Evolution of Extreme Sexual Dimorphisms: Structural and Behavioral Convergence Among Broad-Headed Male Drosophilidae (Diptera)

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ABSTRACT

Males with broad heads (hypercephaly) have arisen 21–24 times in various taxa of flies; 11 instances are in the Drosophilidae. Details of the morphological modification of the male head vary among the hypercephalic taxa, with drosophilids possessing all the types of modifications seen in other hypercephalic flies. Cephalic modifications include distension of the eyes and/or various cranial sclerites or plates (i.e., facial, parafacial, fronto-orbital, occipital plates, and the frontal vitta and ocellar triangle). Reproductive behavior of hypercephalic drosophilids and their close relatives is described for some species and reviewed for others. Measurements are given on eye and head shapes and comparisons are made of approximate optical resolutions. Associated with hypercephaly is aggressive male behavior (head butting and jousting) and vision enhanced for either binocularity (in the pedunculate eye forms) or frontal resolution (those species with conical eyes). Rel-
ative growth was compared among the drosophilids using regressions of $\log_{10}$ measurements of head width on thorax length. Hypercephaly is a consequence, despite the manner of modification, of accelerated growth of certain head sclerites, which is manifested in Zygothrica as well by abnormal growth of setae. Predisplacement of growth onset and hypermorphosis rarely contribute to the sexual dimorphism. Only Zygothrica latipanops males were found to occur in two discrete classes (α and β, or extremely and moderately hypercephalic males). A phylogenetic analysis of the apomorphies associated with hypercephaly provided the following hypothesis: in order from the most to least inclusive feature is territoriality, a frontal approach prior to male fighting, head butting, and then, at the apical node, are hypercephaly with its associated optical features and jousting. No recourse is made to explanations of natural or sexual selection regarding origins of correlated traits.

INTRODUCTION

In the delightful book, "The Natural History of Flies," Oldroyd (1964) said of the small, black dung flies, the Sepsidae (pp. 175–176) that "it is curious that these little flies seem to need so many aids to success in copulation—spotted wings and male display, aphrodisiac odor by the females, special male clasping organs—when other flies manage
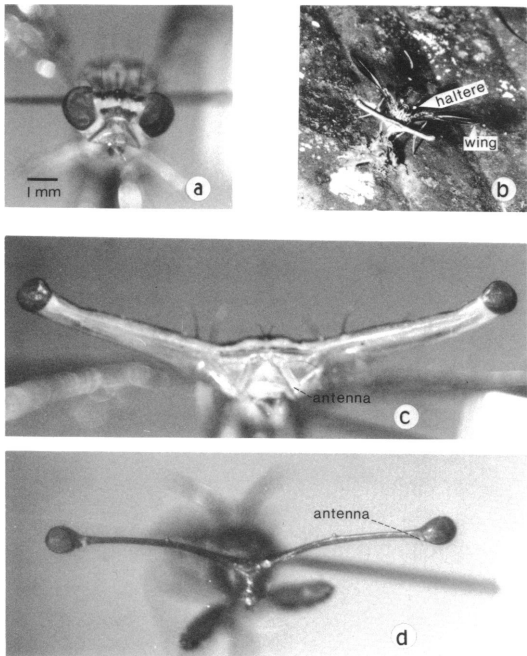
Fig. 1. Examples of hypercephalic Diptera. a–c, *Richardia telescopica*; a, female; b, male feeding on monkey droppings, wings are outstretched (Barro Colorado Island, Panama [BCI]); c, male head, frontal view. d, *Teleopsis* sp. male (female has slightly shorter eye stalks). a, c, and d are to the same scale. Note differences in position of the antennae.

TABLE 1
Hypercephalic Diptera

Number of appearances	Taxa
1	Diopsidae (all genera except *Centrioncus*)
11	Drosophilidae
	Chymomyza spp.
	Drosophila (*Drosophila*) *heteroneura*
	Drosophila (*Hirtodrosophila*) *caputudis*
	Mulgravea asiatica
	Drosophila (*Hirtodrosophila*) *chandleri*
	Zygothrica spp.
1	Micropezidae
	Anaeropsis guttipennis
1–2	Otitidae
	Plagiocephalus spp.
	Ophthalmoptera spp.
2	Periscelididae
	Sphyroperiscelis spp.
	Diopsosoma spp.
2–4	Platystomatidae
	Platystomatinae:
	Achias spp.
	Achiosoma spp.
	Brea spp.
	Laglaizia spp.
	Scholastinae:
	Asyntona
	Mesoctenia
	Pterogenia
	Trigonosoma
	Zygaenula
2	Richardiidae
	Richardia telescopica
	Richardia spp. (nr. *annulata*)
2	Tephritidae
	Pelmatops ichneumonea
	Themara lunifera

without any of these." It is indeed enigmatic why any bizarre sexual dimorphism should come to be, and the frequency with which this question is asked is usually a direct reflection of how bizarre is the feature in question.

Among the most intriguing sexual modifications in insects is male hypercephaly (fig. 1). The well-known example is seen in the Diopsidae, but in most diopsids the male eyestalks are only slightly longer, per unit of body size, than those of the female (Eggers, 1915; Frey, 1928; Deschamps, 1957; Shillito, 1971; Burkhardt and De la Motte, 1985). The dimorphism is much more obvious in seven other families of flies, as seen, for example, in *Richardia telescopica* (Richardiidae) (fig. 1). Hypercephaly has arisen at least 21 times in the Diptera (table 1) and several more times in other insects: twice in the Hymenoptera, in an undescribed chalcid (E. E. Grissell, un-

publ.) and a eurytomid (Yoshimoto and Gibson, 1979); the instances of stalk-eyed Heteroptera (e.g., Stonedahl, 1986) are not sexual dimorphisms.

Numerous explanations have accounted for the presence of eyestalks, mostly because of the attention directed to the Diopsidae. Virtually all of the explanations have been based on proximate-mechanistic factors, particularly sexual selection. Burkhardt and De la Motte (1985) suggested, based on previous optical studies (Burkhardt and De la Motte, 1983; De la Motte and Burkhardt, 1983), that

the eyestalks of Diopsidae impart an enhanced ability to size up opponents and mates, and at distances farther than are possible for "normal"-headed individuals. The "size-up" hypothesis appears to have first been used by McAlpine (1979) for *Achias* (Platystomatidae), but in a slightly different context. He suggested that two fighting males of *Achias* meet with heads almost touching so as to accurately determine the opponents' size. The males thereby avoid unnecessary confrontations and thus injury (little mention was made by McAlpine of long-distance optical resolution and binocularity). McAlpine's hypothesis was espoused by Burla (1988) who observed rival males of *Zygothrica dispar* to freeze head-on before an encounter either ended in retreat or escalated into contact. In trying to account for the hypercephalic males of *Drosophila heteroneura* and their "ramming" behavior, Spieth (1981) suggested a sequence of natural and then sexual selection: bird predation [somehow] selected for a frontward approach of males and for ramming, and intermale competition resulted in the head shape. Intrasexual selection, then, is the most common causal explanation of male hypercephaly. Templeton (1977), however, proposed that the broad head of *Drosophila heteroneura* is a species-specific identification signal that aids females in choosing a mate (intersexual selection). In their most recent paper, Burkhardt and De la Motte (1989) did a female choice experiment, which actually showed that the males of *Cyrtodiopsis whitei* with the broadest heads were favored by females. These authors elsewhere (Burkardt and De la Motte, 1987) hypothesized a sequence of several selection pressures, within and among sexes and species, that act upon diopsid mating repertoires. Finally, Feijen (1984) wrote (p. 80): "A strong argument against the selectional importance of eyestalks for binocular vision is in the large interspecific variation in the ratio eyespan/length of body." That is, if the role of binocular vision is supposedly very finely adapted to reproductive behavior, why is there so much intra- and inter-specific variation in the trait?

Many of the above arguments are intuitively reasonable and are not inconsistent with the observations. The approach here, however, is devoid of selectionist explanations, and is purely comparative, serving to expose convergent patterns of hypercephaly and associated derived traits. Studying this trait in Drosophilidae has the major advantage of male hypercephaly having arisen more often in this family than in any other fly taxon. Also, some phylogenetic work has been done on the family (Grimaldi, 1986a; 1987a, 1987b; 1988), and a great deal is known about the general biology of *Drosophila*.

MATERIALS AND METHODS

Most flies measured in this study were critical point-dried using absolute ethanol. Pinned specimens were selected from various series where there was minimal collapse of the cuticle. Scanning electron microscopy used 10 kV beam current and gold-palladium sputter coating. Techniques for observing fly behavior, especially *Zygothrica*, are provided elsewhere (Grimaldi, 1987b). Morphological terms for parts of the cranium and other tagmata follow McAlpine (1981) and are presented in figure 2.

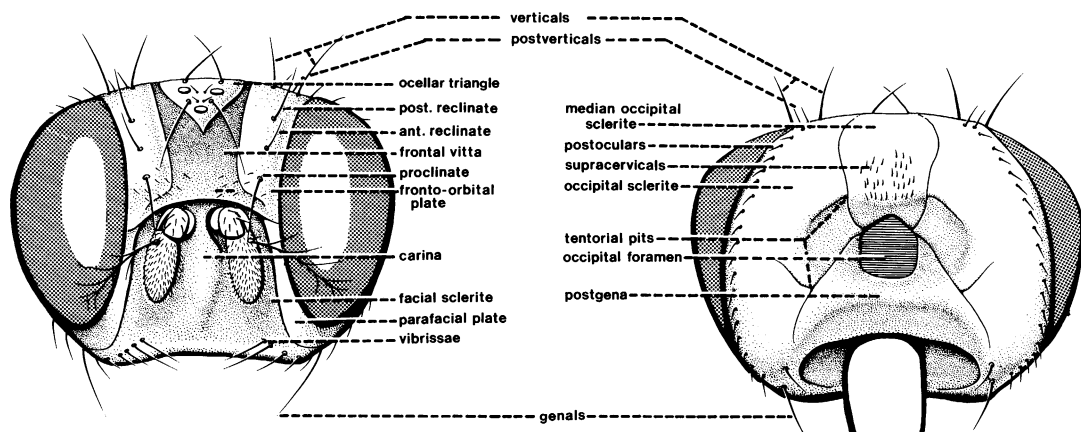Pinned specimens were measured in two

Fig. 2. Frontal and ventral views of a generalized head of Drosophilidae. Terminology follows McAlpine (1981).

ways. One was a Wild M-5 stereoscope with a camera lucida, with the image focused onto the surface of a digitizing tablet (Zeiss). Since the digitizing tablet's measurement error was about ± 0.001 mm, virtually all error was due to positioning of the specimen and movement of the tablet cursor. Also used was a precision stage micrometer. Here, too, error was due almost entirely to the positioning of the specimen. Thorax length (distance from the anterior margin of the notum to the apex of the scutellum) was used as the most reliable and convenient measurement of body size.

