sherman, 1 ♂, 1 ♀, June, 1920 (J. Zetek, B.M.N.H.); 27 ♂, 131 ♀, Apr. 16—Aug. 12, 1920 (J. Zetek, U.S.N.M.); 3 ♀, Mar. 31, 1923 (J. B. Shropshire, U.S.N.M.); 3 ♀, Apr. 2, May 23, 1925 (D. Baker, U.S.N.M.). Ft. Davis, 1 ♂, 21 ♀, Mar. 23, 1925 (D. Baker, U.S.N.M.). Arenal River, 1 ♀, Feb. 2 (C. S. Ludlow, U.S.N.M.). Majagual, 3 ♀, Feb. 15, 1922 (J. B. Shropshire, U.S.N.M.). Cativa, 2 ♀, Apr. 1, 1922 (J. B. Shropshire, U.S.N.M.). Ft. Clayton, 1 ♀, Mar. 5 (C. S. Ludlow, U.S.N.M.). No locality: 1 ♀, Jan., 25 (J. B. Shropshire, U.S.N.M.).

REPUBLIC OF PANAMA: Cascajal River (Portobelo Bay), 1 ♂, May 30, 1908 (A. H. Jennings, U.S.N.M.).

Also reported from PANAMA CANAL ZONE, Corozal, lectotype ♀.

Dyar and Knab (1915: 215) reported that larvae of this species live in the water in crabholes along the coast and that A. H. Jennings obtained them twice in those locations. Apparently these larvae were not preserved nor were the larval and pupal skins of the adults that were reared from at least one of these collections. Jennings (Dyar and Knab, 1915: 215) also obtained this species from a crabhole along the Cascajal River in Puerto Bello Bay. In neither case was the type of crab indicated. Dyar (1928: 265) reports *spanius* breeding in "old tins" and (1928: 261) states that females bite man and even enter houses situated close to their habitats.

The bulk of the material we have seen is from the Atlantic side of Panama, but at least two specimens are apparently from the Pacific side. One of these is the lectotype female selected by Stone and Knight (1957: 197). It was supposedly reared from a larva collected at Corozal, C. Z. Although it is quite possible that *spanius* occurs in the Pacific basin these few records need confirmation. Clarification of this point is of primary importance for further studies on the bionomics and zoögeography of the genus for, as indicated above in the discussion of the group, the Pacific specimens may prove to belong to another species.

DYARI GROUP

This group, represented by a single species, is characterized chiefly by the following: small size, simple forefemur, and absence of mesepimeral scales in both sexes; female antenna moderately and male strongly differentiated; 8th sternite without scales, and cercus without differentiated apical setae in the female; 9th tergite lobe very short and pointed and sidepiece without scales in the male.

3. *Deinocerites dyari* Belkin and Hogue, n. sp.

Adults.—Small in size, wing 2.5–3.5 mm.; pleural integument light, strongly contrasting with rest of body which is dark; antenna, palpus, and proboscis of male and female as illustrated (fig. 24); female antenna with first flagellar segment about equal to 2, 3, and half of 4 combined, proboscis extending only to 8th segment; male antenna with flagellar segments 1 to 6 markedly elongate, segment 1 shorter than 2 and 3 combined, proboscis extending to about middle of seg-

ment 5; mesepimeron without scales; postnotum often with a few hairs; forefemur without spiniforms; claws of fore- and midleg of male all enlarged, subequal (fig. 30), anterior claw of foreleg with a very long, slender, subbasal tooth, anterior claw of midleg with a shorter heavy tooth, posterior claws of both legs simple.

Female genitalia: Eighth sternite without scales on sclerotized apical part.

Male genitalia (fig. 10): Ninth tergite lobe with distal part short, more or less pointed and conical, not reaching more than halfway to median mesal lobe and directed laterad; sidepiece without scales; median mesal lobe with a distinct thumb, seta *c* rather heavy and spiniform but with an apical attenuation, inserted laterad but visible from tergal aspect; apicosternal lobe prominent and with a strong differentiated dorsal seta; dorsal parameres widely separated in tergal aspect, without sclerotized dorsal bridge, apical spine long and strongly curved, ventral teeth large, arising from convex caudolateral border.

Pupa and larva.—Unknown.

Holotype.—♂, Corozal, Panama Canal Zone, Apr. 20, 1919 (J. Zetek, 1183, U.S.N.M. No. 64, 262).

Material Examined (4 ♂, 7 ♀).—PANAMA CANAL ZONE: Corozal, 4 ♂, 6 ♀, Apr. 20, 1919 (J. Zetek, 1183, U.S.N.M., U.C.L.A., holotype and paratypes).

REPUBLIC OF PANAMA: Isla San Jose (Las Perlas), 1 ♀, Apr. 15, 1944 (J. P. E. Morrison, U.S.N.M.).

D. dyari appears to be a transitional form between the Spanius group and the remainder of the genus and may be a relict from the stock from which arose also the Cancer and the Epitedeus groups. This is particularly evident in the differentiation of the male antenna but is also suggested by the degree of development of almost all the other morphological features we have examined. The reduction of the 9th tergite lobe of the male genitalia is undoubtedly secondary.

This species has been found only in the Gulf of Panama but it may extend farther south along the Pacific coast of South America. Its small size is suggestive of an association with smaller land crabs of the family Ocypodidae.

CANCER GROUP

Adults.—Medium in size, wing 2.8–3.8 mm., dark brown to almost black in color; antenna markedly different in total length and in the proportions of flagellar segments in the two sexes; female antenna with first flagellar segment about equal in length to segments 2 to 4 combined or slightly shorter, segments 2 to 13 progressively shorter distad, proboscis reaching 7th flagellar segment but not extending beyond; male antenna with flagellar segments 1 to 6 markedly elongated, segment 1 shorter than 2 and 3 combined, proboscis not reaching segment 5; *ppn* sometimes with a few broad scales; mesepimeron without scales; postnotum without bristles; forefemur without spiniforms; claws of foreleg of male subequal, strongly enlarged, teeth variously developed; claws of midleg of male enlarged, anterior member of pair larger and with a strong subbasal tooth, posterior smaller and simple.

Female genitalia: Eighth sternite without scales on sclerotized apical part, its caudolateral angle in lateral aspect produced, not rounded as in other groups; cercus with a pair of long, slightly or markedly spatulate, apical or subapical specialized setae.

Male genitalia: Ninth tergite lobe with distal part markedly flattened and widened, more or less straight beyond base and overlying the sidepiece dorsally; sidepiece without scales; median mesal lobe with or without mesal thumb, seta *c* heavy, appearing spiniform but usually with a slight apical process or attenuation; apicosternal lobe prominent and with a strong differentiated dorsal seta; dorsal parameres with a variable dorsal bridge; aedeagus cylindrical, in tergal aspect narrow at base then with lateral expansions and constrictions.

Pupa.—Unknown for *melanophylum*; insufficiently known for *cancer* and *magnus* to be described, but conforms to general type for genus.

Larva.—Insufficiently described for *melanophylum*. In general quite similar to *medonaldi* but with the following exceptions.

Head: Hair 6-C usually single, rarely double, very long.

Siphon: Pecten teeth 6 to 8 on each side, bifid or trifid.

The Cancer group is a well-marked complex of three closely related and completely allopatric species whose distribution forms a ring around the Caribbean Sea and extends into Florida and Brazil. The group is most clearly marked by the development of the pair of specialized apical or subapical setae on the cercus of the female and the greatly flattened and broad 9th tergite lobe overlying the side-piece of the male.

Of the three species in the group, *magnus* is the most clearly marked in structure, and *cancer* and *melanophylum* are more alike. Remarkable is the fact that *cancer* occurs on the mainland of Central America, in British Honduras, Republic of Honduras, and Nicaragua, as well as in Jamaica, Cuba, Hispaniola, and Florida whereas *melanophylum* is known only from Panama, Colombia, and western Venezuela. There is thus a wide gap between *cancer* and *melanophylum* in Costa Rica and probably adjacent parts of Nicaragua and Panama. This gap is occupied, as far as we know at present, exclusively by *epitedeus*, a member of another group of the genus. Of interest also is the distribution of *magnus* which begins in the north at Mona Island, less than 40 miles from Hispaniola (where only *cancer* occurs) and extends eastward and then south through Puerto Rico, the Virgin Islands, the Lesser Antilles, and Trinidad to British Guiana, Surinam, and northern Brazil. The boundary between *magnus* and *melanophylum* is not known but it is apt to be in the Gulf of Cariaco in Venezuela.

We suggest therefore from the above-mentioned morphological and geographical relations that *magnus* was cut off to the east from the *cancer-melanophylum* complex very early, and *cancer* and *melanophylum* were separated at a much later date in the region of the Nicaraguan-Costa Rican portal. Although *magnus* shows many more morphological similarities with *cancer* than *melanophylum*, this does not necessarily imply that it was cut off at the northern end and then spread southward; it is possible that these similarities are secondary and that *magnus* was cut off from an ancient stock in the south, in the region of the Gulf of Cariaco, and spread both north and south from this central point. At present, however, we favor the first interpretation. The fact that the populations in Honduras and Nicaragua are definitely referable to *cancer* does not necessarily imply the existence at one time of a continuous land mass from the core of Central America to Florida and including Jamaica, Cuba, and Hispaniola, but it does indicate at least that in the past there have been no major and long-lasting gaps. Otherwise it is very likely that the *cancer* populations would show much more geographical differentiation than they do.

The bionomics of this group are very little known. There are conflicting reports of the blood-feeding habits which may be indicative of racial differences in the species. We have found no record of the species of crabs with which mosquitoes of this group are associated other than the statement that they are the common large land crabs (family Gecarcinidae).

4. *Deinocerites magnus* (Theobald, 1901)

Brachiomyia magna Theobald, 1901, Monograph Culicidae, 2: 344-345. Holotype: Male (described as female), St. Lucia, Low, per Daniels (B.M.N.H., lost, *vide* Mattingly, *in lit*).

Deinocerites troglodytus, Dyar and Knab, 1909, Smithson. Misc. Coll., 52: 260. Lectotype: Female, Trinidad, W. E., June, A. Busek; selection of Stone & Knight, 1957: 197 (U.S.N.M. 12128).

Adults.—Antenna, palpus, and proboscis of male and female as illustrated (fig. 18); female antenna with first flagellar segment distinctly longer than combined lengths of 2 to 4; male proboscis extending to end of 4th flagellar segment; claws (fig. 32) of foreleg of male both with a strong nearly basal tooth; anterior claw of midleg with tooth nearly basal; scaling of pleuron restricted, *ppi* without scales, *ppn* with only a few, *stp* with a long narrow strip of small scales.

Female genitalia (fig. 12): The two specialized cercal bristles not inserted side by side on apex, one distinctly subapical, each bristle with slender stem and with markedly spatulate or spoon-shaped distal widened part; lobe of postgenital plate elongate and with a large differentiated apical bristle; 8th sternite with heavy marginal bristles continued about halfway dorsad on caudolateral border.

Male genitalia (fig. 5): Ninth tergite lobe barely reaching level of median mesal lobe, very broad, and with sinuous external and internal margins; median mesal lobe with rather distinct thumb; the two dorsal parameres closely approximated tergally and with a broad, short, incomplete dorsal bridge; apical spine heavy, long, and only slightly curved; ventral teeth few in number, short, and heavy, and arising in a single row along the truncate lateral border of paramere.

Pupa.—Known only from a single imperfect female specimen, on which even generic characters are difficult to determine. Trumpet index about 4.0.

Larva (Howard, Dyar, and Knab, 1912, fig. 310; Dyar and Knab, 1915: 207, as *troglodytus*).—As for the group, with the following distinctive characters: head hairs 2-C very close together near mid-line, distance between the two less than between 2-C and 1-C on each side in tergal aspect; hair 4-P usually 4- or 5-branched; usually several pecten teeth trifold; hair 7-I rather weak.

Material examined (25 ♂, 51 ♀, 16 larvae, 1 pupa).—PUERTO RICO: Isla Mona, 2 ♂, May 11, 1955 (W. F. Pippin, U.S.N.M.). Isla Verde, 11 ♀, June 1956 (U.C.L.A.). San Juan, 1 larva, Jul. 20, 1948 (H. D. Pratt, U.S.N.M.). Catano, 3 larvae, Oct. 1942 (H. D. Pratt, U.S.N.M.). Ft. Buchanan, 1 ♂, 1 ♀, Jan., 1943 (H. D. Pratt, U.S.N.M.). Dorado, 2 ♂, 2 larvae, Sept. 1, 1938 (G. S. Tulloch, U.S.N.M.). Mayaguez, 9 ♀, Dec. 14, 1935–May 11, 1936 (G. S. Tulloch, U.S.N.M.). Central Aguirre, 3 ♀, Jul. 15, Aug. 15, 1935 (G. S. Tulloch, U.S.N.M.).

VIRGIN ISLANDS: St. Thomas, 1 ♂, Aug. 30, 1932 (Cyril Cregue, U.S.N.M.). St. Croix, 4 ♂, 5 ♀, 6 larvae (H. A. Beatty, U.S.N.M., U.C.L.A.).

