

# AMERICAN MUSEUM *Novitates*

PUBLISHED BY THE AMERICAN MUSEUM OF NATURAL HISTORY  
CENTRAL PARK WEST AT 79TH STREET, NEW YORK, N.Y. 10024  
Number 3190, 30 pp., 16 figures, 1 table March 3, 1997

## The Bird Flies, Genus *Carnus*: Species Revision, Generic Relationships, and a Fossil *Meoneura* in Amber (Diptera: Carnidae)

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### ABSTRACT

Variation in the male genitalia of *Carnus* and other features reveal that specimens from eastern and northern North America are the same as the European species, *C. hemapterus* Nitzsch, 1818. A *Carnus* from western North America is newly described, *C. occidentalis*, n.sp., as are two new species from Florida (*C. floridensis*, n.sp.) and central Mexico (*C. mexicana*, n.sp.). Specimens of two probable additional species from southern Mexico are also discussed, for which only female specimens are available. Single records of the genus from southeast Asia and Africa indicate that the genus is probably global, but yet uncovered in most areas because of the specialized collecting required to find them. All host records of *Carnus* are summarized and new ones presented. The flies

are exclusively nest associates of birds, the adults probably being hematophagous parasites of the nestlings. Larvae of *Carnus* are described for the first time. They are most distinctive for the single, midventral row of eight fleshy protuberances.

A new species of carnid is described in 20 million-year-old (Miocene) amber from the Dominican Republic, *Meoneura vieja*, n.sp., belonging to the sister genus of *Carnus*. This is the first carnid known from the Caribbean. The only other fossil carnid is in Eocene Baltic amber. Ages of the two fossil species are consistent with their phylogenetic rank, and suggest that carnids probably originated in the Paleocene, when many other families of "acalyptrate" Cyclorrhaphan flies were also radiating.

### INTRODUCTION

In the nests of various birds, primarily in the Holarctic Region, a curious tiny fly sheds

its wings: *Carnus*. Europeans have been studying *Carnus hemapterus* Nitzsch since

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the early 19th century (fig. 1), but the genus wasn't even reported in North America until 1942 (Bequaert, 1942), despite the fact that insect inhabitants of North American bird nests had been surveyed before then (e.g., Dobrosky, 1925). Adults of the fly are usually found attached in small groups to bare areas of the axillary region on nestlings. Whether they are feeding on blood or skin secretions has been controversial, as will briefly be reviewed below. This report is a detailed morphological study of adult *Carnus* from throughout the range, originally aimed at examining intraspecific and possible interspecific variation, and which uncovered several new species. The whole study was inspired by the finding of some specimens in the sister genus to *Carnus*, *Meoneura* Rondani, in Oligo-Miocene amber (20 million years old) from the Dominican Republic—only the second fossil species in the family. Description of an interesting *Meoneura* fossil led to a consideration of the generic relationships of *Carnus*, with the possibility of perhaps identifying the ancestral habit of such specialized flies, and the origins of the carnids.

#### MATERIALS, METHODS, ACKNOWLEDGMENTS

Dissection of pinned specimens followed techniques described elsewhere (Grimaldi, 1987). Preparation and study of amber specimens is given in Grimaldi (1993), and a reassessment of the age of Dominican amber is presented by Grimaldi (1995) and, most recently, by Ituralde-Vinent and MacPhee (1996). It is a pleasure to acknowledge the help of Roy Larimer, who has allowed me to sort through his caches of Dominican amber for scientifically valuable specimens, and to Jake Brodzinsky, a constant source of the rare and unusual in Dominican amber. Caroline Chaboo helped with literature searches and prevented various distractions from descending on me. A review and unpublished information on the African *Carnus* were kindly provided by Eliane DeConinck (Royal Central African Museum, Tervuren). I am extremely grateful for the detailed review provided by Terry Wheeler (McGill University), whose knowledge of acalyptrate genitalia was an important source of information.

Mary LeCroy, Dept. of Ornithology (AMNH) kindly checked and updated the taxonomic names and classification of the list of bird hosts. Development of the museum's amber collection is made possible by the generosity of Chairman Emeritus of the museum, Robert G. Goelet. My field and laboratory research on Dominican amber has been sponsored by NSF grant BSR 9020102.

Pinned material was received on loan from the following institutions and their respective curators:

AM	Australian Museum, Sydney (D.K. McAlpine)
CAS	California Academy of Sciences (P.H. Arnaud, Jr.)
CNCI	Canadian National Collection of Insects, Ottawa (J. Cumming)
HNHM	Hungarian Natural History Museum (L. Papp)
HUMB	Zoologische Institut, Humboldt Museum, Berlin (H. Schumann)
INHS	Illinois Natural History Survey (Kathleen Methven)
MHNP	Musée d'Histoire Naturelle, Paris (L. Tsacas)
NHRS	Naturhistoriska Riksmuseet, Stockholm (B. Viklund)
NMNH	U.S. National Museum of Natural History, Smithsonian Institution (W. Mathis)
UTSU	Utah State University (W. Hanson)

#### SYSTEMATICS

##### GENUS *CARNUS* NITZSCH

TYPE SPECIES: *Carnus hemapterus* Nitzsch, 1818.

*Carnus* Nitzsch, 1818: 305; Collin, 1911 (synonymy of *Cenchrudobia*).  
*Cenchrudobia* Schiner, 1862: 435.

DIAGNOSIS: Tiny flies living primarily in bird nests, undoubtedly monophyletic by the following suite of apomorphies: notum having one pair of dorsocentral setae; pleural membrane of abdomen with dense, setiferous spots (more than in other genera of carnids) (figs. 2d; 4a, b; 13); females with abdominal sternites lost (reduced in males) (fig. 13); abdominal tergites reduced in males and females; wings with vein  $A_1$  and crossvein dm-cu lost (fig. 11); wings dehiscent (fig. 2c); adults physogastric, females particularly so.

GENERAL DESCRIPTION: Eye light, cream-

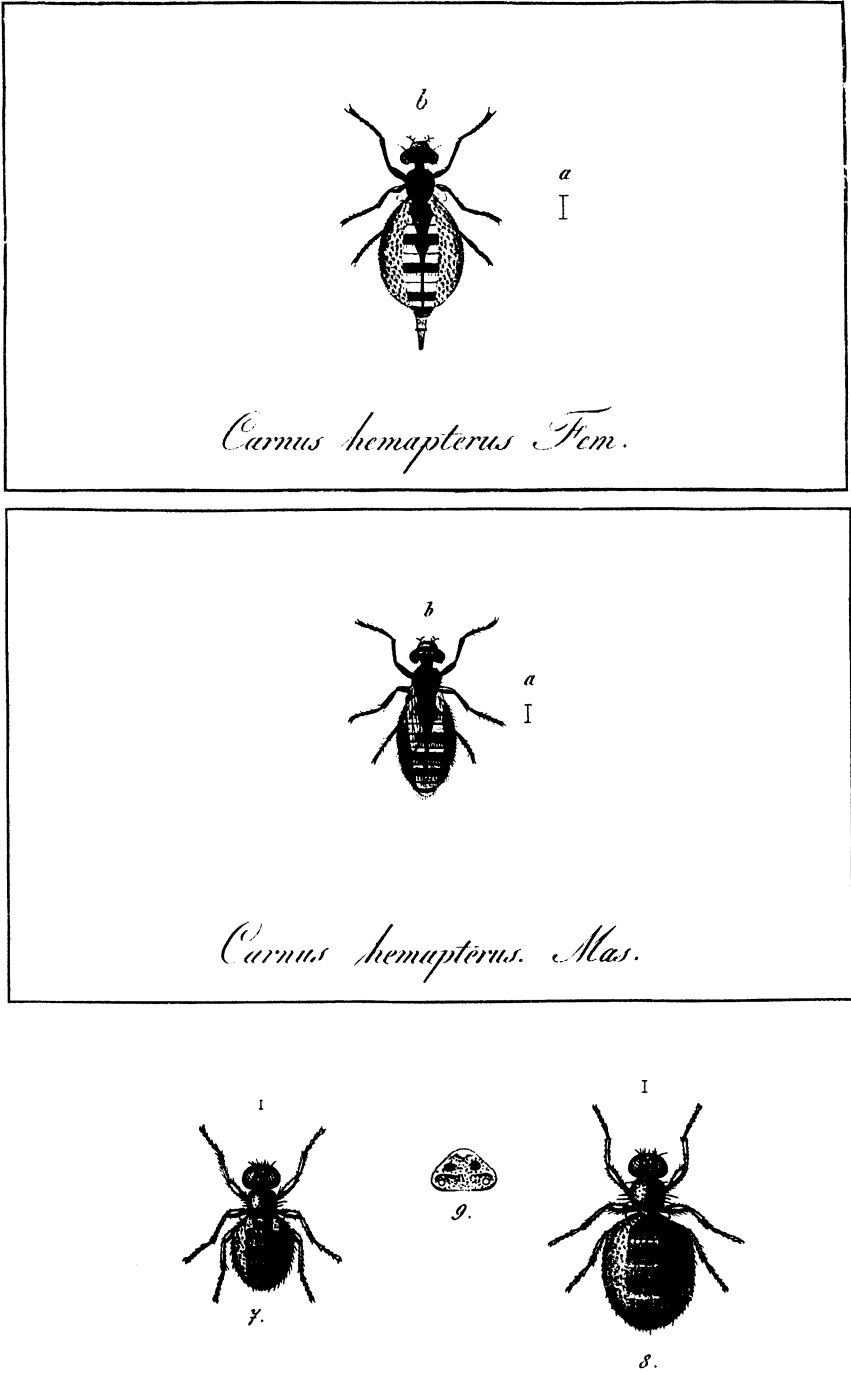


Fig. 1. The earliest accounts of *Carnus*. Top, male and female of *C. hemapterus* (from Germar, 1822); bottom, a normal and engorged female of *C. hemapterus* (from Egger [1854], Verh. Zool. Bot. Ges. Wien 4, p. 3, fig. 2). The genus was not reported in North America until 1942.