Since fly eyes are generally of the neural superposition type, and thus have a single focal point, fairly simple methods can be used to compare estimated optical properties such as resolution and binocularity (Snyder, 1979). Basically, resolution (R, the ability to distinguish two objects which are close together) can be measured as r/D, where r is the radius of eye curvature (in μm) and D is the diameter of the eye facets in the plane of the measured radius (in μm). This estimate does not take into account differences in optical abilities among species based on spectral sensitivity (detection of photons), binocularity, differences in resolving power due to variation in ommatidia number, or, simply, how much light there is in the fly's habitat. Estimates of resolving power and other physical capabilities must eventually be tested with behavioral assays, but such are well beyond the means and efforts here. Fortunately, where it

has been studied in insects, there is good correspondence between optically and behaviorally measured resolution (e.g., Bauer, 1985).

Eye curvature was measured by drawing with a camera lucida at 50× the outside margin of the eye and head, as seen from a dorsal view. The dorsal view was standardized to approximate the position of a drosophilid head when held in a natural, live posture; this position was taken as the dorsal view that maximized head length. Thus, one visual axis was measured, which was a plane approximately horizontal to the substrate and longitudinal to the long axis of the body in a standing fly. Radius of the curvature was measured by comparing with a compass the curve that best fit the outline. The radial length was then measured on paper using the digitizing tablet. For some eyes there were two main axes of curvature: a frontal one and a smaller, posterolateral one (fig. 3a), designated as r and r_1, respectively. Facet diameters were measured at 150–312× (depending on size of the specimen) using scanning electron micrographs (fig. 3b).

THE FLIES

Although not all species of hypercephalic drosophilids are represented in the scanning electron micrographs in figure 4, most of the head structural variation seen in the family is illustrated. Below are descriptions of the relevent behaviors and morphology for the five main taxa of hypercephalic drosophilids.

Chymomyza

Most of the following account comes from Grimaldi (1986a). Five species have hypercephalic males: *Chymomyza microdiopsis* (the most modified), *C. exophthalma, C. diatropa, C. jamaicensis,* and *C. albitarsis.* All belong to the *aldrichii* species group, which is mostly Neotropical in distribution. The first two species belong to one clade, and the remaining three belong to another. Portions of each clade are partly distinguished by the manner in which crania are modified. *Chymomyza* congregate at their oviposition sites on injured tree trunks, and the males usually outnumber the females there by four- to fivefold. Grimaldi (1986a) provided data on relative head size in three of the hypercephalic species and in four species unmodified or slightly modified for the trait; the data are reviewed later in this paper. Widths of the face, the parafacial plates, and fronto-orbital plates have expanded in *C. microdiopsis* and *C. exophthalma,* but the eyes remain relatively unmodified in size and shape. In the other clade the eyes are slightly distended laterally, and the dorsal portion of the fronto-orbital plates has expanded, but the face and parafacial plates are virtually unmodified in width.

Courtship for the *aldrichii* species group has never been observed. Only *Chymomyza amoena,* a member of another species group, has been closely examined (Sturtevant, 1921; Spieth, 1952; Grimaldi, unpubl.). Male display and agonistic behavior has been observed for *C. exophthalma* in Peru (Grimaldi, 1986a) and for *C. diatropa* in Panama (Grimaldi, unpubl.). In both species, the males rapidly zig-zag about on the bark while repeatedly extending the wings and forelegs. The wing and leg movements become more exaggerated as males orient toward and approach each other. Fighting males face off about one-half a body length apart and extend their forelegs while raising the body (fig. 5a). The forelegs, particularly the tarsi, are lashed against those of the opponent. Butting with the head to the head and body of the opponent has never been seen in *Chymomyza.* Apparently, the ventral rows of femoral spines in males is related not to the type of fighting behavior, but to courtship and

$$R = r/d$$
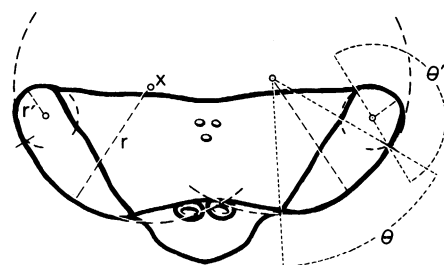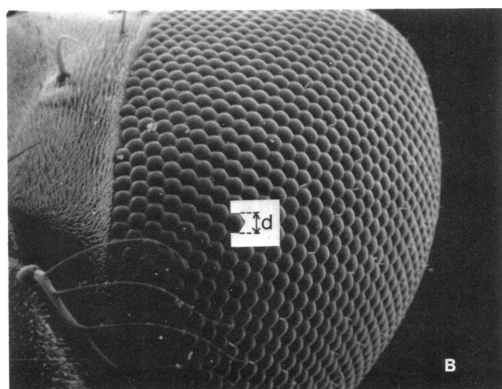
100 μm

Fig. 3. Measurements used for comparing several optical parameters in drosophilids. A, dorsal view of a hypercephalic male *Zygothrica* head. r = radius of curvature of frontal region of the eye, r' = radius of the lateral region, x = origin of circle to which r belongs. B, scanning electron micrograph of frontal region of male *Zygothrica tambopata* eye, showing the measurement for facet size. θ and θ' are the angles circumscribed by their respective radii (these values not measured in this study, but are used in computing interommatidial angles).

copulation, as based on the observations of *C. amoena.* Male *Chymomyza* are probably territorial since they congregate at specific sites but occupy smaller sites therein, frequently display, and fight with each other.

Drosophila (Hirtodrosophila)

Drosophila (H.) caputudis and *D. (H.) chandleri* are very closely related, and like
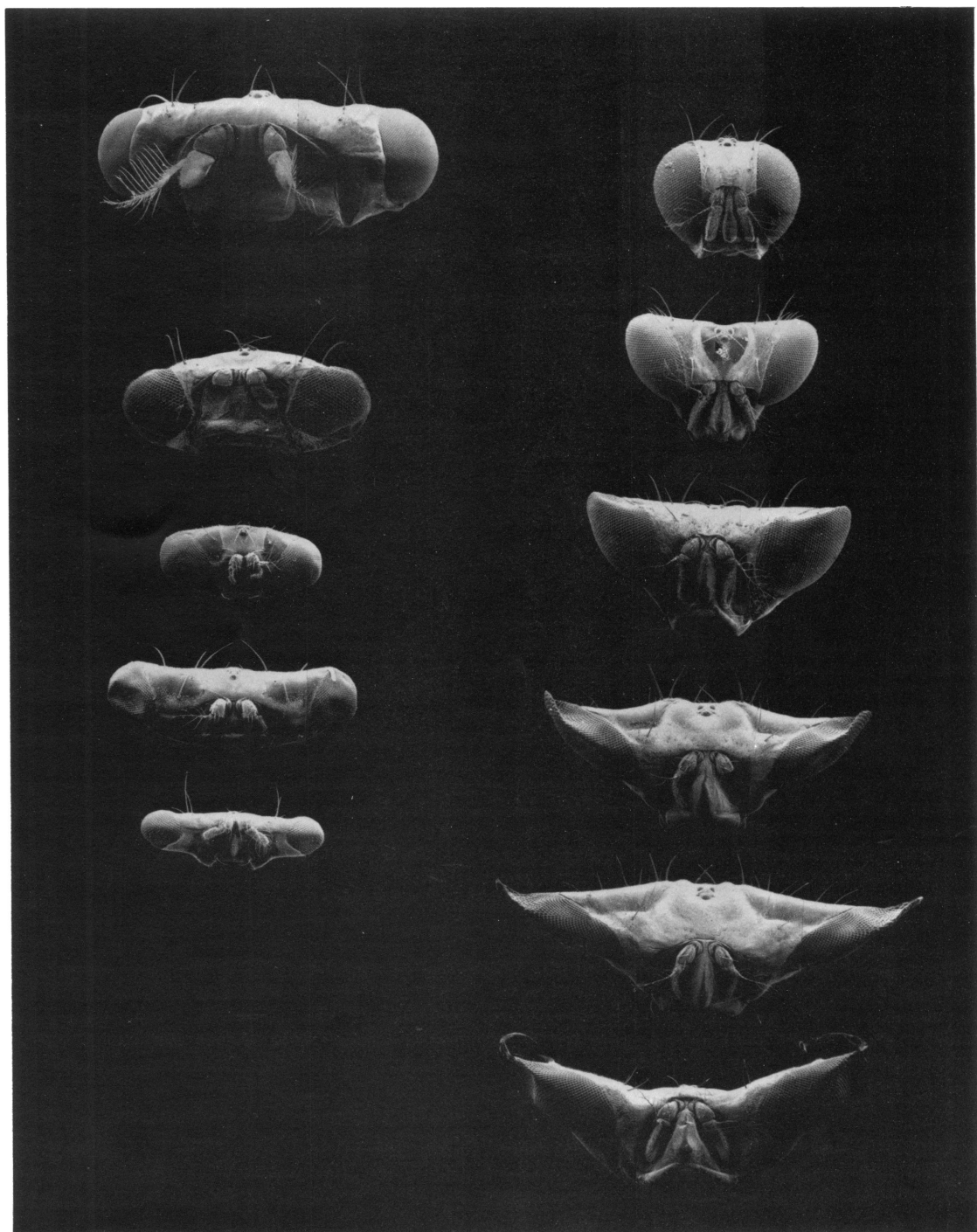
Fig. 4.   Scanning electron micrographs (frontal views) of some male Drosophilidae, all to the same scale; all except *Zygothrica vittinubila* (upper right) are hypercephalic. Left, top to bottom: *Drosophila (D.) heteroneura, Drosophila (Hirtodrosophila) caputudis, Chymomyza diatropa, Chymomyza microdiopsis, Mulgravea asiatica*. Right, top to bottom: *Zygothrica vittinubila, Z. tambopata, Z. pilipes, Z. dispar, Z. latipanops, Z. exuberans*.
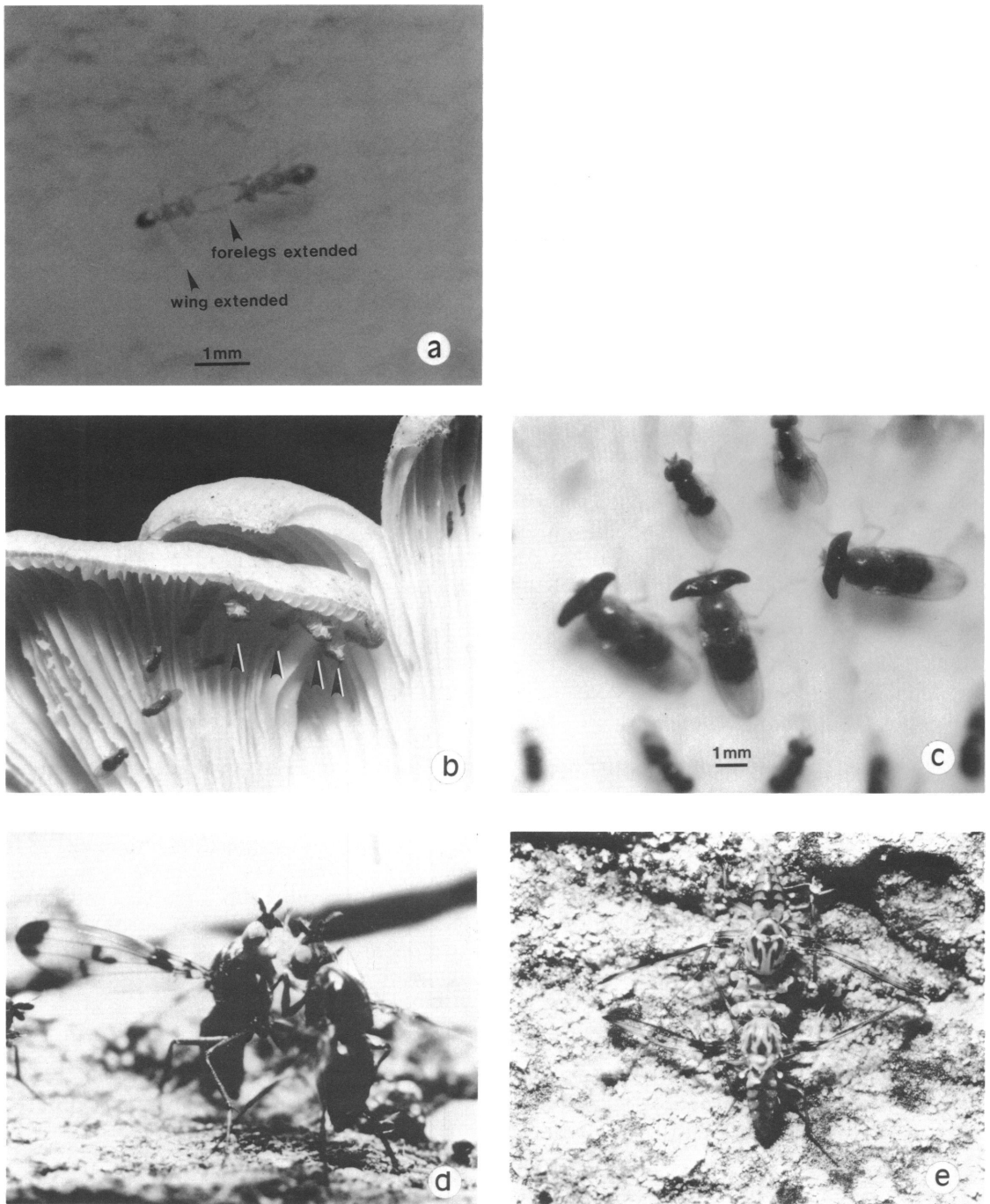
Fig. 5. Habits of some hypercephalic Drosophilidae. **a**, *Chymomyza exophthalma* males slashing with their forelegs. They were observed on the cut end of a tree trunk (BCI, Panama). **b** and **c**, *Zygothrica*. b, arrows indicate positions of four *Z. prodispar* males under the pileus of a mushroom; three of the males are on the edge surveying outward. The small, dark individuals are *Z. virgatinigra*. **c**, three *Z. prodispar* males under the pileus in b. During most of the day the males are quiescent and tolerate each other (b,c: BCI, Panama). **d**, fighting males of *Drosophila silvestris* in the characteristic rearing stance. **e**, fighting (jousting) males of *Drosophila heteroneura* (photos d and e by K. Y. Kaneshiro).

