SYSTEMATICS

Enigmocarnus chloropiformis gen. et sp. nov., and Parallel Evolution of Protandrial Symmetry in Carnidae (Diptera)

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ABSTRACT Enigmocarnus chloropiformis Buck gen. et sp. nov. is described on the basis of a single male from east central Texas. The phylogeny of Carnidae is analyzed based on a matrix of 25 morphological characters, and a key to the World genera of Carnidae is presented. The new genus is characterized by a reduced head chaetotaxy (bristles short and mostly pale), notable gray pruinosity of the body, and a unique configuration of pregenital sclerites (the protandrium), which precludes placement of this species in any previously described genus of Carnidae. Enigmocarnus possesses a nearly symmetrical protandrium like Carnus and Meoneura, but the position of sternite 7 indicates that symmetry evolved independently and on a different path. The protandrial peculiarities exhibited by Enigmocarnus are discussed in the framework of Carnoidea relationships.

KEY WORDS Carnidae, new genus, phylogeny, protandrium, symmetry

In the present article, we describe a new genus and species of Carnidae from North America. *Enigmocarnus* gen. nov. is only the fifth extant genus to be described in this small family after *Carnus* Nitzsch, *Meoneura* Rondani, *Hemeromyia* Coquillett, and *Neomeoneurites* Hennig (*Meoneurites* Hennig is known from Baltic amber only). The new genus exhibits an unusual configuration of sclerites in the male protandrium (pregenital segments) and provides a good example for the usefulness of protandrial characters in phylogenetic reconstruction. All Cyclorrhapha possess a so-called circumverted hypopygium (with a 360° clockwise rotation of the genitalia) (Crampton 1944), which is unique in Diptera and is assumed to have evolved only once in the stem species of the Cyclorrhapha from a postulated inverted (rotated 180° clockwise) ancestral condition (Griffiths 1972). Rotation of the male genitalia to a variable degree has occurred several times independently within Diptera as coupling and mating positions changed during the evolutionary history of the order (e.g., McAlpine 1981). Ontogenetically, rotation is either completed within the puparium before emergence (Schizophora: e.g., Schräder 1927, Gleichauf 1936) or takes place in part before and after emergence ("Aschiza," as far as known; e.g., Kessel 1968). The rotation not only affects the genitalia proper (which are rotated by 360°) but also segment 8 (rotated by 180°) and usually segments 7 and 6, which are rotated up to 90°. Sternites 6 and 7 usually have the appearance of having been dragged clockwise to a degree dependent on their proximity to the completely inverted segment, and this rotation of

segments 7 and 6 is responsible for protandrial asymmetry. The protandrium is further modified through fusion and loss of sclerites and spiracles, which takes place in various ways and to a different extent in different taxa. Such fusion and loss is usually irreversible and therefore of great value for phylogenetic reconstruction (Hennig 1958).

Materials and Methods

Morphology and Terminology. Abdominal morphology was studied on specimens that were cleared in hot 10% KOH and neutralized in glacial acetic acid; cleared parts are stored in glycerin and kept in a microvial with the specimen. The terminology largely follows McAlpine (1981) except for structures of the phallic complex, which were taken from Andersson (1977). The term "protandrium" was coined by Steyskal (1957) and refers to the postabdominal segments before the hypopygium (segments 6–8 or 7 and 8). The segments and sclerites of the protandrium are also referred to as "pregenital segments" and "pregenital sclerites". Costal sector 1 is measured from humeral crossvein to subcostal break, Cs2 from subcostal break to apex of R_{2+3}, Cs3 between apices of R_{2+3} and R_{4+5}.

Photography. Photographs were taken with a Microptics Digital Lab XLT imaging system using a Canon EOS 1 Ds camera and Microptics ML-1000 flash fiber optic illumination system. Each image was assembled from a series of photographs (with different focal planes) using the computer freeware CombineZ (Hadley 2005).

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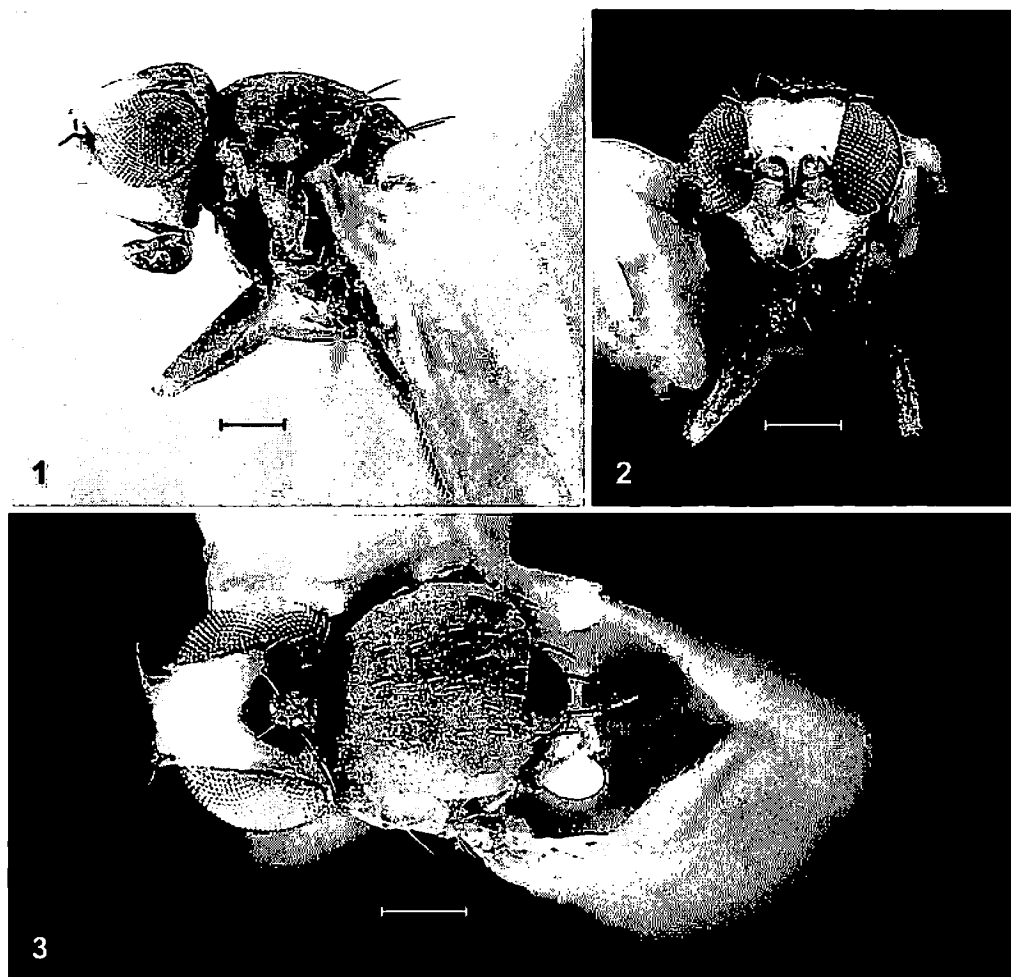
Figs. 1–3.　E. chloropiformis Buck sp. nov., habitus. (1) Head and thorax, lateral. (2) Head, frontal. (3) Head and thorax, dorsal. Scale bar = 0.1 mm.

