Scaptodrosophila aclinata:
A New *Hibiscus* Flower-breeding Species
Related to *S. hibisci* (Diptera: Drosophilidae)

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ABSTRACT. Physiological, ecological and evolutionary studies of *Scaptodrosophila hibisci* have led to recognition of a second species in the Northern Territory (Australia) which is described here as *Scaptodrosophila aclinata* n.sp. The new species is readily distinguishable by reference to the first orbital: it is large and proclinate in *S. hibisci* and small and reclinate in *S. aclinata*. *Scaptodrosophila hibisci* has been collected from the flowers of five *Hibiscus* species in eastern Australia and *S. aclinata* uses eleven *Hibiscus* species in the Northern Territory. Only *H. meraukensis* is a host for both, and there is no evidence of narrow host-specialization. The distributions are apparently disjunct. The two species can be reared in the laboratory on cultured plants. Hybridization studies showed the two species to be partially interfertile; *S. aclinata* has delayed sexual maturation and extended copulation latency when compared to *S. hibisci*. This species pair is already the subject of various eco-physiological and reproductive-biological studies because of so many useful experimental attributes: they are interfertile and can be laboratory-cultured, their hosts and reproductive biology are known, they are abundant and easy to find, and research is underpinned by extensive genetic information already available for *Drosophila*.

There are about 300 drosophilid species recorded from Australia, with some 90% of them described. The genus *Scaptodrosophila* Duda, 1923 (for many years treated as a subgenus of *Drosophila* but see Grimaldi [1990] for revised status) has 81 named species and is by far the largest. The predominance of *Scaptodrosophila* among the 36 genera represented, is striking and distinguishes the Australasian fauna from major drosophilid radiations in other regions—Afrotropical, Neotropical and Hawaiian. In Australia, the other large genera *Drosophila* (35 species), *Hirtodrosophila* (31 species), *Leucophenga* (25 species) and *Mycodrosophila* (24 species) are much smaller by comparison. In general, *Drosophila* species are attracted to fermenting fruit and may be reared easily in the laboratory; whereas *Scaptodrosophila*

species have, in most cases, unknown resource requirements (van Klinken & Walter, 2001) and are difficult to rear in the laboratory. Only 10 of the 35 *Drosophila* species recorded in Australia are endemic and of these 10 only *D. birchii* and *D. serrata* have provided useful research opportunities. In contrast, *Drosophila* species that occur in natural habitats in North America and Africa have provided many important models in the study of evolution, behaviour, physiology and ecology, with field observations being further elaborated by genetic and controlled-laboratory experimentation. The opportunity to explore evolutionary and ecological aspects of the Australian *Scaptodrosophila* radiation, has until recently, been severely hampered by the lack of an amenable model for field and laboratory studies.

In this paper we report the discovery of a sibling species of *Scaptodrosophila hibisci* that offers many of the same—and some new—research opportunities as do some of the important and well-documented *Drosophila* models. This new species, *Scaptodrosophila aclinata*, is readily distinguishable morphologically, has a very specific host-plant relationship, can occur in very large numbers, can be reared under laboratory conditions and can be induced to hybridize (with some negative heterosis) with its sibling species *S. hibisci*.

Scaptodrosophila hibisci (Bock *in* Cook *et al.*, 1977) was found to breed in flowers of *Hibiscus splendens* and *H. heterophyllus*. Both these plant species have been recorded from central Queensland to the Wollongong district in southern New South Wales (Wilson, 1974). Collections of *S. hibisci* have since been made from *H. diversifolius* in New South Wales and Queensland, and from *H. divaricatus* and *H. meraukensis* in Queensland (Starmer *et al.*, 1997; Wolf *et al.*, 2000; Barker unpubl.). With its widespread distribution in eastern Australia, and utilization of a number of *Hibiscus* species as breeding sites, *S. hibisci* has already become a model for the study of population structure and genetic variation, and possible host-plant specialization. Completed studies of this species include ecological aspects, quantitative genetic analyses and reproductive biology (Starmer *et al.*, 1997, 1998, 2000; Polak *et al.*, 1998, 2001; Wolf *et al.*, 2000, 2001).

A number of *Hibiscus* species occur in the Northern Territory and not in eastern Australia. Collections were made in the Northern Territory from 11 *Hibiscus* species (*H. aneuthe, H. arnhemensis, H. byrnesii, H.* cf. *byrnesii, H. fallax, H. menzeliae, H. meraukensis, H. petherickii, H. riceae, H. symonii, H. zonatus*) at 22 locations in May, 1998. Differences between *S. hibisci* and the flies collected in the Northern Territory were noted in terms of the ovariole-number body-size relationship (Wolf *et al.*, 2000), and in microsatellite allele frequencies (Barker unpubl.). Here we describe the Northern Territory fly as a new species, and present results of host-plant specialization and its laboratory hybridization with *S. hibisci*. Given the diverse *Hibiscus* flora in northern Australia and the discovery of cryptic flower-breeding *Scaptodrosophila* species in a variety of *Hibiscus* species throughout the Afrotropical Region, Lachaise & Tsacas (1984) predicted that sibling species of *S. hibisci* would be found in northern Australia.

