# New Species of Cactus-Breeding *Drosophila* (Diptera: Drosophilidae) in the Nannoptera Species Group

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**ABSTRACT** A new species from Mexico, *Drosophila wassermani* Pitnick & Heed, is described, illustrated, and compared with three related species, all belonging to the *D. nannoptera* species group in the subgenus *Drosophila* of the Drosophilidae.

**KEY WORDS** *Drosophila wassermani*, nannoptera species group, cactus-breeding species

THE NANNOPTERA SPECIES GROUP of the subgenus *Drosophila* was first proposed as a monophyletic group by Ward & Heed (1970), based on examination of polytene salivary chromosomes. The group consists of four cactus-breeding species restricted chiefly to Mexico, and no other species or major geographical changes have been added since that time.

The species in the group consist of *Drosophila nannoptera* Wheeler, *D. acanthoptera* Wheeler, *D. pachea* Patterson & Wheeler (Patterson & Wheeler 1942, Wheeler 1949), and a fourth species known in the literature on cactophilic *Drosophila* since 1970 as *D.* species W, which we describe here as *D. wassermani*. It is our pleasure to name this species after its discoverer, Marvin Wasserman, in recognition of his pioneering and monumental work on the cytology of the *D. repleta* species group. Wasserman originally collected this species near Tehuantepec, Oaxaca, Mexico, in August of 1966.

The *D. nannoptera* species group is of biological interest because of the unusual nature of certain male reproductive characters observed within members of the group, such as the production of few, giant sperm, submaximal insemination of females, and partitioning of ejaculate by males among successive females (Pitnick & Markow 1994). In addition, extreme variability in reproductive characters is observable among the species. For instance, the duration of copulation varies from an average of 7.7 ± 0.6 min in *D. nannoptera* to 137.1 ± 8.1 min in *D. acanthoptera;* female *D. pachea* and *D. nannoptera* may remate several times daily, whereas most female *D. acanthoptera* never remate; and *D. wassermani* and *D. acanthoptera* produce relatively short sperm (4.52 ± 0.03 mm and 5.83 ± 0.09 mm, respectively), whereas *D. nannoptera* and *D. pachea* produce very long sperm (15.74 ± 0.30 mm and 16.53 ± 0.29 mm, respectively).

## Materials and Methods

Morphological terminology follows that of Grimaldi (1987); chromosomal terminology follows that of Patterson & Stone (1952). Photographs are of specimens taken from laboratory cultures initiated with flies from the type locality, using a scanning electron microscope (AMR 1000). These specimens were prepared by ethanol dehydration and critical-point drying as described by Rose (1984). Drawings were prepared from laboratory-cultured specimens from other localities, as specified in the text, using a camera lucida. Microscope-slide preparation of the genitalia involved the glycerine jelly technique discussed in Grimaldi (1987). All measurements were made with the ocular micrometer of a stereomicroscope (Wild).

## *Drosophila wassermani* Pitnick & Heed, New Species
(Fig. 1–3)

**Head.** Arista with 3 branches above and 2 below, plus terminal fork. Antennae brown; all segments evenly colored. Frons dark gray, without distinguishing color pattern; ocellar triangle slightly darker. Anterior reclinate seta closer to proclinate seta and of equal length. Face and facial carina tan and slightly shiny. Carina with medial sulcus on anterior third. Palpus with 1 strong apical bristle and 1 strong subapical bristle; the remainder evenly and densely covered with short, erect setae. Eyes dull red with even piling. Ratio of greatest width of cheek: greatest diameter of eye, 0.26. Head wider than thorax in dorsal view.

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**Fig. 1.** Scanning electron micrograph of male showing modified fourth and fifth sternites and asymmetrical cerci. Scale bar = 0.10 mm.

**Thorax.** Brown-gray, mean length (±SEM) 1.07 ± 0.01 mm in males ($n$ = 20), 1.16 ± 0.02 mm in females ($n$ = 20). Scutum with 2 indistinct darker paramedian stripes, these widening and converging posteriorly. Stripes hardly noticeable in older specimens, whose scuti are uniformly dull dark brown-gray. Acrostichal setulae in 8 rows. Scutellum evenly colored. Basal scutellars mildly convergent; apical scutellars converging. Pleurae with 2 irregular darker stripes. Two strong katepisternal setae and 9–12 small setulae; sterno-index, 0.52. Proepisternal and proepimeral bristles absent. Legs tan. Sexes with identical setal patterns.