Phylogenetic Analysis. Parsimony analysis of the character matrix was performed with PAUP* 4.0b10 for Windows (Swofford 2001) by using the "branch and bound" algorithm.

Acronym of Depository. DEBU, Department of Environmental Biology, University of Guelph, Guelph, Ontario, Canada.

Systematics

Enigmocarnus Buck gen. nov.

Type species: Enigmocarnus chloropiformis sp. nov.

Diagnosis. Very small (body length ≈1.3 mm), gray-pruinose flies (Figs. 1–3). Female unknown.

Head. Head with short, inconspicuous, pale bristles (Figs. 1–3), including four pairs of orbital bristles (first and second orbitals inclinate, third exclinate and fourth reclinate), ocellars, slightly divergent postverticals, inner and outer verticals, small inner occipital bristles just inside inner verticals, two pairs of small interfrontals, short vibrissa and two pairs of bristles on facial ridge above vibrissa. Frons with distinct ocellar triangle. Antennae in deep foveae; foveae delimited medially and ventrally by sharply defined carina. Eye distinctly transverse, gena high.

Thorax. Thorax (Figs. 1 and 3) with bristles relatively short and mostly pale including one pair of prescutellar dorsocentrals, two notopleurals, one postpronotal, one postalar, two pairs of scutellars, two anepisternals (one reclinate at anterior margin, one dorsoclinate near middle of ventral portion), and one katepisternal. No distinct supra-alar bristles. Acrostichals in approximately four poorly defined rows. Legs simple. Fore and mid-tibiae with ventroapical bristles, legs otherwise without conspicuous bristles. Wing (Fig. 4) as in the genus Meoneura. Costa extending to R_{4+5}, with humeral and subcostal breaks; subcosta reduced in apical half, last sector of M very faint, crossveins r-m and dm-cu closely approximated and shifted toward base of wing, bm-cu, CuA_2 and A_1 absent, anal lobe well developed.
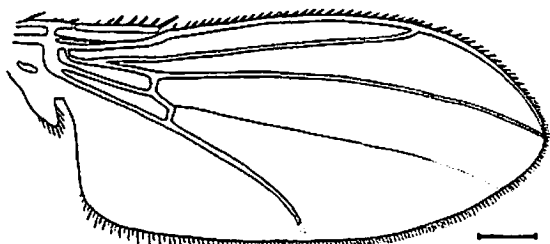
Fig. 4. *E. chloropiformis* Buck sp. nov., right wing. Scale bar = 0.1 mm.

Abdomen. Preabdomen with four large tergites (syntergite 1 + 2, tergites 3–5). Protandrium (fused tergite 6 + sternites 6, 7, 8) nearly symmetrical; tergite and sternite 6 transverse, forming a complete ring; tergite 6 fused with sternite 8 laterally; sternite 7 in mid-ventral position, fused to sternite 6 but free from sternite 8; tergite 7 absent. Spiracles 7 placed slightly asymmetrically. Epandrium saddle L-shaped; surstylus simple, setulose. Cerci rudimentary. Subepandrial sclerite well-developed, free from epandrium posteriorly. Hypandrium with broad and short anterior apodeme, fused to phallapodemic plate. Phallapodeme small. Postgonites simple. Phallus extremely short, distal portion membranous and bare. Ejaculatory apodeme moderately developed.

Etymology. The name refers to the unusual and initially puzzling protandrial morphology of the male.

Recognition. *Enigmocarnus* is separated from other carnid genera in the key below. The genus is very distinctive because of its short, predominantly pale hairing, conspicuous gray pruinosity and unusual facial features. The face below the antennal foveae is high and sclerotized (desclerotized and short to linear in other genera except several undescribed Nearctic species of *Hemeromyia*) with vibrissal angles closely approximated. The narrow face, high gena and shortened vibrissa of *Enigmocarnus* are reminiscent of the canacid ("tethinid") genera *Pelomyia* Williston and *Pelomyiella* Hendel. In dorsal view, the head seems very chloropid-like because of the contrasting and shining ocellar triangle and the short head bristles. The protandrium of *Enigmocarnus* is highly unusual for Carnidae because of the symmetrically placed sternite 7, which is completely free from sternite 8, and the absence of tergite 7, a character only shared with the genus *Neomeoneurites*.

