

**EXTREME HEAD MORPHOLOGY IN PLASTOTEPHRITINAE
(DIPTERA, PLATYSTOMATIDAE), WITH A PROPOSITION OF
CLASSIFICATION OF HEAD STRUCTURES
IN ACALYPTRATE DIPTERA**

Andrew E. WHITTINGTON

Consultant Entomologist, 2 Newhouse Terrace, Dunbar, EH42 1LG, Scotland.

E-mail: awhittington@btopenworld.com

Extreme head morphology in Plastotephritinae (Diptera, Platystomatidae), with a proposition of classification of head structures in acalyptrate Diptera. - Modification of the head capsule in flies is known from several families of Diptera. In nearly all instances the accompanying agonistic behaviour suggests sexual selection for increased morphological change. This paper examines and explores the variety of head modifications found in the Plastotephritinae (Diptera, Platystomatidae) and, in the absence of biological observations regarding sexual behaviour and oviposition, suggests that similar agonistic, territorial behaviour and sexual selection is likely in Plastotephritinae. In addition, a system of classification of head modifications is proposed to aid future discussion and later (possibly phylogenetic) analysis, listing 9 (+ 1 intermediate) categories of head modification in Plastotephritinae and 4 further categories in other dipterous families.

Keywords: Platystomatidae - Plastotephritinae - head modification - agonistic behaviour - sexual selection - morphology.

INTRODUCTION

For many families of Diptera, sexual dimorphism of the head is immediately obvious, for example, males are frequently holoptic, while females are dichoptic. In families where members of both genders are dichoptic, the presence of dimorphism is far less easy to detect, although it may be present to a degree. Furthermore, sexual dimorphism need not necessarily be restricted to the relative proximity of the eyes, since various modifications to the shape of the head capsule are also known.

There are many instances of unusual head shape in Diptera. Indeed, the whole family Diopsidae is renowned for extended eye stalks (hypercephaly). Shillito (1971b) demonstrated sexual dimorphism in 5 species of Diopsidae, and one species each in Tephritidae and Platystomatidae, showing females to approximate normality, while males exist in two forms – female-like or with distinctly elongated eye-stalks. In some species, e.g. *Teleopsis dalmanni* (Wiedemann, 1830) males showing distinct elongation of eye stalks also have modifications to the fore femora, which are lacking in smaller males (Shillito, 1971b).

It has been noted before that Platystomatidae frequently exhibit facial patterning and wing markings, the latter used in semaphoring, for mate attraction and

territorial behaviour, hence the common name “signal flies” (McAlpine, 1998, 2000; Whittington, 1998). In certain genera, e.g. *Achias* Fabricius, 1805 (McAlpine, 1994) and *Laglaisia* Bigot, 1878 elaboration of the head capsule and agonistic behaviour are clearly associated and have been observed in field experiments (McAlpine, 1975).

In a revision of Afrotropical Plastotephritinae, Whittington (2003) noted similar dynamic development of the head capsule in some genera and the probable existence of agonistic behaviour. While such behaviour has not yet been observed for Plastotephritinae, the morphology supporting it is freely available for study.

Plastotephritinae (Diptera, Platystomatidae) range from species with no apparent sexual dimorphism (e.g. *Stellapteryx stellata* Whittington, 2003) to genera with a particularly large variety of head modifications, including the development of eye stalks, protrusion of genal sclerites and dorsal extension of the orbital plate. This paper aims to examine the range of development of the head capsule in Plastotephritinae, of which the Oriental and Afrotropical species have recently been revised (Whittington, 2000, 2003).

MATERIAL AND METHODS

A large number (1100) of pinned specimens of Afrotropical and Oriental Plastotephritinae were examined (see Whittington, 2000, 2003) and drawn using a Wild Heerbrugg M5 microscope, with millimetre calibrated graticule and drawing tube fitted. Samples of these were measured and morphometric analyses were carried out using statistical functions in Microsoft® Excel 2002. All illustrations were previously published in Whittington 2003 (reprinted with permission from Ampyx Verlag).

Body size ranges for Acalyprate flies were accumulated from adult size ranges for families in Soós & Papp (1984a, b, 1988), McAlpine *et al.* (1987) and Papp & Darvas (1998, 2000) and, because these are generalised ranges, must be treated as approximate.

Morphology generally follows White *et al.* (1999) and Whittington (2003). Head widths (Hw) were measured across the extremity of the widest point (the eyes in some genera, the gena in others).

Student's t-test (Elliot, 1983) was applied to test the null hypothesis: *H₀* = *there is no significant difference in the head width of males and females in any particular genus*. *Micronesomyia* Whittington, 2003, for which there was only a single specimen of each sex, was excluded from the analysis. Genera were ranked using untransformed differences between male and female head widths. All samples (except *Conopariella* Enderlein, 1922 for which sample sizes were sufficiently large) were subjected to a log transformation, prior to applying the t-test.