most of the hypercephalic drosophilids have only recently been described (Grimaldi, 1986b; 1988). Nothing is known of their habits, and only 16 specimens from peninsular Malaysia are known for *D. caputudis* and three specimens from Sri Lanka for *D. chandleri*. Close inspection at fungi in these regions, particularly of fleshy, white, bracket forms would probably reveal the habits of the two species. Almost all species in the subgenus *Hirtodrosophila* and their close relatives congregate at such sites (Grimaldi, 1987b). The male heads of both species show remarkable convergence with that of *Chymomyza jamaicensis* and *C. diatropa*: the occipital sclerites and the dorsal (but not the facial) portion of the fronto-orbital plates are laterally expanded, the eyes are slightly distended (due mostly to the dorsal expansion—the distance between the ventral margins of the eyes is unmodified), and the face is almost unmodified in width. All four species also have a dark brown band on the oral margin of the face, which may be related to face-off behavior in males and perhaps affect visual fixation.

Drosophila (Drosophila)

Much has been studied about the hypercephalic species *Drosophila (D.) heteroneura* and its close relatives in the *planitibia* species group, particularly *D. silvestris*. The picture-winged group of Hawaiian *Drosophila* is endemic to that region and *D. heteroneura* and *D. silvestris* are found only in rain forest on the big island of Hawaii. They breed in decaying bark of several arborescent, understory lobeliads, but males will form a lek, as do many of the *planitibia* subgroup species, at a large tree fern with each of them defending a leaflet (Conant, 1978). *Drosophila heteroneura* and *D. silvestris* are probably sister species, as based on electrophoretic data (Craddock and Johnson, 1979; Sene and Carson, 1977), DNA hybridization (Hunt and Carson, 1983), polytene chromosome inversions (Carson, 1971), chromosomal location of a middle-repetitive DNA sequence (Hunt et al., 1984), and sexual behavior (Spieth, 1981, 1982), but these results are not congruent with Kaneshiro's (1976) scheme. An alternative taxonomic placement of some of

the Hawaiian "Drosophila" should be noted. Because of the bare eyes and lack of a facial carina, many of the endemic Hawaiian species would be plesiomorphic with respect to *Drosophila* sensu stricto according to a recent phylogenetic hypothesis (Grimaldi, 1987a).

Male *D. heteroneura* have all of the major cranial sclerites broadened with respect to those of *D. silvestris*: the facial sclerite, parafacial plates, frontal vitta, fronto-orbital plates, and the occipital sclerites are distended. The ocellar triangle, median occipital sclerite, and the eyes contribute little to head shape modification. Males of the *planitibia* subgroup species are very aggressive and highly territorial (Spieth, 1982, 1984). The darkly patterned wings are repeatedly semaphored in both species, but vigorously so in the presence of females and while the fly is faced toward another male. Fighting males of *D. heteroneura* slash with their forelegs and head butt against the head and body of their opponent (fig. 5e). This species has apparently lost the habit of fighting males raising the front end of the body (i.e., in *D. silvestris*, see fig. 5d), with one of them eventually depressing the body of the other. Males of *D. heteroneura* that **joust** (where the heads are in direct contact and there is pushing back and forth) may stay in contact for several minutes (Spieth, 1981). In fact, during the joust, the stout palpal setae found in the males lock into each other. Spieth mentioned (1984) that *D. heteroneura* is "the most pugnacious species of the subgroup." He also indicated that head butting is synapomorphic for *D. heteroneura* and *D. silvestris*, since fighting males of *D. silvestris* also butt heads, albeit briefly.

Mulgravea

This genus includes the hypercephalic species *M. asiatica* (originally as *Lissocephala*, then *Thyreocephala*). The species is a distinctively patterned, tiny fly found in Amami, the Ryukus, Formosa, Burma, Malaya, and Java. Despite its widespread distribution, the sexual behavior and other habits have escaped notice. Its closest relatives, sensu Okada (1985), are the Papuan species *M. bimaculata* and *M. parasiatica*.

Widening of the fronto-orbital plates, the

parafacial plates, facial sclerite, occipital sclerites, and even a modest extension of the frontal surface of the eye all contribute to the extreme hypercephaly of these males. The frontal vitta and ocellar triangle are virtually unmodified in width. Okada (1965) compared the dorsal aspect of male and female *M. asiatica* heads using a D'Arcy Thompson transformation grid, which provided a visual portrayal of the amount of expansion contributed by the fronto-orbital plates.

Zygothrica

Fifteen species belonging to this large, predominantly Neotropical lineage are hypercephalic as males, and in a manner unlike that found in the other drosophilids. Hypercephaly has appeared six times according to the recent, phylogenetic analysis (Grimaldi, 1987b) and each time in clade B. In clade B.1, or the *dispar* species subgroup, hypercephaly has appeared three times: in *exuberans + dispar + prodispar* (these have among the most bizarre heads in the genus), in *Z. dimidiata*, and in *Z. dissimulata* (which have moderately broadened heads). Clade B.2, the *aldrichii* subgroup, has two lineages of hypercephalic flies: *pilipes + radialis*, and *tambopata + microeristes*. Lastly, in clade B.3, the *caudata* subgroup, hypercephaly appears just once, involving *aliucapa + caputrichia + laticeps + latipaps + latipanops* (the last species has extremely hypercephalic males, see below). All of the species aggregate at mostly white, imbricate bracket fungi (figs. 5b, c). At the rendezvous site they feed, court, fight, and mate, but they breed mostly in flowers.

Figure 4 shows an apparently extensive morphocline in head shape for *Zygothrica*. There are actually slight differences among the species subgroups in the extent of modification of certain cranial sclerites, thus supporting the previous hypothesis that hypercephaly in the genus is synapomorphic at several levels and convergent at other levels. Nonetheless, the *Baüplan* of *Zygothrica* hypercephaly is nearly unique for the Diptera and shares a gross similarity only with the pattern in the Papuan genus *Asyntona* (Platystomatidae) and some species of *Richardia* (Richardiidae). Lateral distension of the head in *Zygothrica* is due to expansion of the dor-

sal portion of each fronto-orbital plate and to the occipital sclerites, which have pushed the eyes anterolaterad. Displacement of the eye from the plesiomorphic position has resulted in a broad anterior eye surface and a tapered apex. The ocellar triangle and face are slightly expanded to varying degrees in a few species. Bristowe (1924) was the first to report on the sexual behavior of *Zygothrica*; his anecdotal report likened the jousting of *Z. dispar* males to that of rutting bulls. Only recently have further, detailed observations been made on *Zygothrica* behavior (Grimaldi, 1987b; Burla, 1988). Males of most species, but particularly the hypercephalic species, actively defend sites on fungal sporophores. Most activity occurs during the morning and evening; the flies are quiescent for most of the day (e.g., fig. 5c). Confronting males first turn to face each other, from a distance of about 3–4 cm in *Z. prodispar* and *Z. dispar*. They then rush at each other while flicking out the wings one to several times and rapidly vibrating them. During vibration the wing blade surface is usually held vertical to the ground, so that the broad surface is presented to the opponent. Three hypercephalic species have been examined so far, but many more of them and their close, nonhypercephalic relatives need to be studied. When fighting, hypercephalic males face off at about one head-length's distance while rapidly vibrating the wings, and they then may lunge head-to-head and appear to push each other back and forth (jousting) for up to one minute. Actually, Burla (1988) found in *Z. dispar* that during jousting the male heads are very slightly separated and rarely touch. He also found that territorial residents were the most successful males in encounters, and these males also had substantially wider heads than the intruders. Unquantified observations of *Z. prodispar* and *Z. tambopata* corroborate this finding. Large, very hypercephalic males of *Z. prodispar* were found to be particularly active and aggressive. Burla also reported that *Z. dispar* males form temporary leks. However, at least the other two *Zygothrica* mentioned above are simply territorial since the sites include about as many females as males and because the flies feed on the fungal surface ("resource defense polygamy," sensu Emlen and Oring, 1977).