Key to Extant Genera of Carnidae

1. Last sector of vein M weakened, distinctly weaker than R_{4+5} and CuA_1; crossvein dm, if present, shifted toward wing base, lying distinctly basal of middle of wing; cell *cup* absent (Fig. 4); wing sometimes broken off (dehiscent) 2
- Last sector of M well-developed, as strong as R_{4+5} and CuA_1; crossvein dm located beyond middle of wing; cell *cup* present and closed; wing not dehiscent 4

2. Face below antennal foveae high (Fig. 2). Head bristles inconspicuous and pale (Figs. 1–3). Height of gena at narrowest point about half eye height (Fig. 1). Supra-alar bristles not differentiated (Fig. 3). Thorax heavily gray-pruinose (Nearctic) .... *Enigmocarnus* gen. nov.
- Face below antennal foveae reduced, linear. Head bristles well developed and dark. Genal height usually distinctly less than half eye height. Pre- and postsutural supra-alar bristles differentiated. Thorax shining to dull, never gray-pruinose 3
3. Wing lacking crossvein dm, usually broken off. Postvertical bristles absent. Katepisternal bristle small, hair-like. Female sternites 2–5 absent. Abdomen physogastric. Ectobiontic on birds (widespread) .... *Carnus*
- Crossvein dm present (as in Fig. 4); wing not dehiscent. Postvertical bristles present. Katepisternal bristle well developed. Female sternites 2–5 present. Not ectobiontic on birds (widespread) .... *Meoneura*
4. Second orbital bristle reclinate. Facial carina broad, plateau-like, sclerotized throughout. Proboscis somewhat elongate, prementum longer than wide, not bulbous. Anepisternum bare: two or three subequal katepisternal bristles (Argentina, Chile) ...... *Neomeoneurites*
- Second orbital bristle inclinate. Facial carina narrow, if slightly expanded then median portion pale and desclerotized. Proboscis short, prementum not longer than wide, bulbous. Anepisternum with hairs and bristles; only one katepisternal bristle (Holarctic, Afrotropical) .... *Hemeromyia*

Enigmocarnus chloropiformis Buck sp. nov.
(Figs. 1–14)

Description, male (female unknown): Very small, predominantly gray-pruinose; wing length 1.0 mm.

Head (Figs. 1–3). Frons (excluding ocellar triangle), face, antenna (excluding arista) and anterior two-thirds of gena yellow, becoming paler ventrally; vertex, ocellar tubercle, occiput, posterior third of gena, palpus and prementum gray-pruinose; ocellar triangle (excluding ocellar tubercle) and clypeus shining black but with very thin tomentosity; arista blackish; intermediate areas on each side of ocellar triangle and narrow anterior margin dull brownish. Eye reddish brown. Head bristles pale and very short, longest ones (vibrissa, outer verticals) no longer than ca. twice the distance between posterior ocelli. Orbital bristles very small, anterior two pairs no longer than interfrontal bristles. Lunule narrowly exposed. Face below antennal foveae depressed, sharply delimited laterally by facial ridge, which abruptly curves posteriorly at rounded vibrissal angle; face distinctly narrowed ventrally, at level of mouth margin not wider than width of first flagellomere. Facial foveae deeply excavate, delimited ventrally at level of lower eye margin by sinuate transverse carina, separated from each other
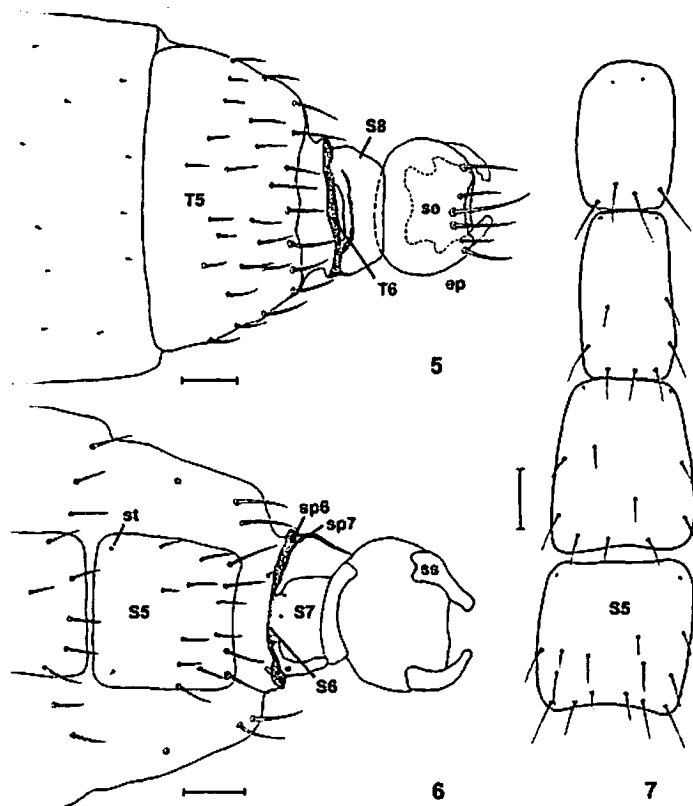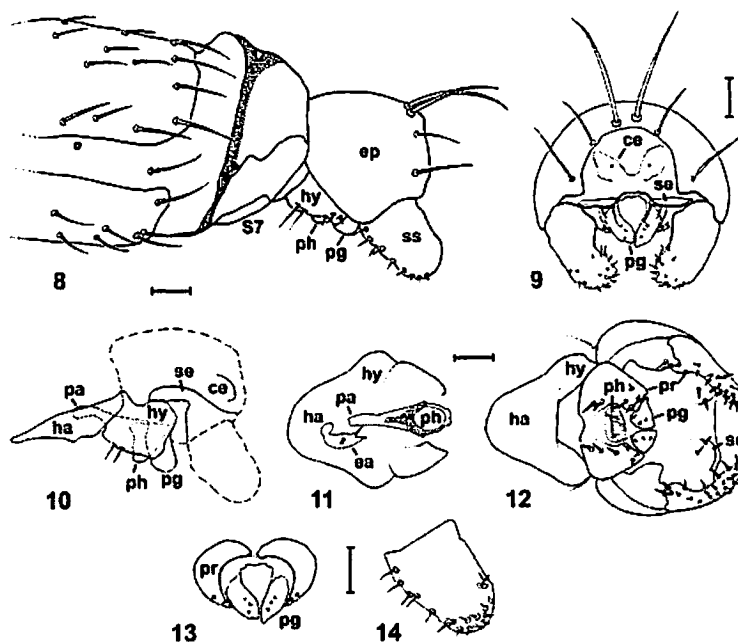
Figs. 5–7. E. chloropiformis Buck sp. nov., male abdomen. (5) Posterior portion of preabdomen and postabdomen, dorsal view (outline of subepandrial sclerite indicated by dashed line). (6) Posterior portion of preabdomen and postabdomen, ventral view (details of hypopygium omitted). (7) Preabdominal sternites. Scale bar = 0.05 mm. Abbreviations: ep, epandrium; S, sternite; se, subepandrial sclerite; st, sensillum trichodeum; ss, surstylus; T, tergite.