Following the t-test, log values of male head widths were plotted against body length for genera resulting in a significant difference and compared to a “standard” genus, *Venacalva* Whittington, 2003. In addition, genera obviously exhibiting hypercephaly, such as *Agrochira* Enderlein, 1911 and *Mesanopin* Enderlein, 1912, were included. R-squared values were derived directly from the Microsoft® Excel 2002 program.

Based on descriptive analyses, both in the literature and provided by morphometrics, a classification scheme was devised to cover examples from a broad range of dipterous families.

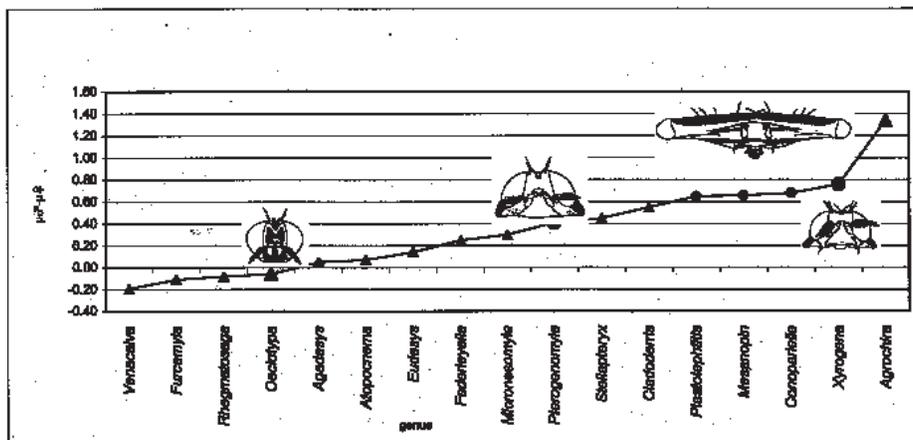


FIG. 1

Untransformed difference between mean head width in male and female samples of Afrotropical and Oriental Plastotephritinae (statistically significant results indicated by circles; non-significant results indicated by triangles). Illustrated genera* indicated by enlarged datapoints from left: *Oeciolyta disjuncta* Whittington, 2003; *Pterogenomyia picta* (Bigot, 1891); *Agrochira parallaxis* Whittington, 2003; and *Xyrogena hyphena* Whittington, 2003 (bottom) [*Reproduced from Whittington, 2003, with permission from Ampyx Verlag].

RESULTS OF MORPHOMETRIC ANALYSIS

Head width in male and female Plastotephritinae exhibit a range of dimorphism (Fig. 1) from almost no discernable difference between sexes (e.g. *Agadasys* Whittington, 2000 ($x_{\text{diff}}=0.05\text{mm}$; $sd_{\text{pooled}}=0.17$; $n=4$)) to very large differences in which males have greatly enlarged heads (e.g. *Agrochira* Enderlein, 1911; $x_{\text{diff}}=1.34\text{mm}$; $sd_{\text{pooled}}=2.06$; $n=31$). As can be seen from the statistical analysis (Tab. 1), these perceived differences are statistically significant in *Pterogenomyia* Hendel, 1914, *Plastotephritis* Enderlein, 1922, *Conopariella* Enderlein, 1922, *Mesanopin* Enderlein, 1912, *Xyrogena* Whittington, 2003.

In some genera, *Oeciolyta* Hendel, 1914, *Rhegmatosaga* Frey, 1930, *Furcanyia* Whittington, 2003 and *Venacalva* Whittington, 2003, females have slightly larger heads than males, resulting in negative values for the difference between means.

Unexpectedly, no significant difference between means of male and female members of *Agrochira* Enderlein, 1911 and *Cladoderris* Bezzi, 1914 were found. Members of *Agrochira* have extreme lateral head modification in the form of stalked eyes, but modification may occur in both sexes, with the result that differences are not statistically significant. In *Cladoderris*, head modification is in the form of lateral and outward extension of the gena, apparently (but not statistically) more pronounced in males (Fig. 2).

It is important to clarify whether or not the observations made reflect increase in size only and that they are in fact allometric. This was tested for genera exhibiting significance in the t-test for head width dimorphism. The R-squared results were compared to *Venacalva* as a "standard" and included the anomalous *Agrochira*. These

TABLE 1. Statistical analysis of head width comparison between sexes in Afrotropical and Oriental Platyptetrinae (Diptera, Platyptetrinae). Genera are ranked according to the untransformed difference of means and Student's t-test was applied to the log normalised data for all except *Conopariella* Enderlein, 1922.