Taxonomy

Morphological terms and morphometric formulae have been given previously (Grimaldi, 1987; McEvey, 1990). Material has been lodged in the following museums:

AM   Australian Museum, Sydney
ANIC Australian National Insect Collection, Canberra
NSMT National Science Museum, Tokyo
NTM Museum and Art Gallery of the Northern Territory, Darwin
QMB Queensland Museum, Brisbane.

Specimens used for SEM images are preserved on stubs in the Australian Museum SEM Unit. Wing-length was measured from the humeral to the wing apex (W) cf. axillary area to apex (L). Specimens have been individually numbered by McEvey, this information is abbreviated "*Reg.*" below.

Scaptodrosophila aclinata n.sp.

Figs. 2, 6–8, 9–12

Type material. HOLOTYPE ♂, Nitmiluk NP, Northern Territory, 14°18.77'S 132°27.00'E, ex *Hibiscus menzeliae* flowers, March 2000, Rick Hope & J.S.F. Barker; *Reg*. 15345, Australian Museum K118208. PARATYPES (24 ♂♂, 40 ♀♀, all Northern Territory): same data as holotype but *Reg*. 15308–15310 ♂♂, QMB; *Reg*. 15311–15316 ♀♀, NTM; *Reg*. 15317–15318 ♂♂, NTM; *Reg*. 15332–3 & 15335–8 ♀♀, QMB; *Reg*. 15334 ♀ (AM K118230, SEM Unit); *Reg*. 15339–15344 (AM K118202–K118207, *Reg*.15342 in SEM Unit) ♂♂; Bardedjilidji Walk, nr Cahill's Crossing [c. 12°26'S 132°58'E], Kakadu NP, *Hibiscus* flowers, 23 Feb. 1996, D.K. McAlpine & G.R. Brown, *Reg*. 15368–15383 (AM K118209–K118224) ♀♀ and *Reg*. 15384–15388 (AM K118225–K118229) ♂♂, AM; Bukalara Plateau, 46 km SSW of Borroloola [c. 16°26'S 136°04'E], 23 Apr. 1976, D.H. Colless, on *Hibiscus* flowers, *Reg*. 15389–15398 ♀♀, *Reg*. 15399–15405 ♂♂, ANIC; McArthur River, 48 km SSW of Borroloola [c. 16°26'S 136°04'E], 14 Apr. 1976, D.H. Colless, malaise trap, *Reg*. 15406 ♀ and 15407 ♂, ANIC.

Distinguishing features. All three orbital setae are reclinate, and foretarsi are unmodified.

Description. Holotype measurements given with paratype range between parentheses where appropriate.

Body length. 2.0 mm (2.0–2.2 mm).

Head. Arista with 3 short, straight rays above and 2 below, plus a small terminal fork. Frons slightly longer than wide (fw:fl = 0.9); with numerous frontal hairs; blackish brown, paler anteriorly (Figs. 2, 8). Ocellar-triangle also blackish brown. Ocellars subequal in length to the postocellar and first orbital setae. Pedicel and first flagellomere yellowish brown. Carina prominent, narrow between pedicels, broad and square below, upper surface flat (Figs. 7, 8). Face yellowish brown. Palpus tan, rounded with 68 setae apically and subapically and about 4 ventrally. Gena curved, slightly broader anteriorly, about one tenth greatest diameter of eye, o:j = 13 (10–16), o:ch = 11 (10–14). Vibrissa single. Eye dark reddish brown with dense pile (Fig. 2). Orbitals short, barely distinguishable from frontal hairs (especially or2), anterior most orbital (or1) reclinate, or2 and or3 also reclinate, in approximate ratio 6:6:7, or1:or3 = 0.9 (0.8–0.9), or1:or2 = 1.0 (1.0–1.2) (Fig. 2). Ocellars (oc) short and pointing posterolaterally,
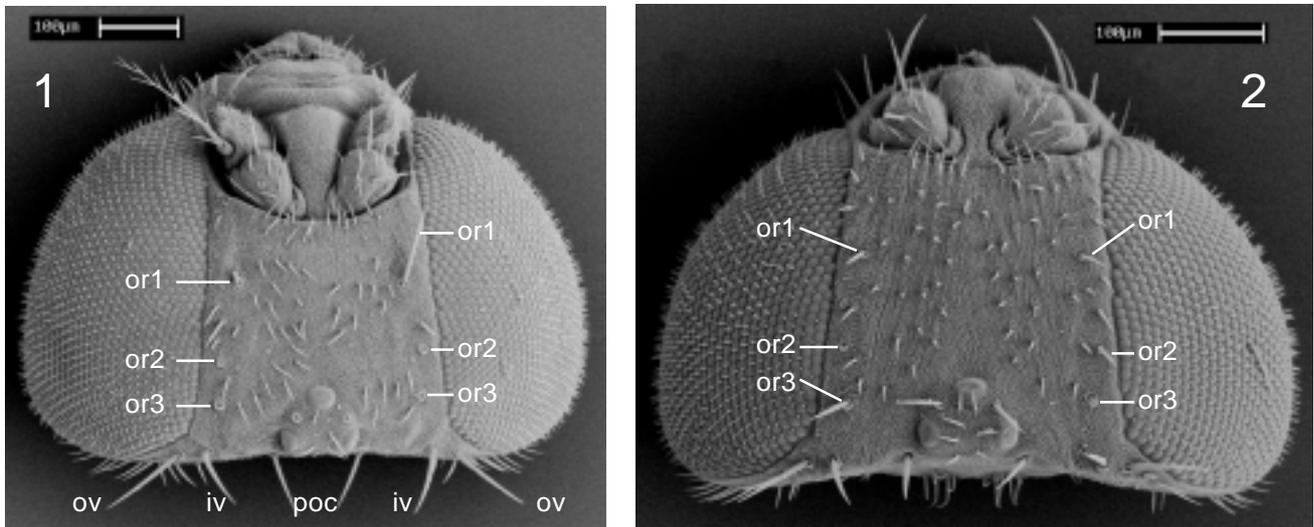
Figures 1, 2. Frontal setation of *Scaptodrosophila hibisci*, left (1), and *S. aclinata* n.sp., right (2). Note the prominent proclinate first orbital (or1) in *S. hibisci* (broken off on left side) and its diminutive reclinate form in *S. aclinata*; see text for abbreviations. (Specimens: *S. hibisci*, *Reg.* 15327, coll. Bellingen NSW, JSFB; *S. aclinata*, *Reg.* 15334, same data as holotype, head on stub in AM SEM Unit, rest of body in Collection). Scale bar = 100 μm.