NETHERLANDS WEST INDIES: Sint Maarten, Philipsburg, 1 larva; below Prinsen Quart., 1 ♀ (E. van der Kuyp, U.S.N.M.).

ANTIGUA: Green Bay, Millars, Old Road, 3 ♂, 2 ♀, Sept. 1–Oct. 14, 1938 (H. E. Box, B.M.N.H.).

GUADELOUPE: 2 ♀, July (A. Busek, U.S.N.M.).

MARTINIQUE: Fort de France, 5 ♂, 3 ♀, July 1905 (A. Busek, U.S.N.M.).

ST. LUCIA: Castries, Botanic Garden, 1 ♀, July 4, 1899 (St. George Gray, B.M.N.H.).

ST. VINCENT: 1 ♂, 1 ♀ (J. J. Buckley, B.M.N.H.). Calliaqua, 1 ♂, 1 ♀ (Low, B.M.N.H.).

BARBADOS: 1 ♀, July, 1905 (A. Busek, U.S.N.M.). Worthing, 1 ♂, 1 ♀, 3 larvae, 1 pupa, June 4, 1907 (Low, B.M.N.H.).

GRENADA: 1 ♂, 1 ♀, Feb. 2, 1900 (W. E. Broadway, B.M.N.H.).

TRINIDAD: 1 ♀, May 11, 1905 (F. W. Ulrich, B.M.N.H.); 1 ♂, 1 ♀, (F. W. Ulrich, U.S.N.M.).

Chaguaramas Bay, 1 ♀, (J. Leacock, U.S.N.M.). Mayaro, 1 ♂, 1 ♀, Dec. 1, 1913 (B.M.N.H.).

BRITISH GUIANA: Morawhanna, 1 ♂, 1 ♀, (Low, 123, B.M.N.H.).

SURINAM: 3 ♀ (45-00, 45-01, 45-02, H) (Amst.).

Also reported from BRAZIL, State of Maranhão (Cerqueira, 1938: 291).

Dyar and Knab (1915: 207), quoting A. Busek's field notes, report this species (as *troglodytus*) from crabholes along the shore and in a mangrove swamp and

indicate that on Trinidad adults do not bite man. On the other hand, Bonne and Bonne-Webster (1925: 173) found "*troglogytus*" entering houses and producing painful bites in Surinam. Cerqueira (1938: 291) reports females, as *cancer*, attracted to horses in Icatu and São Luiz, Maranhão, Brazil.

D. magnus is the most distinct of the three species of the *cancer* group. In most of its morphological adult features it seems also to be the most generalized, and it shows more similarities with *dyari*. It occupies the entire eastern part of the area of distribution of the group, occurring from Mona Island, between Hispaniola and Puerto Rico, at least as far south as northern Brazil. The specimens from British Guiana are undoubtedly *magnus* and in all probability are also those we have seen from Surinam. However, they have had their genitalia removed, and without seeing them we cannot be positive about their identity. The specimens from northern Brazil, reported as *cancer* by Cerqueira (1938: 289-291), also belong to *magnus* to judge by the figures.

We have not analyzed our material critically to determine if there has been local differentiation in *magnus* as might be suspected from the reported differences in feeding habits. We have seen no striking differences in small samples from a large number of localities.

5. *Deinocerites cancer* Theobald, 1901

Deinocerites cancer Theobald, 1901, Monograph Culicidae, 2: 215-216. Lectotype: Female, Jamaica, 8-2-1900, Grabham; not published but marked by Theobald, *vide* Mattingly, *in lit.* (B.M.N.H.).

Deinocerites tetraspathus Dyar and Knab, 1909, Smithson. Misc. Coll., 52: 260. Lectotype: Female, Bluefields, Nicaragua, genitalia mounted on slide 472; selection of Stone and Knight, 1957: 197 (U.S.N.M. 12109).

Adults.—Coloration dark brown; antenna, palpus, and proboscis of male and female as illustrated (fig. 20); female antenna with first flagellar segment about equal to combined lengths of 2 to 4; male proboscis not extending beyond middle of flagellar segment 4; anterior claw (fig. 33) of foreleg of male with a large subbasal tooth, posterior simple; anterior claw of midleg of male with tooth subbasal; scaling of pleuron extensive, *ppl* with a few scales, *ppn* with numerous scales, *stp* with a broad long strip of long scales.

Female genitalia (fig. 13): The two specialized cercal bristles inserted side by side on apex, each bristle with heavy stem and slight apical expansion; lobe of postgenital plate short and without differentiated bristle; 8th sternite with heavy marginal bristles largely restricted to sternal margin, at most continued one-third dorsad on caudolateral border.

Male genitalia (fig. 7): Ninth tergite lobe extending beyond medial mesal lobe, its external and internal margins rather evenly curved, distal part very broad; median mesal lobe without thumb, seta *c* more spiniform than in *magnus* and its base visible from tergal aspect; the two dorsal parameres closely approximated tergally and with a broad incomplete sclerotized dorsal bridge; apical spine slender, moderately curved; ventral teeth slender, long and arising usually from a distinct process from the convex caudolateral border of paramere, two or more teeth often with common base, several additional smaller denticles removed from border.

Pupa.—Known only from a few imperfect specimens on which even generic characters are difficult to determine. Trumpet index apparently about 4.0 or less.

Larva (Carpenter and LaCasse, 1955: 326-327, fig. 286).—As for the group, with the following distinguishing features: head hairs 2-C widely spaced, distance between the two on the midline much greater than that between 1-C and 2-C on each side in tergal aspect; hair 4-P usually 2- or 3-branched; hair 7-I strong; usually no trifold pecten teeth except at base.

Material examined (91 ♂, 146 ♀, 169 larvae, 20 pupae).—FLORIDA: Ft. Pierce, 1 ♂, June 10, 1926 (N. G. Piatte, U.S.N.M.); 3 ♀, June 19, 1937 (No. 1882, U.S.N.M.). Jupiter Is., 12 larvae,

Sept. 16, 1943 (Wanamaker, U.S.N.M.). Palm Beach, 1 ♂, Feb., 1936 (No. 6, T.E.M., U.S.N.M.). West Palm Beach, 1 ♀, May 18, 1945 (U.S.N.M.). Boca Raton, 1 ♂, 1 ♀, Sept. 16, 1943 (U.S.N.M.); 3 larvae Sept. 23, 1943 (Wanamaker, U.S.N.M.); 12 larvae, Apr. 28, 1944 (U.S.N.M., U.C.L.A.); 1 ♀, July 18, 1945 (U.S.N.M.). Fort Lauderdale, 1 ♂, 52 larvae, Oct. 22, 1944 (W. W. Wirth & D. G. Denning, U.S.N.M., U.C.L.A.). Hollywood, 1 larva, June, 1935 (U.S.N.M.). Miami Beach, 1 ♂, Apr., 1944 (W. W. Wirth, U.S.N.M.); 2 ♀, July, 1944 (W. W. Wirth, U.S.N.M.). Miami, 1 ♀, May 23 (U.S.N.M.); 13 ♂, 15 ♀, Oct. 3–Nov. 11, 1921 (G. F. Mozzette, U.S.N.M., U.C.L.A.); 1 ♀, Sept. 9, 1943 (W. W. Wirth, U.S.N.M.). Coral Gables, 1 ♂, Aug., 1934 (No. 8, U.S.N.M.). Key Largo, 1 larva, 1944 (W. W. Wirth, U.S.N.M.). Key West Banks, 3 ♀, June 13, 1924, Mar. 25, Apr. 17, 1925 (Sgt. Mead, U.S.N.M.). No locality: 2 ♂, 1 ♀ (No. 1173); 1 ♀ (No. 1282); 6 ♀ (No. 1302); 4 ♂ (No. 1719); 1 ♀ (No. 1946); 7 ♀ (No. 1990) (U.S.N.M.).

CUBA: Havana, 6 larvae, 2 pupae, Oct. 28, 1903 (J. R. Taylor, 11, U.S.N.M.). Marianao, 20 ♂, 14 ♀, 32 larvae, Mar., 1936 (H. P. Carr, U.S.N.M., U.C.L.A.). Mariel, 16 ♂, 10 ♀ (J. R. Taylor, U.S.N.M.); 1 ♂ (40–66, Amst.). No locality: 13 ♂, 6 ♀ (H. P. Carr, U.S.N.M.); 1 ♂, 2 ♀ (40–63, 64, 65, Amst.).

HAITI: 1 ♂, 1 ♀, Apr. 19, 1932 (S. S. Cook, U.S.N.M.).

DOMINICAN REPUBLIC: Monte Cristi, 1 ♂, 45 ♀, Mar. 18, 1949 (U.S.N.M.). Azua, 1 ♀, Mar. 30, 1928 (P. A. Ricart, U.S.N.M.). Santo Domingo (C. Trujillo), 4 ♂, 1 ♀, Aug., 1905 (A. Busck, no. 10, U.S.N.M.). San Pedro de Macoris, 1 ♀, Mar. 31, 1928 (P. A. Ricart, U.S.N.M.).

JAMAICA: 1 ♀, Oct. 10, 1899 (Grabham, B.M.N.H.); 1 ♀ (Crawford Expedition, B.M.N.H.). Runaway Bay, 1 ♀ (Lord Walsingham, B.M.N.H.). Kingston, 4 pupae (B.M.N.H.); 26 larvae, 14 pupae (U.S.N.M.); 1 ♀ (Grabham, 111, 6·2·9, B.M.N.H.); 1 ♂ (Grabham, 7·2·02, B.M.N.H.); 7 ♂, 2 ♀ (Grabham, U.S.N.M.); 2 ♀, Sept. 9, 1907 (H. Morrison, 459, U.S.N.M.).

BRITISH HONDURAS: Trapp's Key, 1 ♀, Mar. 20, 1909 (40–67, Amst.); 11 ♀, Mar. 20, 1909 (W. H. Sligh, U.S.N.M.).

HONDURAS: Puerto Castilla, 1 ♂, 1 ♀, 24 larvae, Sept. 20, 1943 (K. R. Maxwell, 100, U.S.N.M., U.C.L.A.).

Also reported from NICARAGUA (Bluefields) and GUATEMALA (Puerto Barrios) (Dyar & Knab, 1915: 210).

Dyar and Knab (1915: 205) summarize some of the early conflicting information regarding the bionomics of *cancer*. This species supposedly inhabits holes of land crabs in tidal marshes along the coast (Carpenter and LaCasse, 1955: 327), but there is no record of any specific crab in the literature. Females have been reported to be voracious bloodsuckers, never to bite man (Dyar and Knab, 1915), or occasionally to bite (Carpenter and LaCasse, 1955: 327).

D. cancer is very similar to *melanophylum* in the female and, in a superficial examination, we find only a slight difference in the relative length of the first three flagellar segments. However, the males of the two species are easily differentiated by the claws and the genitalia.

D. cancer occupies the northern part of the western range of the group, extending from Florida through Cuba, Hispaniola, and Jamaica, to British Honduras, the Republic of Honduras, and Nicaragua. We have not made a detailed analysis of the samples of the various populations available to us, but on superficial examination we find no striking, reliable differences within the complex. The inclusion of the Central American populations in *cancer* is based on very slim evidence, a single male, but we feel that it is conclusive. Both the claws and the dorsal paramere of this specimen are definitely of the *cancer* and not of the *melanophylum* type. However, the paramere shows a slight departure from *cancer*, and it may be that the Central American populations have been isolated from the Antillean for a considerable length of time and that they have differen-

tiated from typical *cancer* to a slight degree. The name *tetraspathus* is available for these populations. As far as we know *cancer* occurs in Florida only on the keys and on the southeast coast as far north as the vicinity of New Smyrna (King *et al.*, 1942: 61) and is apparently absent from the west coast. Temperature may be the factor that limits its distribution in this area. As far as we know, neither *cancer* nor any *Deinocerites* occurs in the Bahamas.

6. *Deinocerites melanophyllum* Dyar and Knab, 1907

Deinocerites cancer melanophyllum Dyar and Knab, 1907, Jour. N. Y. Ent. Soc., 15: 200. Lectotype: Male, Colon, Panama, A. Busck, 213; selection of Stone and Knight, 1957: 197 (U.S.N.M. 10865).

Deinocerites monospathus Dyar, 1925, Insec. Insci. menst., 13: 155. Holotype: Female, Fort Sherman, Panama Canal Zone, Apr. 24, 1925, D. Baker; unique, mounted on same slide with normal female of *melanophyllum* (Stone *in lit.*, U.S.N.M. 28309).

Adults.—Coloration somewhat darker than in *cancer* and *magnus*; antenna, palpus and proboscis of male and female as illustrated (fig. 19); female antenna with first flagellar segment distinctly shorter than combined lengths of 2 to 4; male proboscis not extending beyond middle of flagellar segment 4; anterior claw (fig. 31) of foreleg of male with a minute subbasal tooth, posterior simple; anterior claw of midleg of male with tooth subbasal; scaling of pleuron extensive, *ppl* with a few scales, *ppn* with numerous scales, *stp* with a broad long strip of long scales.