Genus	Hw males			Hw females			Untransformed data			Results	
	$\mu\delta$	n	s	$\mu\delta$	n	s	$\mu\delta - \mu\delta$ ranked	pooled s	N	df	Student's-t-test
<i>Venacalva</i> Whittington, 2003	3.48	5	0.67	3.67	7	0.31	-0.19	0.48	12	11	-2.152 NS
<i>Furcamiya</i> Whittington, 2003	4.55	8	0.56	4.66	7	0.69	-0.11	0.61	15	14	0.000 NS
<i>Rhegmatosaga</i> Frey, 1930	3.75	4	0.4	3.83	3	0.35	-0.08	0.35	7	6	-0.262 NS
<i>Oeciotypa</i> Hendel, 1914	3.75	21	0.37	3.81	24	0.46	-0.06	0.41	45	44	-0.669 NS
<i>Agadasys</i> Whittington, 2000	1.8	2	0.28	1.75	2	0.07	0.05	0.17	4	3	0.194 NS
<i>Atopocnema</i> Enderlein, 1922	4.46	16	0.26	4.39	16	0.49	0.07	0.39	32	31	1.193 NS
<i>Eudasys</i> Whittington, 2003	4.5	5	0.5	4.36	5	0.26	0.14	0.38	10	9	0.383 NS
<i>Federleyella</i> Frey, 1932	3.97	23	0.56	3.72	15	0.43	0.25	0.52	38	37	1.113 NS
<i>Micronexomyia</i> Whittington, 2003	4.2	1		3.9	1		0.3				
<i>Pterogenomyia</i> Hendel, 1914	4.13	26	0.6	3.72	46	0.38	0.41	0.51	72	71	2.567 *
<i>Stellapteryx</i> Whittington, 2003	4.28	4	0.59	3.83	3	0.64	0.45	0.6	7	6	0.908 NS
<i>Cladoderris</i> Bezzi, 1914	4.78	10	1.62	4.23	6	0.77	0.55	1.36	16	15	0.727 NS
<i>Plastotephritis</i> Enderlein, 1922	7.33	13	0.53	6.68	12	0.77	0.65	0.72	25	24	2.401 *
<i>Mesanopin</i> Enderlein, 1912	5.37	35	1.36	4.71	32	0.92	0.66	1.21	67	66	2.452 *
<i>Conopariella</i> Enderlein, 1922	5.68	60	1.13	5	72	0.65	0.68	0.96	132	131	4.127 ***
<i>Xyrogena</i> Whittington, 2003	5.71	22	0.99	4.95	30	0.74	0.76	0.92	52	51	3.054 ***
<i>Agrochira</i> Hendel, 1914	4.38	17	2.54	3.04	14	0.86	1.34	2.06	31	30	1.389 NS

Ho= there is no significant difference in the head width of males and females in any particular genus