postocellars (poc) as short as first orbitals, oc:or1 = 1.0 (1.0–1.3), poc:oc = 0.9 (0.9–1.3). Inner (iv) and outer (ov) vertical setae longer than the orbitals, or3:iv = 0.6 (0.6–0.8), iv:ov = 1.0 (0.8–1.1) (Figs. 6, 8).

Thorax. Mesoscutum subshining blackish brown. Dorsocentrals in two pairs; posterior dorsocentrals about twice the length of the anterior setae, and slightly shorter than the anterior scutellar setae, adc:pdc = 0.5 (0.5–0.7), pdc:asc = 0.8 (0.7–0.9). Scutellum and mesoscutum concolorous. Acrostichals in 8 rows, 6 between dorsocentrals. Prescutellar setae developed, adc:pre.sc = 1.0 but less well developed and shorter (0.6) in some paratypes. Halter yellowish brown. Fine propleural seta present. Anepisternum bare. Katepisternal setae barely distinguishable from hairs and all arising near upper edge of sternite, sterno-index = 1.0, m:a kepst = 0.9 (0.7–0.9), p.kepst:pdc = 0.3. Two short humerals; anterior supra-alar about twice as long. Legs with unmodified tarsi and with tarsal hairs strongly curved; mid tibia with 3–4 apical bristles, hind tibia with 2 short ventroapical bristles. Pre-apical bristles absent or not differentiated.

Wing. Length from axillary area to apex 1.56 mm (paratype range 1.45–1.78), length from humeral crossvein to apex 1.36 mm; C-index 1.44 (1.25–1.88), 4v-index 2.19 (2.00–2.70), 4c-index 1.50 (1.29–1.67), 5x-index 1.63 (1.25–1.80), M-index 0.65 (0.52–0.78), ac-index 4.80 (3.60–5.71), C3fringe 0.60 (0.56–0.67). Third and fourth longitudinal veins slightly convergent apically.

Abdomen. Uniformly dark brown, slightly paler than thorax.

Male terminalia (Figs. 9–12). Epandrium narrow, without lateral or ventral broadening, pale tan, with a single large seta ventrally and pubescent hairs restricted to small areas posterodorsally, posterolaterally and narrowly along posterior border in between. Cercus not indented, covered entirely with short hairs and with long setae becoming smaller and shorter ventrally (Figs. 9–10). Surstylus with row of c. 12 short stout prensisetae along inner margin and 6–7 longer setae arranged irregularly behind them. Hypandrium with two long submedian spines; aedeagus expanded apically, with curved apodeme slightly bulbous distally (Figs. 11–12); parameres rounded with cluster of fine sensilla apically.

Female. Forelegs with tarsal hairs only slightly curved (cf. strongly curved in males), otherwise external morphology similar to male.

Female terminalia. Egg guide sclerotized with large marginal teeth.

**Distribution** (Fig. 13). Northern Territory north of 17°S.

In January 2001 no *Hibiscus* plants were found west of Charters Towers on the Barkly Highway, south of 17°11.70'S 133°28.08'E on the Sturt Highway (Northern Territory) or southeast of Halls Creek in the Tanamai Desert (Western Australia–Northern Territory). Mr Terry A. Woodger (Richmond-based botanist, pers. comm.) reports *Hibiscus* from the Selwyn Ranges (c. 21.5°S 140.5°E) and further collecting in that region would be important in order to determine the extent to which populations of *S. aclinata* and *S. hibisci* are geographically isolated.