Female genitalia (fig. 14): Cerebral bristles, postgenital lobe, and 8th sternite essentially as in *cancer* although specialized cercal bristles are slightly more slender and longer in proportion to length of cercus.

Male genitalia (fig. 6): Ninth tergite lobe essentially as in *cancer* except not quite as broad distally and with more sinuous margins; median mesal lobe essentially as in *cancer*; the two dorsal parameres widely separated tergally and with long narrow incomplete dorsal sclerotized bridge; apical spine long, slender, and very strongly curved; ventral teeth short and heavy to minute and in several rows, directed parallel to convex margin so that they appear appressed to body of paramere (considerable variation in size).

Pupa.—Unknown.

Larva (Howard, Dyar, and Knab, 1912, fig. 307; Dyar and Knab, 1915: 209).—We have seen no larvae of this species. There is nothing in the figures or descriptions of Dyar and Knab which would enable us to separate *melanophyllum* from *cancer* but it appears to be distinct from *magnus* on the basis of the greater distance between the two head hairs 2-C as in the case of *cancer*.

Material examined (39 ♂, 119 ♀).—PANAMA CANAL ZONE: Ft. Randolph, 3 ♂, 5 ♀, June 19, 1920 (J. Zetek, U.S.N.M.); 1 ♂, 9 ♀, May 2–16, 1925 (D. Baker, U.S.N.M.). France Field, 1 ♂, 4 ♀, June 19, 1920 (J. Zetek, U.S.N.M.). Cristobal, 1 ♀ (U.S.N.M.). Mount Hope, 10 ♀, Oct. 31, Nov. 5, 8, 1951 (S. J. Carpenter, U.C.L.A.). Margarita, 1 ♂, 9 ♀, Nov. 5, 1921, May 20, Jul. 22, 1922 (J. B. Shropshire, U.S.N.M.). Toro Pt., 6 ♂, 13 ♀, Oct. 29, 1921–Apr. 21, 1923 (J. B. Shropshire, U.S.N.M.). Ft. Sherman, 2 ♂, 2 ♀, June, 1920 (J. Zetek, B.M.N.H.); 13 ♀, Oct. 30, 1951, Feb. 6, 1952 (S. J. Carpenter, U.C.L.A.); 2 ♂, 24 ♀, Apr. 16–Aug. 12, 1920 (J. Zetek, F. A. Blasse, U.S.N.M., U.C.L.A.); 9 ♀, Mar. 31, 1923 (J. B. Shropshire, U.S.N.M.); 8 ♂, 6 ♀, Aug. 8–27, 1923 (Dyar & Shannon, P75, U.S.N.M., U.C.L.A.); 3 ♂, 2 ♀, Apr. 2, 1925 (D. Baker, 8, U.S.N.M.); 2 ♀, Feb. 2 (C. S. Ludlow, U.S.N.M.). Fort Davis, 1 ♂, 5 ♀, Mar. 23, 1925 (D. Baker, U.S.N.M.). Gatun, 1 ♂, Apr. 7, 1908 (A. H. Jennings, U.S.N.M.). No LOCALITY: 2 ♂ (A. H. Jennings, 248), 2 ♂ (A. H. Jennings, 352, U.S.N.M.); 1 ♂ (A. H. Jennings, 40–68, Amst.); 1 ♀ (U.C.L.A.).

REPUBLIC OF PANAMA: Caldera Is. (Portobelo Bay), 2 ♂, Mar. 22, 1908 (A. H. Jennings, U.S.N.M.).

COLOMBIA: Bocas del Toro, 1 ♂ (W. J. Rosenati, U.S.N.M.).

VENEZUELA: Ocumare de la Costa (Aragua), 1 ♂, 1 ♀, Jan. 27, Jul. 5, 1927 (M. Nunez Tovar, U.S.N.M.). Maracay (Aragua), 1 ♂, 3 ♀, 1925, Aug., 1926 (M. Nunez Tovar, U.S.N.M.).

The only specific information pertaining to *melanophylum* is to be found in the original field notes of A. Busek and those of Jennings quoted in Dyar and Knab (1915: 209): "The species is said to inhabit crab-holes along the shore and was once collected in holes from which posts had been withdrawn beside a gravel dump—'simulated crab-holes.'" Some of the statements by Carpenter and LaCasse (1955: 327) about *cancer* undoubtedly refer at least in part to *melanophylum*. This species has been taken in animal-baited traps in Panama and reported as *cancer*.

As noted above, *melanophylum* is very similar to *cancer* in the female, differing only in slightly different proportions of the first three flagellar segments, but is easily differentiated from it in the male claws and genitalia. *D. monospathus* is without doubt an aberrant specimen of *melanophylum*; as a matter of fact the unique specimen is mounted on the same slide with a normal specimen of the latter collected at the same time and at the same locality.

D. melanophylum occupies the southern part of the western range of the *cancer* group, extending from Panama in the west probably to the Gulf of Cariaco in Venezuela in the east. Between the known distributions of *cancer* and *melanophylum* there is a wide gap which coincides with the maximum extent of the last Atlantic-Pacific portal between southern Nicaragua and Panama and which is now occupied by *epitedeus*, a member of another group of *Deinocerites*. Our material outside the Canal Zone is very limited and identification of this as *melanophylum* is only provisional. The single male from Colombia has a larger tooth on the anterior foreclaw than specimens from Panama. In Venezuela our material is from Ocumare de la Costa and from Maracay (Aragua) directly south of the former and situated on the shores of Lake Valencia. The two populations, separated by a good-sized mountain range and utilizing two very different habitats, one littoral marine and the other fresh-water, seem to be entirely similar. These populations conform in general to *melanophylum* from the Canal Zone, but males from both of them have the ventral teeth of the dorsal paramere greatly reduced. For the present we prefer to leave all these populations in *melanophylum* because there is in typical *melanophylum* a wide range in the development of the paramere teeth and because our material is scanty and we know nothing of the characteristics of intervening populations.

EPITEDEUS GROUP

Adults.—Medium in size, wing 2.8–4.8 mm.; general coloration dark brown to almost black; antenna strongly differentiated and usually very long in male but variable in length and development in female; male antenna with flagellar segments 1 to 6 or 1 to 7 markedly elongate, proboscis not reaching segment 5; *ppn* sometimes with a few broad scales; mesepimeron with scales; postnotum often with hairs; forefemur with or without spiniforms; claws of fore- and midleg of male variously modified.

Female genitalia: Eighth sternite without scales on sclerotized apical part except in *epitedeus*, its caudolateral angle rounded in lateral aspect; cercus without specialized apical setae except in species A.

Male genitalia: Ninth tergite lobe with distal part more or less cylindrical, not markedly flattened, slender, directed laterad and sometimes bent mesad more distally, always at least reaching level of median mesal lobe; sidepiece without scales; median mesal lobe with a well-developed mesal thumb, seta *c* usually distinctly bristlelike and always arising from lateral face

of lobe; apicosternal lobe prominent, with a large differentiated tergal seta; dorsal parameres with dorsal bridge variable, sometimes practically absent.

Pupa.—Known only for *mcdonaldi* and very imperfectly for *epitedeus*.

Larva.—Completely unknown for *howardi* and very imperfectly known for *epitedeus*. As described for genus; hair 5-C variable, 2- to 5-branched; hair 6-C single to 3-branched; antennal spicules variable; mental plate triangular, longer than broad.

The Epitedeus group is the most heterogeneous of the four groups of *Deinocerites*, but a number of characters (the presence of mesepimeral scales being the most conspicuous) unite the five known species and indicate that the group is probably of monophyletic origin. Our impression is that this group represents one major phyletic line in the genus and that the various species have been thrown off from time to time in connection with the complex fragmentation and isolation of the land areas in the region it occupies, Central America and Mexico, and that these species have not succeeded in establishing new subsidiary lines of evolution but have formed hybrids in several cases. We find it impossible at present to reconstruct the complex history of this group. However, on the basis of degree of morphological similarity we have some clues as to the probable sequence of separation of known forms within the group.

The group probably arose contemporaneously with the Dyari and Cancer groups through a tripartite splitting of the then existing stock, with Dyari developing in the south, Cancer in the center, and Epitedeus in the north. In the Epitedeus group the mesepimeral scales were developed at the outset. *D. mcdonaldi* and species A are apparently the earliest known offshoots of the group since they lack the development of anterior spiniforms on the forefemur which is characteristic of the other three species. *D. mcdonaldi* is known only from three localities at the mouth of the Gulf of California, two on the mainland and one in the Cape region of Baja California, but it is probable that it will be found elsewhere in the Gulf of California. Species A is represented by a single female from the Pacific coast of Costa Rica. It seems to be quite similar to *mcdonaldi* and at the same time has several features of the Cancer group, notably specialized cercal bristles. We believe that it arose as a hybrid between the early *mcdonaldi* stock and a member of the Cancer group. *D. epitedeus* seems to be the next segregate since it lacks the posterior spiniforms found in the remaining two species of the group. The presence of scales on the 8th sternite of the female, the development of the 9th tergite of the male, and the great elongation of the antenna suggest to us that it may have arisen as a hybrid between *spanius* and the early *pseudus* stock. *D. pseudus* is the dominant modern species of the genus in the Pacific basin. It has overlapped the range of *mcdonaldi* (see below under *howardi*) in the north and has crossed into the Gulf of Mexico either through the portal or the isthmus of Tehuantepec. It is apparently the only species on the Pacific coast from at least as far north as Zehuatanajo (Guerrero) in Mexico all the way to central Costa Rica where it overlaps with species A, and extends to Panama where it overlaps with *dyari* and apparently even penetrates into the Atlantic basin. The last species, *howardi*, occurs in Bahía de Banderas, Mexico, where the ranges of *mcdonaldi* and *pseudus* overlap, and it almost certainly arose through hybridization between these two species.

Little specific information is available on the bionomics of the Epitedeus group.

D. epitedeus and *D. pseudus* have been reported from animal-baited traps but nothing is known about the blood-feeding habits of the other species. *D. pseudus* has been taken from the holes of *Cardiosoma crassum*, a gecarcinid, and *mcdonaldi* is known to use both large and small crabholes.

7. *Deinocerites mcdonaldi* Belkin and Hogue, n. sp.

Adults.—Wing about 3.0–4.0 mm., general coloration dark brown to blackish; antenna, palpus, and proboscis of male and female as illustrated (fig. 15); antenna of female short, proboscis reaching 9th flagellar segment, flagellar segment 1 slightly longer than segments 2 to 4 combined, 2 less than 1.5 of 8, and less than twice as long as 12; antenna of male very long, proboscis reaching base of 4th flagellar segment, segments 1 to 7 markedly elongate, but progressively shorter, 1 less than 2 and 3 combined, 2 more than three times as long as 8 and more than five times as long as 12; mesepimeron with a patch of scales; postnotum usually with a few small hairs in upper part; forefemur (fig. 25) with bristles not modified into spiniforms; claws (fig. 36) of foreleg of male greatly enlarged, subequal, and with a small subbasal tooth, those of midleg only slightly enlarged, subequal, and simple.

Female genitalia: Eighth sternite without scales on sclerotized apical part; cercus without specialized apical bristles.

Male genitalia (fig. 40): Ninth tergite lobe with distal part long, cylindrical, slender, directed outward, and slightly hooked apically and reaching level of median mesal lobe, but not extending beyond; median mesal lobe with seta *c* slender, long, bristlelike; dorsal parameres with an incomplete short broad dorsal bridge; apical spine moderately long and heavy and strongly curved; ventral teeth short, arising from the convex ventrolateral border without a process or lobe.

Pupa (figs. 38, 39).—Cephalothorax: Very lightly and uniformly pigmented; hairs 1–3-C short, branched; 2, 3-C moderately removed from caudal border of sclerite and moderately spaced; 4-C short, usually 4-branched; 5-C very long, usually 2-branched; 6-C short, single; 7-C moderate, usually 2-branched; 8-C rather long, single; 9-C short, usually double; 10, 11-C rather short and close together, usually double; 11-C short, usually triple.

Trumpet: Index about 4.0–4.5; inserted about halfway between middorsal line and wing base; strongly pigmented, blackish on tracheoid, brown distad; tracheoid in basal third.

Abdomen: Uniformly and lightly pigmented except for darker sclerite between float hairs (1-I); larger hairs very strongly pigmented; float hair (1-I) with simple branches at base, becoming fringed or moderately dendritic distally; hairs 1-II inserted very close together near mid-line, very similar in appearance to 1-I, may serve as additional pair of float hairs; chaetotaxy as figured; distinctive features from other known species as follows: hair 1-VII shorter than tergite VIII; 5-VII very short and multiple, 7-III–VI distinctly removed from posterolateral margins of tergites, 7-VII well removed from lateral margin.

Female genitalia: Genital lobe conical, projecting beyond 9th tergite lobe for distance almost equal to length of latter; cercal lobe very strongly developed extending full length of genital lobe.