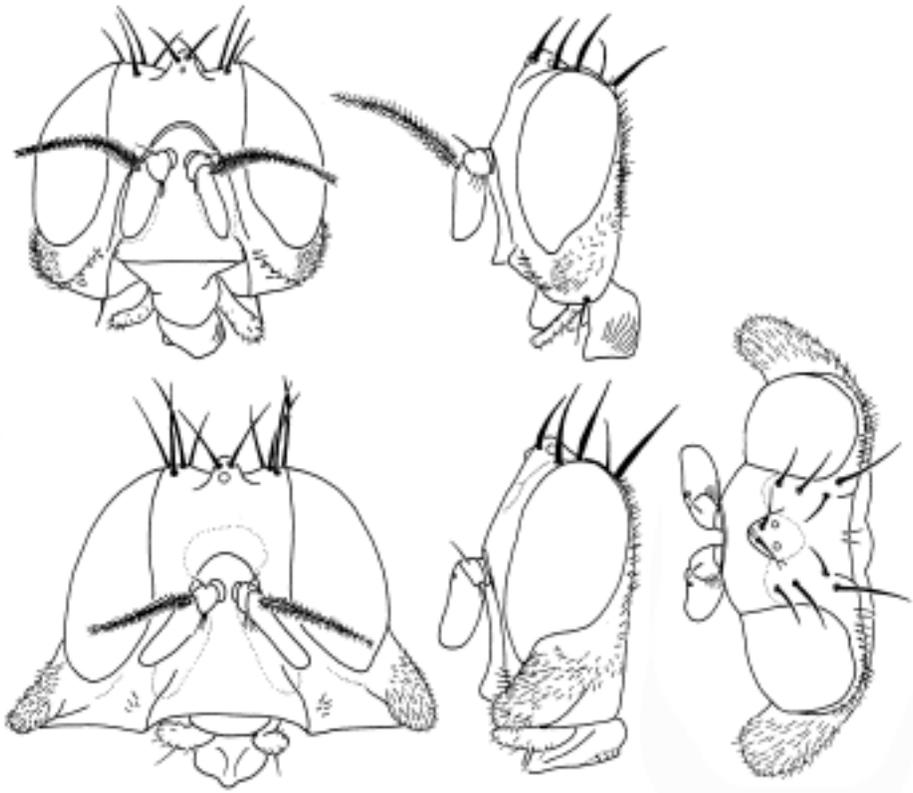


FIG. 2

Dimorphic heads of female (top) and male (bottom) *Cladoderris convexa* Whittington, 2003 [Reproduced from Whittington, 2003, with permission from Ampyx Verlag].

TAB. 2. Comparison of R^2 values of body length and head width coefficients with significance results from Student's t-test between sexes in Afrotropical and Oriental Plastotephritinae (Diptera, Platystomatidae). Genera are ranked according to the untransformed difference of means and Student's t-test was applied to the log normalised data for all except *Conopariella* Enderlein, 1922.

Genus	R^2	Equation of the slope	Student's t-test	Implications of R^2
<i>Venacalva</i>	0.9499	$y = 1.002x + 0.0024$	NS	Increase in body size may be associated with increase in head width
<i>Plastotephritis</i>	0.0473	$y = 0.2401x + 0.6824$	*	Head width may be independent of body length
<i>Mesanopin</i>	0.0042	$y = 0.1216x + 0.7786$	*	Head width may be independent of body length
<i>Conopariella</i>	0.2554	$y = 0.5848 + 0.3954$	***	There is some change in head width as body size increases
<i>Xyrogena</i>	0.0178	$y = 0.2114x + 0.6142$	***	Head width may be independent of body length
<i>Agrochira</i>	0.8561	$y = 2.1092x - 0.7704$	NS	Increase in body size may be associated with increase in head width