**Abdomen.** Pale gray; each tergite with darker posterior banding, this indistinct and attaining level of anterior tergite medially and sometimes laterally. Abdomen almost black in older specimens. Males with slight, rounded protrusion on midposterior margin of third sternite; fourth sternite forms broad point overlapping fifth sternite (Fig. 1); basal width of this process 50% that of sternite. Fifth sternite divided by deep cuticular fold along midline (Fig. 1). Abdomen length ≈1.6 mm in males, 1.9 mm in females.

**Wings.** Uniformly transparent gray, relatively short: length ≈2.3 mm; length-to-width ratio 2.25. Two bristles at tip of costal section I, upper slightly longer; heavy bristles on basal 2/5 of costal section III. Wing indices: C, 2.78; 4V, 1.68; 5x, 1.11; M, 0.52.

**Fig. 2.** Scanning electron micrographs of male external genitalia: (A) epandrial lobes, cerci, surstyli, and decasternum. (B) surstyli. Scale bars = 0.03 mm.

**Male Genitalia.** Immature testes light yellow, becoming yellow-orange to orange in older specimens; 4 outer and 3.5 to 4 inner coils; each testis 7.76 ± 0.16 mm long ($n$ = 10); sperm 4.52 ± 0.03 mm long ($n$ = 5 males [Pitnick & Markow 1994]). Epandrium with enlarged, flattened lobes curling toward anteroposterior axis; terminus of lobes with 5–9 long bristles and dense covering of shorter bristles (Fig. 2a). Cerci not fused to epandrium, directionally asymmetric with left lobe convex and right lobe concave (Figs. 1 and 2a). Numerous, irregularly arranged, stout bristles on medial margins of cerci; thinner, longer bristles laterally (Figs. 1 and 2a). Surstylus without micropubescense, with 14–16 irregularly arranged primary teeth, 22–25 secondary teeth, and 5–8 marginal bristles, mostly on a lateral finger-shaped protuberance (Fig. 2). A second, longer, thinner protuberance on anterior margin (Fig. 2a). Hypandrium shorter than epandrium, trapeziform; bow spurious. Aedeagus bent, dorsoapically pointed; distiphallus pointed, ventral region subapically bearing pair of strongly sclerotized spurs (left one directed downward and

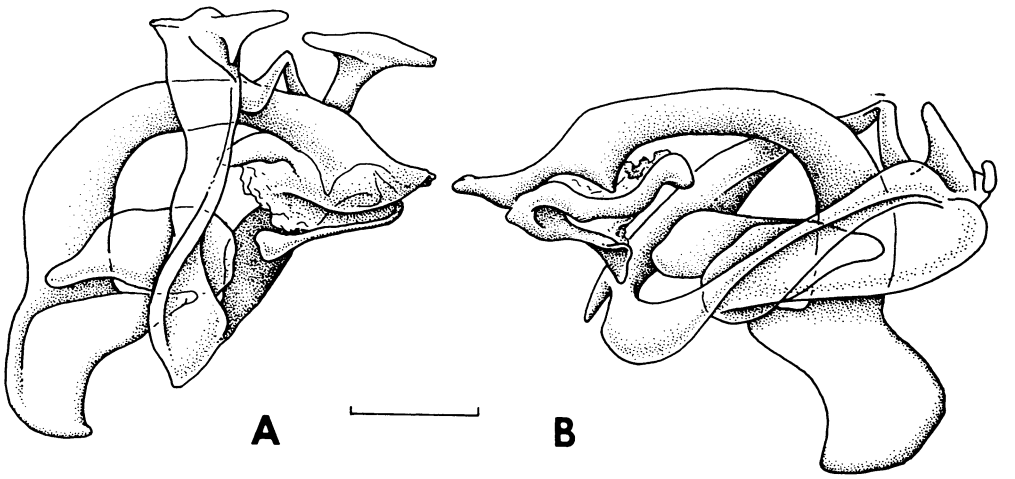


Fig. 3. Intraspecific variation in aedeagi, aedeagal apodemes, parameres, and hypandria; oblique lateral views: (A) from 36 km north of Tehuantepec, Oaxaca; (B) from near Tuxtla–Gutierrez, Chiapas. Scale bar = 0.10 mm.