Male genitalia: Genital lobe projecting beyond middle of paddle.

Paddle: Only slightly longer than broad; paddle hair usually at least as long as paddle.

Larva (fig. 41).—As described for the genus and with the following diagnostic features.

Head: Hair 5-C longer than antenna, 3- to 5-branched; 6-C longer than 5-C, usually 2- or 3-branched; mental plate very small, triangular, longer than broad and with long, filamentous marginal spicules.

Thorax: Hairs 3, 4-M well developed; hair 6-T moderately long, single.

Abdomen: Hair 7-I well developed, conspicuous; 6-II–V strong, usually double, 6-V usually single; hair 13-V usually 3- or 4-branched. Siphon as figured; hairs 1a-S very short and inconspicuous; 2-S short; pecten usually of 4 or 5 teeth on each side, individual tooth usually bifid, rarely trifid.

Anal segment: Hair 2-X usually 7- to 9-branched; ventral brush with 7 or 8 pairs of hairs (4-X); anal papillae evident.

Egg.—Unknown.

Holotype.—♂, with associated larval and pupal skins, San Blas, Nayarit, Mexico, June 26, 1956 (W. A. McDonald, U.C.L.A. 199–116, U.S.N.M. No. 64,263).

Material Examined (55 ♂, 26 ♀, 86 larvae, 23 pupae).—MEXICO: San Blas (Nayarit), 37 ♂, 17 ♀, 86 larvae, 23 pupae, June 26, 28, 1956 (W. A. McDonald, U.C.L.A. 199, 204, U.S.N.M., U.C.L.A., B.M.N.H., holotype and paratypes). San Jose del Cabo (Baja California), 1 ♂, July 13, 1948 (W. G. Downs, 1239, U.S.N.M.). Las Penas (Puerto Vallarta, Jalisco), 1 ♂; 2 ♂, May 10, 1903, 14 ♂, 9 ♀, June, 1906 (A. Duges, U.S.N.M., U.C.L.A.).

Adults, as well as larvae and pupae, were found in crabholes in a mangrove area near a road at Matanchen, near San Blas, Nayarit, Mexico. Some of the crabholes had a diameter of 2 inches, others up to 6 inches. The species of crabs were not identified. It is probable that both Ocypodids and Gecarcinids were present in the area.

D. mcdonaldi seems to be the most generalized and the oldest known segregate of the *epitedeus* group. It is distinguished from all the other species in the group except species A by the lack of development of spiniforms either in the anterior or the posterior rows of bristles of the forefemur. Very striking is the similarity of the male claws and genitalia in this species and in *howardi*; they are so much alike that we cannot distinguish them in these features. At present *mcdonaldi* is known only from one locality on the Gulf side of the Cape region of Baja California and two localities on the mainland of Mexico near the mouth of the Gulf of California. The single specimen from the Cape is quite similar to the others. In all probability *mcdonaldi* will be found in the Gulf of California proper and possibly on the west coast of Baja California as well.

8. *Deinocerites* species A

A single imperfect female from Tarcoles on the Pacific coast of Costa Rica shows a combination of a number of characters of *mcdonaldi* with a cercus suggestive of the Cancer group: the forefemur lacks spiniforms; the mesepimeron has a small but distinct patch of scales; the 8th sternite is broadly rounded on the caudolateral angle but has some enlarged marginal bristles; the cercus has 5 subapical specialized setae, the most ventral 3 with recurved and twisted apex; the antenna seems to be longer than in *mcdonaldi* or any member of the Cancer group. We believe that this form may represent a species of hybrid origin between the *mcdonaldi* stock and an ancient stock of the Cancer group. Since we have no male of this form we leave it without a specific name for the present.

9. *Deinocerites epitedeus* (Knab, 1907)

Dinomimetes epitedeus Knab, 1907, Jour. N. Y. Ent. Soc., 15: 120–121. Lectotype: Male, Port Limon, Costa Rica, F. Knab, 344a, genitalia on slide 286; selection of Stone and Knight, 1957: 197 (U.S.N.M. 10291).

Adults.—Wing about 2.8–3.5 mm.; antenna, palpus, and proboscis of male and female as illustrated (fig. 21); female antenna with flagellar segments 1 to 4 greatly elongated, segment 1 only slightly longer than 2 and less than 1.4 of 3, proboscis extending slightly beyond middle of segment 5; male antenna greatly elongated, almost twice length of proboscis which extends only to near end of flagellar segment 3, flagellar segments 1 to 6 markedly elongate, segment 1 only slightly longer than 2, and less than 1.4 of 3; postnotum usually with two or more small bristles near lower end; forefemur (fig. 27) with an anteroventral row of spiniforms but with

the posterodorsal row of bristles not replaced by spiniforms at base; claws (fig. 34) of foreleg of male strongly enlarged, anterior with a moderately large submedian tooth, posterior simple; claws of midleg of male moderately enlarged, anterior with a moderate submedian tooth, posterior simple.

Female genitalia: Eighth sternite with numerous scales in upper part.

Male genitalia (fig. 8): Ninth tergite lobe with distal part very long and slender, angled outward near base, then bent mesad to parallel sidepiece and extending beyond level of median mesal lobe; median mesal lobe with a rather small thumb, seta *c* rather strongly flattened and expanded but with attenuate apex; dorsal paramere with very broad but short incomplete bridge; apical spine very slender and long; ventral teeth long and frequently several joined at base but not arising from a distinct lobe.

Pupa (Lane, 1955, fig. 576).—Known only from two imperfect exuviae; seems to be similar to *medonaldi* except that hair 1-I with primary branches plumose and not secondarily dendritic and trumpet index is more than 6.0; paddle hair markedly longer than paddle.

Larva (Howard, Dyar, and Knab, 1912, fig. 309; Dyar and Knab, 1915: 198–199).—Known only from imperfect exuviae; appears to be similar to *medonaldi* but differs in following characters: hair 5-C double, 6-C long and single; mental plate with some of the teeth bifid apically; the long anal papillae figured by Dyar and Knab seem to be artifacts owing to flattening of the specimen on the slide as another specimen shows them to be about the same as in *medonaldi*.

Material examined (68 ♂, 107 ♀, 2 larvae, 2 pupae).—COSTA RICA: Puerto Viejo, 1 ♀ (H. W. Kumm, B.M.N.H.).

PANAMA CANAL ZONE: Ft. Randolph, 1 ♀, Aug. 17, 1923 (Dyar & Shannon, P89, U.S.N.M.). France Field, 3 ♂, 3 ♀, June 19, 1920 (J. Zetek, U.S.N.M.). Margarita, 1 ♂, 2 ♀, May 20, 1922 (J. B. Shropshire, U.S.N.M.). Toro Pt., 1 ♀, Jan. 8, 1922, (J. B. Shropshire, B.M.N.H.); 14 ♂, 10 ♀, Nov. 23, 1921–Apr. 21, 1923 (J. B. Shropshire, U.S.N.M., U.C.L.A.). Ft. Sherman, 1 ♂, 1 ♀, Mar. 31, 1923 (J. B. Shropshire, B.M.N.H.); 41 ♀, Oct. 30, 1951–Feb. 6, 1952 (S. J. Carpenter, U.C.L.A.); 2 ♂, 2 ♀, 1916 (L. H. Dunn, U.S.N.M.); 1 ♂, 1 ♀, 1918 (L. H. Dunn, U.S.N.M.); 1 ♀, Aug. 17, 1923 (Dyar & Shannon, P75, U.S.N.M.); 2 ♀, Mar. 31, 1923 (J. B. Shropshire, U.S.N.M.); 23 ♂, 14 ♀, Apr. 12, 1919–July 23, 1924 (J. Zetek, U.S.N.M.). Ft. San Lorenzo, 2 ♂, 6 ♀, Dec. 2, 1921 (J. B. Shropshire, U.S.N.M.). Fort Davis, 1 ♂, Apr. 19, 1925 (D. Baker, B.M.N.H.); 2 ♀, Apr. 19, Jul. 18, 1925 (D. Baker, U.S.N.M.). Arenal River, 1 ♀, Feb. 2 (C. S. Ludlow, U.S.N.M.). Gatun, 1 ♀, Aug. 13 (J. Zetek, U.S.N.M.); 2 ♀, July 8, 1913 (J. Zetek, U.S.N.M.). Majagual, 2 ♀, Dec. 3, 1921 (J. B. Shropshire, U.S.N.M.). Cativa, 1 ♀, Apr. 1, 1922 (J. B. Shropshire, U.C.L.A.). Ancon, 1 ♀, 1912 (J. Zetek, U.S.N.M.). No locality: 1 ♂ (A. H. Jennings, 40–69, Amst.); 3 ♀ (129), 1 ♂, 1 ♀ (150), 7 ♂, 4 ♀ (158), 3 ♂ (177), 1 ♀ (180) (A. H. Jennings, U.S.N.M.).

REPUBLIC OF PANAMA: Colon, 1 ♂ (A. Busck, 40–71, Amst.); 1 ♂, 1 ♀, 1 larva, 1 pupa (A. Busck, 22, U.S.N.M.). Caldera Is. (Portobelo Bay), 5 ♂, 2 ♀, 1 larva, 1 pupa (A. H. Jennings, 160, U.S.N.M.).

All the known information on the bionomics of *epitedeus* is summarized in Dyar and Knab (1915: 199). Apparently these authors were greatly impressed by the supposedly long anal papillae of the larva of this species (see above) and they tried to make a case for *epitedeus* utilizing crabholes with fresh water. It is evident that it uses crabholes with brackish water at least under certain situations. This species has been taken in animal-baited traps in Costa Rica (Kumm *et al.*, 1940: 392) and in Panama (Carpenter and LaCasse, 1955: 327, reported as *cancer*).

D. epitedeus is a very clearly marked species in which are combined some of the characteristics of the *Epitedeus* and *Spanius* groups. In general external characters, such as mesepimeral scales and anterior spiniforms of the forefemur, it resembles *pseudus*. On the other hand, the 9th tergite lobe of the male genitalia and the scales of the 8th sternite of the female are strongly suggestive of *spanius*. The

antennae of both sexes are longer than in any other species in the genus except *howardi*. We interpret *epitedeus* as a species formed through hybridization between a *pseudus*-like ancestor and *spanius*.

D. epitedeus occurs chiefly in the Atlantic basin, from Costa Rica to Panama. In the Canal Zone it apparently crosses over to the Pacific coast to a limited degree. Its present range fills the gap between *cancer* and *melanophylum* in the general area of the former Nicaraguan-Panamanian portals.

10. *Deinocerites pseudus* Dyar and Knab, 1909

Deinocerites pseudus Dyar and Knab, 1909, *Smithson. Misc. Coll.*, 52: 260. Lectotype: Female, Ancon, Canal Zone, Panama, A. H. Jennings, 378; selection of Stone and Knight, 1957: 197 (U.S.N.M. 12053).

Adults.—Wing about 2.8–4.8 mm.; antenna, palpus, and proboscis of male and female as illustrated (fig. 21); female antenna with flagellar segments other than 1 not markedly elongate, progressively shorter distad, basal flagellar segments quite variable in length, proboscis reaching to near end of segment 8; male antenna greatly elongate, almost twice length of proboscis which extends to about middle of segment 4, flagellar segments 1 to 7 markedly elongate, segment 1 about 0.85 of combined length of 2 and 3 and almost 2.0 of 3; postnotum without bristles; forefemur (fig. 26) with an anteroventral row of spiniforms and with posterodorsal row of bristles continued as an irregular row of short spiniforms; claws (fig. 35) of foreleg of male subequal, greatly enlarged and thickened and without teeth; claws of midleg of male subequal, slightly enlarged, slender and without teeth.

Male genitalia (fig. 11): Ninth tergite lobe quite variable, usually not extending distad of median mesal lobe, usually with a distinct apical curvature and expansion; median mesal lobe with thumb large and seta *c* thickened; dorsal paramere with only a slight indication of a narrow dorsal bridge; apical spine short and broad; ventral teeth short and heavy and on a prominent lobe which in tergal aspect projects about as far distad as the apical spine.

Pupa.—Unknown.

Larva (Howard, Dyar, and Knab, 1912, fig. 308; Dyar and Knab, 1915: 212).—In general very similar to *medonaldi* but with the following distinctive features: hair 6-C very long and usually single; hair 5-C usually 3- to 5-branched; mental plate with simple marginal teeth; antennal shaft basad of hair 1-A with more numerous and distinct spicules than in any other species; hair 1-VII very heavy, single or double, by far the strongest hair of segment; hair 1-VIII usually 6-branched; pecten teeth 5 or 6 on each side, bifid, unusually long.

Material examined (82 ♂, 88 ♀, 29 larvae).—MEXICO: Tampico (Veracruz), 1 ♂, 2 ♀ (Jos. Goldberger, U.S.N.M.). Nautla (Veracruz), 10 ♀, May, 1903 (A. Duges, U.S.N.M.). Vera Cruz, 1 ♀, on steamer (U.S.N.M.). Las Penas (Puerto Vallarta, Jalisco), 4 ♂, 3 ♀, May 10, 1903 (A. Duges, U.S.N.M.). Zihuatanejo (Guerrero), 1 ♂, 1 ♀, 1903 (A. Duges, U.S.N.M.).