medially by a narrow keel. Gena at narrowest point approximately half as high as eye, receding toward mid-line in frontal view, sparsely setulose with most setulae arranged in one irregular diagonal row from vibrissal angle to posterodorsal corner; posteroventral corner with one relatively long bristle. Clypeus with very narrow transverse median portion and long posterior arms. Antenna small; scape minute, hidden by pedicel; pedicel with one blackish dorsal bristle; first flagellomere discoid, with nearly circular outline. Arista micropubescent, very short, slightly longer than width of first flagellomere. Proboscis porrect, small, and with bulbous prementum as typical for Carnidae. Palpus very small and short, lacking conspicuous bristles. Eye distinctly transverse with inclined long axis, greatest diameter ≈1.2× eye height. Postgena flattened, meeting gena at nearly right angle.

Thorax (Figs. 1 and 3). Thorax mainly gray-pruinose, with small darker subshining areas on anepisternum (anteroventral spot behind fore coxa), katepisternum (anteroventral spot partially hidden by fore coxa, oblique posterodorsal spot along hind margin below katepisternal bristle), anterior portion of meron, hind margin of metepimeron, and ill-defined medial area of mediotergite. Thoracic bristles and hairs pale except dorsocentrals, posterior notopleurals, postalars

and scutellars which are dark. Anterior scutellars slightly shorter than posterior pair, about as long as prescutellar dorsocentral and postalar. Postpronotal and notopleurals shorter, posterior notopleural slightly stouter than anterior one. Acrostichals few in number, arranged in four irregular rows, prescutellar pair not enlarged. Anepisternum with one bristle plus one hair on hind margin, one dorsoclinate hair in posterodorsal corner, one dorsoclinate ventral bristle and one hair on disc. Proepisternal and proepimeral setae absent. Katepisternum setulose, with one dorsal bristle and several longer bristles ventrally. Pleuron otherwise bare. Postscutellum developed.

Legs. Legs mostly gray, except apex of fore femur, base and apex of tibiae and basal segments of tarsi, which become gradually more yellowish brown toward their extremes; pruinosity almost uniform except small subshining patches dorsobasally on fore femur and posteriorly on mid and hind coxae. Hairing of legs pale except dark apicoventral bristle of mid tibia and small, spine-like bristles of ventral surface and apex of tarsomeres. Fore femur with four posteroventral bristles that are only about half as long as diameter of femur. Apicoventral bristles of fore and mid tibiae short, not exceeding width of tibia.

Figs. 8–14. *E. chloropiformis* Buck sp. nov., male genitalia. (8) Posterior portion of preabdomen and postabdomen, lateral view. (9) Hypopygium, posterior view. (10) Internal genitalia, lateral view (outline of epandrium and surstylus indicated by long dashed lines). (11) Hypandrium and phallic complex, dorsal view. (12) Hypopygium, ventral view. (13) Pregonites and postgonites, posterior view. (14) Right surstylus inner view. Scale bar = 0.025 mm. Abbreviations: ce, cercus, ea, ejaculatory apodeme: ep, epandrium: ha, hypandrial apodeme; hy, hypandrium; pa, phallapodeme; pg, postgonite; pr, pregonite; S, sternite; se, subepandrial sclerite; ss, surstylus.

Wings (Fig. 4). Wings with the generic characteristics of *Meoneura*, with subangulate apex where R_{4+5} reaches wing margin; wing membrane slightly whitish opaque. Upper costagial bristle pale, lower one black. Relative lengths of costal sectors 1:2:3 is 1:2.4:1.53. First sector with a single row of black spinules; spine just in front of subcostal break less than twice as long as others. Spinules of second and third sector smaller, denser and in two rows, except near base of second sector and in apical third of third sector where spinules are sparse and in a single row; spinules stopping short before reaching R_{1+5}. R_{2+3} nearly straight; R_{4+5} distinctly curved posteriorly; M without distinct kinks at crossveins r-m and dm-cu. Crossvein r-m at level of subcostal break; dm-cu removed from r-m by ≈1.5x its length. CuA_1 reaching wing margin as a fold; CuA_2+A_1 developed as a hardly discernible fold that disappears about halfway toward wing margin. Halter white, stem brown.