then forward, right one directed downward at sharper angle), these embracing large membranous sac. Aedeagal apodeme shorter than aedeagus, laterally flattened. Paraphysis with 1 sensilla (Fig. 3). Geographic variation in adeagus morphology evident (Fig. 3); specimens from type locality similar to Fig. 3a.

**Female Genitalia.** Spermatheca chitinized, elliptical (long axis: 216 ± 3 μm; short axis: 156 ± 1 μm; $n = 5$). Ventral receptacle 3.00 ± 0.05 mm long ($n = 5$); ≈21 coils. Ovipositor somewhat pointed, 9–12 teeth marginal (usually 10); 2–3 teeth on outer surface.

**Eggs.** One pair of filaments, slightly longer than egg, widely expanded along terminal 2/3 into thin blades with central midrib. Mean (±SEM) egg length 512.8 ± 1.9 μm, width 183.3 ± 3.8μm, filament length 539.7 ± 2.9 μm ($n = 10$).

**Larvae.** Mouth hooks curving slightly downward, without teeth on ventral edge. Pictured in Mangan (1982).

**Puparia.** Golden brown, translucent. Horn with 6 short filaments, 8 longer filaments. Horn (plus filaments) short, ≈17% length of puparium itself.

**Metaphase Chromosomes.** Autosomes include 1 pair of rods, 2 pairs of Js, and 1 pair of short heterochromatic rods with satellites. The X is a large V and the Y is a short heterochromatic rod. Because polytene chromosomes show seven arms plus a dot, there must have been (at least in the original lineage) one X-autosome fusion to form the X, two pericentric inversions to form the Js, and addition of heterochromatin to the microchromosomes to form the short pair of rods. The culture examined was No. 113.14 of M. Wasserman's original collection (Ward & Heed 1970).

**Type Material.** HOLOTYPE male, PARATYPE males, and ALLOTYPE females from laboratory culture SP888 initiated from flies collected from necrotic tissue of unidentified columnar cacti northwest of Tehuantepec, near La Reforma, Oaxaca, Mexico, by S. Pitnick and R. Mangan in August 1988. All material deposited in American Museum of Natural History, New York.

**Distribution, Ecology, and Hybridization.** Originally collected by Marvin Wasserman on 14–16 August 1966, 3 km north of Tehuantepec, Oaxaca, *D. wassermani* is believed to be distributed widely in the lowlands of southern Mexico and Guatemala, although it may be only locally abundant because it is not commonly collected (Heed 1982). It is strictly cactophilic and has been aspirated in the field and reared in the laboratory from the necrotic tissues of *Stenocereus griseus* (Haw.) Buxb. by Bernard L. Ward, 36 km north of Tehuantepec, Oaxaca, in 1970 and of *S. pruinosus* (Otto) Buxb. by Robert L. Mangan and Jean S. Russell, near Ixtepec, Oaxaca, in 1976. *Drosophila acanthoptera* was reared simultaneously with *D. wassermani* from both these host plants. Other rearing records of *D. wassermani* include a *Pachycereus marginatus*-like plant near Zacapta, Guatemala, by R. L. Mangan in 1973 and *Stenocereus standleyi* (G. Ort.) Buxb. near Tomatlan, Jalisco, by W. B. Heed in 1981. The latest rearing record (1987) was from *S. pruinosus* collected near Tuxtla-Gutierrez, Chiapas, by William J. Etges.

Two studies have attempted unsuccessfully to form hybrids between *D. wassermani* and its close relatives. Ward & Heed (1970) found that no sperm was transferred in all possible crosses between all four species, suggesting strong sexual isolation. Subsequently, Russell et al. (1977) confirmed the isolation between *D. wassermani* and *D. nannoptera* but found that *D. wassermani* males could transfer sperm to *D. pachea* females (14 of 21 dissections).