EL SALVADOR: Espíritu Santo, 1 ♂, 1 ♀ (H. W. Kumm, 570, U.S.N.M.).

NICARAGUA: Corinto, 1 ♂, Jan. 7 (779), 1 ♂, Mar. 31 (791), 1 ♀, Mar. 31 (793), 1 ♂, Apr. 11 (794), 5 ♂, 6 ♀, June 23, 1943 (806) (P. A. Woke, U.S.N.M.); 3 ♀, Aug. 5, 1944 (14), 3 ♂, 3 ♀ (K. R. Maxwell, U.S.N.M.).

COSTA RICA: Rio Aranjuez, Puntarenas, 6 ♂, 7 ♀ (F. Knab, 336, 339, U.S.N.M.); 1 ♂ (40–70, Amst.). Bonilla, 2 ♀ (H. W. Kumm, 75, U.S.N.M., B.M.N.H.).

PANAMA CANAL ZONE: Ft. Sherman, 1 ♂, 1916 (L. H. Dunn, U.S.N.M.). Monte Lirio, 1 ♂, 1919 (C. S. Ludlow, 1229); 4 ♀, Jul. 7 (U.S.N.M., U.C.L.A.). Gatunella Riv., 1 ♀, Apr. 25, 1919 (J. Zetek, U.S.N.M.). Empire, 1 ♂, Aug. 23, 1913 (J. Zetek, U.S.N.M.). Miraflores, 1 ♂, June 19, 1909 (A. H. Jennings); 1 ♂, 1 ♀, July, 1912 (J. Zetek, U.S.N.M.). Corozal, 2 ♂, Dec. 12, 1907 (A. H. Jennings, U.S.N.M.); 2 ♂, 1 ♀, Aug. 28, Oct. 1, 1913 (J. Zetek, B.M.N.H.); 18 ♂, 23 ♀, June 10, 1913–June 27, 1920 (J. Zetek, U.S.N.M., U.C.L.A.); 2 ♀, 1916 (L. H. Dunn, U.S.N.M.); 2 ♀, July 11, 1925 (D. Baker, U.S.N.M.); 1 larva, May 13, 1935 (W. H. Komp, U.S.N.M.). Albrook Field, 1 ♂, 9 larvae, May 10, 1934, Jan. 16–May 24, 1942 (W. H. Komp, U.S.N.M.). Ancon, 13 ♂, 5 ♀, May 4, 1908–May, 1909 (A. H. Jennings, 87, 378, 440, U.S.N.M.).

No locality: 5 ♂, 1 ♀ (A. H. Jennings, 69, 352, 371, 411, U.S.N.M.); 1 ♀, Feb., 1944 (L. Roth, U.S.N.M.).

REPUBLIC OF PANAMA: La Chorrera, 4 ♂, 11 larvae, June 27, 1944 (R. Van Doran, R. H. Arnett, 11-1, U.C.L.A.). Panama City, 2 ♂, 1916 (L. H. Dunn, U.S.N.M.). Bella Vista, 1 ♂, 1 ♀, Aug. 5, 1915 (U.S.N.M.). Isla Taboga, 1 ♂, June 14, 1911 (A. Busck, U.S.N.M.). Isla San Jose (Las Perlas), 1 ♂, May 5, 1941 (J. P. E. Morrison); 1 larva, July 21, 1944 (W. H. Komp, U.S.N.M.). No locality: 3 larvae (55-1), 4 ♀ (57-1), 4 larvae (64-1), 2 ♂, 2 ♀ (49-57-1) (A. H. Arnett, *leg.*, U.C.L.A.).

All the information about the bionomics of *pseudus* is summarized in Dyar and Knab (1915: 212). Knab collected this species near Puntarenas, Costa Rica, in the holes of *Cardiosoma crassum* Smith "in mangrove swamps situated back along the inlets. The water is brackish, sometimes near the surface of the holes, sometimes deeper down." Jennings found larvae in crabholes in Panama on a hillside in a swamp at Corozal, on a flat at Miraflores and Ancon, "generally near the shore but sometimes back from it." This species has been collected on horses and in houses in Costa Rica (Kumm *et al.*, 1940: 392) and El Salvador (Kumm and Zuniga, 1942: 406). Among the material we have examined is a specimen collected on a steamer at Veracruz, Mexico.

D. pseudus is the dominant species of the Pacific basin. In the north it has penetrated in the Atlantic into the Gulf of Mexico, and possibly also in the south, although the few specimens in Panama may be only strays. Throughout its range it is quite variable, particularly in size and in the proportions of the basal flagellar segments in the female and even in the male genitalia, especially the length and shape of the 9th tergite lobe. However, it is always readily recognized by the characteristic development of the ventral spiny process of the dorsal paramere in the male. We have not analyzed carefully the samples of various populations, but a superficial examination gives no indication of any major differentiation anywhere in the range of the species. Of particular interest is the fact that the populations in the Gulf of Mexico are entirely similar to those in the Pacific basin, even the supposed difference in size (Dyar and Knab, 1915: 213) falls well within the range of variation observed elsewhere, particularly at the southern end of the distribution of the species in Panama.

As indicated elsewhere *pseudus* and *mcdonaldi* overlap at Bahia de Banderas on the west coast of Mexico, and here also occurs *howardi* which we interpret as a distinct species formed through hybridization of the other two. In the south *pseudus* overlaps with *dyari*, species A, and an unknown member of the *spanius* group. The presence of *pseudus* in the Gulf of Mexico may be owing either to dispersal through the last Tehuantepec portal or subsequent to it over the isthmus.

11. *Deinocerites howardi* Belkin and Hogue, n. sp.

Adults.—Wing about 3.5 mm.; antenna, palpus, and proboscis of male and female as illustrated (fig. 22); female antenna with first flagellar segment tremendously elongated, almost equal to segments 2 to 5 combined, proboscis not quite reaching segment 7; male antenna tremendously elongate, more than twice length of proboscis which reaches only to about middle of flagellar segment 3, segments 1 to 7 markedly elongate, segment 1 only about 0.75 of combined lengths of 2 and 3; postnotum without bristles; forefemur with spiniforms almost exactly as in *pseudus*; claws of fore- and midlegs of male (fig. 37) almost exactly as in *mcdonaldi*.

Male genitalia (fig. 9): Ninth tergite, sidepiece, and its lobes, clasper, dorsal paramere, and aedeagus almost exactly as in *mcdonaldi*, we have not been able to find any significant differences.

Pupa and larva.—Unknown.

Holotype.—♂, Las Penas (Puerto Vallarta), Jalisco, Mexico, May 10, 1903 (A. Duges, U.S.N.M. No. 64,264).

Material examined (4 ♂, 2 ♀).—MEXICO: Las Penas (Puerto Vallarta, Jalisco), 1 ♂; 3 ♂, 2 ♀ May 10, 1903 (A. Duges, U.S.N.M., U.C.L.A., holotype and paratypes).

This is a most interesting form that combines the characteristics of *pseudus* and *mcdonaldi* and occurs in the zone of contact of these strongly differentiated species. In general features both sexes resemble *pseudus* in having anterior and posterior spiniforms on the foreleg (these are not developed in *mcdonaldi*) and in completely lacking postnotal bristles (usually present in *mcdonaldi*). In the male the claws and the genitalia are identical—as far as we can determine—with those on *mcdonaldi* and most strikingly different from those of *pseudus*. In addition *howardi* has features in the flagellar segments which are peculiar to it and represent an intensification of the condition found in the opposite sexes of *pseudus* and *mcdonaldi*. In the female it has an antenna even longer than in *pseudus* (*mcdonaldi* has the shortest), and in the male, longer than in *mathesoni* (*pseudus* has the shortest). We interpret *howardi* as a distinct species that arose through hybridization between *mcdonaldi* and *pseudus* soon after the latter invaded the range of *mcdonaldi*. There is also the possibility, of course, that our specimens represent merely interspecific hybrids. Which of these interpretations is correct can be determined only through the study of the problem in Bahia de Banderras.

Nothing whatever is known about the bionomics of *howardi*.

SUMMARY

Deinocerites, characterized in the adult stage chiefly by articulated 9th tergite lobes and two pairs of parameres in the male and elongate first flagellar segment in both sexes, in the pupa by two pairs of float hairs, and in the larva by lateral head pouches, basal lobe of mandible, small mental plate, and presence of head hair 2, is considered to be an ancient derivative of the stock which also gave rise to *Culex*. It was probably differentiated on an island in the American Mediterranean Region, and its association with crabholes is probably of long standing. Differentiation of species appears to have taken place on islands in the central area, with relicts and species of hybrid origin occurring at the adjoining continental margins. Eleven species in four groups are recognized. The Spanius group is the most generalized and ancient known and is represented by *mathesoni*, n. sp., in the southwest corner of Texas and *spanius* (D. and K.) chiefly on the Atlantic coast of Panama. The second group is represented only by *dyari*, n. sp., from the Gulf of Panama. The Cancer group consists of three complementary allopatric species forming a ring around the Caribbean Sea and extending north to Florida and south to Brazil; *cancer* Theo. occurs from Florida through Cuba, Hispaniola, Jamaica to British Honduras and Nicaragua, *melanophyllum* D. and K. from Panama to the Gulf of Cariaco in Venezuela, and *magnus* (Theo.) from Mona Island through Puerto Rico, Lesser Antilles, Trinidad to the Guianas, and northern Brazil. The Epitedeus group consists of five species largely confined to

the Pacific coast of Central America and Mexico; *pseudes* D. and K. is the dominant modern form that crosses into the Gulf of Mexico at Tehuantepec and spills over to the Atlantic at the Canal Zone; *mcdonaldi*, n. sp., is found at the mouth of the Gulf of California on the Mexican mainland and in the cape region of Baja California; the remaining three species appear to be hybrid in origin, species A from the Pacific coast of Costa Rica between the *mcdonaldi* and *cancer* stocks, *epitedeus* (Knab) from the Atlantic side of Costa Rica and Panama between the *pseudes* and *spanius* stocks, and *howardi*, n. sp., from Bahia de Banderas, Mexico between *mcdonaldi* and *pseudes*.

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FIGURES

EXPLANATION OF FIGURES

Fig. 1. Distribution of the genus *Deinocerites*.

Fig. 2. Phylogeny of known species of *Deinocerites*.

Figs. 3-11, 40. Male genitalia of species of *Deinocerites*: tergal aspect of right (morphological) half; phallosome complex complete; lateral aspect of left dorsal paramere enlarged in inset.

Figs. 12-14. Female genitalia of species of *Deinocerites*: left lateral aspect of entire genitalia from segment 8 distad.

Figs. 15-24. Heads of male and female *Deinocerites*: left lateral aspect of antenna, palpus and proboscis; joint in male proboscis not shown; scales of flagellar segments 1 and 2 not shown; outline of head diagrammatic; sketches drawn from pinned specimens.

Figs. 25-27. Forefemora of female *Deinocerites*: inner (anterior) aspect of left femur in upper figures; outer (posterior) aspect of right femur in lower figures.

Figs. 28-37. Claws of fore- and midleg of male *Deinocerites*: from left to right, inner (anterior) claw of foreleg, outer (posterior) claw of foreleg, inner (anterior) claw of midleg and outer (posterior) claw of midleg.

Fig. 38. *Deinocerites mcdonaldi*. Pupa: left lateral aspect of anterior part of cephalothorax; enlarged trumpet in inset.

Fig. 39. *Deinocerites mcdonaldi*. Pupa: dorsal (on left) and ventral (on right) aspects of metanotum and abdomen of male; terminal segments of abdomen of female in inset.

Fig. 41. *Deinocerites mcdonaldi*. Larva: dorsal (on left) and ventral (on right) aspects of head, thorax and proximal abdominal segments; left lateral aspect of terminal abdominal segments; details of tip of antenna, mental plate, middle comb scale of posterior row, and subapical pecten tooth.