TABLE 2
Mean Facet Diameters (μm) of Hypercephalic
Drosophilidae

	Acute zone	Ventral/ dorsal	Apical
Chymomyza microdiopsis	20.4	14.7	15.6
Chymomyza diatropa	18.2	15.4	15.4
Drosophila caputudis	30.0	24.0	24.0
Mulgravea asiatica	16.0	11.2	14.2
Zygothrica prodispar	19.0	19.0	25.2
Zygothrica pilipes	14.7	14.1	14.1

OPTICAL COMPARISONS

Tables 2 and 3 present data on, respectively, facet diameters (in μm) and estimated optical resolution (as measured per equation given in the Materials and Methods section). The facet diameters of *Chymomyza amoena*, *Mulgravea* sp., and *Zygothrica orbitalis* (species unmodified for hypercephaly) were not measured; the resolution values in table 3 for these species were calculated based on facet measurements of their closest relatives. Instead of "fovea," the term "acute zone" seems most proper since the eye region of highest resolution is not a single, discrete point, but an area or areas grading into the remainder of the eye (Land and Eckert, 1985). Although the acute zone was not measured, which is generally done in degrees from the eye equator (Land and Eckert, 1985), in some drosophilids this region was obviously where there was a round cluster of large facets in the frontal region. Land and Eckert (1985) found that the region of highest resolution coincided with the area of largest facets in *Calliphora erythrocephala* (Diptera: Calliphoridae) (they measured resolution by mapping pseudopupil displacement onto a sphere). In the "acute zone," *Drosophila caputudis* had the largest facets, then *Chymomyza microdiopsis*, *Zygothrica prodispar*, *Chymomyza diatropa*, *Mulgravea asiatica*, and finally *Zygothrica pilipes*. This order is opposite the rank order (from highest to lowest) of measurements in r (radius of curvature of the frontal region of the eye). Generally, then, the eyes with the broadest frontal surfaces (especially *Zygothrica*) had the smaller facet diameters in this region. Given that there is a direct relationship between diameter and

TABLE 3
Optical Resolution Comparisons for Male
Drosophilidae

	R (=r/d)	R_1	r, μm	r_1, μm
*Chymomyza amoena	23.1	—	420	—
Chymomyza diatropa	33.6	14.1	612	218
Chymomyza microdiopsis	17.9	14.4	366	224
Drosophila caputudis	16.8	9.3	505	223
Mulgravea asiatica	26.2	9.8	420	140
*Zygothrica orbitalis	18.0	—	338	—
Zygothrica pilipes	53.1	12.1	780	170
Zygothrica prodispar	37.6	4.8	700	120

* Species unmodified for hypercephaly.
r = mean radius of eye curvature (frontal region), d = mean facet diameter from various regions of eye; R_1 and r_1 are resolution and radius measurements for lateral region of eye.

light-gathering ability (sensitivity) of a facet (Snyder, 1979), it is not surprising that species of *Zygothrica* congregate at white fungi even though brown-colored forms are more common on the tropical forest floor.

Zygothrica appears to have the best frontal resolution, which was estimated at generally twice as acute as that of other hypercephalic species. It should be noted that, on average, males of *Z. pilipes* had broader heads than those of *Z. prodispar*, but in the latter species the range is much greater (see section on allometry). *Chymomyza diatropa* males have broad anterior eye surfaces, and subsequently this species ranked third among the nine for which resolution was calculated. The thorough work of Burkhardt and De la Motte (1983) showed that the span between eyes proportionally increases long-distance depth perception in diopsids. It can safely be assumed that, because the eyes are separated by at least three to four times that which is "normal," diopsid-like species such as *Mulgravea asiatica* and *Chymomyza microdiopsis* are able to resolve images at depths of at least three or four times that which their unmodified relatives can perceive.

In the hypercephalic species for which an additional, lateral curve was fitted onto the eye surface, the radius of this curve was always much smaller than the radius for the frontal region. In *Zygothrica*, because of their apically pointed eyes, the lateral curve of the eye was especially minute (about one-sixth

of the frontal). Also in *Zygothrica*, the facets at the tip of the eye are spaced far apart, and even lost in *Z. exuberans* and extremely hypercephalic males of *Z. dispar*. Thus, the lateral portion of the hypercephalic eyes must have much less resolution than the frontal region. Despite the lateral impairment, hypercephalic males generally have the tips of the eyes extended beyond the lateral surfaces of the thorax, and so these flies should have a rearward, albeit limited, perspective.

The extent of differences in resolution among individuals of *Z. prodispar* is shown in figure 6. A positive, highly significant (p ≤ .01) relationship exists between head width and the radius of eye curvature of the frontal region, with values ranging between 0.29 and 1.09 mm. This variation may be related to a threefold difference in resolving power among the smallest and largest males of *Z. prodispar*, as well as other species such as *Z. dispar* which have such disparate variation in head size. Higher resolving power and better depth perception could probably be translated into an increased ability of hypercephalic males to distinguish distant objects, patterns, and motion. Such an ability, no doubt, would be related to distinguishing conspecifics from other flies, perhaps even distinguishing among conspecifics, and may reduce the time a territorial males takes to react to an intruder.

ALLOMETRY AND HEAD GROWTH

Figure 7 shows four possible types of heterochrony, or differential growth, between species x and y. If the onset of head growth in x is later than in y, but growth rates are equal, the result is **hypermorphosis** of x with respect to y. **Acceleration** occurs when the slope of x is steeper than that of y, and may occur irrespective of the onset of growth. So, the parameters traditionally useful to compare among species are the y-intercepts and slopes (see also, McKinney, 1988). If the slope of the allometric relationship within a species is not significantly different from that of close relatives, then body size is the main variable explaining, in this case, head breadth (Lande, 1985). Even though y-intercepts (in this paper, the axis for head width [HW]) are traditionally used in allometric analyses, it can be a misleading method because it often re-
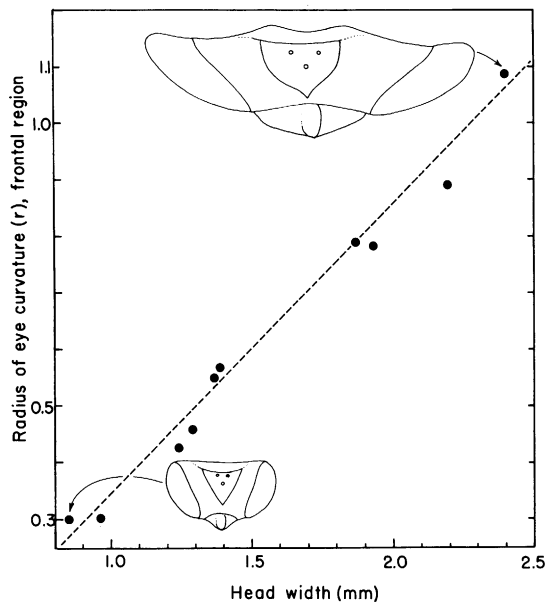

Fig. 6.   Relationship between head width and radius of eye curvature (r, in mm) of the frontal region in males of *Zygothrica prodispar*. The range in variation shown here is the maximum found among specimens from a single collection taken in Panama, and is about as great as that from all sites within the overall distribution of this highly variable species.

quires extensive extrapolation beyond the endpoints of the regression. Such reasoning led to several instances where biologically meaningless, negative y-intercepts were calculated. Thus, here we present both HW (y) intercepts and, more properly, minimum HW values. Given below for each group of hypercephalic Drosophilidae is a discussion of the relative roles of predisplacement and acceleration in head peramorphosis.

Chymomyza. Plots of relative head size for species of this genus are provided in Grimaldi, 1986a. Slopes varied from +2.00 in *C. microdiopsis* to about +0.60 in several nonhypercephalic species, such as *C. amoena* and *C. procnemoides*. The y-intercepts and minimum head width values varied little among the hypercephalic species, but did differ dramatically between these species and the nonhypercephalic ones. Growth acceleration accounts most for *Chymomyza* hypercephaly. Although the trend is not significant (p ≥ .06), the scatter plot suggested that males

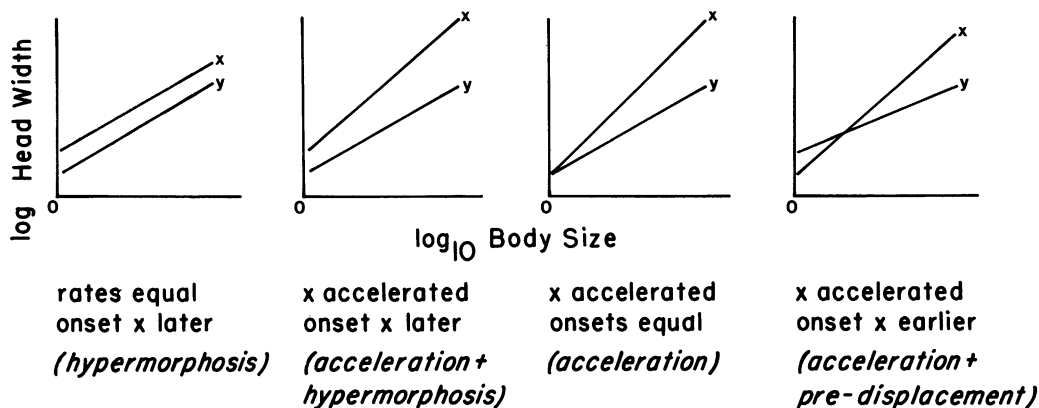| rates equal onset x later	x accelerated onset x later	x accelerated onsets equal	x accelerated onset x earlier
(hypermorphosis)	(acceleration + hypermorphosis)	(acceleration)	(acceleration + pre-displacement)

Fig. 7. Basic models of the differential (peramorphic) growth of x as compared to y and the terms used to describe each mode.

of *Chymomyza microdiopsis* fall into two groups based on relative head width.

Drosophila (Hirtodrosophila). Little can be said of *D. caputudis* because comparison to its closest known, nonhypercephalic relative, *D. (H.) yakushimana* Okada (Grimaldi, 1986b), has yet to be done. Only two males of *Drosophila chandleri* are known, so this species was not included in the regression plot. In the event that sufficient material of these close relatives becomes available, then such measurements can be compared with the data in figure 8 for *D. caputudis*.