Preabdomen. Preabdomen very sparsely haired, hairs pale; tergites 1 and 4 (Fig. 5) with minute hairs, tergites 2 and 3 bare except for a few sensilla trichodea laterally and some outstanding hairs on margin, tergite 5 with moderately developed and more numerous hairs (Fig. 5). Pleural membrane very sparsely haired, hairs almost completely restricted to a single row at hind margins of segments 3–5, not arising from sclerotized bases (Fig. 6). Abdominal tergites subshining, dark gray (seeming "greasy"), except for tergite 1, lateral fourths of tergites 2 and 5 (excluding anterior margin), which are more strongly pruinose. Abdominal sternites gray-pruinose.
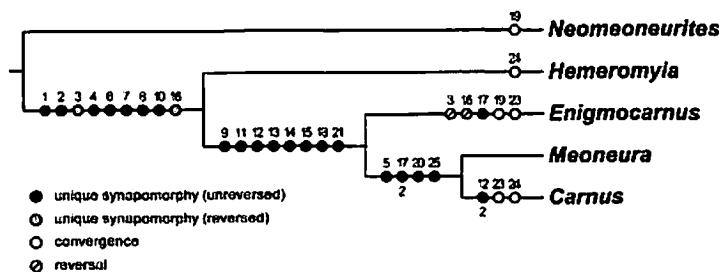

Fig. 15. Genus-level phylogeny of Carnidae. Character numbers given above the circles; states for multistate characters are given below the circles.

Protandrium (Figs. 5 and 6 and 8). Pregenital sclerite (fused tergite 6 + sternites 6, 7, 8) bare except for sensilla trichodea of sternites 6 and 7 (Fig. 6). Tergite 6 very short, laterally fused to sternite 8 (Fig. 5). Tergite 6, lateral portions of sternite 6 and a narrow band along anterior margin of sternite 8 strongly sclerotized and darker. Sternite 6 extremely short, its sensilla trichodea shifted anteriorly (lying outside sclerotized area), placed symmetrically. Spiracles 6 placed symmetrically within fused tergite + sternite 6 (Fig. 6). Sternite 7 rectangular, broadly fused with sternite 6 along anterior margin, sensilla trichodea slightly shifted toward left side. Right spiracle 7 shifted slightly ventrally, lying in pleural membrane (Fig. 6); left spiracle slightly displaced dorsally near ventral margin of syntergosternite 6 + 8 (this sclerite is not clearly delimited ventrally; it cannot be clearly determined whether spiracle lies in sclerite or pleural membrane). Sternite 8 large, truncated semiconical, broadly articulated with epandrium posteriorly.

Male genitalia (Figs. 8–14). Epandrium saddle-shaped, shining black, posteromedially with a small dull spot, with three unequal pairs of strong bristles (Fig. 9), otherwise bare. Surstylus (Figs. 8 and 14) broad and rounded, setulose in marginal areas, without outstanding hairs or bristles. Cerci (Fig. 9: ce) reduced to a pair of weakly sclerotized plates on each side of anus, each bearing one small setula. Subepandrial sclerite a broad plate with two pairs of setulae near hind margin (Figs. 5 and 12: se), free from epandrium, posterolaterally continuous with inner surface of surstyli. Hypandrium (Figs. 11 and 12) with broadly triangular apodeme and clearly delimited posterior portion consisting of indistinguishably fused phallapodemic plate plus pregonites (termed gonopods by Sabrosky 1987). Phallapodeme short and curved (Fig. 10: pa). Pregonites setulose, embracing phallus on each side (Fig. 13: pr); articulating posteriorly with postgonites. Postgonites developed as simple lobes, each with three small setulae (Fig. 13: pg). Phallus very simple (Fig. 12: ph), not clearly divided into basi- and distiphallus; distal portion broadly truncate and expanded toward apex, bare. Ejaculatory apodeme (Fig. 11: ea) as long as phallapodeme, with deflected, knob-like apex.

Etymology. The name refers to the chloropid-like frons of this species.

Type Material. HOLOTYPE ♂. U.S.A.: Texas, Bastrop Co., Colorado River E Utley at Rd. 969, 8-IV-2000, sandy river bank, sweeps, M. Buck (DEBU).

Homology of Protandrial Sclerites. The homology of sclerites pertaining to segments 6–8 is established based on the location of spiracles and sensilla trichodea of sternites 6 and 7. Sternal sensilla trichodea are part of the ground plan of Cyclorrhapha (Wheeler 1960), where they usually occur near the anterior margin of all sternites except male sternite 8. Spiracles are present on segment 6 and usually 7 (the latter missing in *Carnus*, some *Meoneura*, see Fig. 16, and according to Griffiths 1972, in one species of *Hemeromyia*). The protandrium of *Enigmocarnus* is unusual for Carnidae in possessing a midventrally placed ster-
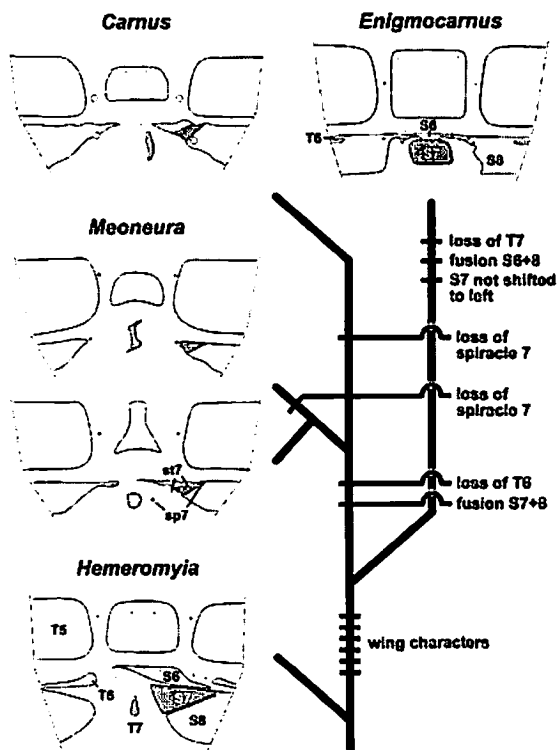