SOURCE OF SPECIMENS IN FIGURES

D. mathesoni: Brownsville, Texas

D. spanius: Ft. Sherman, Panama Canal Zone

D. dyari: Corozal, Panama Canal Zone

D. magnus: Castries, St. Lucia (♀); Martinique (♂)

D. cancer: Kingston, Jamaica

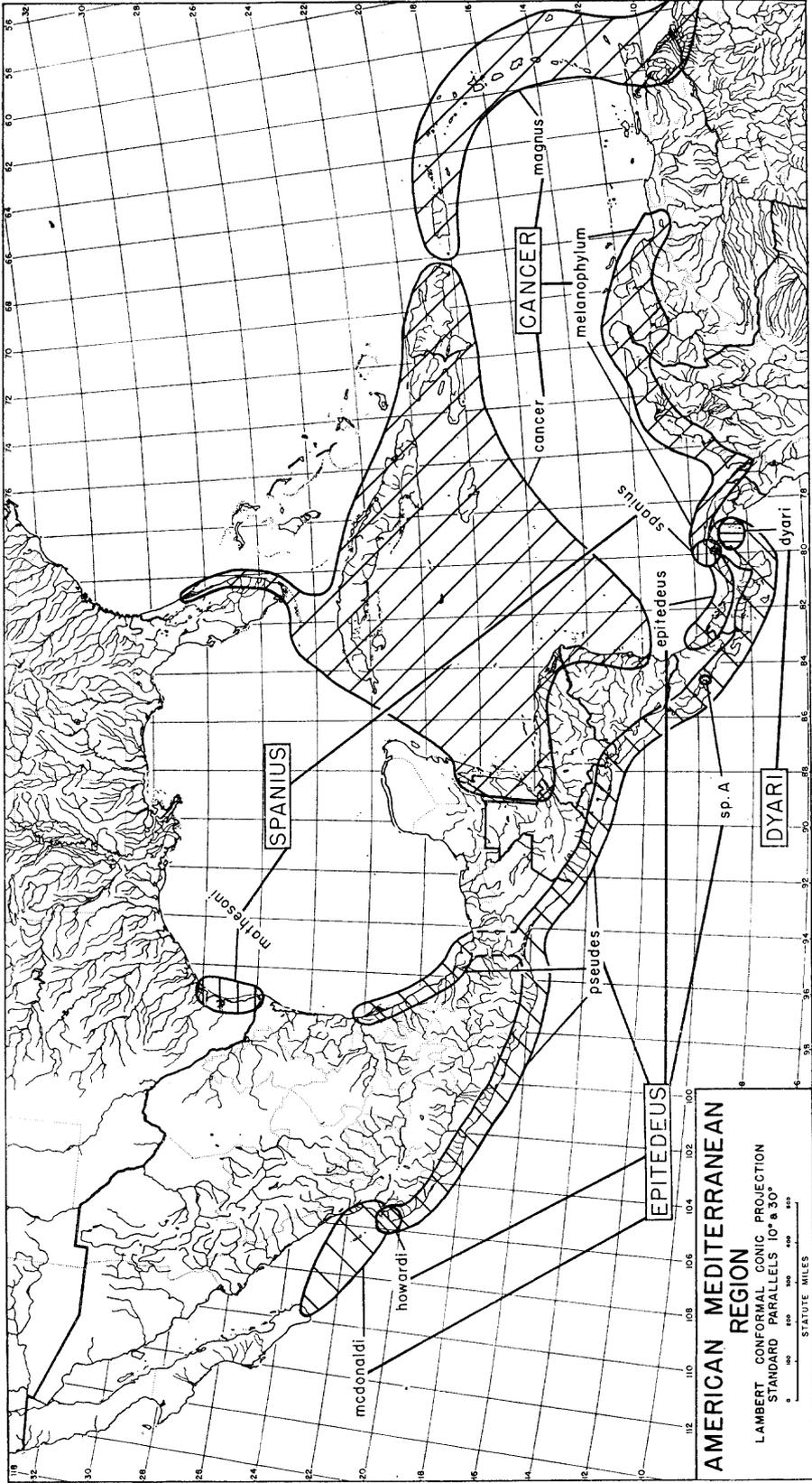
D. melanophyllum: Ft. Sherman, Panama Canal Zone

D. mcdonaldi: San Blas, Nayarit, Mexico

D. epitedeus: Ft. Sherman, Panama Canal Zone

D. pseudus: Corozal, Panama Canal Zone

D. howardi: Las Penas (Puerto Vallarta), Jalisco, Mexico



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Fig. 1. Distribution of the genus *Democerites*.

PACIFIC BASIN | ATLANTIC BASIN

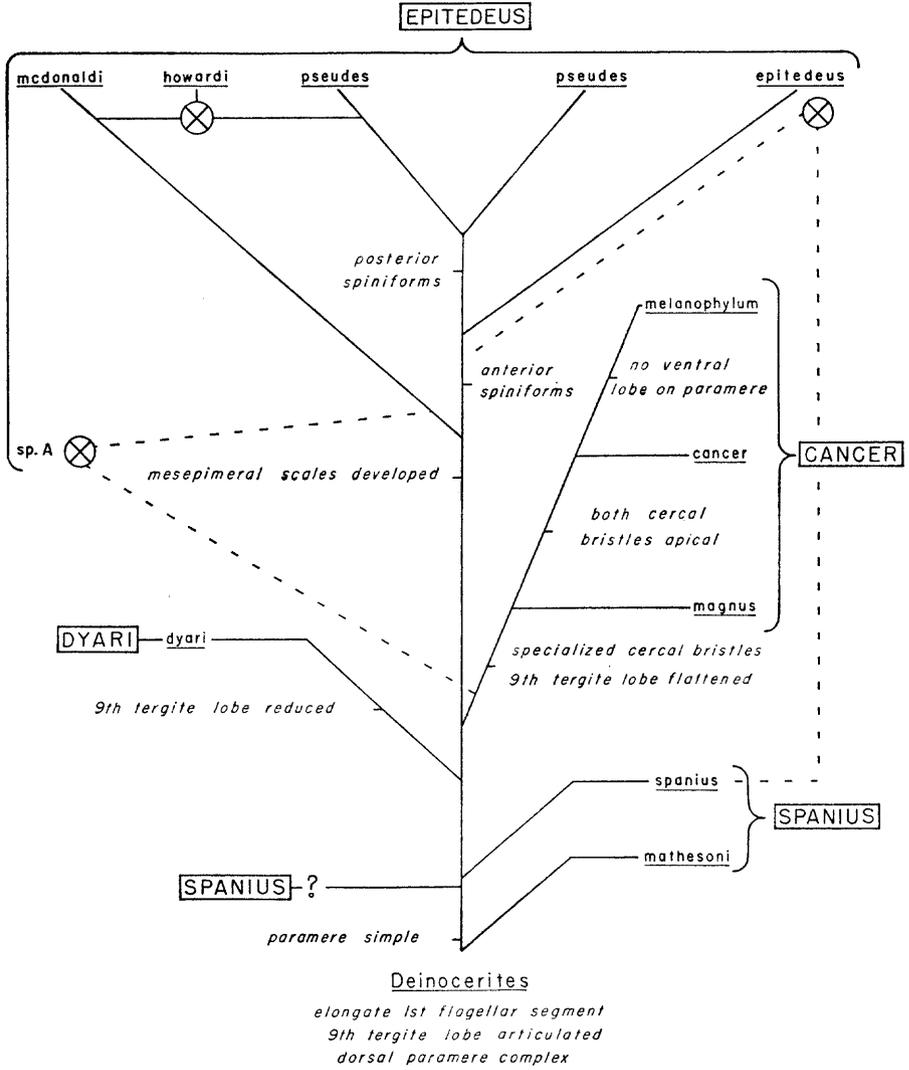
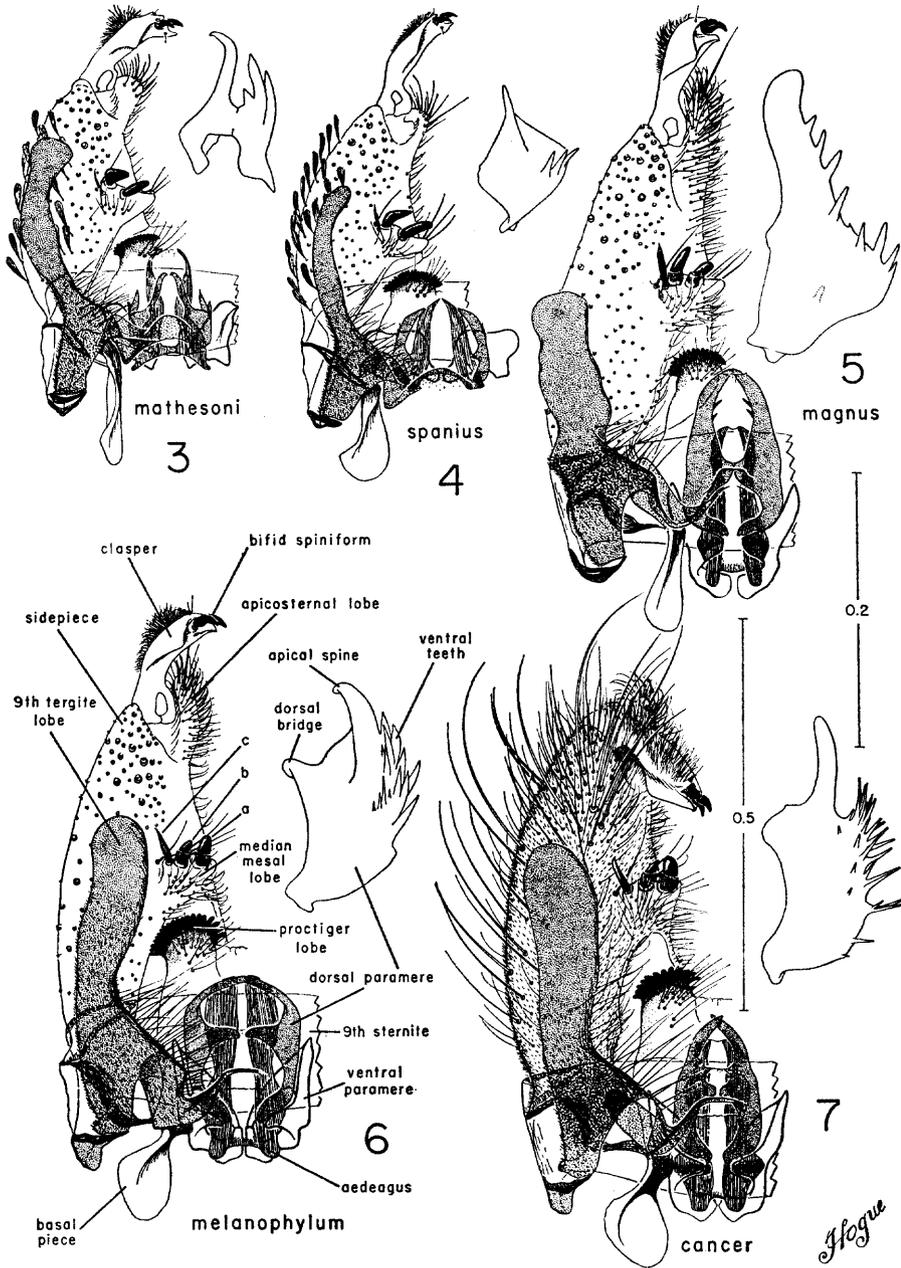
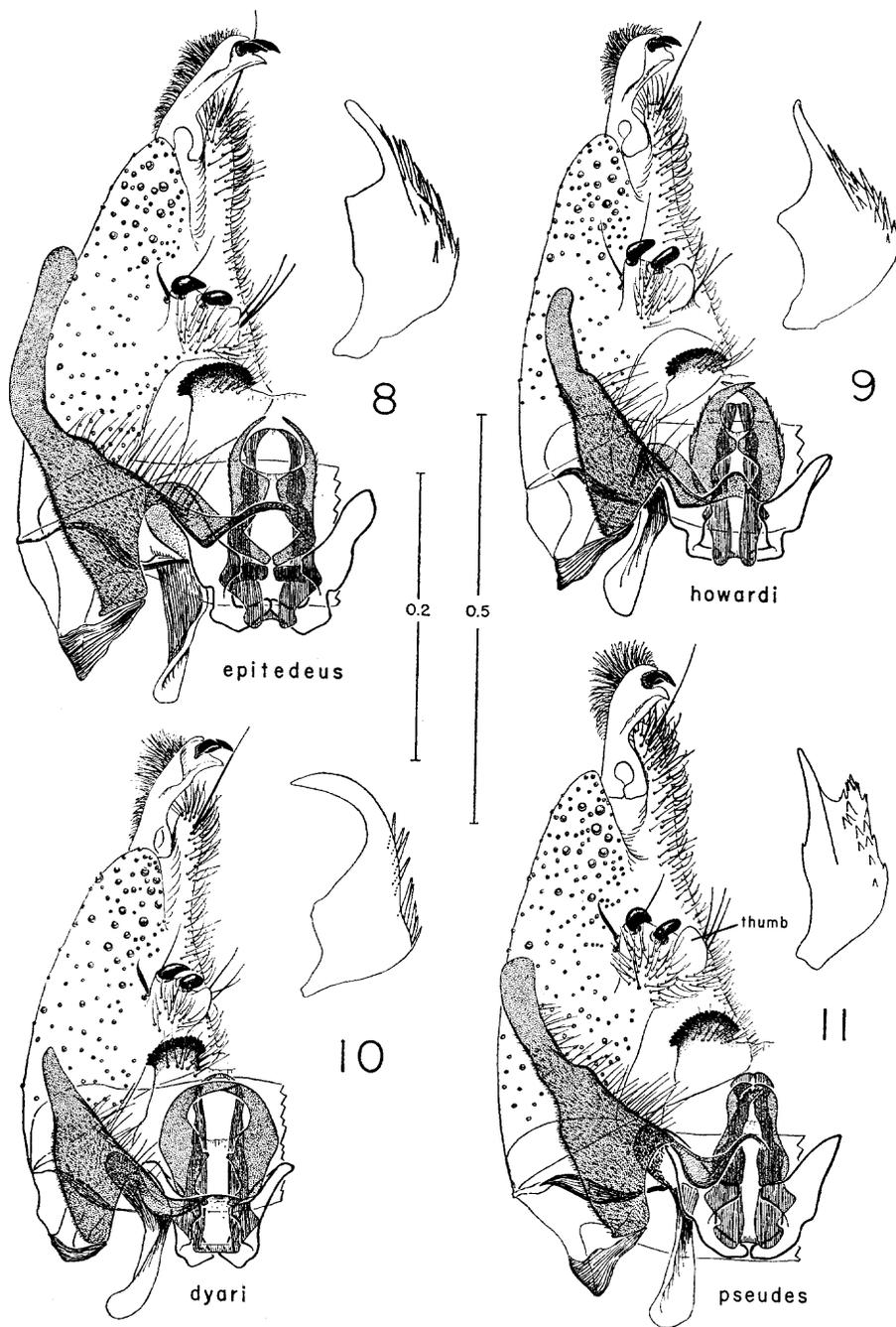