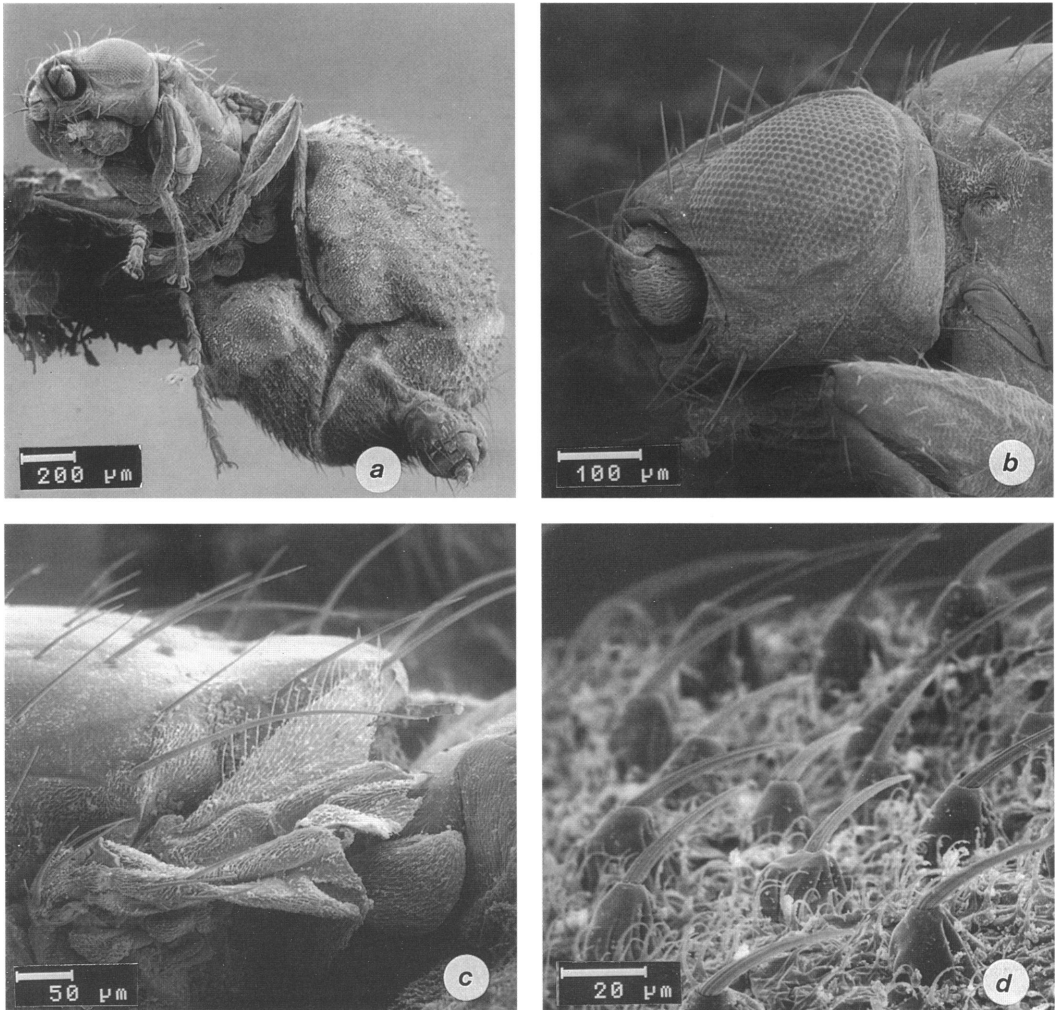


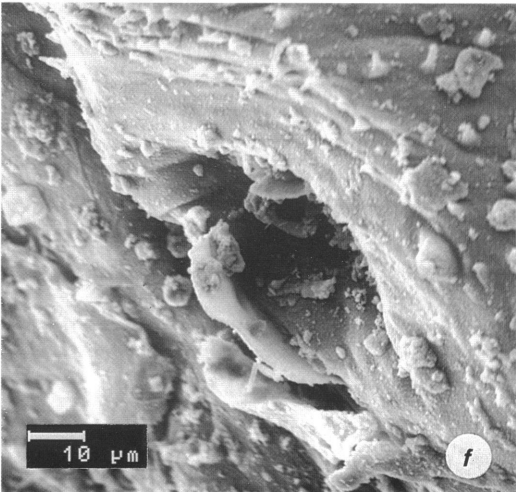
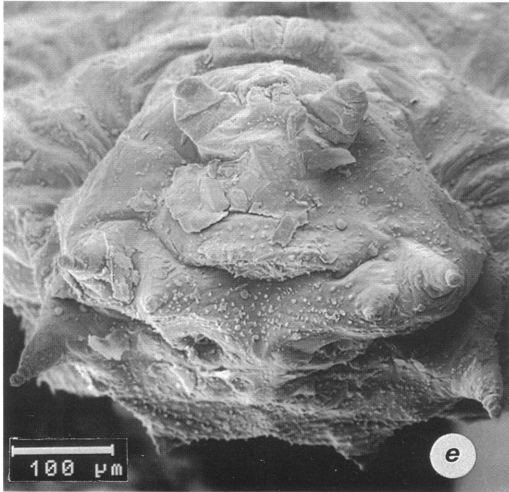
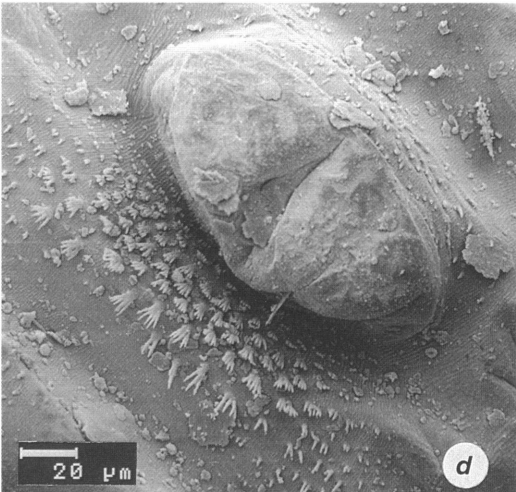
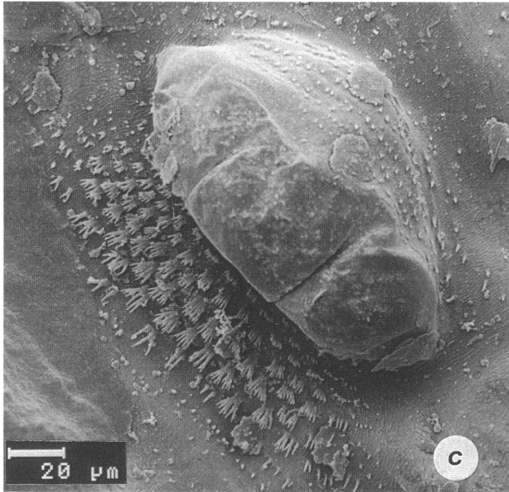
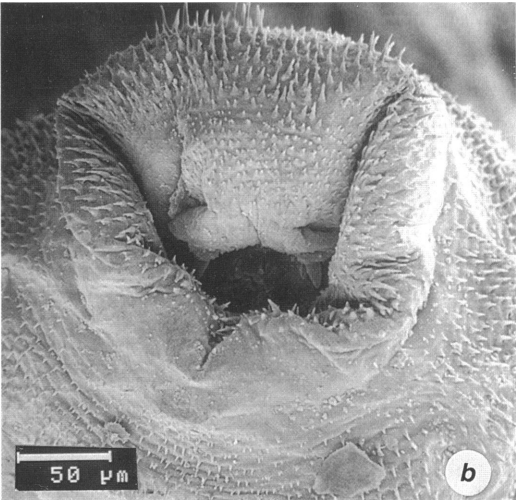
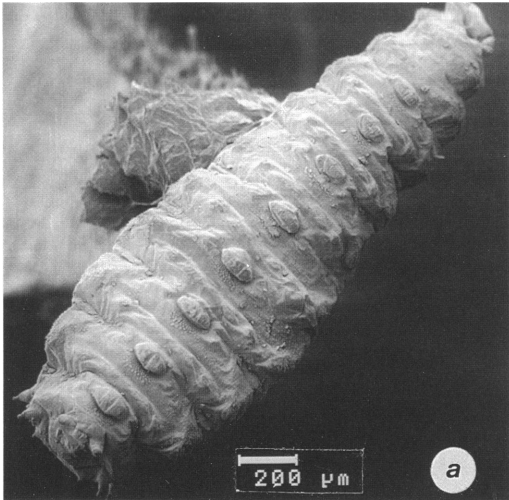
Fig. 2. A more modern view of *Carnus*: scanning electronmicrographs of *C. occidentalis*, n.sp. **a.** Habitus, physogastric female (ventral view). **b.** Head, profile. **c.** Base of dehiscent wing, which is broken along the line from the subcostal break through the anterior crossvein. **d.** Setulae in the abdominal, pleural membrane. Each seta is anchored in a sclerotized, conical base.

colored, slightly ovoid, bare (no interfacetal setulae); 1 pair anterior, inclinate orbital setae and 2 pairs posterior, lateroocline orbital setae present; postocellar setae lost; face virtually nonexistent, merely a deep, vertical sulcus (closure of sulcus varies greatly); aris-

ta about same length as orbital setae, with short pubescence; 2 pairs vibrissae present, ventral one slightly thinner, setae ventral to these upturned; proboscis with labellum small, labium heavily sclerotized, broad, sometimes bulbous; antennal bases lying in deep fossae.

→

Fig. 3. Third instar larva of *Carnus occidentalis*, n.sp. **a.** Entire larva (ventral). **b.** Cephalic region (head is collapsed into the oral cavity). **c.** Ventral protuberance on abdominal segment 5. **d.** Ventral protuberance on abdominal segment 7. **e.** Posterior end (dorsal surface is up). **f.** Cavity into which posterior spiracle is recessed.



Notum with following setae (per side): 1 postpronotal, 1 presutural, 2 notopleurals, 1 dorsocentral, 1 postsutural supra-alar, 1 prescutellar acrostichal; acrostichal setulae in no noticeable rows, most numerous at anterior end; 2 pairs of scutellar setae. Legs with coxae, femora, and most of each tibia brown, tarsi yellowish. Female tergites reduced to narrow, rectangular shape, tergite 1 and 5 heavily sclerotized, others much more lightly so.

Male genitalia with epandrium complete; cerci small, unsclerotized, without setae or setulae; hypandrium narrow, U shaped; aedeagus (phallus) short, bulbous, membranous; paraphysis (paramere) triangular.

*Carnus hemapterus*

Figures 4a; 5a, b; 6–8; 13

*hemapterus* Nitzsch, 1818: 305; Germar, 1822: pl. 24, 25; Hennig, 1937: 72.; Sabrosky, 1965 (catalog): 729.

*Cenchrudobia eggeri* Schiner, 1862: 436.

*Carnus setosus* Stobbe, 1913: 193.

**DIAGNOSIS:** Found throughout the Palearctic region and eastern and northern North America, and distinguished from *occidentalis*, n.sp., by the relatively longer surstylus (apical width/total length 0.40) (fig. 6), and by the long paraphysis in lateral view (0.54 greatest width/length) (fig. 7). Distinguished from *orientalis* as given below. Comparisons between eastern North American and European specimens revealed no consistent differences, although the ventral lobe of the epandrium in some European *Carnus* was longer and thinner.

**MATERIAL EXAMINED:** **AFRICA:** Egypt, 25 km W. Marsá Matrúh, W. Desert, IV/28/59, M.N. Kaiser, nest of *Corvus corax*, 3♂ (diss. no. 9), 2♀ (NMNH); **CANADA:** **British Columbia:** Osoyoos L., N. end, 21/IV/85, R.J. Cannings, in saw whet owl nest, 1♂ (diss.), 2♀ (CNC). **New Brunswick:** F'ton [Fredericton], VI/27/51, N.R. Brown, "nest and young of *Sphyrapicus varius*", 2♀ (CNC); Priceville, near Docketown, VII/6/68, ex: nest of yellow-bellied sapsucker, 2♀ (CNC). **Ontario:** no specific information. **EUROPE:** **England:** Oxford, III/54, J.R. Vockeroth, 1♀ (CNC). **Hungary** (all in HNHN): Aranyosgándány, gyurgyalag fész-

ekböl, Kelt VIII/13/70, Papp, 1♂; Alcsüt, VI/20/63, Csókófésze K ből Kelt, Warga, 3♂ (diss. no. 18); Szentendre, III-V/70, Papp, 3♂ (diss. no. 17). **Sweden:** Sk. Malmö. Belleviegården, Kläckt ur holk nr. *Sturnus vulgaris*, 28/IV/86, 10♂ (diss. nos. 19, 20), 4♀ (NRS). **Switzerland** (all in HNHN): Kaufdorf, Sur poussin de Cherèche, 3/VI/79, Baude, 1♂ (diss. no. 16), 2♀; Anière (GE), nest of *Falco tinnunculus*, 9/VI/79, Baude, 3♂.

**USA:** **Colorado:** Colorado Springs, VI/18/70, R.M. Stabler, ex: Sparrow Hawk, 1♂ (diss. no. 7), 2♀ (NMNH); **Indiana:** Wayne Co., Centerville, 5/VIII/61, G.L. Ward, *Sturnus vulgaris* nestling, 1♂ (diss. no. 4) (NMNH). **Maryland:** Howard Co., 4/VI/85, ex: young kestrels in nest box; Lowry, Martin, and Wallace, 2♂ (diss. nos. 1, 11), 2♀ (NMNH). **Massachusetts:** Middlesex Co., Cambridge, 7/VII/81, N.E. Woodley, 2♂ (diss. no. 12) (NMNH). **New Jersey:** Cape May Co., Avalon, VI/5/79, W.G. Robichaud, ex: osprey nestling, 1♂ (diss. no. 2), 1♀ (NMNH). **New York:** Albany, IV/4/72, J.A. Wilcox, 2♂ (NMNH); *Tompkins Co.*, Ithaca, ex: falcon (no date or coll.), 1♂, 1♀ (INHS); Jamesville, J.R. Philips, VI/24/76, ex: nest of American kestrel, 2♂ (CNC). **Rhode Island:** Richmond, VI/1/71, A. Lavallee, 3♂ (diss. nos. 3, 10), 3♀ (NMNH). **Utah:** Cache Co., Smithfield, 27/V/74, T.L. Whitworth, magpie nest in willow, 7♂ (diss. no. 21), 8♀ (UTSU, 1 of each sex in AMNH); West Nibley Lumber Mill, 16-18/IV/74, T.L. Whitworth, magpie nest, Nos. 1758, 1788, 3♂ (diss. no. 22), 2♀ (UTSU).

**HOSTS:** Bequaert (1942) summarized the hosts and localities for European specimens and records of *Carnus hemapterus*, which included 29 species of birds in 15 families. He noted that there was a slight predilection for birds nesting in sheltered areas or cavities, but never a species that was a ground or swamp nester. Capelle and Whitworth (1973) reviewed all the North American records, which included 15 species of raptors, passerines, and woodpeckers, but, again, no ground nesters. Fitzner and Woodley (1983), Main and Wallis (1974), and Wilson (1977) added new records of raptor and woodpecker hosts. Additional records are added here from museum specimens that have been studied. Ap-

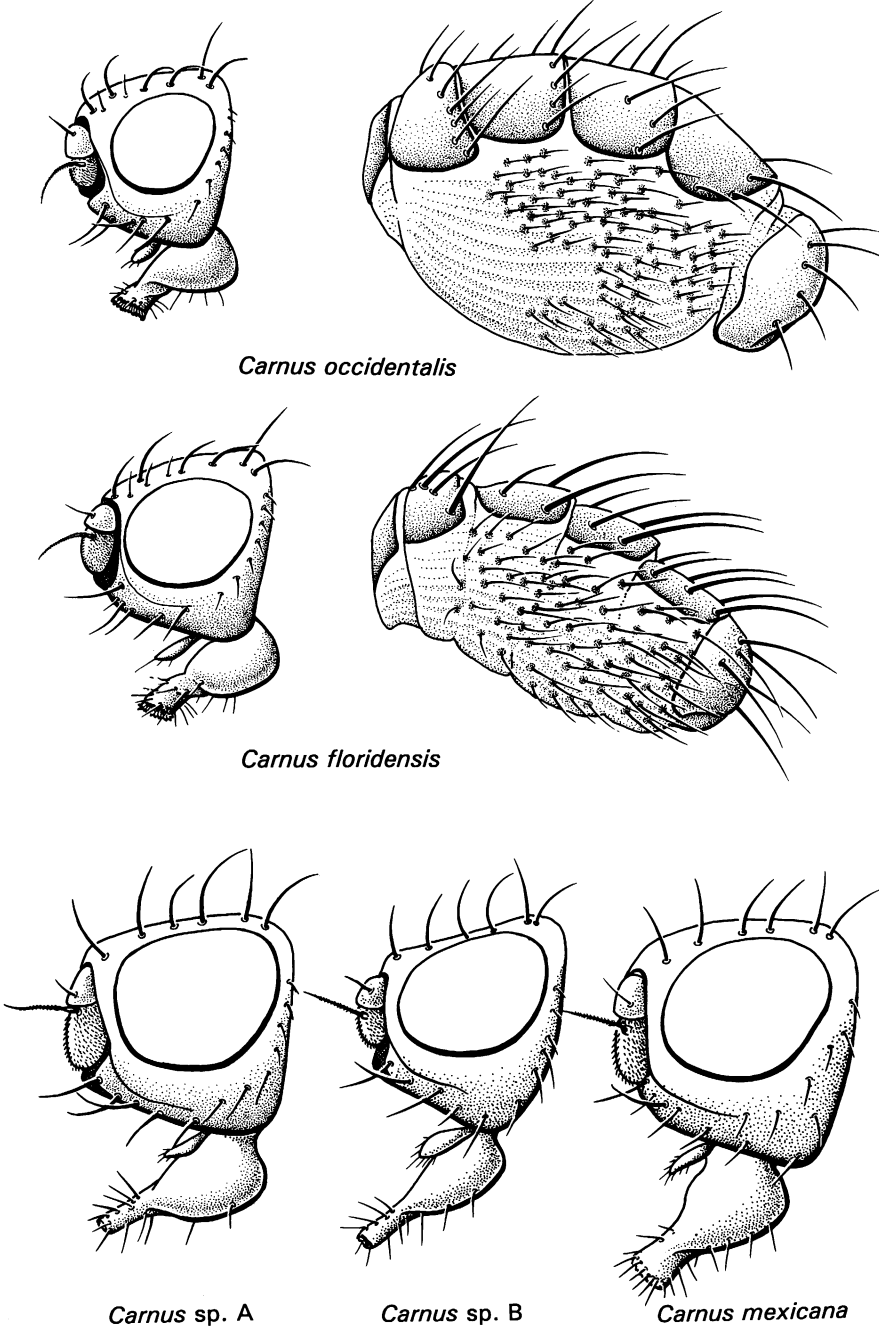


Fig. 4. Heads and abdomens of *Carnus occidentalis*, *floridensis*, *mexicana*, and two species from Chiapas, Mexico known only from females.