Other specimens examined. Specimens from eastern Australia in the AM and previously determined as *Scaptodrosophila hibisci* by Bock or McEvey were re-examined and found to be correctly identified. Mt Cahill specimens (ANIC, see paratype series above) were found to be incorrectly identified as *hibisci*. A series of *Scaptodrosophila aclinata* flies from Tolmer Falls, 13°11.60'S 130°42.32'E, Litchfield NP, Northern Territory, 1998, J.S.F. Barker, were dissected and discarded—this represents an additional locality for the new species.

Remarks. *Scaptodrosophila aclinata* n.sp. is closely related to *S. hibisci* (Bock *in* Cook *et al*., 1977) because it has very
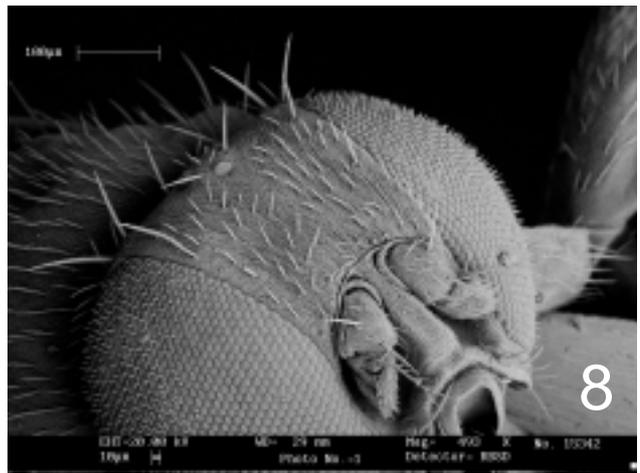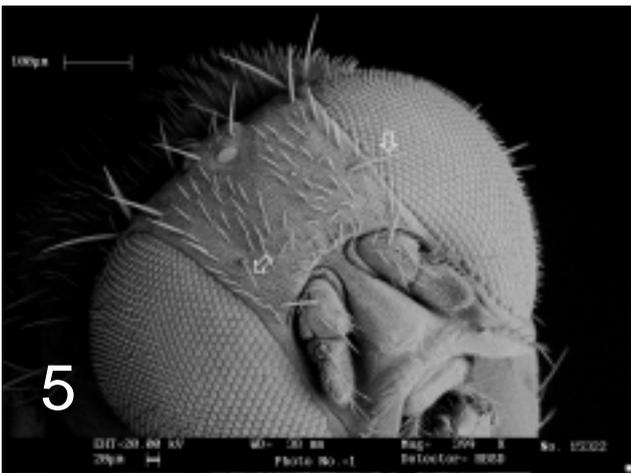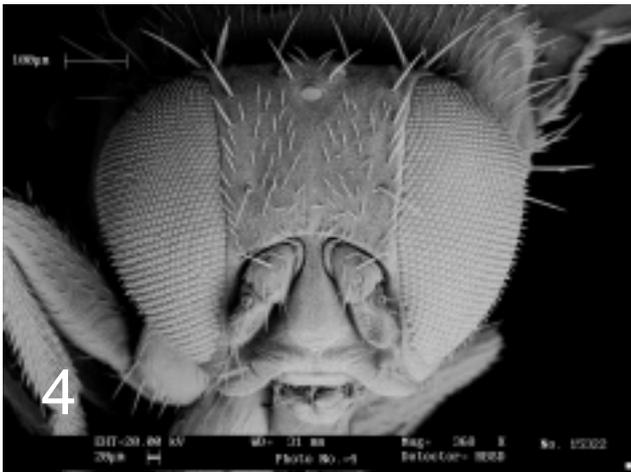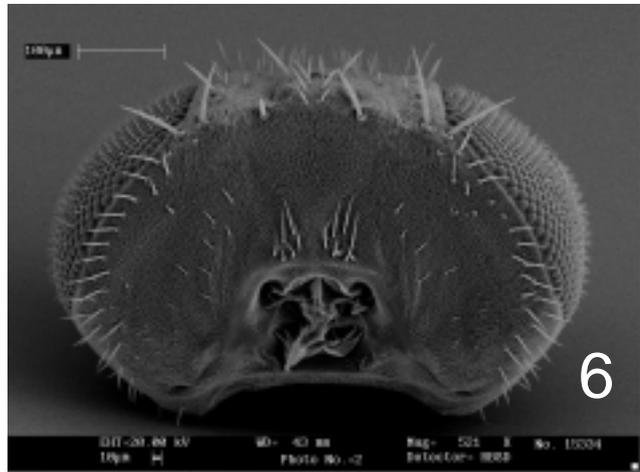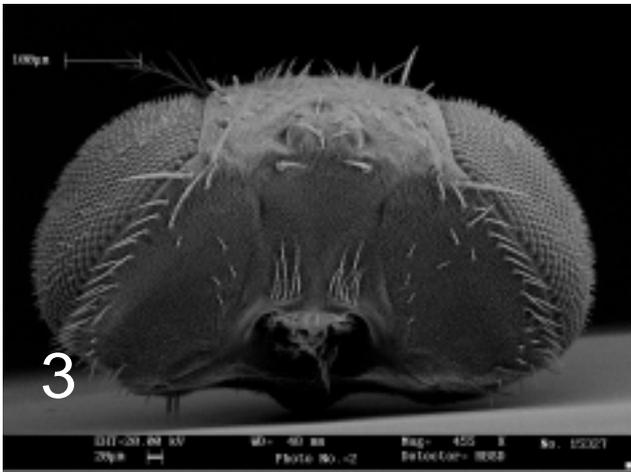
Figures 3–8. Comparative views of the head of *Scaptodrosophila hibisci* (left) and *S. aclinata* n.sp. (right). View of the back of the head showing supracervical setae: Fig. 3, *S. hibisci* (*Reg.* 15327); Fig. 6, *S. aclinata* n.sp. (*Reg.