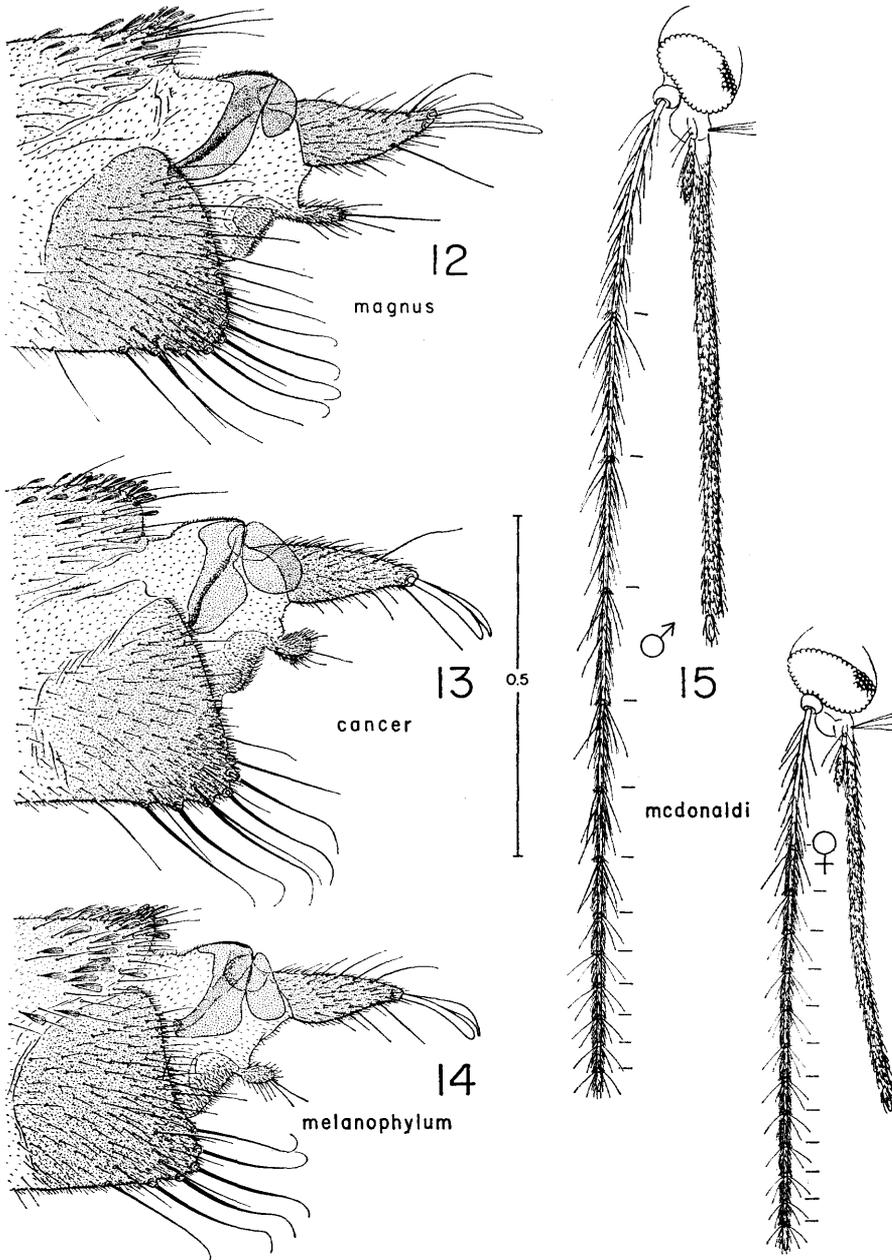
Fig. 2. Phylogeny of known species of *Deinocerites*.



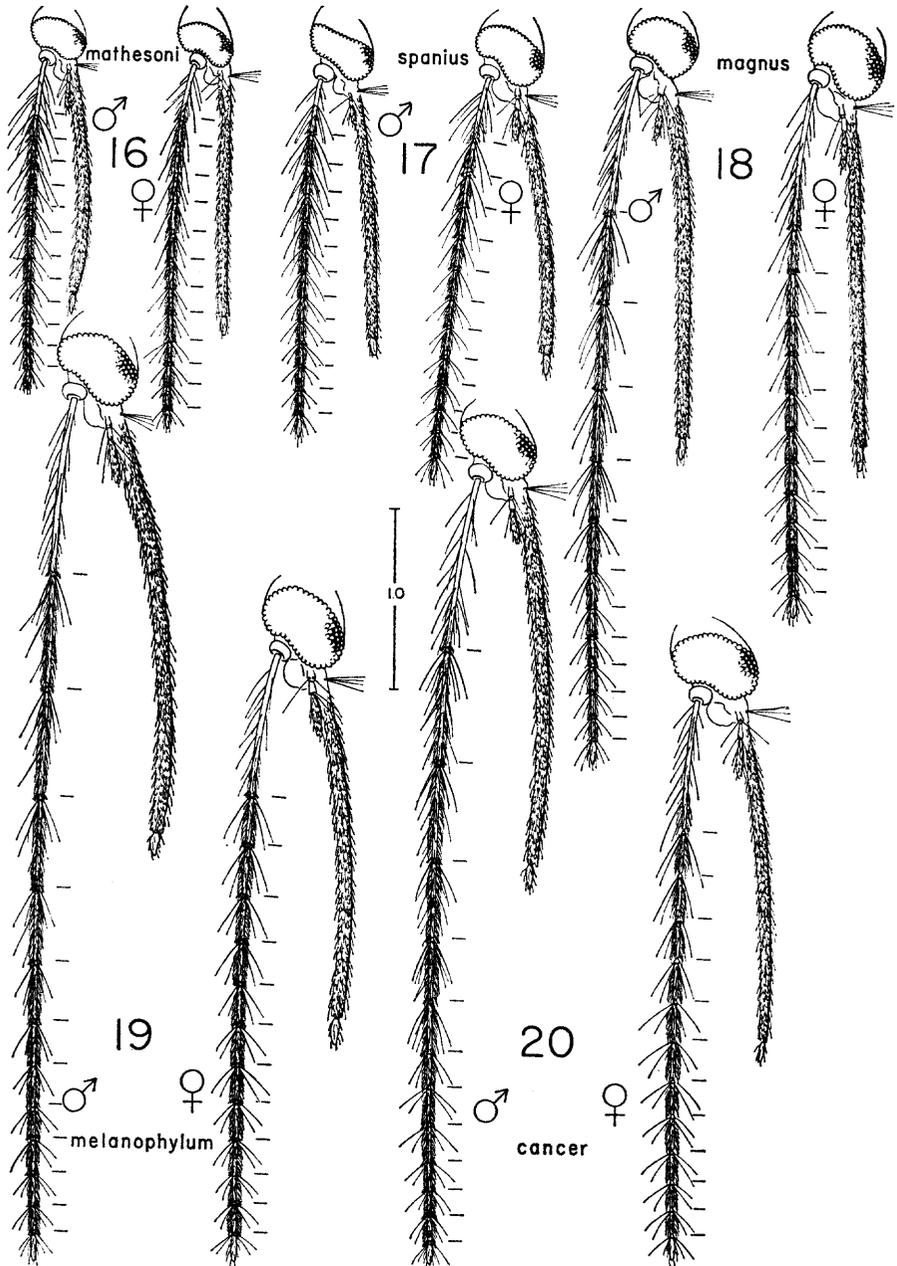
Figs. 3-7. Male genitalia of species of *Deinocerites*: tergal aspect of right (morphological) half; phallosome complex complete; lateral aspect of left dorsal paramere in inset.



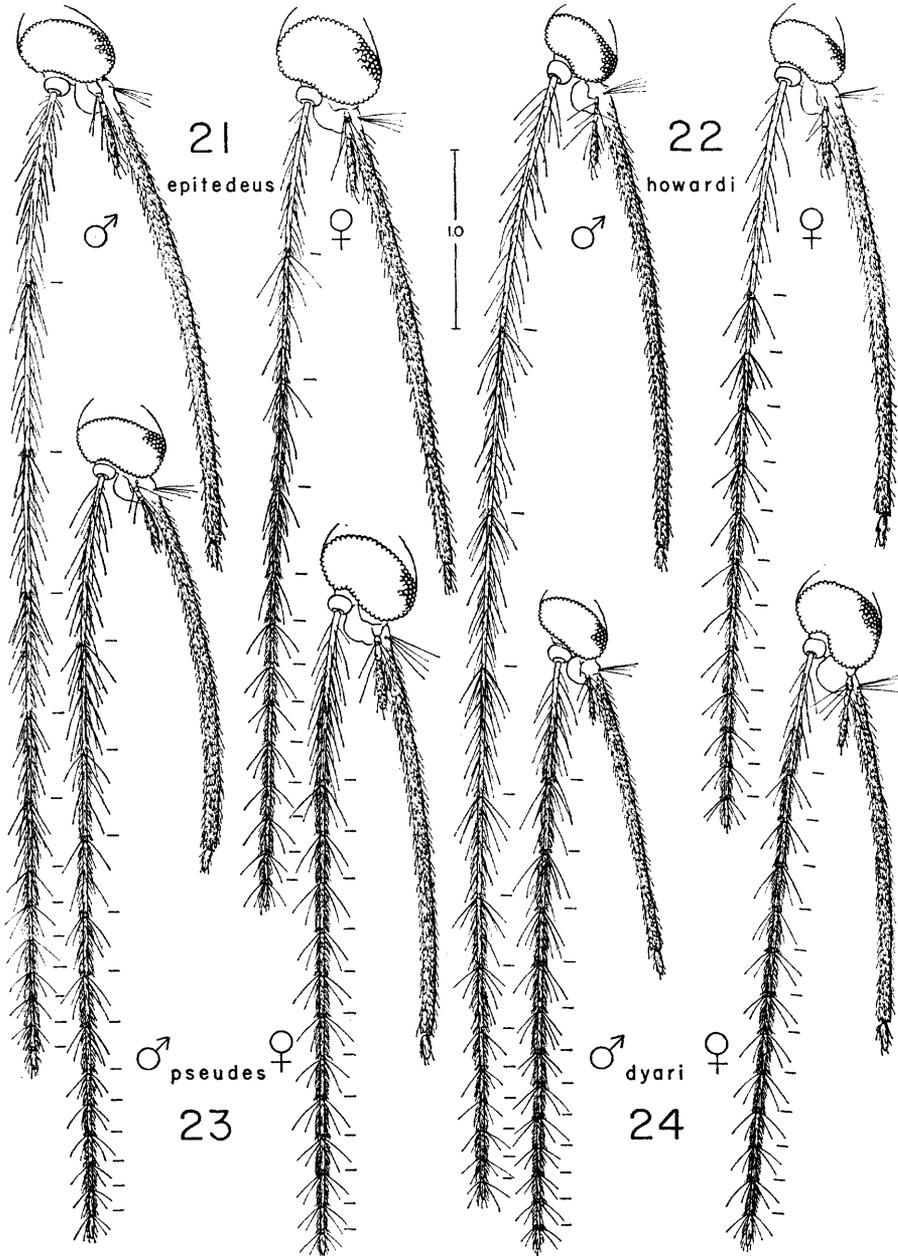
Figs. 8-11. Male genitalia of species of *Deinocerites*: tergal aspect of right (morphological) half; phallosome complex complete; lateral aspect of left dorsal paramere in inset.