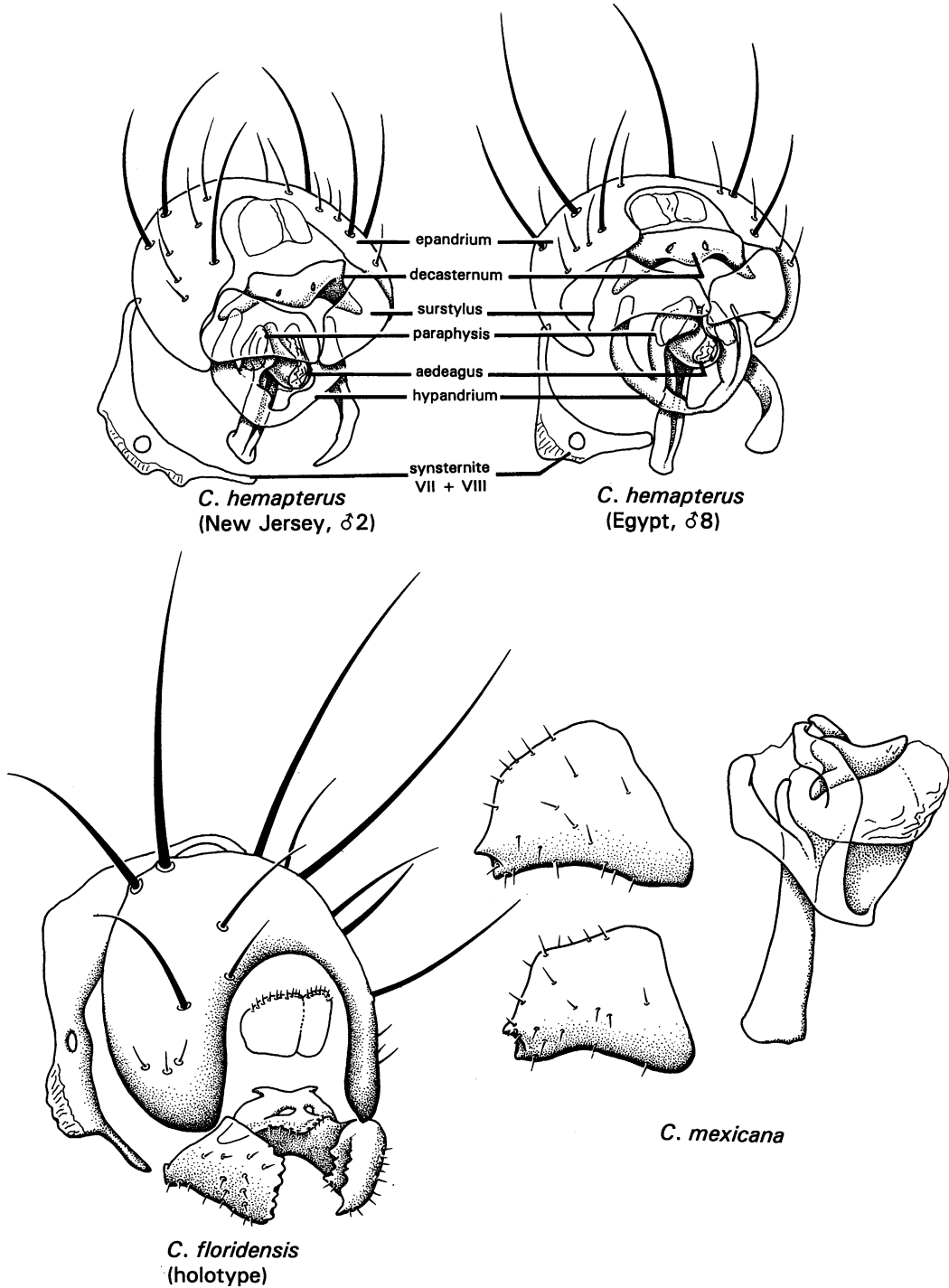
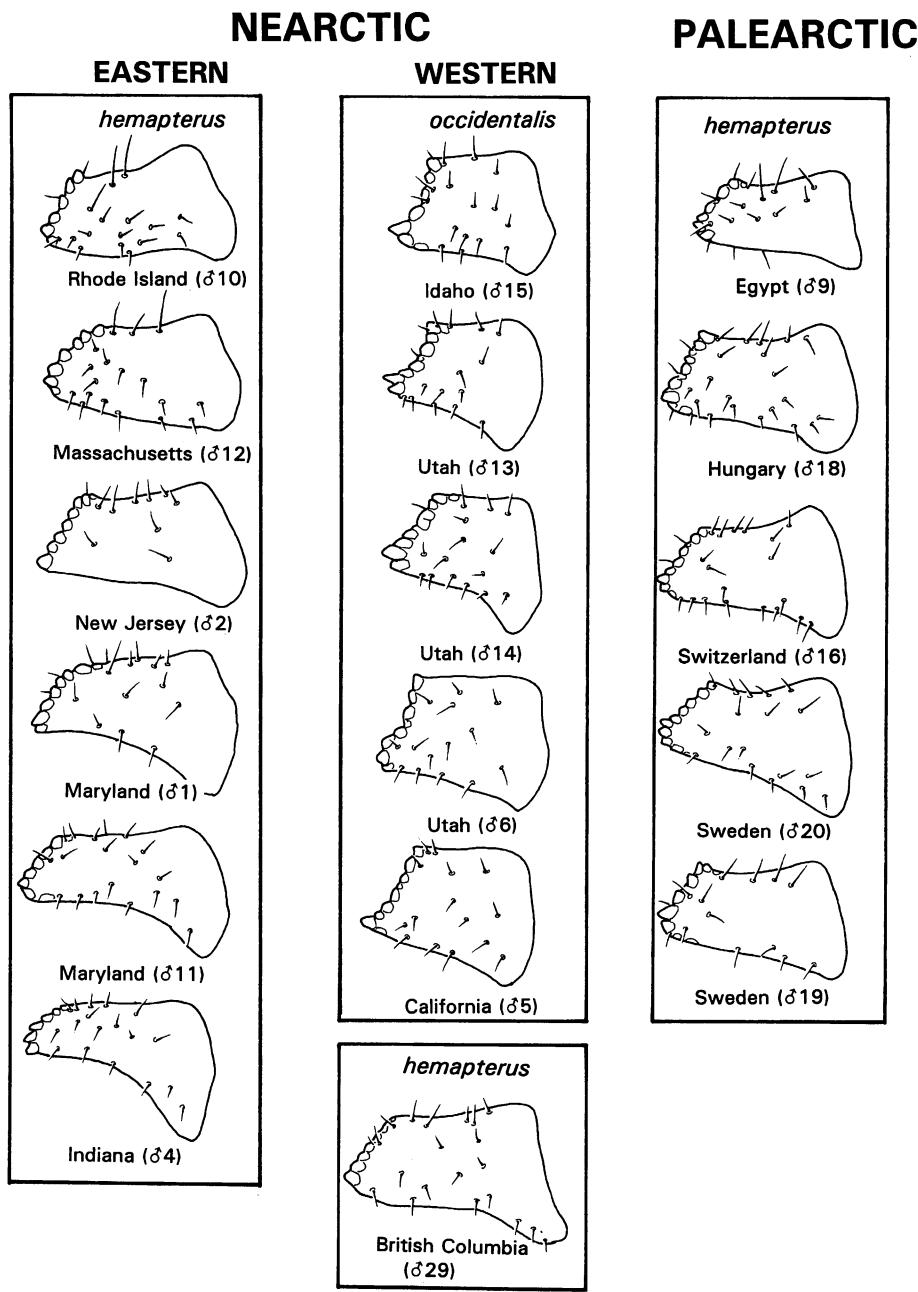


Fig. 5. Male terminalia of *Carnus*. Epandrium, surstyli, and genitalia of *C. hemapterus*, from New Jersey and Egypt, and of *C. floridensis*, n.sp. (holotype). Genitalia and surstyli of *C. mexicana*, n.sp.





inal membranes in freshly collected flies. Bequaert (1942) noted that the mouthparts were not similar to other higher flies that had rasping structures on the labellum, such as *Stomoxys* (Muscidae) and tsetse flies (Glossinidae), and so were probably unable to penetrate the skin. Capelle and Whitworth (1973) found, as did Fitzner and Woodley (1983), small groups of 3–8 adults feeding in bare axillary regions of nestling Swainson's hawks and red-shafted flickers. Of most interest was that Fitzner and Woodley observed dried blood spots in the axillary region where the flies were found. Evidence does not preclude, and in fact suggests, that the flies are blood feeders. This could be simply addressed by first starving the flies, letting them feed, and then examining their gut contents soon after their removal from the host. Simply removing the flies from a host in nature would not guarantee that the fly has fed recently.

**REPRODUCTION:** Reports conflict as to whether *Carnus* is ovoviviparous. De Meijere (1913) cited Brauer (1880) as stating that first-instar larvae were extracted from the abdomen of a gravid female [presumably based on specimens from Germany]. Capelle and Whitworth (1973) mentioned that a female from Utah laid eggs.

**LARVAE:** Until now, the larvae have been undescribed, although de Meijere (1913), Hennig (1937), and Capelle and Whitworth (1973) illustrated the puparium. The puparium is distinctive for its produced posterior spiracles and pronounced, evenly spaced annuli (numbering about 16–22). Using material from the Capelle and Whitworth study, the third-instar larva is most distinctive for the midventral row of eight fleshy protuberances, one per abdominal segment (figs. 3a, c, d). This is apparently unique for the Cyclorrhapha. The protuberances are not extensions of the creeping welts, since there are no curved spinules on them (figs. 3c, d), as is seen in the assorted cyclorrhaphan larvae with paired "prolegs" (e.g., *Ephydra* [Ephydriidae], *Cladochaeta* [Drosophilidae]). Function(s) of the protuberances are unknown, but unlikely to serve in locomotion because there are no spinules. Each protuberance has either a single, central slit or a pair of paramedian slits (figs. 3c, d). The ce-

phalic region is entirely covered with simple (unbranched) spinules (fig. 3b). The posterior end has five pairs of lobes (fig. 3e), and the posterior spiracles are retractable enough to be entirely recessed (fig. 3f).

**DISTRIBUTION:** European records of *Carnus hemapterus* were summarized by Bequaert (1942), which included the following countries: Austria, Finland, Germany, Italy, Lithuania, the Netherlands, Romania, Switzerland, and Yugoslavia. Additional records are Spain (Carles-Tolra [1993]), Hungary (Papp, 1984; this study), eastern Russia (Papp, 1984), and Sweden (Papp, 1984; this study). Papp (1984) also listed "Nearctic and Afrotropical Regions" under the distribution of *C. hemapterus*; some of these records, as shown below, refer to other species.

American records of *Carnus* were most recently reviewed by Capelle and Whitworth (1973), with new records cited by Fitzner and Woodley (1983) and Cannings (1986). States and provinces previously reported are: Arizona (Bequaert, 1951: species identity uncertain, specimens were possibly *occidentalis*, n.sp.), Baja California (Bequaert, 1951; Sabrosky, 1965: probably *occidentalis*, n.sp.), British Columbia (Bequaert, 1951; Cannings, 1986), Florida (Bequaert, 1942: probably *C. floridensis*, n.sp., see below), Indiana (Wilson, 1977), Massachusetts (Main and Wallis, 1974), New Brunswick (Sabrosky, 1965), New Jersey (Kirkpatrick and Colvin, 1989), New York (Bequaert, 1942), Utah (Lloyd and Philip, 1966; Capelle and Whitworth, 1973: included *hemapterus* and *occidentalis*, but these species were not distinguished at the time), Washington state (Fitzner and Woodley, 1983, specimens of which could have been *occidentalis* or *hemapterus*). Additional records, based on material examined for this study, include Colorado, Maryland, and Rhode Island. Fitzner and Woodley remarked that the species was unknown from the midwestern (Great Plains) states (e.g., Dakotas, Minnesota, Iowa, Nebraska, Kansas, Texas, New Mexico, Wyoming, and Montana, although it has been found in Colorado). Two slide-mounted specimens were examined from the CAS, labeled as "Rocky Mt. Laboratory, 19 June, 1963, G. D. Lloyd, Nest 21-2N," which is in Hamilton, Montana (P. H. Arnaud, Jr., per-

sonal commun.) (orientation of the mount prevents a definitive identification, but the male specimen appears to be *hemapterus*). Previous authors maintained that this might represent a disjunction of eastern and western populations. *Carnus hemapterus* clearly occupies the eastern half of North America, and northern latitudes west to northern Utah and southern British Columbia (fig. 9). *Carnus occidentalis*, n.sp., is the fly former authors called *hemapterus* from southwestern North America.