* 15334). Frontal setation and facial morphology, Figs. 4–5, *S. hibisci* (*Reg.* 15322, coll. Bellingen NSW, JSFB); Figs. 7–8, *S. aclinata* n.sp. (*Reg.* 15342). Note the complete lack of proclinate setae (arrowed in *hibisci* Fig. 5) in the anterior frontal half of *S. aclinata* n.sp. (Fig. 8).
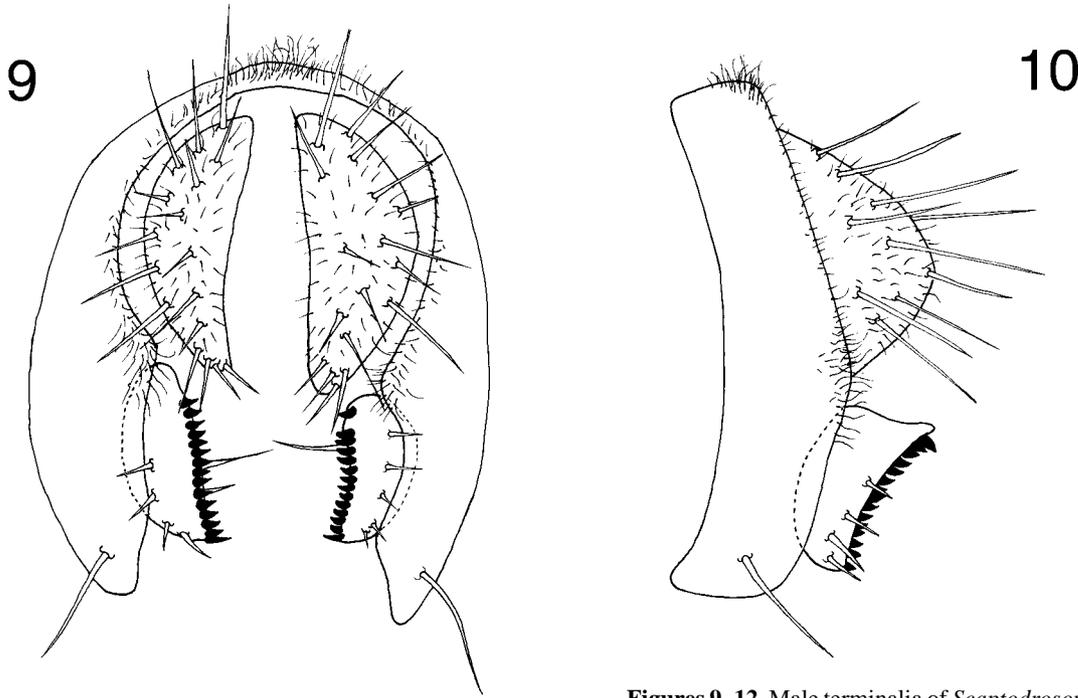
Figures 9–12. Male terminalia of *Scaptodrosophila aclinata* n.sp. (*Reg*. 15344, AM K118207) 9–10, hypandrium, caudal and lateral views; 11–12, epandrium, ventral and lateral views.
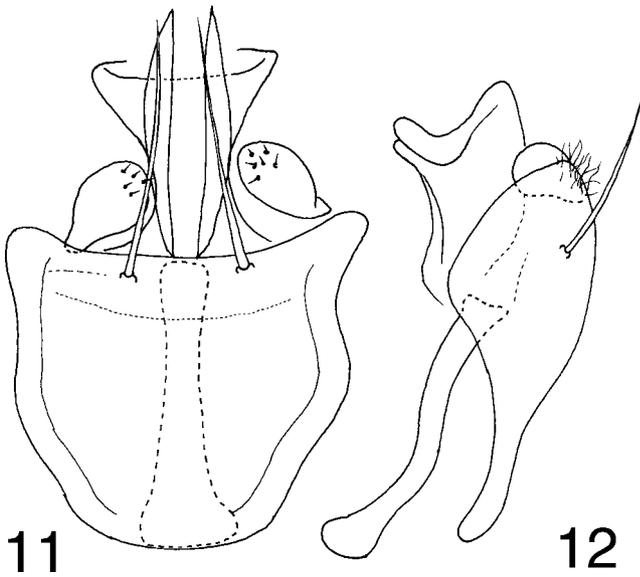
similar morphology (Figs. 1–8) and habitat preference, and it produces progeny—albeit with reduced fertility—when hybridized (Table 1). However, it is distinctly different by virtue of the first orbital being proclinate and relatively large in *hibisci* and reclinate and relatively small in *aclinata*. Of less significance is that the humeral setae are larger and the overall coloration darker in *S. hibisci*. Other differences have been noted in ovariole-number to body-size relationship (see "*Drosophila hibisci*—Northern Territory flies" in Wolf *et al*., 2000) and microsatellite allelic frequencies (Barker unpubl.).