Drosophila heteroneura. Specimens of this species and *D. silvestris* were obtained mostly from laboratory stocks and, as a result of constant developmental regimes, little size difference was found among individuals (unfortunately, at least *D. heteroneura* is quite rare in the field, and wild individuals have not been found for the last several years). No significant differences ($p \geq .05$) were detected within or between species for the overall regression (fig. 9), which may be a result of the use of lab material or actually indicate that accelerated growth is not involved in the hypercephaly. However, significant differences were found between species for the means of both HW and ThL. In both species, males had significantly larger ($p < .05$) HW values than the females, while the variances of HW and ThL were not significantly different ($p > .05$). Hypermorphosis seems to account most for the hypercephaly of male

D. heteroneura, but there needs to be a greater range in body size among the specimens to confirm this.

Mulgravea. Two species were measured, *M. asiatica* and an undescribed species in the genus closely related to *asiatica* that is not hypercephalic (fig. 8). $r^2 = 3.99$ for males of *M. asiatica* and is 0.75 for males and females of *Mulgravea* sp. and for the females of *M. asiatica*. Obviously, the 2.50 y-intercept for *M. asiatica* males compared to +0.40 for *Mulgravea* sp. males and females is an artifact of extrapolation, and yields a predisplacement of approximately 500×! Based on minimum y-values for each species, predisplacement may not account at all for *M. asiatica* hypercephaly, but only acceleration.

Zygothrica. Burla (1954, 1955) was the first to describe the allometry of male *Zygothrica* heads. He compared HW and ThL among males of *Z. dispar*, *Z. prodispar*, *Z. laticeps*, and *Z. orbitalis* (the last is not hypercephalic). Although these two studies showed that the slope of the HW-ThL regression was highest for *Z. prodispar*, y-values have not been compared. Perhaps the most intriguing result from Burla's studies was the quantification of a bimodal distribution of male *Z. dispar* head widths relative to thorax lengths. This feature appears obvious to the trained eye, such that males can be sorted into moderately (β-males) and very broad-headed (α) individuals without measuring them. However, the presence of biphasic male allometry has not been cor-
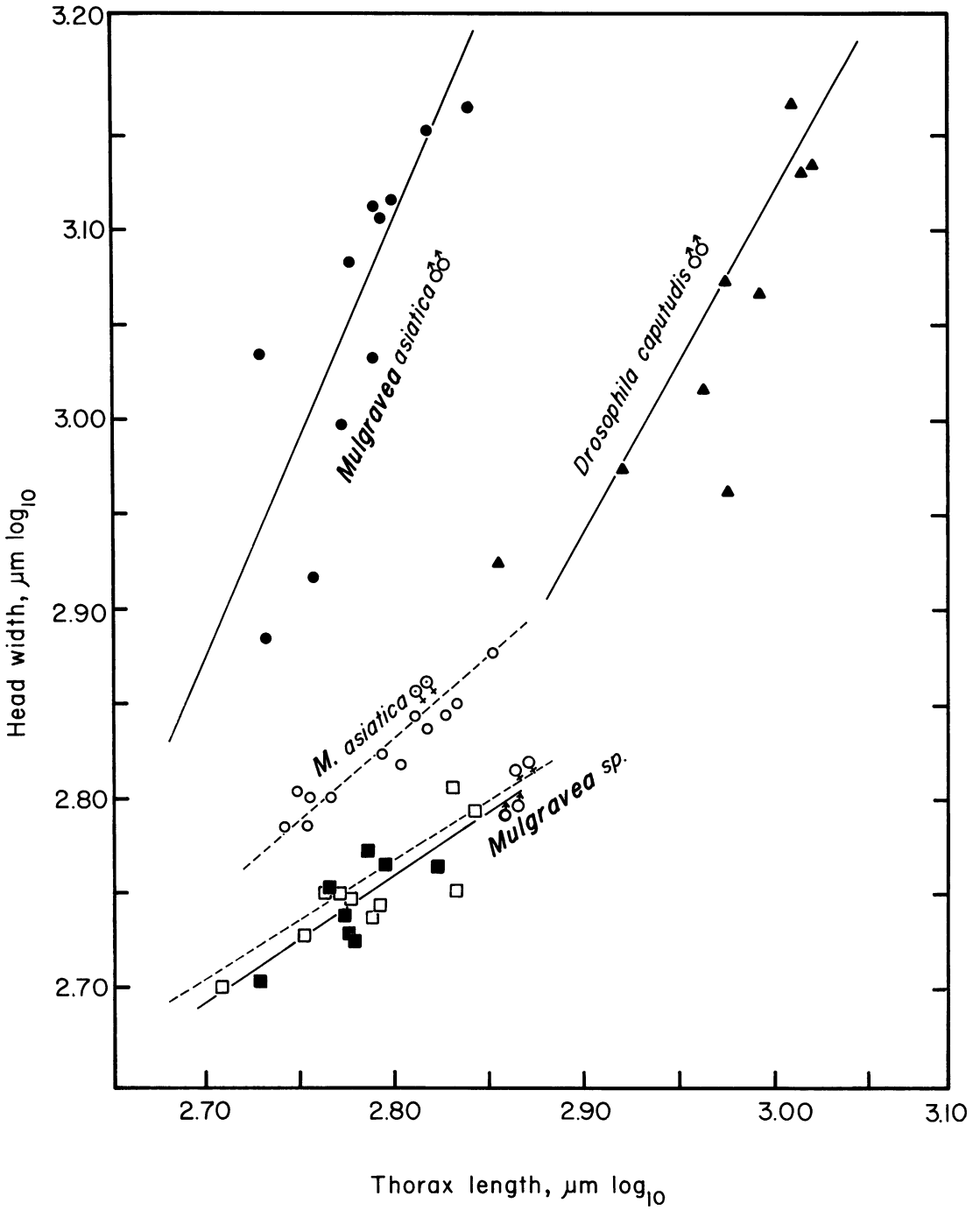
Fig. 8. Relative head sizes in *Mulgravea* spp. and in *Drosophila caputudis* (see text for discussion of regression parameters). In all regression figures the solid symbols are males and the empty ones are females.
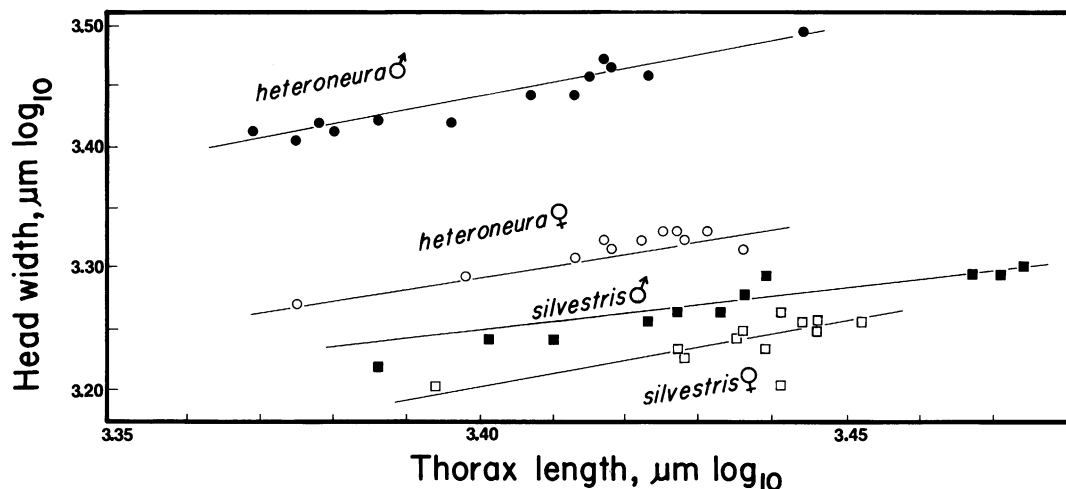
Fig. 9. Relative head sizes in two species of Hawaiian *Drosophila*.

roborated here for *Z. dispar*, nor found in any of the hypercephalic *Zygothrica* species except for one. Sample sizes of the rarer species should eventually be increased so as to more rigorously test for biphasic allometry, but the preliminary indication is that the trait will be rare in *Zygothrica*. In view, too, of the recent discovery of numerous new hypercephalic species (Grimaldi, 1987b), comprehensive data are presented here that compare *Zygothrica* head allometry.

All of the statistical analyses used Version 5 of SAS. Regressions were initially made of $\log_{10}$ transformed values of HW on ThL for each sex of 15 species in *Zygothrica*. Sample sizes (N), y-intercepts and their standard errors, minimum y values, slopes and their standard errors, and r^2 values are presented in table 4. Comparisons were made between species, and between sexes in some cases, for slopes and minimum y-values. For *Z. dispar*, *Z. prodispar*, and *Z. microeristes*, the males were divided into groups based on collecting locality, and locality regressions were compared as a check for geographic variation in allometry. Since no geographically distinct groups were found, individuals were pooled where necessary from several collecting localities. ANOVAs and a posteriori multiple comparison tests examined for differences among mean HW and ThL values within each species group. T- tests and F-tests compared the means and variances, respectively, of the sexes within each species. Principal compo-

nents analyses (PCA) on the covariance matrix of the males of each species were used to test for the existence of α- and β-males.

Spearman's rank correlation coefficients (r_s) indicated that there was little relationship between HW (y)-intercepts and minimum y values for males in the *aldrichii* and *dispar* subgroups. The r_s for the *caudata* group (-0.87) was strongly negative, and was calculated with the division of *Z. latipanops* into α- and β-males. The only other negative relationship was for *aldrichii* subgroup males (-0.40). For each group r_s was higher when sexes were pooled as well as when all of the *Zygothrica* species were included. Every attempt possible was made to include specimens representing the range in size for measurements of each species; thus, with the lack of correlation discussed above, it would appear that minimum y value, not y-intercept, is most appropriate to estimate size at the initiation of head growth in *Zygothrica*. All regressions are displayed as scatterplots in figures 10–12. Allometric descriptions of the head for each of the three *Zygothrica* species subgroups that have hypercephalic members are given below.