An apparent absence of *Carnus* in mid-western North America may be attributable to the poor sampling for these flies, but the distinct identity of the western North American species (reported below) suggests the disjunction to be real. Indeed, an examination of bird nests from western Montana revealed no *Carnus* (Jellison and Philip, 1933). Prior to the present study, virtually no comparisons had been made among individuals of *Carnus* from various localities. Bequaert (1942) mentioned that he was unable to compare European and American specimens, but did note (on the basis of old descriptions) that the setation in the abdominal pleural membrane was slightly different in the American specimens, and the "[external] male terminalia [were] virtually identical." Given that apparent Holarctic species are often two species, Nearctic and Palearctic (albeit subtly different), separate identities are not surprising.

### *Carnus orientalis*

*Carnus orientalis* Maa, 1968: 33.

**DIAGNOSIS:** Separated from *hemapterus* and *occidentalis* by *orientalis* having a narrower interocular distance; labium shorter and slightly longer; cheek not as deep; abdominal sternites (males) almost square (rectangular in other species); abdominal pleural membrane with setulae sparser in both sexes; female tergites much larger than any other species in the genus. Species status is unquestionable based on somatic features alone, but diagnostic features of male genitalia could not be deciphered from Maa's descriptions or illustrations.

**SPECIMENS:** Known only from the type series of 8 dealate males and 11 females from

Malaysia ("Selangor, Rantau Panjang, 8 km N. Klang, ex: juvenile fish owl"). Holotype is in the Bishop Museum, Honolulu (no. 7604), paratypes in the Natural History Museum, London; and the National Museum of Natural History, Smithsonian Institution.

It should be noted that an intensive survey of nearly 70 bird nests, from 23 species and eight families of birds, done in Hokkaido, northern Japan, revealed no *Carnus* (Iwasa et al., 1995).

### *Carnus occidentalis*, new species

Figures 2, 3, 6, 7

**DIAGNOSIS:** Very similar to *C. hemapterus* but consistently distinguished from it by male genitalia in *occidentalis* having a shorter, deeper surstylus that is almost square (apical width/total length approximately 0.57, vs. 0.30 to 0.45 in *hemapterus* [fig. 6]); paraphysis (paramere) in lateral view much shorter, almost triangular (greatest width/greatest length = 0.75, vs. 0.55 in *hemapterus*) (fig. 7).

Head, notum, pleura light, shiny brown to black; proclinate interfrontal setae cruciate; ocellar setae almost parallel; antenna with pedicel tan, flagellomere 1 dusty gray. Notum with apical scutellar setae cruciate, leg coloration typical for genus. Setulae on abdominal pleural membrane short, longer ones dorsad. Male genitalia: synsternite VII + VIII, a vestigial pair of crescentic sclerites flanking epandrium; paraphysis (paramere) longer than wide; surstylus with blunt teeth on medial edge, trapezoidal in shape, longer than wide.

**TYPES:** Holotype (male): UTAH: *Box Elder Co.*, Mantua, Devil's Gate, ex: flicker [species], 14/VII/68, T.L. Whitworth. In AMNH. Paratypes: 14♂ (diss. no. 23), 19♀ from same series as holotype (in AMNH and UTSU).

**OTHER MATERIAL:** **California:** *Contra Costa Co.*, Walnut Creek, V/12/50, S. Kent Carnie, "Host: *Falco peregrinus anatum*, undersides of wing at elbow jt., among pin feathers and down," 1♂ (diss. no. 5), 1♀ (NMNH). **Idaho:** *Boise Co.*, Lucky Pk. Nur. 14/VI/84, R. Meadows, "Malaise trap," 1♂ (diss. no. 15). **Utah:** *Box Elder Co.*: Devil's Gate, VII/69, T.L. Whitworth, flicker nest,

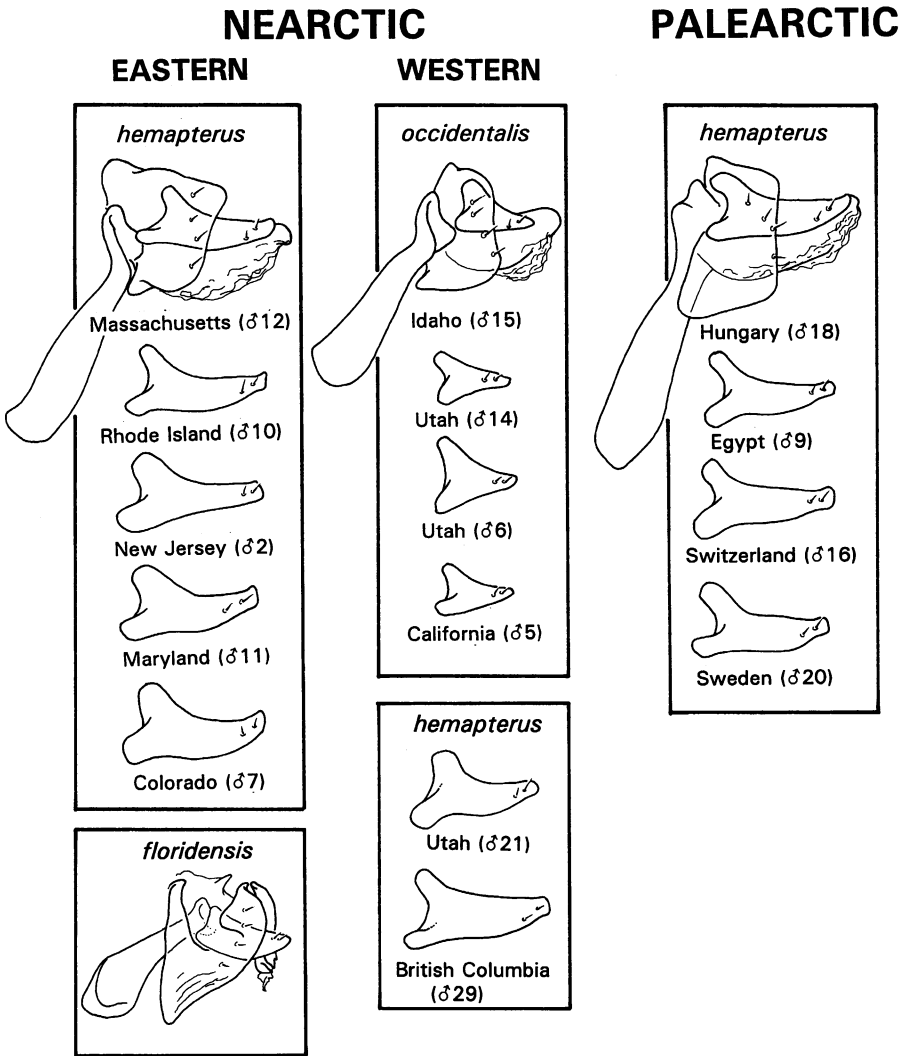


Fig. 7. Variation in and comparison between paraphyses and other parts of the male genitalia in *C. hemapterus*, *C. occidentalis*, and *C. floridensis*.

9♂, 2♀ (diss. nos. 13, 14); 5 mi NW Brigham City, 25/V/93, C.D. Marti, "from abdomen of *Tyto alba* chicks", 2♀; *Davis Co.*: 3 mi W. Kaysville, 25/V/93, C.D. Marti, 3♀, "paras. of *Tyto alba* chicks"; *Summit Co.*, Heiner's Canyon, nr. Coalville, 25/VI/64, G.D. Lloyd, ex: hawk nest, 12-3N (1♂, 1♀: CAS); nr. Coalville, 6500 ft, G.D. Lloyd, 25/VI/64, on nestling sparrow hawk, 3♂ (diss. no. 6). *Willard BSN*, 9/VII/69, Capelle and Whitworth, on flicker nestling, 33♂, 24♀ (in UTSU and AMNH).

**ETYMOLOGY:** "Western," referring to its location in North America.

**DISCUSSION:** Distribution of this species overlaps that of *C. hemapterus*, at least in northern Utah. It should be noted that the brief survey by Lee and Rychman (1954) of owl nests in California revealed no *Carnus*.

*Carnus floridensis*, new species  
Figures 4b, 5c, 8

**DIAGNOSIS:** Eye light, cream-colored, contrasting with dark blackish-brown body

(head, all of thorax, labium, femora, most of each tibia). Antenna with pedicel and flagellomere I dark, black-brown. Ocellar setae divergent; proclinate interfrontal setae convergent but not cruciate; labium bulbous. Setulae on pleural membrane of abdomen black, about twice the length of setulae in other species. Female tergites narrow, except tIV ( $W/L = 2.2$  [vs.  $2.4-3.6$  in other species]); tergites with long setae on posterior margin, about twice the length of setae in other species. Male genitalia with epandrium having long, stout setae, about twice the length of other species; synsternite VII + VIII complete dorsally; aedeagal apodeme short (ca.  $0.7\times$  length in other species); paraphysis a simple, triangular shape; surstylus rectangular, not trapezoidal, with blunt teeth on the apical edge.

**TYPES:** Holotype (male): **FLORIDA:** *Wakulla Co.*, 15/V/92, on woodpecker nestling (diss. no. 24). Paratype: female, same data. Both specimens in AMNH.

**ETYMOLOGY:** In reference to the type and only known locality, in Florida, USA.

***Carnus mexicana*, new species**

Figures 4e, 5d-e, 8b

**DIAGNOSIS:** Coloration light brown to tan, all tarsi yellowish white. Head: Proclinate interfrontal setae convergent, but not cruciate; ocellar setae parallel to slightly divergent; vibrissae with large distance between two ipsilateral ones (distance approx.  $5\times$  the diameter of the seta). Thorax: scutellar setae with apical pair parallel to convergent (in very replete females they are cruciate from pressure of the abdomen). Abdomen: pleural setae short; female tergites narrower than in other species, especially tII, tIII ( $W/L = 3.2$  [vs.  $3.8-4.0$  in other species]); apical sternite in female less sclerotized and smaller (by approx. one-half the size) in other species. Male genitalia: synsternite VII + VIII complete; surstylus with just 2 blunt apical teeth, roughly triangular in shape; paraphysis triangular, longer than wide.

**TYPES:** Holotype (male): **MEXICO:** *Durango*, 10 mi W. El Salto, ex: flicker young. Paratypes: 15♀, 7♂, same data. Holotype and 18 paratypes in CNC; 4 paratypes in AMNH.

**ETYMOLOGY:** In reference to Mexico, the only known locality.

***Carnus* sp. A**

Figures 4c; 8c

**FEATURES:** Larger black species; ocellar setae divergent; proclinate interfrontal setae upright, almost parallel, another pair posterior and nearly cruciate. Proboscis slightly longer and thinner than in other species (except *Carnus* sp. B), labellum small and narrow. Abdominal setae (pleural setulae and tergal setae) black, long. Male unknown.

**SPECIMENS:** **MEXICO:** *Chiapas*, 8 mi E. San Cristobal, 19/V/69, B. Peterson, ex: owl nest. 2♀. In CNC.

**DISCUSSION:** Both this species and *Carnus* sp. B appear to be distinct species on the basis of somatic features only. However, since the other species of *Carnus* in this study are most consistently diagnosed on the basis of male genitalia, I hesitate to describe these as new species without additional material. *Carnus* sp. A and B are sympatric at least in southern Mexico, but were reared from different hosts.

***Carnus* sp. B**

Figure 4d

**FEATURES:** Body entirely dark, black-brown, except for eyes and light yellowish tarsi. Proboscis slightly longer and thinner than in other species (except *Carnus* sp. A), labellum narrow. Proclinate interfrontal setae virtually upright, convergent to almost parallel. Eye longer than high, cheek very deep; vertex flat in profile. Apical scutellar setae with tips virtually touching. Tergites not observed well, since specimens considerably shriveled, but pleural and tergal setae long, as in *floridensis*.