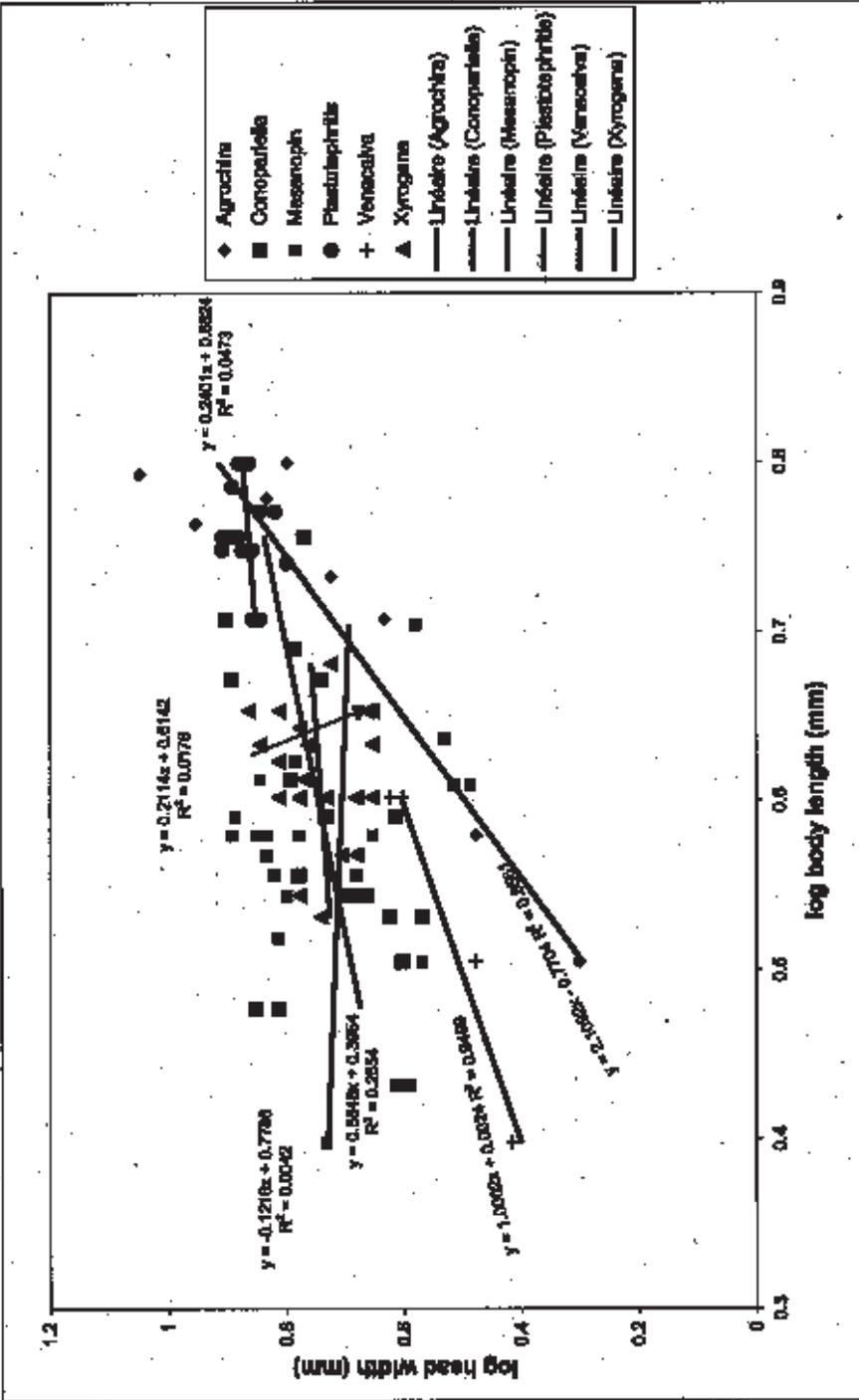


FIG. 3. Relationship between male body length and head width in hypercephalic Plasiatropinae.

results clearly suggest that there may be allometric growth in *Mesanopin*, *Plastotephritis* and *Xyrogena* (i.e. changes in head width may be independent of increase in body size) (Tab. 2). Conversely, an association between increase in body size and increase in head size is suggested by the results for *Conopariella*, *Agrochira* and *Venacalva* (in order of increasing association) (Tab. 2). This is graphically represented in Fig. 3, by trend lines approaching horizontal ($m < 0.25$ in $y = mx + c$) for *Mesanopin*, *Plastotephritis* and *Xyrogena*, but steeply sloped ($m > 0.5$ in $y = mx + c$) for *Conopariella*, *Agrochira* and *Venacalva*.

DISCUSSION

Most instances of modification of the head capsule in other families of flies suggest that sexual selection accounts for development of these ornaments. Such selection usually infers competition for resources, most commonly of an ovipositional nature. These developments of the head carry some evolutionary “cost” offset by the advantages of heightened success in mating and therefore competitive advantage for offspring.

In Acalyprate flies, such modifications are clustered non-randomly in acalyprates (Wilkinson & Dodson, 1997) and are concentrated in, but not exclusive to, the tephritoid lineage (Wilkinson & Dodson, 1997; Sivinski, 1999). Accounting for this concentration runs into difficulties. Sivinski (1999) made three suggestions, the first of which concerns comparatively large body size in tephritoids with modified heads (compared to other acalyprates), suggesting increased ability of males to control access to resources by females and or other potential mating males.

Contrarily, in Plastotephritinae, body size is noticeably small, much more like the other acalyprate families Sivinski (1999) considered. For Plastotephritinae: $\mu_{\text{body length}} = 4.09 \pm 1.19$ mm (range 1.7-12.0mm); $n = 285$; $\mu_{\text{wing length}} = 4.46 \pm 1.26$ mm (range 2.2-12.0mm); $n = 286$). The very large range in body and wing sizes are accounted for mainly by large specimens of *Pterogenomyia picta* (Bigot, 1891), within which the ranges are 6.5-12.0 and 7.3-12 for body and wing length respectively. Disregarding *Pterogenomyia picta* the values are lower: $\mu_{\text{body length}} = 4.00 \pm 0.95$ mm (range 1.7-7.5mm); $n = 280$; $\mu_{\text{wing length}} = 4.38 \pm 1.06$ mm (range 2.2-7.8mm); $n = 281$). These figures compare to a mean body length and range of 67 families of Acalytratae: $\mu_{\text{body length}} = 5.12 \pm 4.58$ mm (range 0.5-20.0mm); $n = 122$ (see Appendix).

Secondly, Wilkinson & Dodson (1997) and Sivinski (1999) proposed that lineages of large species numbers may be more likely to result in particular adaptations. In Plastotephritinae we observe an unusual diversity and concentration of head capsule development compared to the number of known species: 9 categories out of the 12 listed below in 18 genera and 80 species (Afrotropical and Oriental). This may suggest that either there are many more Plastotephritinae species yet to be described or that we cannot link adaptation to species numbers within distinct lineages.

Thirdly, long life span provides for many more mating opportunities and may enhance female learned behaviour, leading to adaptive modification (Wilkinson & Dodson, 1997; Sivinski, 1999), or lead to lower per capita costs among resource defending males (Wilkinson & Dodson, 1997), but little is currently known about memory in flies. Even less is known about Plastotephritinae life spans and sexual

behaviour, thus behavioural paradigms cannot be verified for this subfamily. Wilkinson & Dodson (1997) & Dodson (1999) proposed a more likely scenario: viz. antlered flies are more often encountered in the tropics, simply because greater species richness leads to a greater chance for rare traits to be expressed.