The *dispar* Species Subgroup. Both *Z. antedispar* and *Z. exuberans* had sample sizes too low for statements to be made regarding their regressions, and they are presented in the plots in figure 10c simply for visual comparison. *Zygothrica dispar* (fig. 10a) and *Z. prodispar* (fig. 10b) both had significant diff-

TABLE 4
Regression Values for *Zygothrica* Species

	Y-intercept	SE of intercept	Min. Y-value	Slope	SE of slope	r²
Males						
Male latipanops (N = 16)	−2.189	3.120	—	1.729	0.954	0.190
A-male latipanops (N = 8)	−13.293	8.850	1.46	5.162	2.710	0.165
B-male latipanops (N = 8)	−8.810	2.053	3.26	3.721	0.626	0.620
caudata (N = 4)	0.305	0.866	3.10	0.878	0.265	0.845
latipaps (N = 3)	−0.658	0.501	3.08	1.178	0.154	0.983
posthona (N = 5)	−0.674	0.410	3.14	1.187	0.043	0.996
microeristes (N = 62)	−2.063	0.445	2.95	1.678	0.146	0.686
pallida (N = 32)	−0.388	—	2.88	1.099	—	0.954
pilipes (N = 9)	−3.670	1.170	2.19	0.828	0.379	0.828
radialis (N = 37)	−2.686	0.340	2.96	1.873	0.111	0.891
tambopata (N = 34)	−2.981	0.414	2.97	1.962	0.134	0.869
antedispar (N = 4)	3.500	0.424	3.02	−0.152	0.136	0.387
dimidiate (N = 15)	0.833	0.978	2.96	0.178	0.317	0.795
dispar (N = 106)	−6.528	0.480	2.94	3.177	0.157	0.798
exuberans (N = 6)	−4.140	2.867	3.39	2.444	0.916	0.640
prodispar (N = 119)	−3.898	0.396	2.89	2.284	0.128	0.730
heteroneura (N = 15)	−0.613	0.424	3.40	1.191	0.124	0.876
silvestris (N = 12)	0.320	0.365	3.22	0.858	0.106	0.867
Females						
latipanops (N = 4)	1.195	0.612	3.22	0.401	0.184	0.703
latipaps (N = 4)	−0.544	0.382	3.16	1.136	0.115	0.980
posthona (N = 7)	1.639	0.652	3.16	0.471	0.200	0.528
microeristes (N = 26)	0.044	0.196	2.95	0.965	0.064	0.905
pilipes (N = 5)	−2.520	0.901	2.98	1.785	0.288	0.928
radialis (N = 17)	0.084	0.433	2.98	0.952	0.139	0.757
tambopata (N = 18)	0.271	0.374	2.98	0.887	0.120	0.775
antedispar (N = 2)	2.411	—	3.04	0.202	—	1.000
dimidiata (N = 16)	0.510	0.413	2.92	0.813	0.133	0.728
dispar (N = 33)	0.283	0.252	2.97	0.892	0.081	0.795
prodispar (N = 24)	0.491	0.359	2.95	0.820	0.116	0.696
heteroneura (N = 11)	0.012	0.456	3.27	0.966	0.133	0.853
silvestris (N = 11)	0.117	1.037	3.20	0.908	0.302	0.502

ences in the male and female regressions (p ≤ .05 for both slopes and intercepts). Growth acceleration appears to be the main factor in the hypercephaly of these two species. *Zygothrica dimidiata* and *Z. antedispar*, which did not have sexually dimorphic regressions, were also the two species of the group with positive male y (HW)-intercepts. For *Z. dispar* and *Z. prodispar*, mean HW was significantly larger in the males, while, as is true for most flies, mean ThL was larger in females. Also interesting is the finding that these are the only two species of the group for which there were significant differences in the variance of either trait. In both species the males were more variable in HW than were females.

Slopes and intercepts of males were different among species (p ≤ .05), but this was not true for the pooled sexes and for females only. Thus, a comparison of male regressions excluding *Z. antedispar* and *Z. exuberans* showed the slopes and intercepts to be different (p ≤ .05). *Zygothrica antedispar* is the member of this group studied here that is not hypercephalic, even though it is among the largest of the species. It is also the only member that had a negative slope, though this could be a result of small sample size. For mean HW, *Z. exuberans* and *Z. antedispar* were at opposite extremes of the range, whereas they were indistinct for ThL and together separated from the other three species
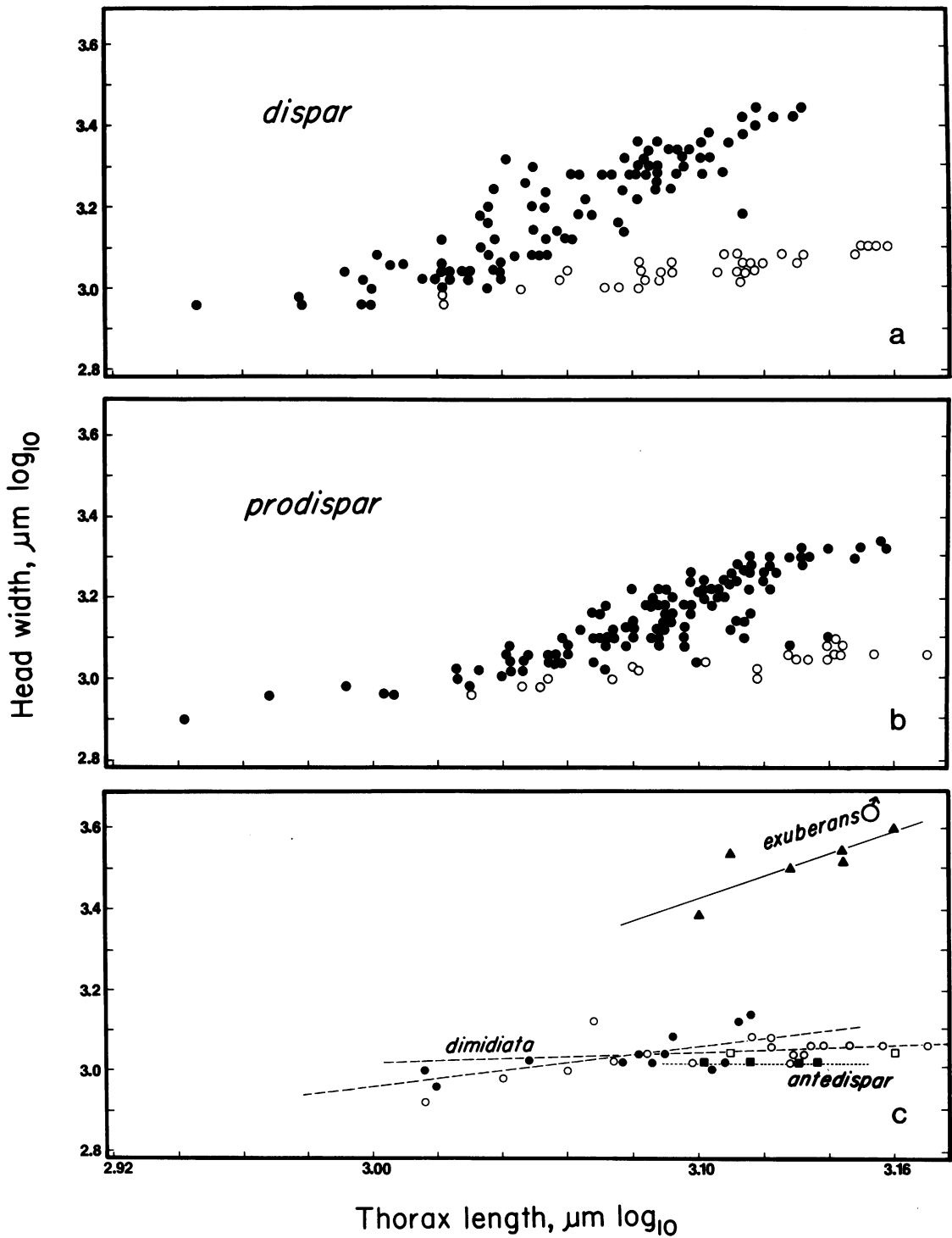
Fig. 10.   Relative head sizes in five species of the *Zygothrica dispar* species subgroup.
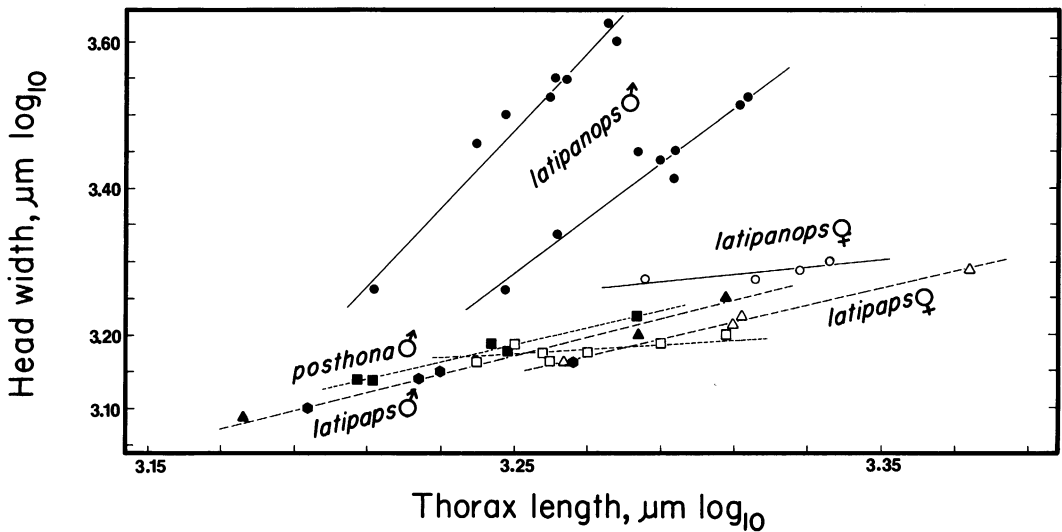
Fig. 11.   Relative head sizes in three species of the *Zygothrica caudata* species subgroup.

(Duncan's multiple range test). *Zygothrica dispar* and *Z. prodispar* males group apart from *Z. dimidiata* based on HW even though all three species have similar ThL. The ANOVA indicated that females, in contrast to males, showed no significant differences among species in mean HW or ThL.

The *caudata* Species Subgroup. With the exception of *Z. latipanops*, the sample sizes for this group are too small to have much confidence in the regressions (fig. 11). Significant differences in the slope and intercepts were found between sexes of *Z. latipanops* and *Z. posthona*. Regression comparisons among species indicated no significant differences when the sexes were pooled or for just the male regressions. However, significant differences were found for both the slopes and intercepts of the females! These differences may be due to small sampling effects and perhaps as well to smaller female variances. *Zygothrica latipanops* is similar to *Z. dispar* and *Z. prodispar* in that males are much larger and more variable in HW than are females, which are larger in ThL. Males of *Z. latipanops* were divided into two principal components, the major difference of which was primarily along the second principal component (for which ThL weights most [p < .05 for equal ThL means]). Slopes and in-

tercepts of the two male groups were significantly different (e.g., fig. 11). This is the only one among four *Zygothrica* species analyzed for which biphasic allometry was found. Not surprisingly, this is the most modified in relative head width among all *Zygothrica* species. In this subgroup, too, acceleration accounts for hypercephaly.

The *aldrichii* Species Subgroup. *Zygothrica pilipes*, which had the lowest sample size in the group, was the only species that had no allometric sexual dimorphism (for this species, females are more hypercephalic than is found in any other *Zygothrica*). For all species the male y-intercept was negative, and for *Z. pilipes* this was true for females as well. *Zygothrica pallida* was the member of the group studied here that is not hypercephalic, and it showed the same allometric relationship to other members of its group that the nonhypercephalic species *Z. antedispar* showed to other members of the *caudata* subgroup (fig. 12). Accelerated growth of male heads accounts for the sexual dimorphism in this subgroup.