The new species keys to couplet 80 in Bock's (1982) key to the Australian species of *Drosophila*. Formation of a

triplet at that level with the addition of: "Frontal macrochaetae greatly reduced, first orbital not proclinate… *aclinata*" would lead to a correct identification.

Three other anthophilic drosophilids from northern Queensland and New Guinea are superficially similar: *Scaptodrosophila moana* (McEvey) from Torres Strait and Cape York Peninsula, and *S. aproclinata* (Okada & Carson) and *S. paraguma* (Okada & Carson) from Wau. *Scaptodrosophila moana* has a very distinctive arista with a single upper ray quite unlike the three rays above and two below arrangement in *aclinata* n.sp.; *moana* also has a well-differentiated and proclinate first orbital seta. *Scaptodrosophila aproclinata* and *S. paraguma* have not been examined but they are described as having only two reclinate orbitals, a condition that would make them very hard to separate from *aclinata* n.sp. However, *aproclinata* is also described as having extraordinary tarsal modification and finely pubescent arista (tarsi are unmodified and aristae are not finely pubescent in *aclinata* n.sp.); while *paraguma* is described as having an arista pubescent in the distal half, a mesopleural (= anepisternal) seta, and a deeply constricted cercus (the anepisternum is bare and the cercus is not constricted in *aclinata* n.sp.). The prensisetae of the *aclinata* surstylus are most unlike the arrangement in *S. paraguma*.

The unusually short rays of the arista and the overall reduction in cephalochaetae appears to be characteristic of a number of drosophilids associated with flowers.

Etymology. The specific name refers to the unusual inclination of the first orbital seta—proclinate in most other drosophilids including *Scaptodrosophila hibisci* but reclinate in this species.
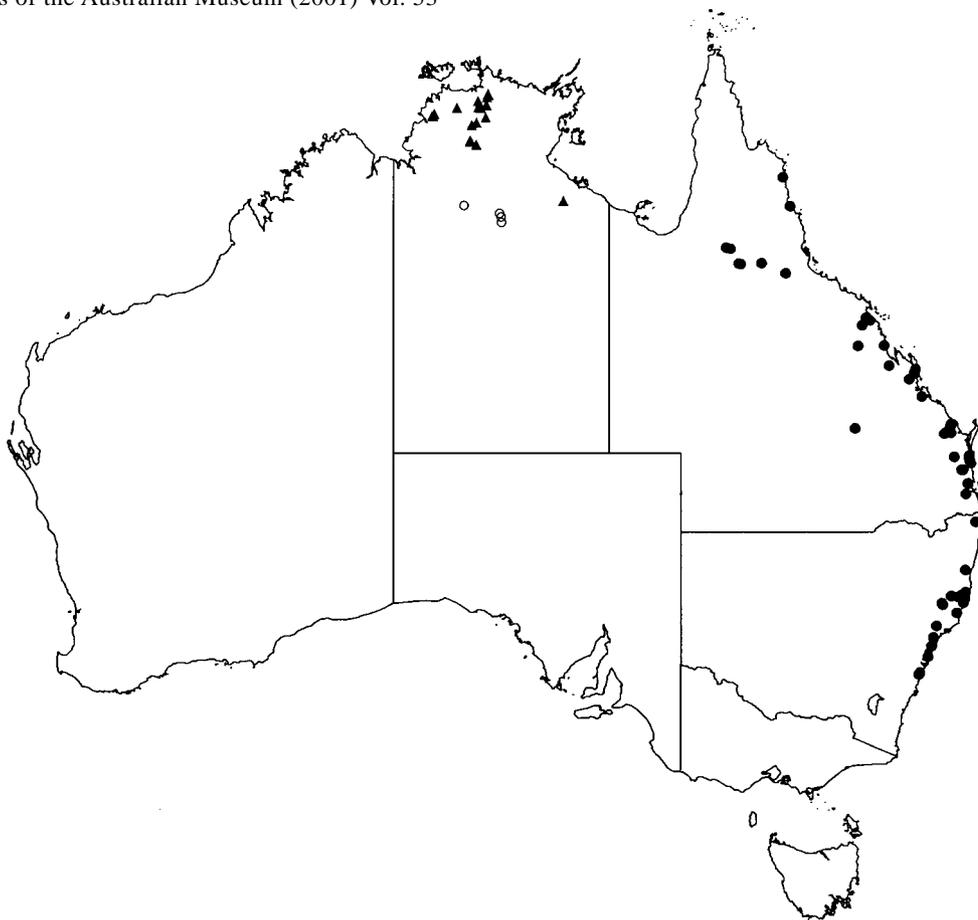
Figure 13. Distribution of *Scaptodrosophila aclinata* (▲) and *S. hibisci* (●) in Australia (Papua New Guinea record for *S. hibisci* not shown). *Hibiscus* flowers examined for *Scaptodrosophila* flies (January 2001) without result (○).