Fig. 16. Evolution of the protandrium in the higher Carnidae. Protandria shown in ventral view as if cut open dorsomedially and flattened. Limits of sternites 6–8 approximate in all genera except *Hemeromyia* (sternites fused indistinguishably). Crossbars indicate significant apomorphic changes (wing characters: see characters 9, 11–15 of phylogenetic analysis). Drawings other than *Enigmocarnus* based on the following exemplar species: *Hemeromyia* sp. (U.S.A.: Arizona, Buckeye), *Meoneura vagans* (Fallén) (U.S.A.: New Mexico) (bottom), *Meoneura* sp. (Bolivia: Santa Cruz, Boyuibe) (top), *Carnus hemapterus* Nitzsch (Canada: British Columbia) (all material deposited in DEBU). Abbreviations: S, sternite; st, sensillum trichodeum; sp, spiracle; T, tergite.

nite 7, which occupies approximately the same position as tergite 7 in other carnid genera. The homology of sternite 7 is clearly established through the presence of a pair of sensilla trichodea and the (nearly) unrotated spiracles. Neomorphic accessory sclerites, which occur in a few other families do not bear sensilla trichodea. Homology with tergite 7 can also be excluded because of the presence of sensilla trichodea. Carnid genera that do possess a midventral tergite 7 (*Hemeromyia* and *Meoneura;* cf. Figure 16) have right spiracle 7 displaced ventrally for a considerable distance. In this case, spiracle 7 is located toward the left side of tergite 7 or near its anterior margin (not on the right side of the sclerite as in *Enigmocarnus*).

Biology. The biology of *Enigmocarnus chloropiformis* is unknown. The holotype was swept along a sandy river bank, either over the sand itself or from the weedy vegetation behind the shore. Sweeps from this habitat yielded predominantly Ephydridae such as

Paralimna Loew, *Hydrochasma* Hendel and *Ochthera lauta* W.M. Wheeler, 1896.

Phylogeny

Phylogenetic relationships within the Carnidae were studied previously by Grimaldi (1997) and Buck (2006). Buck (l.c.) showed that the Carnidae in the present sense (i.e., to the exclusion of *Australimyza* Harrison, contra Colless and McAlpine 1970, Grimaldi 1997) is monophyletic. The monophyly of *Carnus* is well established, whereas the monophyly of *Hemeromyia* and especially *Meoneura* is only weakly supported (Buck 2006). Thorough revisions of the World fauna of the latter two genera are necessary to clarify their phylogenetic status. The new genus *Enigmocarnus* is defined by five autapomorphies (plesiomorphic states in parentheses): 1) Bristles of head very short (normally developed). 2) Bristles of head and body mostly pale (dark). 3) Sclerotized part of face below antennal foveae high (narrow to linear). 4) Body with conspicuous gray pruinosity (shining or weakly pruinose). 5) Male sternite 7 in midventral position (displaced toward left side of body). Further autapomorphies include characters 16, 17, 19, and 23 of the phylogenetic analysis below.

The present analysis does not include the monotypic genus *Meoneurites*, which is known only from two females in Baltic amber (Hennig 1965). *Meoneurites* is the sister group of *Neomeoneurites*, which includes two extant species from Chile and Argentina (Hennig 1972, Wheeler 1994). The clade of *Meoneurites* – *Neomeoneurites* is defined by four synapomorphies: (plesiomorphic states in parentheses): 1) Prementum elongate (simple). 2) Katepisternum with two dorsal bristles (one bristle). 3) Ovipositor greatly elongated, longer than remainder of body from head to posterior margin of segment 5 (moderately elongated). 4) Female tergites 6 and 7 with long anterior apodemes (without apodemes). The monophyly of *Neomeoneurites* is evidenced by four autapomorphies (plesiomorphic states in parentheses): 1) Mouth margin somewhat projecting forward (not projecting). 2) Number of rows of acrostichals reduced to a single median row in anterior half of thorax (several rows). 3) R_{4+5} and M convergent apically (parallel to slightly divergent). 4) Female tergite 6 medially divided (entire). Five other characters mentioned by Buck (2006) as having apomorphic states for *Neomeoneurites* cannot be assessed for *Meoneurites* and could be either autapomorphies for *Neomeoneurites* or synapomorphies for *Meoneurites* + *Neomeoneurites* (plesiomorphic states in parentheses): 1) Ventral appendage of stipes absent (present). 2) Lacinia reduced (present). 3) Male sternite 8 fused to right side of hypandrium (not fused). 4) Hypandrium with a pair of large posteroventral projections (without projections). 5) Surstyli greatly reduced, indistinguishably fused to epandrium (separate from epandrium). *Meoneurites* shows only one character that is apomorphic with regard to *Neomeoneurites*, the presence of three instead of two pairs of marginal scutellar bristles. To