GENERAL GROWTH CONSIDERATIONS

Similarities are seen in the modification of head setae in some hypercephalic *Zygothrica*
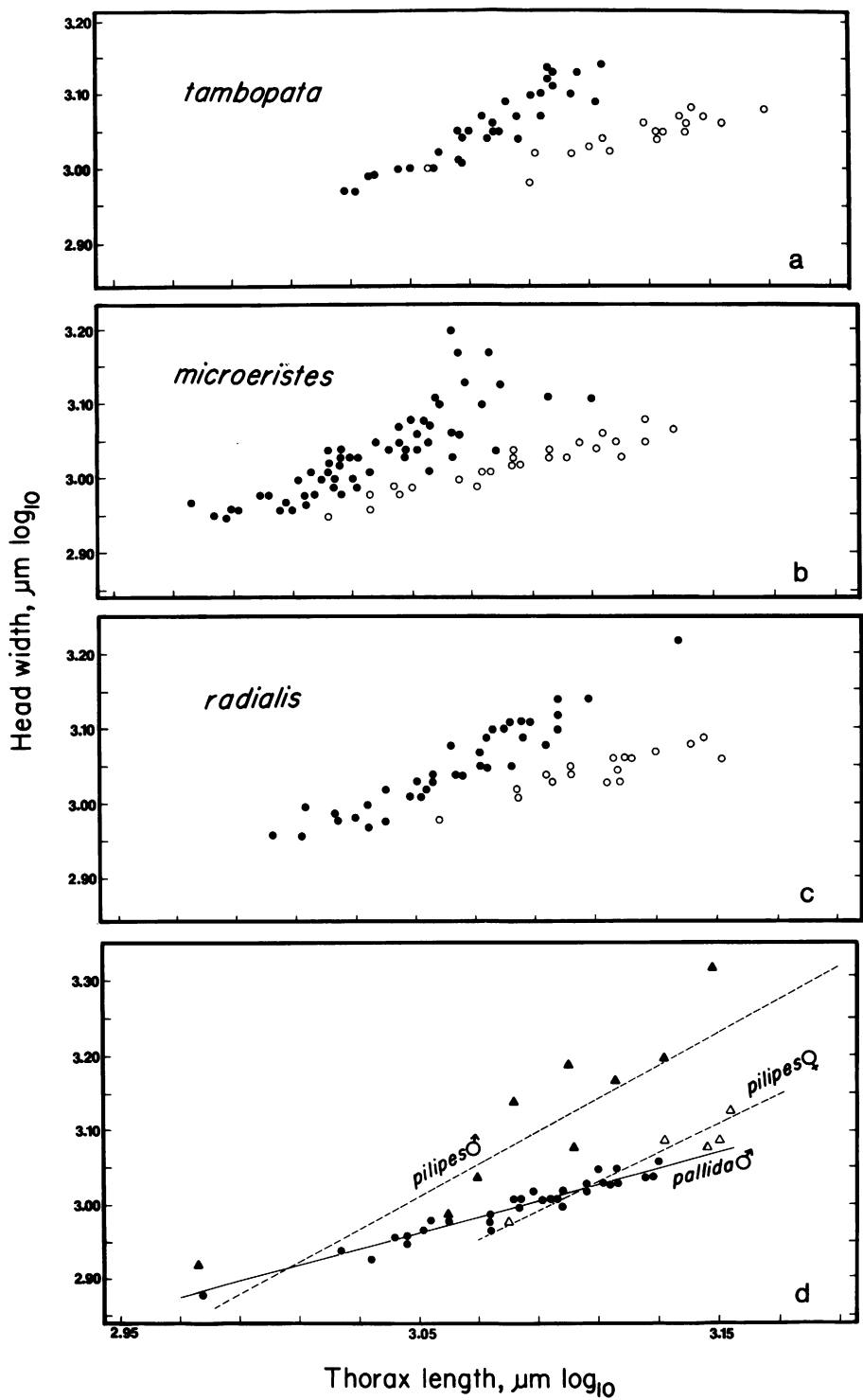
Fig. 12.   Relative head sizes in five species of the *Zygothrica aldrichii* species subgroup.
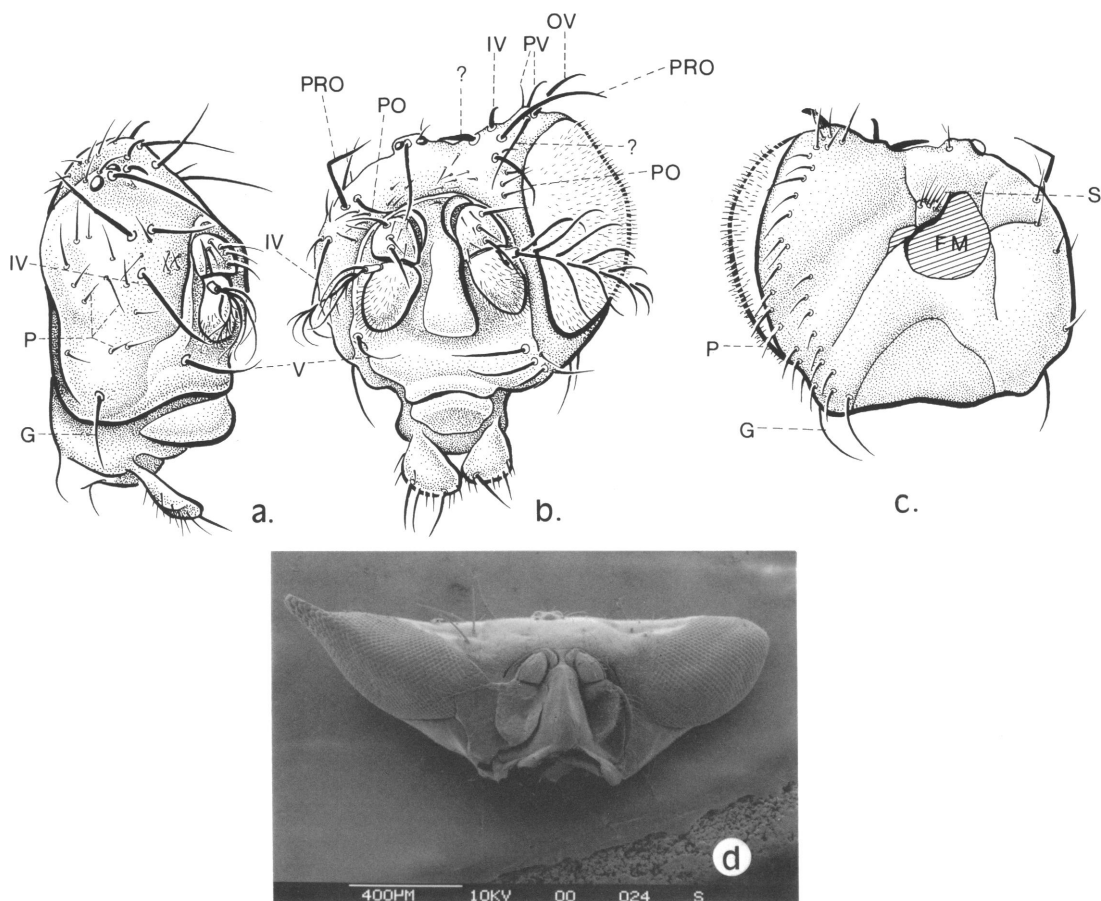
Fig. 13. Abnormal head growth in some drosophilids. **a–c**, *Drosophila recens*, unilateral eyeless mutant (a, lateral; b, frontal; c, posterior views). Setal abbreviations same as in fig. 14 plus the following: G, genal; PO, proclinate orbital; PRO, posterior reclinate orbital; S, supracervical; V, oral vibrissa. Note duplication and kinking of some setae in the same manner as for extremely hypercephalic *Zygothrica* (fig. 14). **d**, scanning electron micrograph of *Zygothrica dispar* male head (frontal view). Of nearly 5000 specimens examined for this species, this individual was the only one with asymmetrical eyes. Drosophilid eyes develop independently from separate anlage. The asymmetry is either rarely produced, rarely viable, or its rarity is due to a combination of both factors.

and those *Drosophila* mutants that have various degrees of eyelessness (*ey*). Three instances of *ey* are known in *Drosophila*: *D. melanogaster* (reviewed in Lindsley and Grell, 1968), *D. pseudoobscura* (Farmer, 1984), and *D. recens* (Jaenike, 1985) (fig. 13). For all three species a gradation of partial to completely unilateral or bilateral eyelessness can occur. Proportional to the degree of eyelessness is the extent of loss, duplication, and/or malformation of the ipsilateral orbital and vertical setae (this fact corroborates early anlage studies which showed that development

of either side of the head is independent of the other—e.g., fig. 13d). Ipsilateral to the lost or reduced eye is an arista that is lost or malformed, but the base of the antenna, the face, and the contralateral portions of the head are rarely affected. The setae are sometimes duplicated, and nearly always are stubby or crooked.

The smallest males of several hypercephalic *Zygothrica* have relatively normal setae on the head and thorax. While no acrostichal setal modifications occur in the *Drosophila ey* mutants, there is an obvious

and direct relation, within and among *Zygothrica dispar, Z. exuberans,* and *Z. prodispar,* between the degree of hypercephaly and the size of postvertical, postocular, and acrostichal setae (fig. 14). In addition, in the most hypercephalic individuals of *Z. dispar* and *Z. microeristes,* several of the verticals and/or postverticals are crooked. In *Z. latipanops* (not figured), the most hypercephalic males have duplicated proclinate orbital and dorsocentral setae. Thus, gross expansion of a cephalic sclerite apparently accelerates the growth of the setae that lie on it (during the pupal stage) and, in extreme cases, the development of normal, straight setae is disrupted. Perhaps a similar mechanism affects the hypermorphic interfacetal (eye) setulae in *Drosophila (H.) chandleri* (see Grimaldi, 1988) and the unrelated species in *Diopsosoma* (Diptera: Periscelidiidae). Both of these hypercephalic taxa have a patch of long, stout, scaliform setulae in the middle of each eye, which may be related to a particular environmental condition and manner of vision, a result of cephalic hypermorphosis, or perhaps a combination of both. These growth patterns suggest the involvement of a general inducer affecting particular areas of the head and all structures within such regions, such as has been hypothesized for color patterns in lepidopteran wings (Nijhout, 1986).

Convergent patterns in drosophilid hypercephaly illustrate that various sets of cranial sclerites are involved. For example, in all instances of fronto-orbital plate widening there is a widening of the occipital plates as well; likewise for the face in conjunction with the fronto-orbital plates. In only some instances of eye distension are the parafacial plates also distended. These patterns are no doubt a reflection of the eye-antennal anlage structure and growth (Ouweneel, 1970; Ransom, 1982), and they at least corroborate that the eye behaves like and should have the same developmental origin as the other cephalic sclerites (Butt, 1960). It might be of great benefit to select and cross some hypercephalic and non-hypercephalic drosophilids, and determine the genetic bases of head shape modifiers. Unfortunately, most of the hypercephalic drosophilids are either quite rare or are very demanding for laboratory culture.