What does appear evident is the likelihood that the modifications of heads in Plastotephritinae indicates a process of sexual selection and agonistic behaviour, similar to species of lineages closely affiliated in the phylogeny of the Tephritoidea and other subfamilies of Platystomatidae (McAlpine, 1975, 1979, 1982, 1994; Dodson, 1999). In particular McAlpine (1979) discussed agonistic behaviour, head butting and function in *Achias* Fabricius, 1805. Furthermore, some genera exhibiting head modifications also have unusual leg modifications. Elaborate armature of the fore femora (Fig. 4), another agonistic character trait, occurs in *Agrochira*, *Furcamyia* and *Mesanopin*, suggesting a “wing-lock” mating position (Dodson, 1999; also see Eberhard, 2001 with respect to similar mechanisms in Sepsidae), while scoop shaped modifications to the hind tibia (possibly for pheromone transfer (White, 1999)) occurs in *Atopocnema*, *Stellapteryx* and *Xyrogena* (Fig. 4).

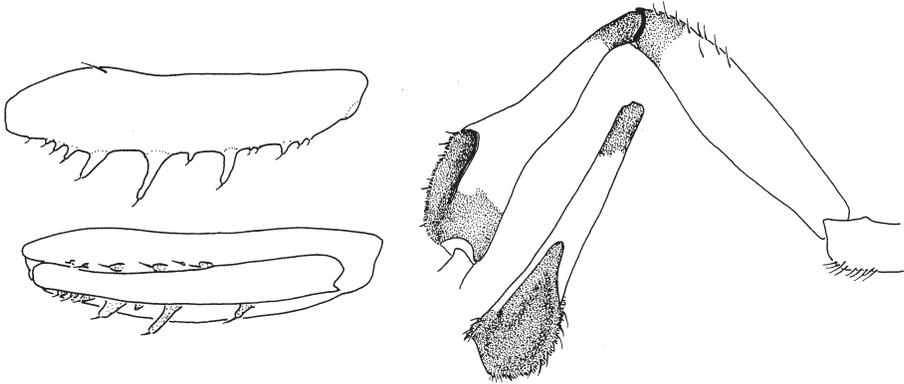


FIG. 4

Male femora of *Agrochira achoides* Enderlein, 1911 (left; top = lateral view, bottom = ventral view) and hind tibia of *Xyrogena gratiosa* (Enderlein, 1922) (right; top = lateral view, bottom = dorsal view) [Reproduced from Whittington, 2003, with permission from Ampyx Verlag].

An unexpected result in the statistical tests carried out on Plastotephritinae heads was that the genus exhibiting the widest span, viz. *Agrochira* resulted in a non-significant t-test (Tab. 1). Similarly, in *Cladoderris*, which has broadened genae, the t-test was NS (Tab. 1). Small sample sizes may contribute to the unexpected results for *Agrochira* and *Cladoderris*, but more telling, is the pooled standard deviation about the means, which are much greater than the difference between gender means. This is because males range from “female-like” or “normal” dimensions to exceptional enlargements, thus artificially enhancing the lower dimensions. This is a feature which occurs in other genera as well, e.g. *Conopariella*, but is offset by large sample sizes. The range normal-to-extreme, is most pronounced in *Conopariella tibialis* (Hendel, 1914) (Fig. 5) and, as already mentioned, is a feature in other families with head