Table I. Character state matrix for extant genera of Carnidae

Species	Character no.		
	1 1234567890	2 1234567890	12345
Ancestor	0000000000	0000000000	0?000
Neomeoneurites	0000?00000	0000000010	00000
Hemeromyia	1111011101	0000010000	01010
Enigmocarnus	1101??1111	1111101110	111??
Meoneura	1111111111	1111112101	11001
Carnus	1111111111	1211112101	10111

our knowledge more than two pairs of marginal scutellar bristles do not occur elsewhere in the Carnoidea except in some Chloropidae genera where they evolved independently from marginal scutellar hairs, and in the fossil *Phanerochaetum* Hennig, a doubtful member of the Cryptochetidae (McAlpine 1989). In our matrix (see below), *Meoneurites* shows identical character states as *Neomeoneurites* for all characters that can be assessed from the original description (i.e., characters 1–4, 7, 9–15, 24; after Hennig 1965).

The character matrix includes 25 morphological characters (Table 1). Ancestral states were determined previously in the context of a phylogenetic analysis of the superfamily Carnoidea (Buck 2006) or (for newly included characters 3, 8, 9, and 12) through outgroup comparison with Australimyzidae. Ancestral states are coded with (0), derived states with (1) or (2) (ancestral state of character 22 unknown).

Characters Used for Phylogenetic Analysis

Head

1. Second orbital bristle from front: 0 – reclinate; 1 – inclinate.
2. Third orbital bristle from front: 0 – reclinate; 1 – exclinate.
3. Supra-antennal bristles (=anterior pair of interfrontal bristles): 0 – simple, 1 – enlarged. ACCTRAN optimization.
4. Prementum: 0 – slightly swollen; 1 – strongly swollen.
5. Labrum: 0 – simple; 1 – with internal knob-like projection (cf. Buck 2006: Fig. 11K).
6. Labela, number of pseudotracheae: 0 – five or six pairs; 1 – four pairs or less.

Thorax and Wing

7. Anepisternum: 0 – simple; 1 – with upcurved bristle near ventral margin.
8. Coxopleural streak: 0 – present; 1 – absent.
9. Costa: 0 – extending to M; 1 – extending to R_{4+5}.
10. Subcosta: 0 – reaching costa; 1 – fading away before reaching costa.
11. Vein M, last lector: 0 – strong; 1 – weakened.
12. Vein dm-cu: 0 – removed from wing base; 1 – shifted toward wing base; 2 – absent. Character unordered.
13. Vein bm-cu: 0 – present; 1 – absent.

Table 2. Step matrix for character 17

From:	To: 0	1	2
0	-	1	1
1	∞	-	1
2	∞	∞	-

14. Vein CuA_2+A_1: 0 - present, strong at least in basal third; 1 - absent or abbreviated and fold-like.

15. CuA_2 (closing vein of cell cup): 0 - present; 1 - absent.

Preabdomen

16. Pleural membrane: 0 - setulae with simple base; 1 - setulae arising from sclerotized bases. ACCTRAN optimization.

Male Postabdominal Characters

17. Tergite 6: 0 - present and free; 1 - present, fused to sternite 8 laterally; 2 - absent or indistinguishably fused to synsternite 6-8. Transition costs between character states are specified in a step matrix (Table 2).

18. Sternite 6: 0 - free; 1 - fused to sternite 7.

19. Tergite 7: 0 - present; 1 - absent.

20. Sternite 7: 0 - (largely) free from sternite 8; 1 - completely fused to sternite 8.

21. Sternite 8: 0 - setulose; 1 - bare.

22. Phallapodeme: 0 - free from hypandrium; 1 - connected to hypandrium through phallapodemic plate (ancestral state unknown). Phallapodeme connected to the hypandrium in the Carnidae ground plan according to Wheeler (1994) but outgroup evidence is equivocal (Buck 2006).

23. Distiphallus: 0 - elongate; 1 - extremely shortened. DELTRAN optimization.

Female Postabdominal Characters

24. Spiracle 7: 0 - present; 1 - absent.

25. Spermathecae: 0 - well developed and sclerotized; 1 - rudimentary and weakly sclerotized, or absent.

Results of Phylogenetic Analysis. The analysis yields a single most parsimonious tree (Fig. 15; tree length = 33, consistency index = 0.76, retention index = 0.78, rescaled consistency index = 0.59). Enigmocarnus is the sister group of Meoneura + Carnus. The possible paraphyly of Meoneura with regard to Carnus (Grimaldi 1997, Buck 2006) is of no consequence to the phylogenetic validity of the new genus. The monophyly of the Meoneura genus group (Enigmocarnus + Meoneura + Carnus) is demonstrated primarily through the suite of apomorphies that characterizes the Meoneura-type wing (characters 9, 11–15). Figure

16 shows the evolution of the Carnidae protandrium and indicates some of the most significant evolutionary changes on the cladogram. Tergite 6, tergite 7, and sternite 7 have followed different evolutionary pathways in the stem lineages of Enigmocarnus and Meoneura + Carnus. In Enigmocarnus, 1) tergite 6 has become partially fused to the pregenital sclerite (either completely lost or indistinguishably fused to pregenital sclerite in Meoneura + Carnus; Figs. 6 and 7 of Sabrosky 1987 seem to support the latter interpretation); 2) tergite 7 has been lost (present in all other genera except Neomeoneurites where it was lost independently; Hennig 1972, Wheeler 1994); 3) sternite 7 is largely free and only fused to sternite 6 anteriorly (indistinguishably fused to both sternite 6 and 8 in Meoneura + Carnus).