Despite the fact that *Zygothrica dispar*

probably is not biphasically allometric for male hypercephaly, the subsequent discovery that *Z. latipanops* indeed is indicates that biphasic allometry in male secondary sexual features extends across several orders of insects. Numerous other hypercephalic Diptera have yet to be tested. Biphasic allometry in male horn size and shape occurs repeatedly in various beetle taxa, including Ciidae, Leiodidae, Scarabaeidae, Staphylinidae, Tenebrionidae, and other families. Besides beetle horns and wide fly heads, we are unaware of any studies on other orders where a male sexual character has been tested for a biphasic distribution, so it is difficult to say exactly how widespread male biphasic allometry is. However, given the repeated appearance of the trait among at least some insects, one must conclude that environmental factors, such as differences in larval nutrition, have only minor involvement, and probably act in conjunction with some more influential, genetic-developmental factors. The expression of the trait is very similar to those exhibiting **threshold effects,** the mechanism of which is usually seen in physiological processes (e.g., enzymatic rates) but which we believe could also be involved in morphogenesis. It is possible that at least some structures are subject to threshold effects during development, but due to the scale of measurement and error, threshold effects are most likely to be detected in exaggerated features: the greater the variance in the size and/or shape (as was found to be the case for the hypercephalic drosophilids), the more defined morphs become.

CONVERGENCE AND "ADAPTATION"

Figure 15 is a phylogenetic hypothesis (cladogram) of the five drosophilid taxa where hypercephaly occurs, with several morphological and behavioral apomorphies added. The monophyly and relative relationships of these genera and of groups therein are supported mostly on the basis of morphological features different from those in the analysis. Several aspects of the diagram require detailed discussion. Somewhat obvious is the fact that an altered visual field, either an improvement in frontal resolution (for apically tapered eyes) or binocularity (for the pedun-

HEAD, DORSAL SURFACE   **PROFILE OF NOTUM**

dispar

SMALL MALE

LARGE MALE

exuberans

LARGE MALE
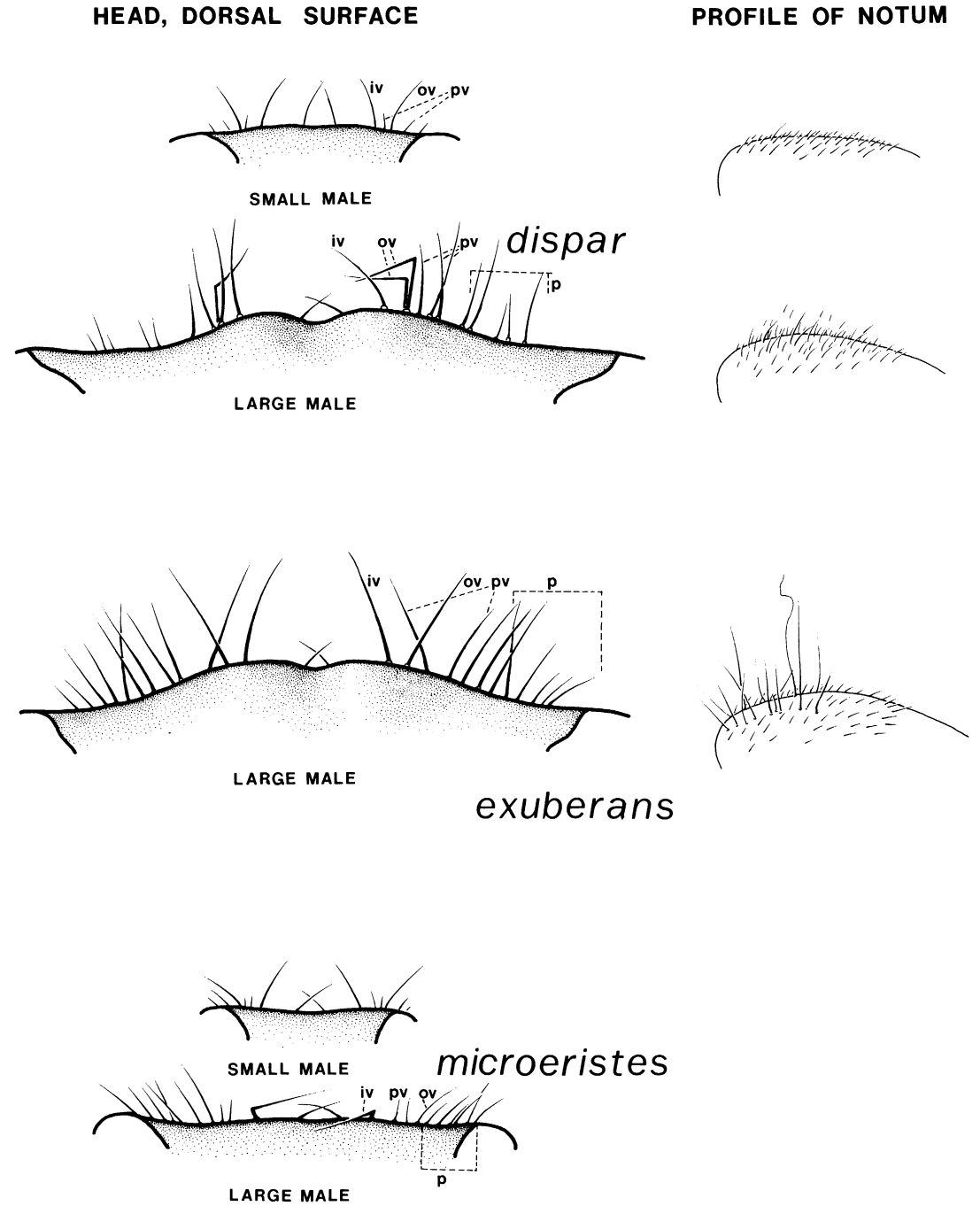
microeristes

SMALL MALE

LARGE MALE

Fig. 14.   Head (dorsal surface) and notal setae (dorsal thorax in lateral view) in some hypercephalic *Zygothrica*. Shown are a large and small *Z. dispar* male, a large *Z. exuberans* male, and a large and small male of *Z. microeristes*. iv, inner vertical seta; ov, outer vertical seta; p, postocular seta; pv, postvertical seta.

culate forms) is always associated with mod-ification of head shape. The data are limited, but it appears that jousting by fighting males is concomittant with hypercephaly. Studies
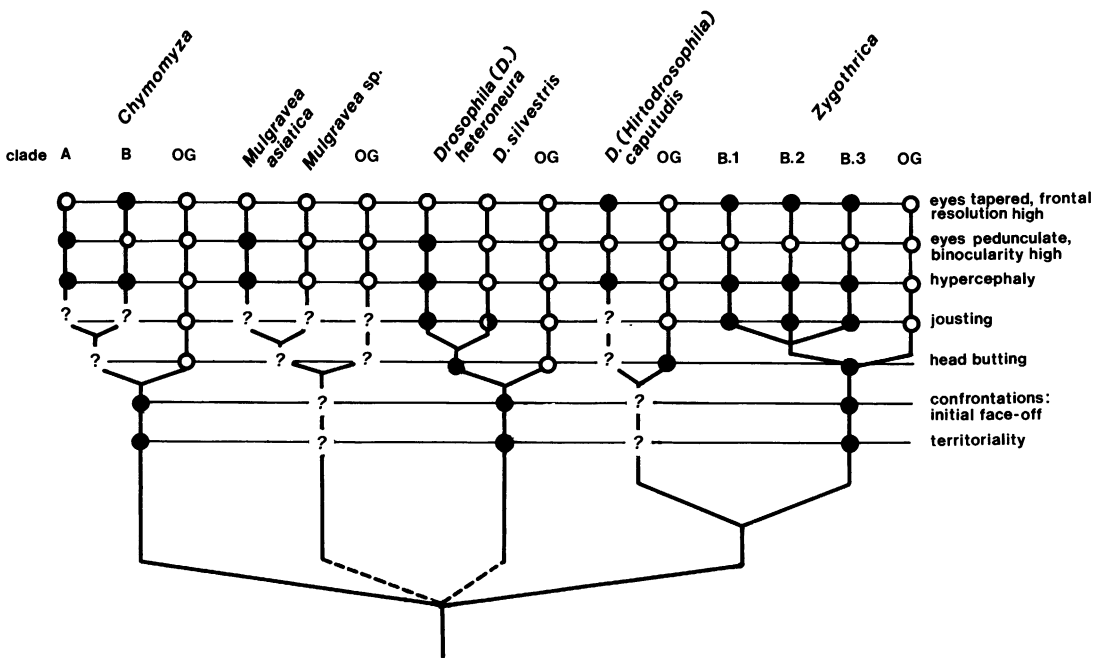
Fig. 15. Phylogenetic hypothesis of various traits associated with male hypercephaly in several taxa of Drosophilidae. Not all of the features that distinguish between the various clades (e.g., *Zygothrica* B.1, B.2, B.3) have been included. "OG" is the most closely related outgroup for each of the various taxa, and was used to polarize the state of each morphological and behavioral apomorphy. Apomorphic states are dark circles, plesiomorphic states are empty circles. Although the apomorphies at the right of the figure are convergent among most of the higher groups, they are defined as synapomorphies for the more terminal taxa on the basis of differences in structural and behavioral details. The relationships of *Mulgravea* and the Hawaiian *Drosophila* to the other taxa have yet to be detailed; ? indicates missing data, see text for discussion.

on the very hypercephalic species *Chymomyza microdiopsis* and *Mulgravea asiatica* would provide the best test of this prediction. Males that fight by using the head very briefly to butt the body or head of the opponent are more widespread in drosophilids than are jousting males, and such males are found among the outgroup taxa. For example, the nonhypercephalic species *Zygothrica orbitalis* doesn't joust, but does use the head for brief butting, and the situation is similar for *Drosophila silvestris*. Of the several species of *D. (Hirtodrosophila)* that have been observed by Grimaldi, males behaved this way; but, again, for *Chymomyza* and *Mulgravea* more data are needed. For the three taxa that are known well enough, it appears that territoriality and confrontations where males initially face each other are traits even more widespread than is head butting. In *Myco-*

drosophila, which is closely related to the subgenus *Hirtodrosophila*, males are territorial but, in at least two Neotropical species observed by Grimaldi, fighting males back into each other and slash with the hind legs.

Thus, there are apparently certain preconditions ("preadaptations," sensu Cuénot [1936] and ultimately others) associated with the rise of male hypercephaly in the Drosophilidae, and probably other flies as well: territoriality, face-to-face confrontations, then head butting, and jousting. There is a general trend for the hypercephalic drosophilids to be more aggressive than their unmodified relatives; that is, engage in more confrontations. Therefore, we interpret jousting to be just a prolonged bout of head-to-head butting, taking place between aggressive individuals that are not prone to immediately back away in an encounter as are most nonhypercephalic

flies. Thus, there are alternative explanations to such adaptationist ones as McAlpine's "size up" hypothesis. We do admit that understanding the evolution of this sexual dimorphism may be enhanced by studies of selection and developmental mechanisms. For example, given the improved binocularity or resolution associated with hypercephaly, why are just a few taxa hypercephalic? There could be insufficient selection pressure and/or genetic variation for hypercephaly in most species of Drosophilidae. Perhaps selection for hypercephaly in some taxa imparts substantial developmental consequences (e.g., Carson and Teramoto, 1984), more severe than those discussed for *Zygothrica*? Such questions can only be posed now that the descriptive and comparative basis has been established.

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