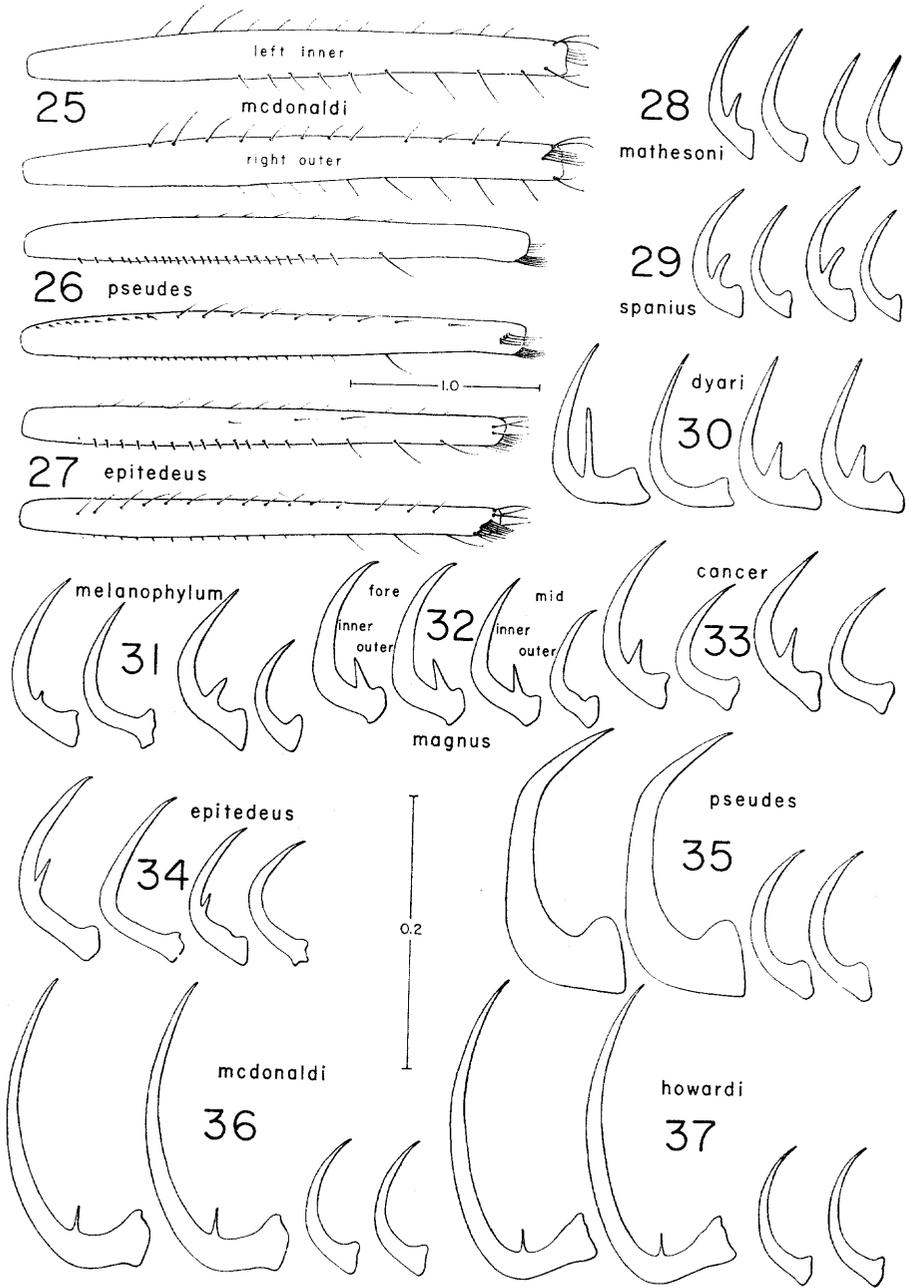
Figs. 12-15. Figs. 12-14, female genitalia of species of *Deinocerites*: left lateral aspect of entire genitalia from segment 8 distad. Fig. 15, heads of male and female *D. mcdonaldii*: left lateral aspect of antenna, palpus, and proboscis; joint in male proboscis and scales of flagellar segments 1 and 2 not shown; outline of head diagrammatic; sketches drawn from pinned specimens.



Figs. 16-20. Heads of male and female *Deinocerites*: left lateral aspect of antenna, palpus, and proboscis; joint in male proboscis and scales of flagellar segments 1 and 2 not shown; outline of head diagrammatic; sketches drawn from pinned specimens.



Figs. 21-24. Heads of male and female *Deinocerites*: left lateral aspect of antenna, palpus, and proboscis; joint in male palpus and scales of flagellar segments 1 and 2 not shown; outline of head diagrammatic; sketches drawn from pinned specimens.



Figs. 25-37. Figs. 25-27, forefemora of female *Deinocerites*: inner (anterior) aspect of left femur in upper figures; outer (posterior) aspect of right femur in lower figures. Figs. 28-37, claws of fore- and midleg of male *Deinocerites*: from left to right, inner (anterior) claw of foreleg, outer (posterior) claw of foreleg, inner (anterior) claw of midleg and outer (posterior) claw of midleg.

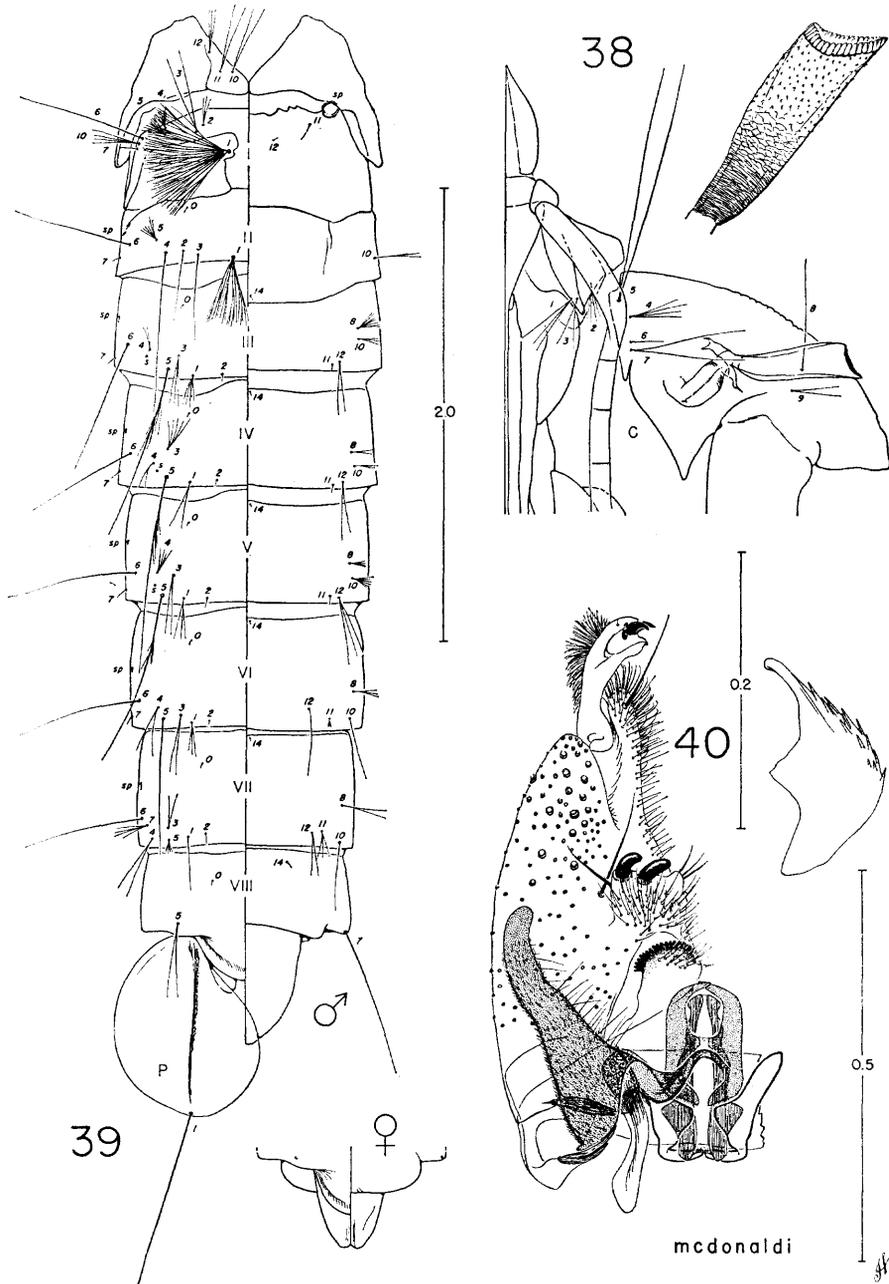


Fig. 38-40. Fig. 38, pupa of *Deinocerites mcdonaldi*: left lateral aspect of anterior part of cephalothorax; enlarged trumpet in inset. Fig. 39, pupa of *Deinocerites mcdonaldi*: dorsal (on left) and ventral (on right) aspects of metanotum and abdomen of male; terminal segments of abdomen of female in inset. Fig. 40, male genitalia of *Deinocerites mcdonaldi*: tergal aspect of right (morphological) half; phallosome complex complete; lateral aspect of left dorsal paramere in inset.

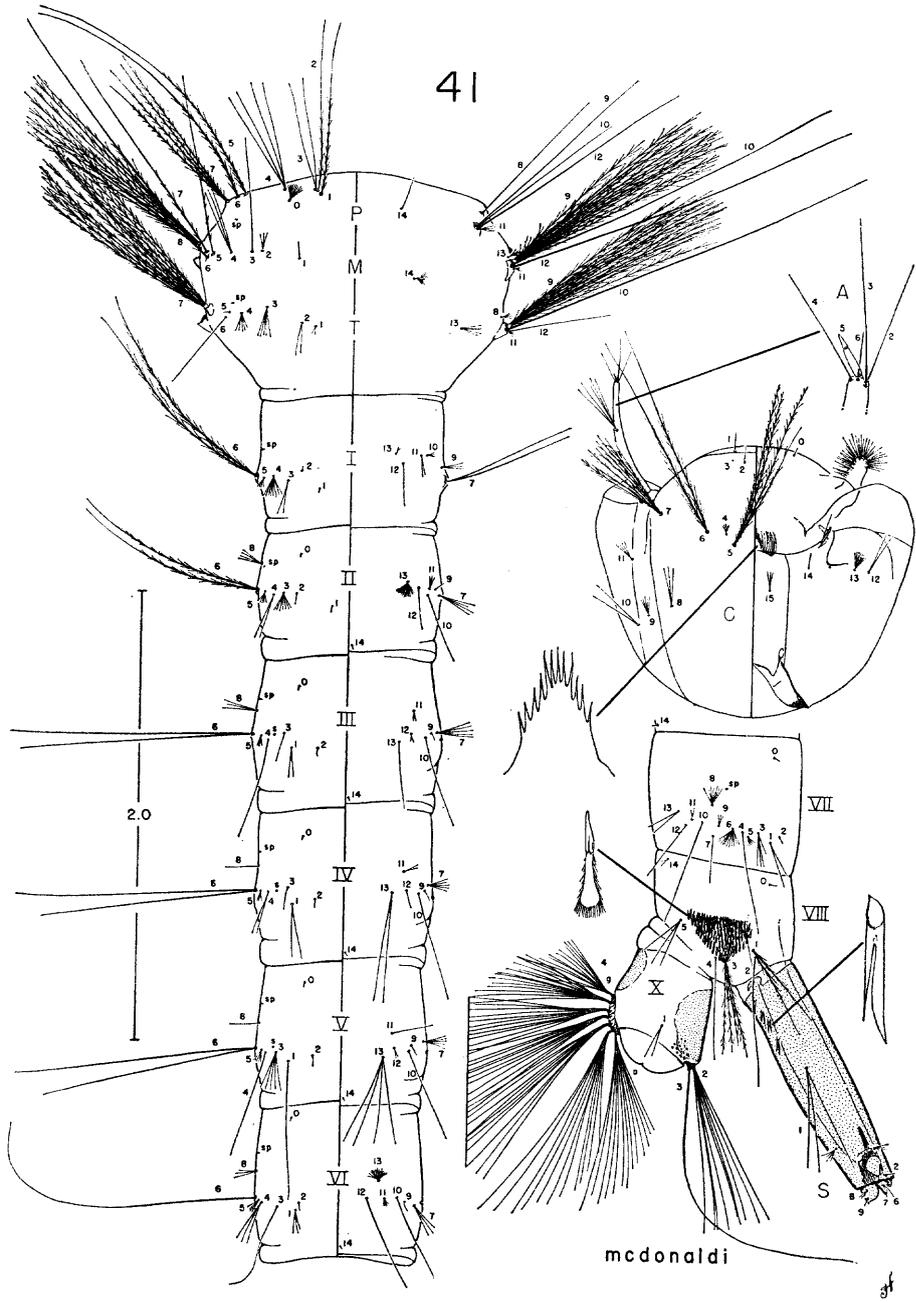


Fig. 41. Larva of *Deinocerites mcdonaldi*: dorsal (on left) and ventral (on right) aspects of head, thorax, and proximal abdominal segments; left lateral aspect of terminal abdominal segments; details of tip of antenna, mental plate, middle comb scale of posterior row, and subapical pecten tooth.