Host-plant specialization

Two populations of *S. hibisci*, each derived from a locality in nature that has only one of the two *Hibiscus* species, *H. heterophyllus* or *H. diversifolius*, were used to test preferences for oviposition of each population on each species. Wild caught flies (50♂♂, 70♀♀) from Bellingen (*H. heterophyllus* 30°25.155'S 152°49.425'E) were set in a population cage and maintained breeding on *H. heterophyllus* flowers for six weeks. Wild caught flies (250♂♂, 340♀♀) from Tyagarah (*H. diversifolius* 28°34.933'S 153°32.258'E) were held at 20°C in sugar-agar vials for three days, and then a population cage was set up for each population with 50 males and 50 females. One *H. heterophyllus* and one *H. diversifolius* flower were added to each cage, each day. Two days after addition to a cage, flowers were removed to sand bottles (Starmer *et al*., 1998), and all emerging progeny scored daily until there were no further emergences. After 28 days, all remaining flies in the cages were collected and counted.

Results. Over the 28 days, the Tyagarah population derived from *H. diversifolius* produced more progeny than the Bellingen population from *H. heterophyllus* (mean progeny/day = 14.0 and 9.6 respectively, P = 0.07), and survived

better (mean numbers at end of test period = 33♂♂, 29♀♀ and 12♂♂, 15♀♀ respectively). *Hibiscus heterophyllus* flowers were preferred by flies from both populations (mean progeny/day = 16.0 and 7.4 respectively, P < 0.001). The regressions of proportion of progeny from *H. heterophyllus* on day were not significant for either cage. Thus all two way interactions were tested in ANOVA against population of origin × *Hibiscus* species × day as error. None were significant.

Discussion. For two species (*H. heterophyllus* and *H. diversifolius*) which it does utilize in nature, *S. hibisci* laboratory populations from each of these species in nature produced more progeny on the former. However, as the population of origin × *Hibiscus* species interaction was not significant, there is no evidence for host plant specialization.

Both *S. hibisci* and *S. aclinata* n.sp. have been found breeding only in flowers of the *Furcaria* section of the genus *Hibiscus* in Australia. However, *S. hibisci* has been recorded breeding in flowers of okra [*Abelmoschus (= Hibiscus) esculentus*] in New Guinea (Okada & Carson, 1982), and we have bred it on okra flowers in the laboratory.

Scaptodrosophila hibisci has been collected from flowers of five *Hibiscus* species and *S. aclinata* from 11 species. Only one of these *Hibiscus* species, *H. meraukensis*, is

Table 1. Results of test crosses for hybridization, copulation latency and duration and interfertility between *Scaptodrosophila hibisci* (*h*) and *Scaptodrosophila aclinata* n.sp. (*a*); ft. = fertile.

mating type	mating ♂ × ♀	number pairs tested	number mating <1h	number mating <3h	% mated <3h	copulation latency[c] (min) mean±sd	copulation duration (min) mean±sd	number pairs tested for progeny	progeny number mean±sd	no. pairs tested to first ft. egg	mean day first ft. egg
parent	*h* × *h*	18	16	nt[b]	0.89	19.3±19.1	5.6±3.9	8	66.0±33.1	12	1.83
	a × *a*	11	7	10	0.91	37.7±35.0	4.8±1.6	6	11.7±9.5	5	5.00
F₁	*a* × *h*	23	7	12	0.52	81.4±69.0	6.1±3.0	11	10.0±8.7	8	4.88
	h × *a*	20	8	13	0.65	43.6±33.3	2.9±3.5	4	0.4±0.5	3	4.67
F₂	(*a* × *h*) × (*a* × *h*)	11	7	9	0.82	26.8±34.3	5.6±2.7	2	0	—	—
	(*h* × *a*) × (*a* × *h*)	2	0	0	0	—	—	—	—	—	—
backcross	*a* × (*a* × *h*)	7	5	5	0.71	8.5±6.6	3.3±1.0	3	35.0±16.1	3	1.00
	h × (*a* × *h*)	8	8	8	1.00	6.6±8.7	4.4±2.9	3	19.7±12.3	4	4.25
	(*a* × *h*) × *a*	1	0	0	0	—	—	—	—	—	—
	(*a* × *h*) × *h*	3	1	3	1.00	60.7±49.8	8.1±8.0	0	—	—	—