**SPECIMENS:** **MEXICO:** *Chiapas*, 8 mi E. San Cristobal, 19/V/69, B. Peterson, ex: Sparrow hawk nest. 10♀ (in CNC).

**African *Carnus* sp.**

DeConinck (1986), cited by Barraclough (1994), reported the first *Carnus* from sub-Saharan Africa. Locality: **ZAIRE:** near Mitwaba,  $08^{\circ}51'S$ ,  $26^{\circ}43'E$ , Kaswabilenga, 14/X/47, René Verheyen, on nestlings of the

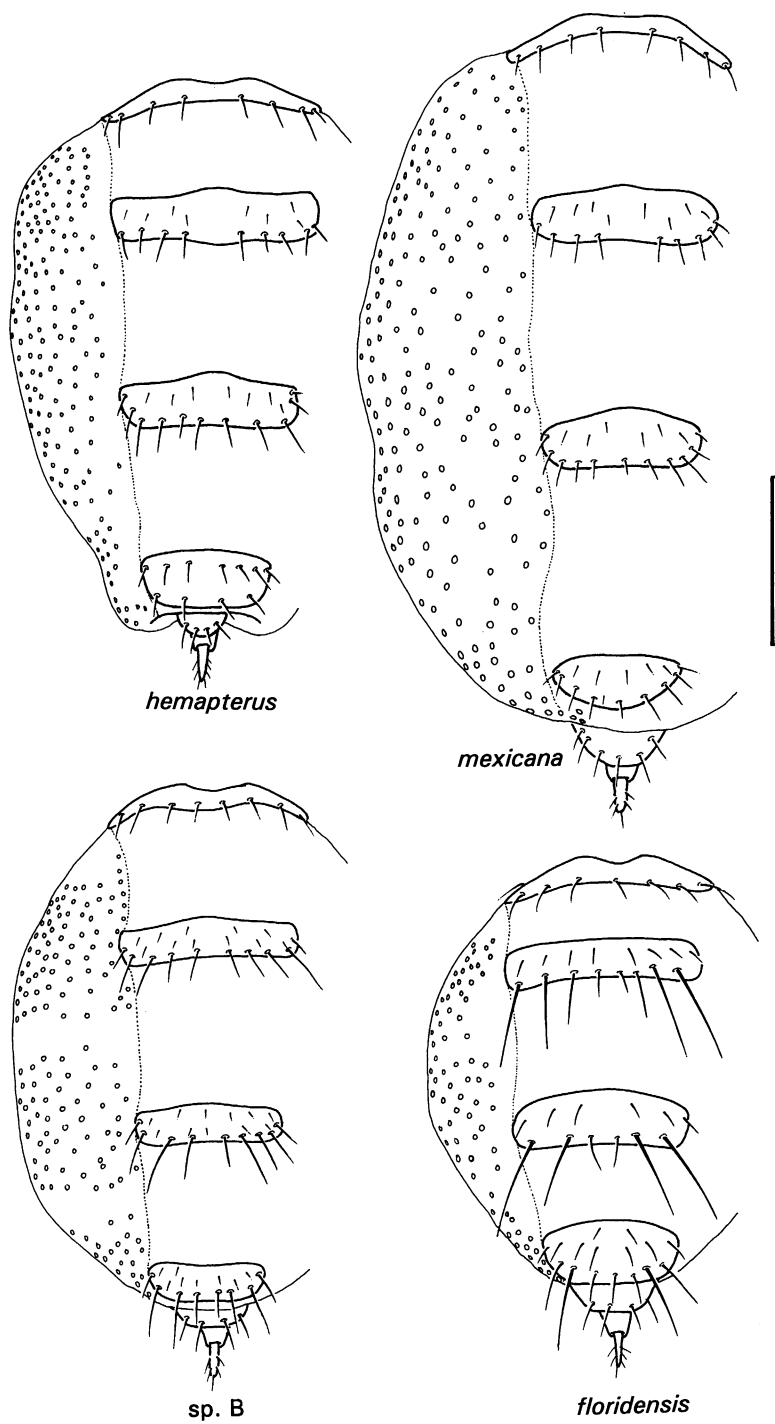


Fig. 8. Female tergites in *Carnus*. Distension of the abdomen is trivial variation.

kingfisher, *Halcyon albiventris*. Since this kingfisher is widespread through South Africa, Gabon, Zaire, Kenya, and Somalia, the fly is thought to be similarly widespread. If this *Carnus* is as polyphagous as the European and North American species, it probably feeds on many birds. A description of this species will be published by DeConinck.

## GENERAL DISCUSSION

All but one of the more than 65 records of *Carnus* associate the fly with nests of tree-nesting birds (appendix 1) (the one exception is the mention by Maa [1968] of *Carnus hemapterus* on the gray egret, *Ardea cinerea*, in The Netherlands). More than one-third of the records report *Carnus* in raptor nests, 10 records in woodpecker nests, 9 with corvids, and the remaining records being one to four reports each in various families of smaller, perching birds (passeriformes). The apparent predilection for raptors may be due to the conspicuous size of the nests, and the carrion debris that falls into the bottom of the nest, in which larval carnids would breed. Later I discuss why tree-nesting birds are parasitized.

Behavior of the flies and field observations indicate that the flies specifically feed on blood and/or oily and other secretions of nestling birds. This is probably their sole way of life, given the distinct adaptations of *Carnus* for avian ectoparasitism, such as dehiscent wings; short, stiff setae over much of the body; and physogastry. Presumably, an enormous clutch of eggs or one or more large larvae are produced with the volume of blood/oil meal that distends the female abdomen two to three times the size of the rest of the body. Physogastry is also seen in the hippoboscids fly *Melophagus*, a hematophagous ectoparasite of ungulates, although the physogastry is not as pronounced as in *Carnus*. Interestingly, additional protein for vitellogenesis in *Carnus* may be derived from autolysis of the flight muscles, which was shown to occur in histological studies by Mercier (1928). A feature that preadapts *Carnus* well to ectoparasitism are antennae deeply recessed in fossae (which exists in the other genera of carnids).

A few studies indicate that, while parasit-

ism rates of birds may be high, the flies have little noticeable effect on the birds. *Carnus hemapterus* was found on 91 of 103 (88%) nestling barn owls (*Tyto alba*) in southwestern New Jersey (Kirkpatrick and Colvin, 1989). The flies were on the chicks only until the fifth week. In Germany, *Carnus hemapterus* infested nestlings of the starling, *Sturnus vulgaris*, from hatching, and the heaviest infestation was when the nestlings were six and seven days old (Walter and Hudde, 1987). Parasitism apparently did not reduce breeding success of the starlings.

Adults of *Carnus* probably do not disperse with their avian hosts. No reports have ever been made of banded, mist-netted, wild-captured or even domestic birds having *Carnus* on them. The flies may just be much easier to detect in a nest or nest hole and on nestlings and fledglings. However, *Carnus* lacks modifications seen in fleas and other ectoparasitic Diptera (such as hippoboscids, streblids, and nycteribiids), which allow the parasite to grip the hairs or feathers of its flying or moving host. These include an extremely flattened body (for moving among hair and feathers) and combs (ctenidia) or strong claws for gripping. *Carnus* also lacks the distinctive ectoparasite feature of reduced eyes. If *Carnus* must disperse to nests simply by its own flight, instead of by phoresy, then the broad range of hosts seen in *C. hemapterus* must be directly related to this method of host colonization.

Three of the five species of *Carnus* are each known from only a single series or pair of specimens from one nest (e.g., *orientalis*, *mexicanus*, *floridensis*). This applies as well to three additional, undescribed species from Mexico and Africa. No records exist from South America, or from India, southern China, Indochina, or even from central and eastern Russia; and one doubts if appropriate efforts to sample flies like *Carnus* have ever been made in these regions. Given the spotty records of *Carnus* from Africa and Central America, and the poor sampling of them from an area as intensively studied as North America, it would not be surprising if *Carnus* were found on all continents except Australia (and Antarctica, of course). In fact, based on land areas, and the diversity of tropical bird faunas, *Carnus* is likely to be sev-

eral times more diverse in the African, Indopacific, and New World tropics than are presently known to exist in northern temperate regions. Fifty world species of *Carnus* would not be an unreasonable number to expect, but this would require an extremely ambitious program of field work to decipher.

### GENUS *MEONEURA*

Figures 11b, 12b, 14, 15

*Meoneura* Rondani, 1856: 128; Hennig, 1937: 59 (subsequent citations and synonyms).

#### *Meoneura vieja*, new species

**DIAGNOSIS:** Easily distinguished from *Carnus* and other *Meoneura* with abdominal spots on the basis of the distinctive male genitalia, with surstyli that are deeply forked, for virtually one-half their length (similar to that in the living species *Meoneura anceps* Frey, *M. californica* Sabrosky, and *M. milleri* Gregor); surstyli without brushes of long setae; ventral lobe beneath the cerci bifurcate, with several fine setae at tips of the lobes. Abdominal segments 3–5 with tergites virtually devoid of setae; pleural membrane with setulae more numerous than in most *Meoneura*.

**DESCRIPTION:** *Head:* Unicolorous brown. Eyes bare, without fine pile, much lighter in color than rest of head. Orbital setae: 2 posterior pairs strongly laterocline; 2 anterior pairs inclinate, all approximately equal in size (anteriormost orbitals slightly shorter); a much smaller, finer setula lying between each orbital seta; ipsilateral setae and setulae in line. Pair of small mediofrontal setae present; convergent, with ends touching. Two pairs small inclinate setae bordering ocellar triangle. Ocellar triangle extended to ca.  $0.6\times$  length of frons. Ocellar setae thick (slightly thicker than other setae on head), strongly divergent. One pair of fine, parallel post-ocellar setae present. Inner vertical setae longest on head; pair of outer vertical setae divergent, ca.  $0.7\times$  length of inner verticals. Face with narrow carina lying between 2 deep fossae; base of carina forming membranous triangle at oral margin. Fossae have steep, definite edges extended laterally to inner margin of eye and ventrally to just between vibrissae. Antenna with pedicel with 1 stout seta on anterior surface; arista ca.  $2.5\times$

length of flagellomere I. Vibrissae stout, subtended by 4 pr. of subvibrissal setae: pair immediately ventral to vibrissae smallest, next pair similar in size and orientation to vibrissae; setae of large lateral pair upturned and divergent; lateralmost pair convergent. Proboscis with small palps and labellum; prementum only slightly bulbous, considerably smaller than in *Carnus*. Face width/head width = 0.41; cheek depth/eye depth = 0.34.

*Thorax:* Notum with flat dorsal surface; acrostichal setulae well developed, not in rows. Setae: 1 large postpronotal; 1 presutural (lateral); 2 notopleurals (anterior one slightly stouter); 1 pr. large prescutellar acrostichals; 2 supra-alars; only 1 (large) pair of dorsocentrals; 2 pr. scutellars. No color patterns distinct on thorax or abdomen. *Wings:* completely hyaline. Section of costal vein proximal to sc break with row of 5 stout, black, spinelike setae (no indication of a line of weakness in this area).  $R_{2+3}$  short. Costal vein ending midway between apices of  $R_{2+3}$  and  $R_{4+5}$ . Crossveins dm-cu and r-m present, separated by a distance approximately 1.5 times length of crossveins. Vein  $M_1$  very light, barely noticeable. Vein  $A_1$  largely absent. Wing length = mm. *Legs:* Forefemur with dorsal row of 3 and ventral row of 4 long setae; midtibia with 2 large apical setae; hind femur with ventral row of 5–6 stiff short setae on distal half, one seta twice the size of others.

*Abdomen:* Male and female tergites 2–4 virtually devoid of setae, with only 2–3 setae near lateral margins. Tergite 5 with normal setation, including row of larger setae along posterior margin. Tergite 6 minute, with several long setae, segment 7 with 2 lateral plates. Pleural membrane of segments 1 and 2 without setulae; segment 3 with 4–5 setulae, each one arising from dark spot at its base; segments 4 and 5 with more setulae than normally found in *Meoneura*. Female sternites small. Ovipositor telescoping (segments 6, 7, 8), apically membranous. Surstyli of male genitalia without brushes of long setae; ventral lobe beneath cerci bifurcate, with several fine setae at tips of lobes.

**TYPES:** *Holotype:* Male: AMNH DR-14-600, in amber from the Miocene of the Dominican Republic (Grimaldi, 1995), although specific provenance is unknown. Genitalia



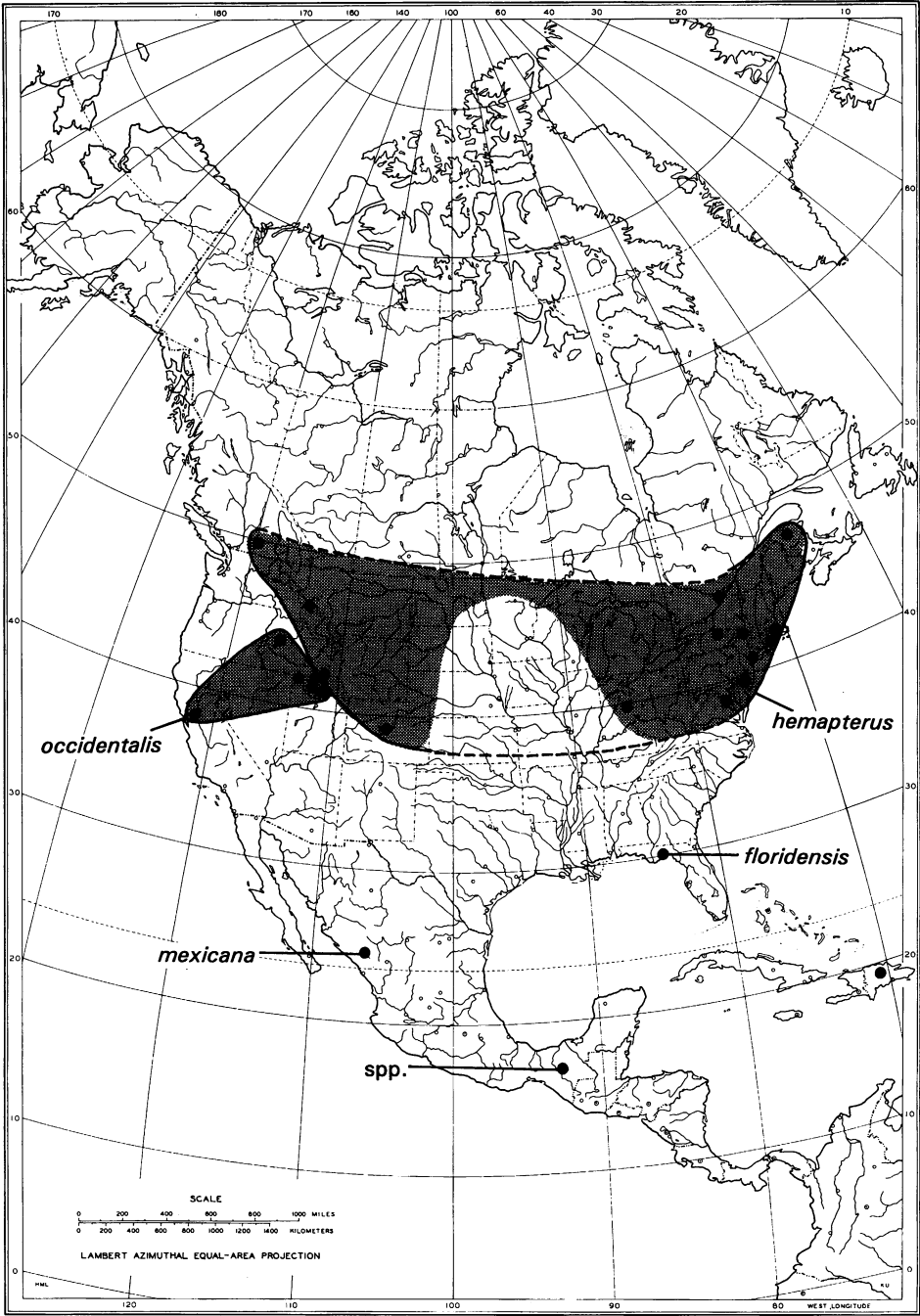


Fig. 9. Records of *Carnus* in the New World.