Discussion

The discovery of the new genus Enigmocarnus is remarkable because it sheds new light on the evolution of the protandrium within the Carnidae. Two distinct conditions can be observed in the previously described genera (Fig. 16): Neomeoneurites and Hemeromyia have strongly asymmetrical protandria with discrete tergite 6 and sternites 6, 7, and 8, whereas Meoneura and Carnus possess just one, nearly symmetrical pregenital sclerite in their place (the fossil genus Meoneurites is known from females only; Hennig 1965). The pregenital sclerite of Meoneura and Carnus is obviously a product of fusion of sternites 6-8, possibly including remnants of tergite 6 as well. The fused, symmetrical condition has to be considered apomorphic for two reasons. First, asymmetrical protandria occur in the ground plan of all major lineages within the Carnoidea (Buck 2006): most importantly in the sister group of Carnidae (Australimyzidae + Inbiomyiidae), but also in the Chloropidae family group (Canacidae s.l. + (Cryptochetidae + (Milichiidae + Chloropidae))) and in Acartophthalmidae. Second, the fusion of sclerites is probably an irreversible process. Sclerite fragmentation occurs in several groups but there are no documented examples of a simple reversal to the ancestral state. Fragmentation of sclerites either leads to symmetrical fragments (frequently a pair of lateral sclerites, e.g., some Drosophilidae and Hippoboscoidea, cf. Griffiths 1972), or it results in irregularly shaped fragments that are dissimilar to the original sclerites involved in the fusion process (e.g., some Sphaeroceridae; Marshall 1995).

At first glance the new genus Enigmocarnus seems to fall within the group of Carnidae genera with symmetrical and fused protandrial sclerites. The similarities between Meoneura + Carnus and the new genus furthermore include clearly apomorphic features such as the Meoneura-type wing venation. However, close examination of the protandria of the three genera shows fundamental differences between Enigmocarnus and Meoneura + Carnus. Enigmocarnus differs from all other Carnidae by the midventral, (nearly) symmetrical sternite 7. In other genera, this sternite is either strongly asymmetrical and shifted to left side of

the body (*Neomeoneurites* and *Hemeromyia*), or it is fused indistinguishably to sternites 6 and 8 (*Meoneura* and *Carnus*). Outgroup comparison clearly shows that the condition found in *Enigmocarnus* is derived. Other Carnoidea families have sternite 7 (when present) asymmetrical and displaced to the left side of the body (cf. Acartophthalmidae: Andersson 1977, Fig. 6B; Australimyzidae: Griffiths 1972, Figs. 74 and 75). In families where sternite 7 has become part of a synsternite, the portion homologous to sternite 7 is in a dorsal or dorsolateral, not in a ventral position (cf. Inbiomyiidae: Buck 2006, Fig. 6D; Milichiidae: Brake 2000, Figs. 12, F and I and J; Chloropidae: Andersson 1977, Fig. 23F). Additional evidence for the derived status of a midventral sternite 7 comes from the absence of tergite 7. The Carnidae ground plan includes a midventral tergite 7 in nearly the same position that is occupied by sternite 7 in *Enigmocarnus* (Fig. 16: *Hemeromyia, Meoneura*. and *Carnus*; see also Griffiths 1972: Fig. 134). The ventral shift of sternite 7 in *Enigmocarnus* was only possible after previous elimination of tergite 7.

The presence of a discrete, midventral sternite 7 has important implications for the evolutionary scenario leading to the development of protandrial symmetry in the Carnidae. The "shift" of sternite 7 to the middle requires that sclerite be free from sternite 8 in the *Enigmocarnus* ancestor. As mentioned previously, all Carnidae with discrete sternites 7 and 8 possess a strongly asymmetrical protandrium. This means symmetry has evolved twice in Carnidae: once in *Enigmocarnus* and once in *Meoneura* + *Carnus*. In other words, the lineages of *Enigmocarnus* and *Meoneura* + *Carnus* must have separated *before* symmetry evolved. This is an interesting finding, because there are few documented examples in Schizophora where symmetrical protandria have evolved more than once within a single family. McAlpine (1985) illustrates the protandria of a variety of Heleomyzidae genera. In this family, strongly asymmetrical protandria are prevalent and clearly represent the ancestral condition. However, there are at least four examples of symmetrical protandria, three of which evolved *within* different genera. Brake (2000) studied the morphology of Milichiidae, most of which have symmetrical protandria. Protandrial configuration and outgroup comparison clearly establishes asymmetry as the ground plan condition for this family as well. When mapping the distribution of asymmetrical protandria on Brake's cladogram, it seems that asymmetry evolved at least four times within the family.

The presence of a midventral sternite 7 also has interesting implications for the hypothesized ontogenetic development of the *Enigmocarnus* protandrium. As is known from the very few developmental studies on circumversion (Schräder 1927, Gleichauf 1936), rotation of the Schizophora terminalia occurs before emergence from the puparium. This means there are two possible scenarios for the ontogenetic development of sternite 7 in *Enigmocarnus:* First, sternite 7 (including sensilla trichodea) and spiracles 7 could rotate clockwise as in all other Carnoidea, and

then rotate back counterclockwise into almost their original position. Second, sternite 7 and spiracles 7 could remain in place and omit the usual rotation (nevertheless, a slight clockwise displacement of right spiracle 7 still takes place; cf. Figure 16). The latter alternative seems more likely than the first alternative. Interestingly, neither scenario has been observed or postulated before in Cyclorrhapha. There are no observations indicating a clockwise followed by a counterclockwise rotation of postabdominal segments within the puparium. To our knowledge, it also has never been suggested that rotational movements that usually take place during ontogeny can be lost or suppressed in certain evolutionary lineages. These theoretical considerations provide interesting starting points for future developmental studies of the Cyclorrhapha protandrium.

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