**Diagnostic Characters.** Several characters permit *D. wassermani* to be distinguished easily from sister-species. To the naked eye, *D. wasser-*

*mani* males are medium brown with ventrum orange-brown; *D. nannoptera* and *D. pachea* males are black with ventrum darker orange and black; *D. acanthoptera* males are light brown with ventrum pale yellow.

Sternites of *D. nannoptera* and *D. pachea* are heavily pigmented black, lacking enlarged or protruding areas as in other species; sternites 4 and 5 are square and intact in *D. nannoptera;* sternites are rectangular and sternite 5 is split in *D. pachea.* Sternites of *D. acanthoptera* lack pigmentation; those of *D. wassermani* are light yellow-brown. As in *D. wassermani,* sternite 3 of *D. acanthoptera* has a slight rounded protrusion on the posterior margin, sternite 4 has a larger protrusion, and sternite 5 is split. However, in *D. acanthoptera,* enlargement of sternite 4 is smaller than that of *D. wassermani;* it is rounded rather than pointed and extends posteriorly to overlap only 50% of sternite 5.

The external genitalia of males also differ in ways easily discernible using a dissecting microscope. Epandrial lobes are short and narrowed to thin points in *D. nannoptera* (see Fig. 74: Vilela & Bächli 1990); short and rounded in *D. acanthoptera* (see Fig. 73: Vilela & Bächli 1990); long and directionally asymmetric, with left lobe longer than right lobe in *D. pachea;* and large and elaborate in *D. wassermani* (Fig. 2a). Surstyli of *D. nannoptera, D. pachea,* and *D. acanthoptera* are similar, with 8–10, 8–10, and 6–7 teeth, respectively, in a single row (Vilela & Bächli 1990). Surstyli of *D. wassermani* are remarkably different (Fig. 2b).

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## References Cited

**Grimaldi, D. A. 1987.** Phylogenetics and taxonomy of *Zygothrica* (Diptera: Drosophilidae). Bull. Am. Mus. Nat. Hist. 186: 103–268.

**Heed, W. B. 1982.** The origin of *Drosophila* in the Sonoran Desert, pp. 65–80. *In* J.S.F. Barker & W. T. Starmer [eds.], Ecological genetics and evolution. The cactus-yeast-*Drosophila* model system. Academic, Australia.

**Mangan, R. L. 1982.** Adaptations to competition in cactus breeding *Drosophila,* pp. 257–272. *In* J.S.F. Barker & W. T. Starmer [eds.], Ecological genetics and evolution. The cactus-yeast-*Drosophila* model system. Academic, Australia.

**Patterson, J. T. & W. S. Stone. 1952.** Evolution in the genus *Drosophila.* Macmillan, New York.

**Patterson, J. T. & M. R. Wheeler. 1942.** Description of new species of the subgenera *Hirtodrosophila* and *Drosophila.* Univ. Tex. Publ. 4213: 67–109.

**Pitnick, S. & T. A. Markow. 1994.** Male gametic strategies: sperm size, testes size, and the allocation of ejaculate among successive mates by the sperm-limited fly *Drosophila pachea* and its relatives. Am. Nat. 143: 535–569.

**Rose, V. M. 1984.** Method of preparation of *Drosophila* for scanning electron microscope studies. Drosoph. Info. Serv. 60: 223–224.

**Russell, J. S., B. L. Ward & W. B. Heed. 1977.** Sperm storage and hybridization in *D. nannoptera* and related species. Drosoph. Info. Serv. 52: 70.

**Vilela, C. R. & G. Bächli. 1990.** Taxonomic studies on neotropical species of seven genera of Drosophilidae (Diptera). Bull. Soc. Entomol. Suisse 63 (suppl).

**Ward, B. L. & W. B. Heed. 1970.** Chromosome phylogeny of *Drosophila pachea* and related species. J. Hered. 61: 248–258.

**Wheeler, M. R. 1949.** Taxonomic studies on the Drosophilidae. Univ. Tex. Publ. 4920: 157–195.

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