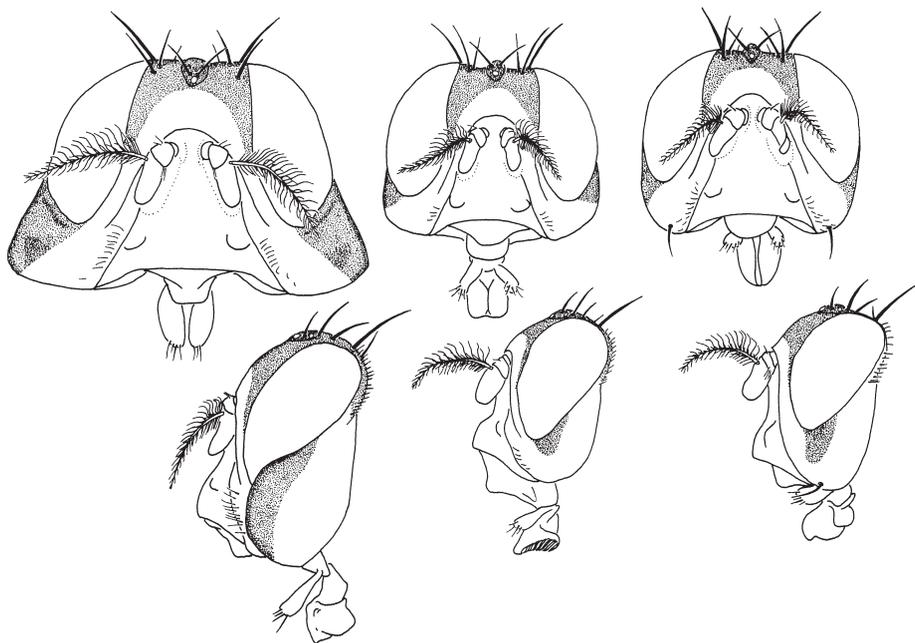


FIG. 5

Male (left and centre) and female (right) head variation in for *Conopariella tibialis* (Hendel, 1914) [Reproduced from Whittington, 2003, with permission from Ampyx Verlag].

modifications. In a sexual selection sense, it becomes difficult to argue the rationale behind head modification if both sexes exhibit gross modification and start to look alike. Undifferentiated, or diminutive, specimens have been noted in other families in which hypercephaly occurs (Diopsidae (Shillito, 1971b), Tephritidae (McAlpine & Schneider, 1978; Moffett, 1997); Platystomatidae (McAlpine, 1975, 1982, 1994)) and may be a result of deficiency in food quality and/or quantity (Kawano, 1998; Knell *et al.*, 1999; Marshall, 2000).

It was also unexpected that the R-squared results for *Agrochira* suggest a development other than allometric. This suggests that increase in head width and body size are in some way linked (or associated). What we may be observing here has been alluded to before as dependence in resource availability during larval growth (McAlpine, 1979; Kawano, 1998; Knell *et al.*, 1999; Marshall, 2000). Despite this, allometric growth would be expected in hypercephalic species, and again I refer the reader to results based on low sample size ($n=8$ males).

The other R-squared results were much as expected: for *Mesanopin*, *Plastotephritis* and *Xyrogena* the results suggest changes in head width may be independent of increase in body size; and for *Conopariella*, and *Venacalva* there appears to be an association between increase in body size and increase in head size (Tab. 2; Fig. 3). The near horizontal (or shallow) slopes of the trends for *Mesanopin*, *Plastotephritis* and *Xyrogena* suggest that hypercephalic Plastotephritinae are unlike other well known examples of allometric growth such as Stag beetles (Lucanidae) (Kawano,

1998) in which mandible size increases proportional to body size. Nevertheless, the conclusions reached by Kawano (1998) match the pattern seen in Plastotephritinae, viz. each genus has its own allometric scheme (distinguished by the slope of the allometric regression).

There is also the urge to link phylogeny and functionality with unusual modification. In the absence of more complete knowledge of the plastotephritine fauna (particularly that adjacent to the Pacific Fringe, which is as yet unrevised) and of biological data for the Plastotephritinae, such conclusions would be premature, although discussion is possible based on examples from other families of flies.

The view that eyestalks have no real function and are merely freak-developments, has largely been refuted. In Diopsidae, evidence suggested that increase in span and narrowing of eyestalks was a unifying evolutionary trend within the family, supported by corresponding elaboration of the head capsule and prothorax (Hennig, 1965; Shillito, 1971a). In more recent works (Baker & Wilkinson, 2001; Meier & Baker, 2002) it has become clear that, although the basal split between the Centricinae (lacking eye-stalks) and the Diopsinae (having eye-stalks) is well supported by both morphological and molecular approaches, the phylogenetic association between short and long eye stalks is not a linear progression and thus cannot be viewed purely as a unifying evolutionary trend. In other words, the macro-evolutionary change in eye span is flexible throughout the clade (Baker & Wilkinson, 2001).

Visual acuity is greatly enhanced at distance (but not close to the head) as eye span increases and body size is correlated not only to eye span, but also to an increase in the number of ommatidia (Burkhardt & de la Motte, 1983). In later studies, Burkhardt *et al.* (1994), found that the number of offspring was directly proportional to body length and that eye span increased by the square of body length in *Cyrtodiopsis whitei* (Curran, 1936). Contrarily, they also found that the offspring of large and small males did not differ significantly in body size. This correlates well with the knowledge that adult size is a product of resource availability during larval growth.

Territoriality was suggested by Grimaldi (1987) as a likely prerequisite condition for the evolution of hypercephaly and semaphore patterns in Drosophilidae. So, while observed changes in gross head capsule morphology may not indicate an evolutionary lineage and a unifying trend, it can be said that it may be a selective force driving evolutionary change to produce the end result that we observe.