are well preserved and exposed. *Paratypes*: female, in excellent condition, AMNH no. 11842A. Originally in large, clear, deeply colored piece of amber also containing a sta-

phylinid beetle. Area around carnid was removed and polished into a small piece so as to better view the face. A fine crack along the midventral line of the abdomen obscures

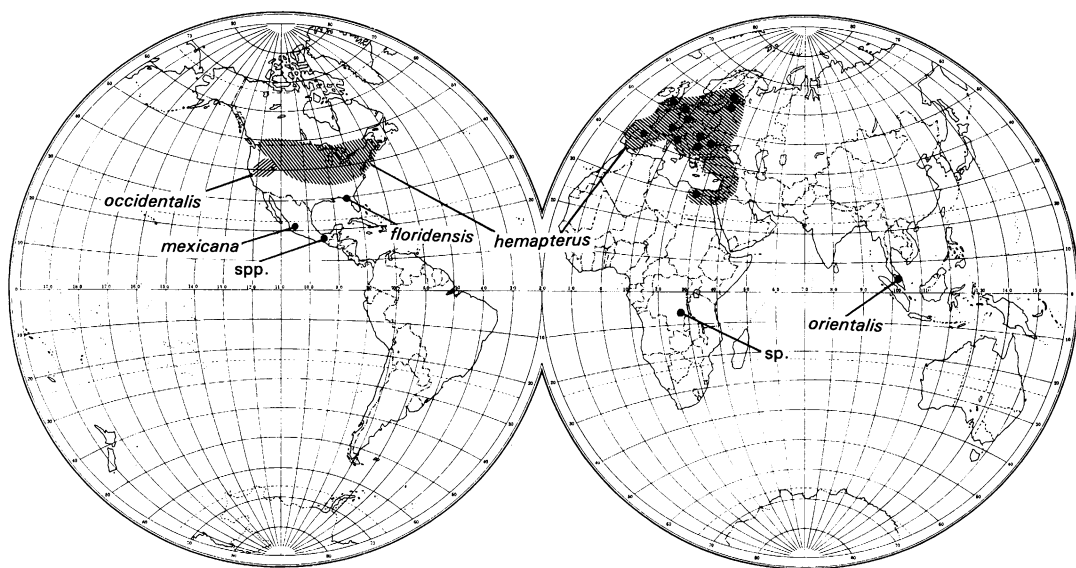


Fig. 10. Global distribution and records of *Carnus*.

this area somewhat: the piece must be carefully positioned and lit to view the sternites. Paratype, female, AMNH DR-14-599, specific locality in Dominican Republic unknown.

ETYMOLOGY: Spanish for "old man," referring to age of the specimen.

### GENERAL DISCUSSION

**GENERIC RELATIONSHIPS:** Below is a list of apomorphic characters used in constructing the cladogram of genera and other groups of carnids (fig. 16). The characters were polarized based on comparison to the outgroup family Milichiidae, which has been generally recognized as the sister group to the Carnidae. Since the characters are completely consistent with each other (fig. 16), the cladogram was not analyzed with computerized algorithms. Character numbers given below appear on the cladogram, and dates of the two amber fossils are superimposed for estimates of the minimum age of several clades.

1. Apomorphic: Upper fronto-orbital setae directed outward/laterad; lower (anterior) fronto-orbitals directed inward/mediad. Plesiomorphic: All fronto-orbitals directed mediad or posteriad.

2. Apomorphic: One pair of dorsocentral setae present. Plesiomorphic: Two pairs.
3. Apomorphic: Pair of (proclinate) inner frontal setae present. Plesiomorphic: None present.
4. Apomorphic: Aedeagus (phallus) long, coiled, with extensive spicules. Plesiomorphic: short, bare.
5. Apomorphic: Female cerci fused (McAlpine, 1989). Plesiomorphic: Cerci not fused.
6. Apomorphic: Bases of antennae (pedicel, flagellomere I) recessed into deep fossae. Plesiomorphic: Fossae not present.
7. Apomorphic: Facial carina broad, at least width of antenna. Plesiomorphic: Carina very narrow.
8. Apomorphic: Male tergite VI reduced or lost. Plesiomorphic: not reduced or lost.
9. Apomorphic: Abdominal pleural membrane with sparse to many fine setulae, each with a sclerotized base. Plesiomorphic: Pleural membrane bare.
10. Apomorphic: Apical half of vein  $M_1$  very weak. Plesiomorphic: Vein  $M_1$  as strong as other veins.
11. Apomorphic: Labium enlarged to bulbous. Plesiomorphic: Width of labium no more than rest of proboscis.

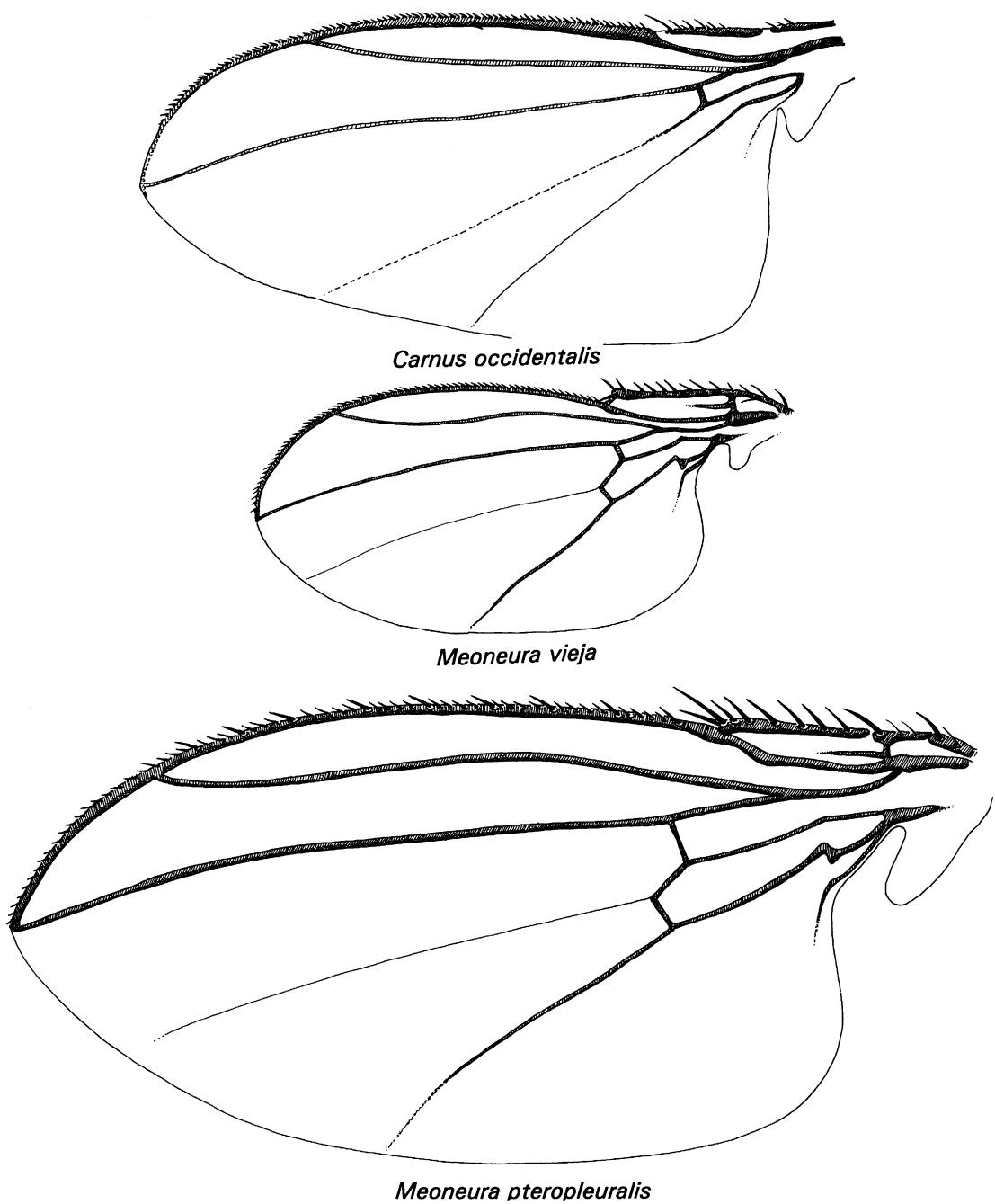
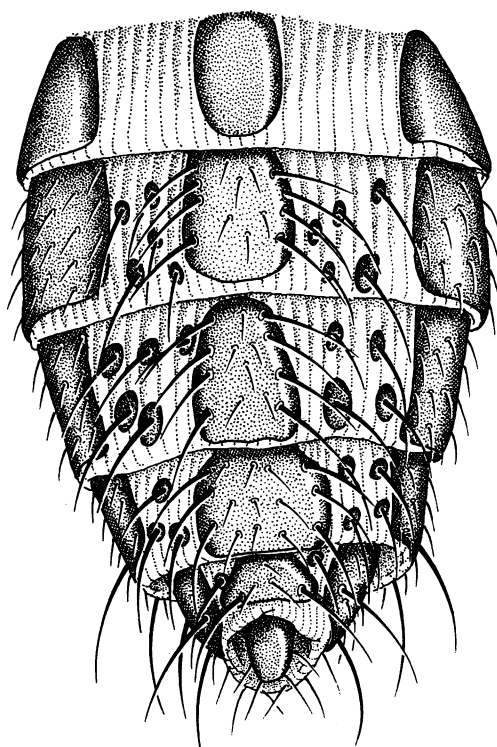
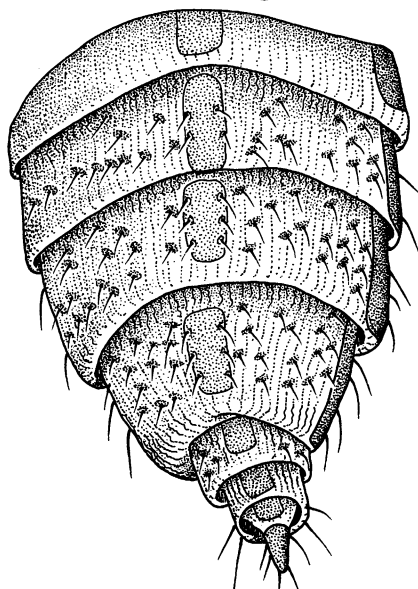


Fig. 11. Wings of *Carnus* and *Meoneura*: *Carnus occidentalis*, n.sp.; the amber fossil, *Meoneura vieja*, n.sp.; and *Meoneura pteropleuralis* Sabrosky. All to the same scale.

12. Apomorphic: Anal vein very reduced or lost. Plesiomorphic: Anal vein distinctly present, extended almost to margin of wing.
13. Apomorphic: Small basal wing cell (bm-cu) not closed. Plesiomorphic: Cell closed.
14. Apomorphic: Vein Sc incomplete or lost. Plesiomorphic: Vein Sc present, strong, often extending to costal vein.
15. Apomorphic: Rs vein meets vein R slightly proximal to inner end of the basal cell. Plesiomorphic: Rs meets R distal to end of basal cell.
16. Apomorphic: Male tergite VI lost. Plesiomorphic: Tergite VI reduced.
17. Apomorphic: Portion of costal vein proximal to subcostal break with 2 rows of large, spinelike setae. Lengths of setae about  $2.5\times$  width of costal vein. Plesiomorphic: Setae shorter and thinner, lengths no more than  $1.5\times$  width of costal vein.
18. Apomorphic: Crossveins very close together, separated by distance equal to or slightly greater than length of crossvein. Plesiomorphic: Crossvein distance much greater, at least several times the length of either crossvein.
19. Apomorphic: Postvertical setae cruciate. Plesiomorphic: Setae convergent or parallel.
20. Apomorphic: Setulae in pleural membrane of abdomen long and thick, with large, heavily sclerotized base to each seta (McAlpine [1989] erroneously indicated that this feature was restricted to males). Plesiomorphic: Setae much smaller, without such heavily sclerotized bases.
21. Apomorphic: Surstylus (male genitalia) deeply bilobed. Plesiomorphic: Not lobed; a simple, undivided lobe.
22. Apomorphic: Broad lobe or pair of lobes on surstylus with fringe of long setae. Plesiomorphic: Without fringe.
23. Apomorphic: Setulae in pleural membrane of abdomen very numerous (several hundred per side). Plesiomorphic: Much sparser, 50 or less.
24. Apomorphic: Abdominal sternites of female lost. Plesiomorphic: Present.