[b] not tested

[c] time to first copulation (averaged only for pairs that mated)

known to occur within each of the disjunct distributions of the two *Scaptodrosophila* species, and it is utilized by both. Thus there is no field evidence of host plant specialization for these *Scaptodrosophila* species. However, the hybridization tests (Table 1) were done using *H. diversifolius*, which is utilized by *S. hibisci* in nature, but which is not known to occur within the distribution of *S. aclinata*. In both parental and F₁ crosses, *S. aclinata* females produced fewer progeny than *S. hibisci*, indicating poorer adaptation of the former to this *Hibiscus* species, to which it is not exposed in nature, or possibly a lower intrinsic fecundity.

Hybridization studies

Adults of *Scaptodrosophila hibisci* and *S. aclinata* n.sp. were reared from flowers of *H. heterophyllus* collected at Bellingen, N.S.W. and flowers of *H. menzeliae* collected at Nitmiluk National Park, Northern Territory. Some, where females were collected as virgins, were used in single pair matings in both parental and F₁ crosses (both reciprocals). The remainder were added to population cages (one for each species, and one for each reciprocal cross to produce F₁ progeny). For all pair matings, males were generally one day older than females, and most females were collected and used within 2 h of eclosion, using very light CO_2 anaesthetization. All flies for crosses were placed singly in vials with about 7 ml 1.5% agar, and allowed 1 h to recover from anaesthetization. The predetermined male was then gently aspirated and added to its paired female, and pairs observed for copulation for 3 h. Copulation latency and copulation duration were recorded. All observations were done between 09h00 and 14h00 at 25°C. At the end of the observation period, each mated pair was placed in a 200 ml bottle with moist sand in the base, and a small tube with water holding a single *H. diversifolius* flower. The pairs

were transferred to a fresh flower each day for 10 days, with the previous days flower transferred to a bottle with sand. Four days later, 10 ml distilled water was added to each of these bottles. Progeny emerging from these flowers were collected daily, sexed and counted. From parental matings, progeny were used in backcrosses or added to the appropriate parental cage. Some of the F₁ progeny, plus F₁ flies from the cage crosses, were used in F₂ and backcross matings, with the remainder stored (sexes separate in agar vials) for use on subsequent days.

Flies in population cages were maintained by adding one or two fresh flowers to the cage each day, with the previous days flowers transferred to a bottle with sand for progeny collection.

Sufficient flowers were not available on some days to set up all pairs that copulated. Further, some pairs were not carried through for 10 days because of death or loss of one or both of the pair. Thus the number of pairs tested for progeny production is less than the number that copulated, while the number of pairs recorded for day of first fertile egg lay is greater than the number tested for progeny, except where some pairs copulated, but produced no progeny.

Discussion. The results are summarized in Table 1. These two species are partially interfertile, and clearly are closely related. The proportion of pairs mating and average progeny numbers are less for the F₁ crosses than for parentals, while no progeny were obtained from the F₂ crosses. Two of the backcrosses appear exceptional, both in proportion of pairs mating and in progeny numbers. However, this is possibly a function of the much older males used in these crosses, viz. average of 9–10 day old versus average of two day old in all other crosses.

In all crosses, the pairs were kept together for 10 days, so that further matings may have occurred during this period.

Previous study of *S. hibisci* (Polak *et al.*, 1998) has shown that mature males prefer young virgins, as compared with older virgin and non-virgin females, and that a mating plug fills the entire uterus at copulation. For the *S. hibisci* parental matings here, copulation latencies for < 2 h and 2 day old females were 12.5 and 30.1 min (but not significantly different). The sexual maturation and copulation dynamics of *S. aclinata* seem to be different. Mean copulation latency was about twice as long as for *S. hibisci*, while copulation latencies for < 2 h, 1 and 4 day old females were 49.7, 39.2 and 10.9 min respectively (again not significantly different). However, male age was highly correlated with female age, and both copulation duration and progeny numbers increased with parental age. These observations, together with the later day of first fertile egg lay, suggest delayed sexual maturity in this species, as compared with *S. hibisci*. For the F_1 cross (*S. hibisci* male×*S. aclinata* female), mean copulation duration is shorter than for all other crosses. However, six of the 13 pairs mated more than once in the 3 h observation period—five twice and one three times. In all cases, the first copulation was short (< 1 min), and the overall mean copulation duration, using last copulation for multiple matings was 4.2±4.1 min, similar to the means of other crosses.

Hibiscus meraukensis is known (records of the Queensland Herbarium) from a number of localities in northwest Queensland—the region between the known distributions of these two *Scaptodrosophila* species (Fig. 13). Further field work in this region is needed to determine if either species is present there, and whether they ever occur sympatrically under natural conditions. The form of orbital setation in hybrids is also in need of further investigation so that any naturally occurring hybrids may be identified as such.

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