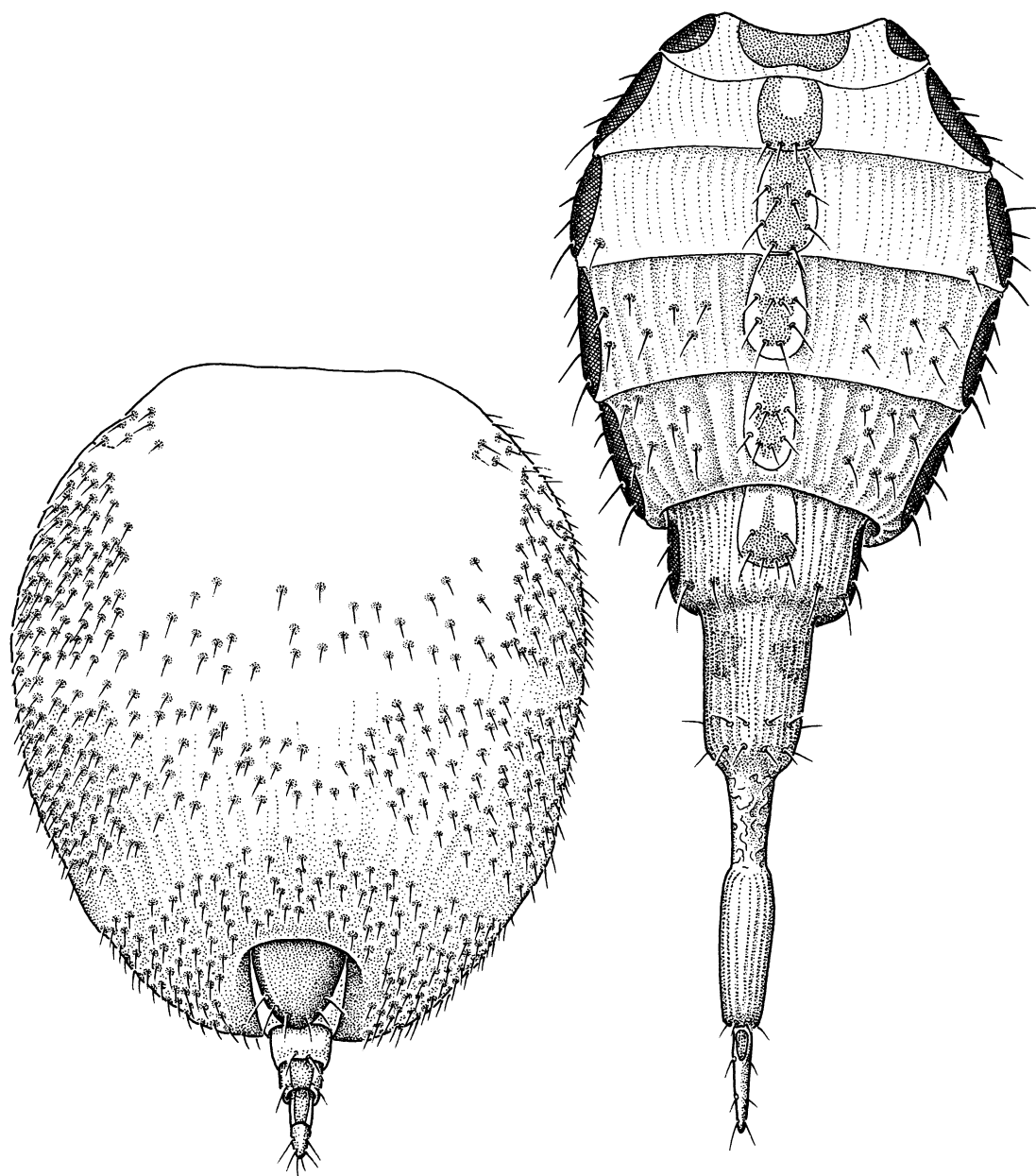


*Meoneura digitata*



*Meoneura vieja*

Fig. 12. Female abdomens of two *Meoneura* (ventral view): *M. digitata* Sabrosky (extant) and *M. vieja*, n.sp. (fossil). Setation in *vieja* is actually typical for most of the living *Meoneura*, that in *digitata* is highly derived.



*Carnus hemapterus*

*Meoneura* sp.

Fig. 13. Female abdomens of *Carnus hemapterus* and *Meoneura* sp. (from Yellowstone National Park, Wyoming). Telescoping terminal segments of the *Meoneura* are everted.

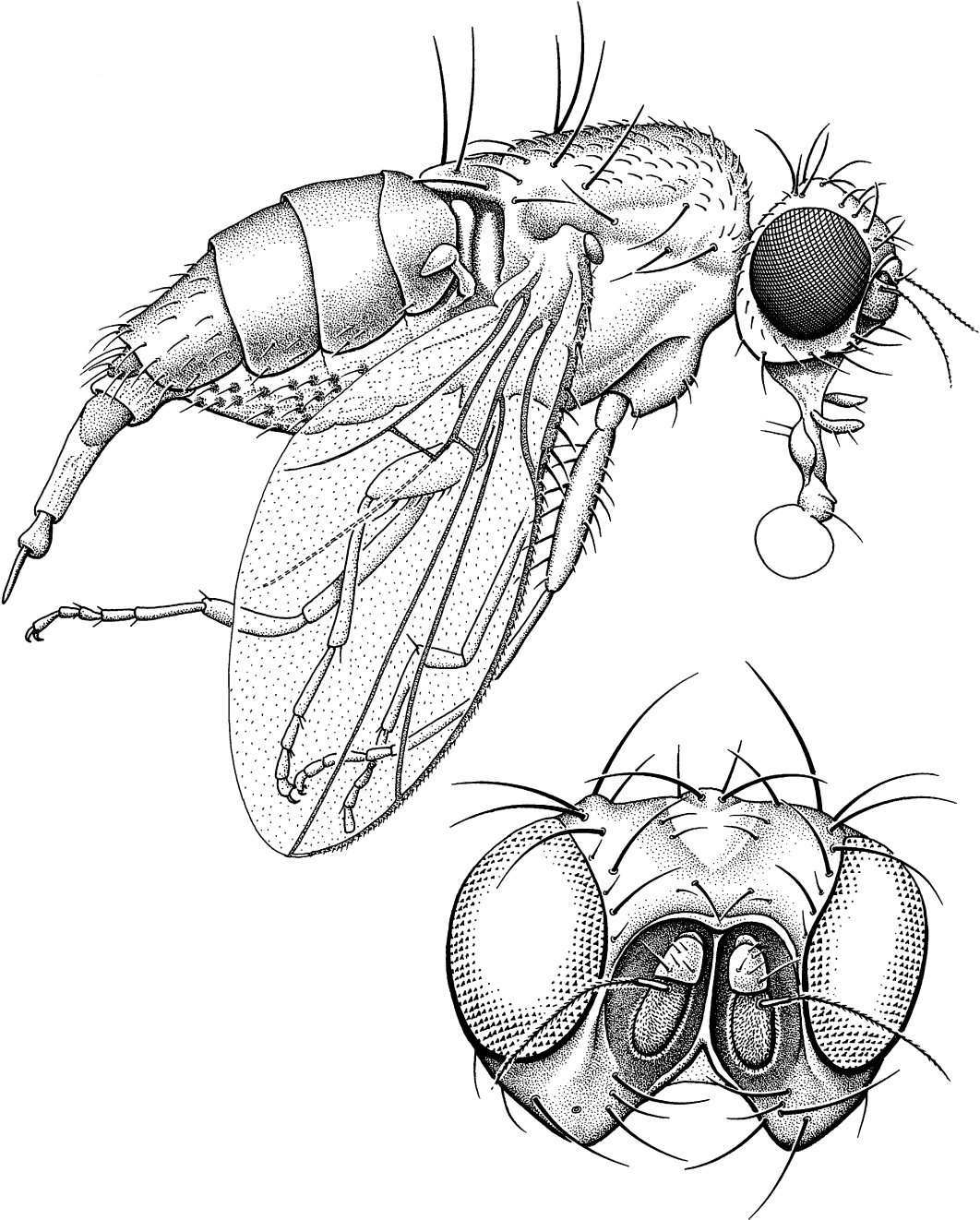


Fig. 14. Paratype female of *Meoneura vieja*, n.sp. (AMNH 11842A) in Dominican amber. Habitus and frontal view of the head.

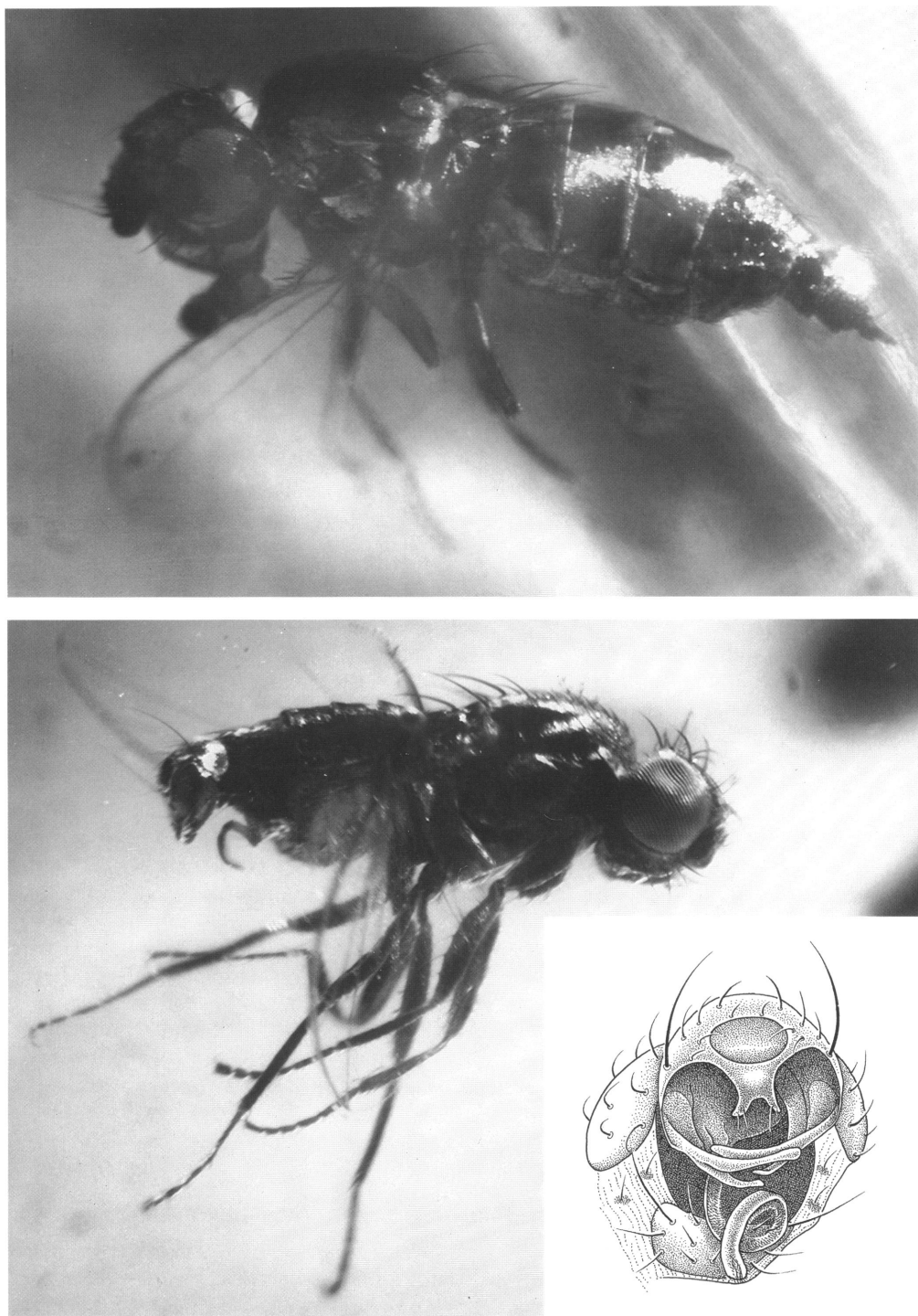


Fig. 15. Photomicrographs of *Meoneura vieja*, n.sp., in Dominican amber. Above, female paratype (DR-14-599); below: male holotype (DR 14-600), with rendered detail of genitalia in terminal view.

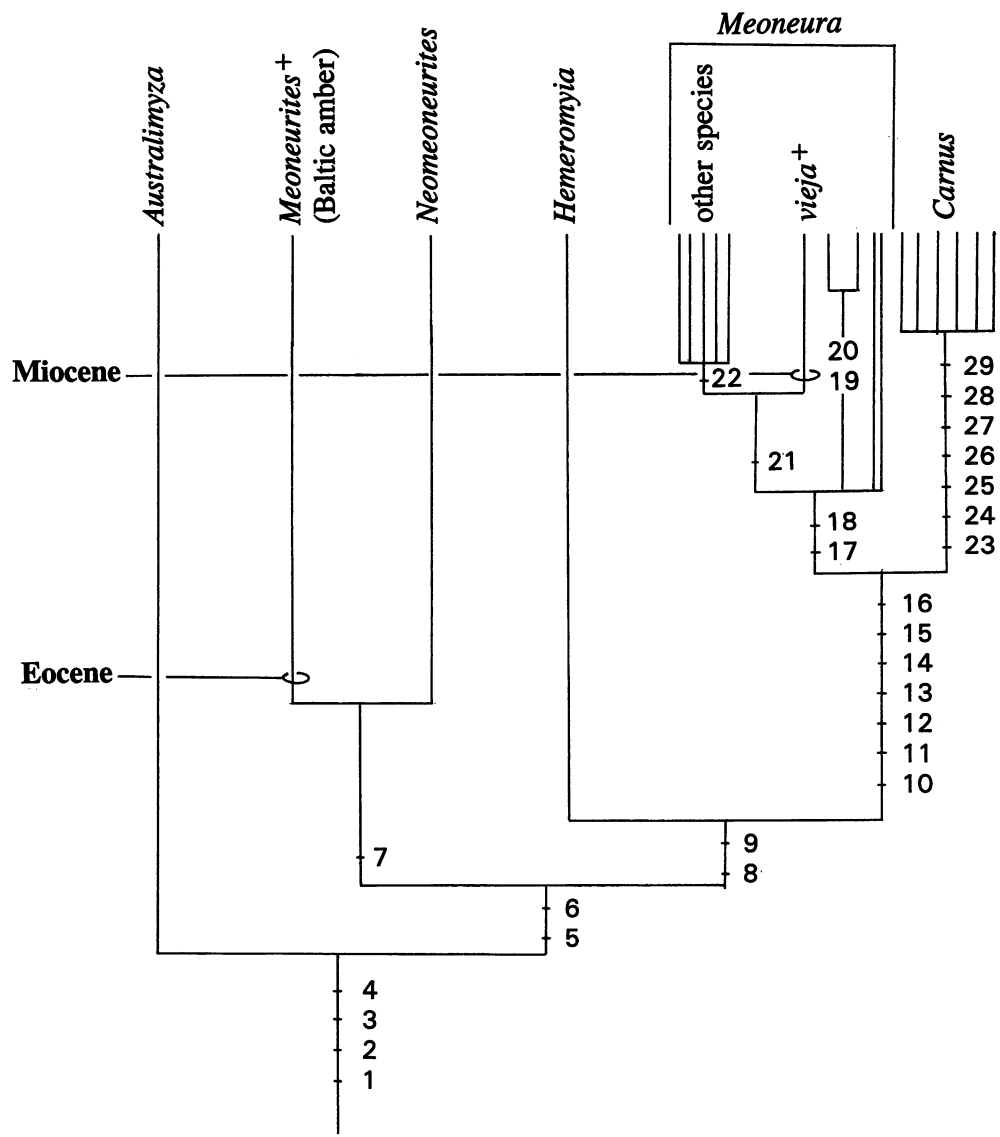


Fig. 16. Cladogram of generic relationships in the Carnidae. No attempt was made here to define monophyly of *Australimyza*, *Meoneurites*, *Neomeoneurites*, and *Hemeromyia*.

- 25. Apomorphic: Physogastry. Plesiomorphic: No physogastry.
- 26. Apomorphic: Crossvein dm-cu lost. Plesiomorphic: Crossvein present.
- 27. Apomorphic: Wing dehiscent. Plesiomorphic: Not dehiscent.
- 28. Apomorphic: Aedeagus (phallus) short, abbreviated, without vestiture. Plesiomorphic: Long, coiled, with spicules.
- 29. Apomorphic: Abdominal tergites re-

duced, especially in females. Plesiomorphic: Tergites extend laterad.

The inclusion of *Australimyza* Harrison, as a subfamily in the Carnidae, has been proposed elsewhere (Colless and D.K. McAlpine, 1991; J.F. McAlpine, 1989), although Griffiths (1972) indicated there was no close relationship between this genus and carnids. *Australimyza* is composed of 6 described and



many undescribed species from New Zealand and Australia, where they breed in beach wrack. The clade of *Neomeoneurites* (two species in Chile [Hennig, 1972; Wheeler, 1994]) and the Baltic amber fossil, *Meoneurites* Hennig (1965), is defined on the basis of a broad facial carina (character 7). Wheeler (1994) discussed several apomorphic male genitalic features of living *Neomeoneurites*, the existence of which are unknown for the fossil *Meoneurites*. It is interesting that, without the Baltic amber fossil, one would have assumed that the early history of the carnids was entirely an austral one (as based on *Australimyza* and *Neomeoneurites*). The extinction of present-day austral taxa from northern latitudes has actually been discussed elsewhere, specifically with respect to organisms in Baltic amber (Ander, 1942). The next taxon on the cladogram is *Hemeromyia*, a genus of four Palearctic, two Nearctic, and one African species. Little is known of its biology, but the report by Cole (1969), of specimens in New Mexico reared from the nest of a mouse (*Peromyscus truei*), is consistent with what is known of the habits of other carnids.

The close relationship between *Meoneura* and *Carnus* has never been questioned and rests on substantial morphological criteria: characters 10–15, above. It is possible, in fact, that *Carnus* may eventually be found to be paraphyletic with respect to *Meoneura*, since only two characters of *Meoneura* are known thus far to be apomorphic with respect to *Carnus*: the spinose base of the costal vein in *Meoneura* (character 17), and the close proximity of the crossveins on the wing of *Meoneura* (character 18) (which is impossible to evaluate for *Carnus*, since the distal crossvein is lost). Thus, effectively only one apomorphy establishes the monophyly of *Meoneura* with respect to *Carnus*. The question of *Meoneura* paraphyly could probably be answered with a complete, worldwide revision of the genus. It should be noted that characters 26 (loss of crossvein dm-cu) and 10 (atrophy of vein M<sub>1</sub>) in *Carnus* may be developmentally very closely associated: striking convergence of both features appears in *Paramyia nitens* (Milichiidae). *Paramyia* has even lost vein A<sub>1</sub> as in *Carnus*, but the basal cells remain.

Male genitalia of *Meoneura* offer a plethora of features for cladistic analysis of the genus. However, for purposes here only certain obvious features were selected to group some species. One feature, character 20, groups the North American species *Meoneura pteropleuralis* Sabrosky and *M. digitata* Sabrosky (fig. 12, top). At least four North American species (*californica*, *lamellata*, *flavifacies*, and *wirthi*) and one European species (*milleri* Gregor) are grouped on the basis of characters 21 and 22. The fossil *Meoneura* appears to be a basal member of this clade, since it possesses character 21 but not 22. One should not expect this preliminary attempt at cladistics of *Meoneura* to necessarily make much biogeographic sense, particularly in light of the very poor Neotropical sampling of this genus. However, it can be assumed on the basis of these relationships that the genus *Meoneura* possibly originated in the lower Miocene to late Oligocene.

With an Oligo-Miocene origin of *Meoneura*, and appearance of the more plesiomorphic clade, *Meoneurites* + *Neomeoneurites*, by the time of the Eocene Baltic amber, the Carnidae can be assumed to appear by the Paleocene. Given the virtual lack of higher cyclorrhaphan fossils from the Cretaceous, carnid origins in the Paleocene would be entirely consistent with radiations of the modern families of Cyclorrhapha in the earliest Tertiary.

**EVOLUTION OF HOST USE:** Like most carnids, *Meoneura* is closely associated with feces of mammals and birds. In fact, there are several records of *Meoneura* in close association with birds. *Meoneura lamellata* was reported about the "openings of sand martin's burrows" in England (Collin, 1930), and in the nests of bank swallows in Alaska (Sabrosky, 1959). Two records associate *Meoneura* with marine birds: Collin reported *M. seducta* as being probably associated with gannets on Grasholm Island. (Collin, 1937) and an undetermined species of the fly was associated with a penguin rookery on Gough Island (in the south Atlantic, in the Tristan de Cunha group) (Barracough, 1994). There are two records of *Meoneura* reared from old bird nests: *M. neottiophila*, in England (Collin, 1930); and *M. hungarica*, from a *Juncus*

nest in Hungary (Papp, 1977b). Clearly, the ancestral *Carnus* also bred in bird nests, like some *Meoneura*.

The almost exclusive use by *Carnus* of tree-nesting birds, vs. ground nesters, may relate to the development of the young birds. Most ground nesters have precocial young that leave the nest quickly after hatching; tree nesters have predominantly altricial young (nestlings), which live in the nest for several weeks. For the flies to parasitize young precocial birds, emergence of adult flies would need to be perfectly synchronized with the hatching of the birds. Nestlings are parasitized instead of adult birds probably because their skin is more accessible, with at best a layer of down that the flies must penetrate. Since adult *Carnus* lack the extremely flattened and hardened bodies seen in other dip-

terous ectoparasites, the preening and ruffling of stiff, adult contour feathers would probably prevent the adult flies from reaching the skin. Whatever the mode of host evolution, the parasitic lifestyle of *Carnus* adults is derived from behavioral and morphological specializations that further used the contents of the nest: its inhabitants.

The *Meoneura* in amber were preserved almost certainly when flying around trunks of the amber tree (*Hymenaea*). It is plausible that they were breeding in or searching for the nests of birds in *Hymenaea* trees, since feathers are also preserved in Dominican amber. One feather, in fact, has been identified as from a woodpecker (family Picidae), probably closely related to the extant Antillean Piculet (*Nesocittes micromegas*) (Laybourne et al. 1994).

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APPENDIX

Bird Host Family/Species	Location	Nest (N)/ Bird (B)	Carnus Species	Ref.
ARDEIDAE:				
<i>Ardea cinerea</i>	Netherlands	B	hemap	f
PANDIONIDAE:				
<i>Pandion haliaetus</i>	New Jersey	B	hemap	i
ACCIPITRIIDAE:				
<i>Haliaetus albicilla</i>	Finland	N	hemap	a
<i>Aquila heliaca</i>	Yugoslavia	B	hemap	a
<i>Buteo swainsoni</i>	Washington	B	h/occ	b
<i>Buteo jamaicensis calurus</i>	Utah	B	h/occ	c
FALCONIDAE:				
<i>Falco peregrinus</i>	California	B	occid	i
	Finland	N	hemap	a
	Germany	B	hemap	k
<i>Falco tinnunculus</i>	Austria	N	hemap	a
	Germany	N	hemap	a, k
	Switzerland	N	hemap	i
<i>Falco cherrug</i>	Romania	B	hemap	a
<i>Falco mexicanus</i>	Utah	B	h/occ	c
<i>Falco sparverius</i>	Colorado	B	hemap	i
	Maryland	B	hemap	i
	New York	B	hemap	i
	Utah	B	h/occ	c, d
	Mexico	N	sp. B	i
<i>Falco</i> sp.	Italy	B	hemap	a
COLUMBIDAE:				
<i>Columba livia</i>	Finland	N	hemap	a
<i>Columba oenas</i>	Finland	N	hemap	a
	Germany	B	hemap	k
TYTONIDAE:				
<i>Tyto alba</i>	Germany	N, B	hemap	a, k
	New Jersey	B	hemap	j
	Utah	B	occid	i
STRIGIDAE:				
<i>Otus asio</i>	Florida	N/B	flori?	a
	Arizona	B	occid?	e
<i>Bubo ketupu</i>	Malaya	B	orient	f
<i>Aegolius acadicus</i>	Brit. Columbia	B	hemap	i
“owl”	Mexico	B	sp. A	i
<i>Aegolius funereus</i>	Finland	N	hemap	a
<i>Athene noctua</i>	Germany	B	hemap	k
PICIDAE:				
<i>Picoides major</i>	Austria	N	hemap	a
	Finland	B	hemap	a
<i>Picus viridis</i>	Germany	B	hemap	a
<i>Dryocopus martius</i>	Finland	N	hemap	a
<i>Colaptes auratus</i>	Mexico	N	mexic	i
	New York	B	hemap	i
	Utah	B	occid	d, i
Williamson’s sapsucker	Utah	B	h/occ	d

APPENDIX Continued

Bird Host Family/Species	Location	Nest (N)/ Bird (B)	Carnus Species	Ref.
<i>Sphyrapicus thyroideus</i>	Utah	B	h/occ	d
	New Brunswick	B, N	hemap	i
pileated woodpecker	Oregon	N	h/occ	g
“woodpecker”	Florida	B	flori	i
JYNGINAE:				
<i>Jynx torquilla</i>	Germany	B	hemap	a
	Switzerland	B	hemap	a
HIRUNDINIDAE:				
<i>Delichon urbica</i>	Finland	N	hemap	a
TURDIDAE:				
<i>Turdus philomelos</i>	Finland	N	hemap	a
<i>Turdus iliacus</i>	Finland	N	hemap	a
<i>Phoenicurus phoenicurus</i>	Finland	N	hemap	a
SYLVIIDAE:				
<i>Regulus regulus</i>	Finland	N	hemap	a
<i>Sylvia atricapilla</i>	Germany	N	hemap	a
PARIDAE:				
<i>Parus atricapillus</i>	Finland	N	hemap	a
<i>Parus ater</i>	Finland	N	hemap	a
<i>Parus major</i>	Germany	B	hemap	k
CERTHIDAE:				
<i>Certhia familiaris</i>	Finland	N	hemap	a
FRINGILLIDAE:				
<i>Fringilla coelebs</i>	Finland	N	hemap	a
PLOCEIDAE:				
<i>Passer domesticus</i>	Switzerland	N	hemap	a
STURNIDAE:				
<i>Sturnus vulgaris</i>	Finland, Germany, Italy, Sweden			
	Switzerland	N/B	hemap	a, i, k
	Indiana	B	hemap	g, i
	Wisconsin	N/B	hemap?	d
CORVIDAE:				
<i>Pica pica</i>	Finland	N	hemap	a
	Utah	B	hemap	a, d, i
<i>Corvus corone cornix</i>	Finland	N	hemap	a
	Egypt	N	hemap	i
<i>Corvus corone</i>	Lithuania	B	hemap	a
	Germany	B	hemap	a, k
<i>Corvus monedula</i>	Netherlands	N, B	hemap	a
	Finland	B	hemap	a
	Germany	B	hemap	a, k

References: a, Bequaert (1942); b, Fitzner & Woodley (1983); c, Lloyd & Philip (1966); d, Capelle & Whitworth (1973); e, Bequaert (1951); f, Maa (1968); g, Wilson (1977); h, Guigan et al. (1983); i, this study (museum specimens); j, Kirkpatrick & Colvin (1989); k, Walter & Hudde (1987).