Other elaborations to the head capsule have recently been examined in Clusiidae, Tephritidae and Platystomatidae including various extensions to the genae often referred to as "antlers", modified vibrissae, broadened heads and elongate antennae (Dodson, 1997, 1999; Marshall, 2000; McAlpine, 1975, 1979; Moffett, 1997). These extensions are commonly lateral displacements of some sclerites comprising the head capsule, such as lateral displacement of the eyes or lateral development of the genal sclerite. These are the more obvious cases and most often the extremes are used as examples. In nearly all of these studies, sexual dimorphism inferred sexual selection for copulatory and/or ovipositional advantage, i.e. agonistic behaviour, and represent a resource defence mating mechanism (Tephritidae, Phytalmiinae: Dodson, 1997) or a lek defence mechanism (Clusiidae: Marshall, 2000; Drosophilidae: Grimaldi, 1987). Astoundingly, in manipulative experiments, Wilkinson & Dodson (1997) found that head elaboration was not necessary to win contests.

An alternative (or perhaps complimentary) hypothesis is that selection is not by agonistic means, but by female preference for large males (or males with large ornaments) as has been observed in harems of *Cyrtodiopsis whitei* (Curran, 1936) and *C. dalmanni* (Wiedemann, 1830) (Diopsidae). This is not the result of exclusion of males with short eye-stalks, but the selection, by females, of males with long eye-stalks (Burkhardt & de la Motte, 1988; Wilkinson & Reillo, 1994; Wilkinson *et al.*, 1998). In genera which also have leg armature and elaboration of other body parts, such as occurs in *Mesanopin*, presence of the spines on the fore femora mitigate against this and for an agonistic response between males. There is currently no observed behaviour to suggest that the spines have a species specific clasping function as observed for some Sepsidae (Eberhard, 2001). It is also not clearly understood why females of some species have also developed these spines on a diminished scale (e.g. *Mesanopin palaga* Whittington, 2003, fig. 406) or even fully (e.g. *Mesanopin biplexum* Whittington, 2003, fig. 338). Thus, female selection and male agonistic behaviour seem possible within the same species (Knell *et al.*, 1999). Furthermore, de la Motte & Burkhardt (1983) reported that female diopsids also use their eye-stalks in aggressive encounters. Indeed, Wilkinson *et al.* (1998) indicated that, in the case of *Cyrtodiopsis dalmanni* (Wiedemann, 1830), because female selection was sex chromosome meiotic driven, genetic variation for fitness should exist and allow elaboration of male ornamentation. Wilkinson & Dodson (1997) also noted that males of diminutive body size, had little to gain by developing “expensive” elaborations.

Various parallels between elaboration of head capsules in flies and the antlers of cervid mammals have been made – hence the name “antlered flies”. Partly this is based on the apparent and, in some cases the observed, behaviours of “rutting”, “rearing” and “challenging” using various head modifications. As a consequence, we too easily slip into the belief that these are “aggressive weapons” rather than visual displays. In antler-shortening experiments, Wilkinson & Dodson (1997) and Dodson (1999) found that the head modifications in *Phytalmia* were honest signals of body size and hence prowess, rather than weapons in a “size matters” arms race. Relative body size remained the dominant determinant in contest outcome in these experiments.

CLASSIFICATION

The adaptation of the morphology of the head capsule in Plastotephritinae is so varied, that an appropriate classificatory scheme is proposed, based on morphological examination of numerous Plastotephritinae (Whittington, 2000, 2003). This classification was then arranged into a diagrammatic flow chart, following trends along lines of apparent morphological development. These trends are not proposed as phylogenetic events in the evolutionary sense, since no cladistic analysis has been undertaken, quite simply because these are not necessarily monophyletic lineages and because some characters described quite clearly arise in paraphyletic groups (i.e. are repeated evolutionary events within the acalytrate lineage as suggested by Wilkinson & Dodson (1997). Wilkinson & Dodson (1997) provide a phylogenetic diagram of the distribution of eye stalks and “antlers” in acalytrate families and also tabulate the presence of head projections in 8 acalytrate families. The classification presented below, goes further, in that it teases out the different types of projections, although it does not use all the

examples mentioned by Wilkinson & Dodson (1997). For example: Diopsidae eye-stalks differ fundamentally in form from all other observed eye-stalks, in that the antennae are also borne on the extremes of the stalks, whereas in all other instances they are positioned in the centre of the face.

The ground-plan shape of the head is best represented by the semi-globose form familiarly found in the vast majority of acalyptrate flies. From this basic form (represented here by *Venacalva margarita* Whittington, 2003), morphology is divergent in nine major pathways, identified by the types listed below, with examples in progressive order towards the extreme condition. Modifications are not necessarily restricted to single types of change in the head structure and therefore species used as examples may be listed in more than one type. For example, *Conopariella picipennis* (Enderlein, 1922) is listed under type 2 and 3, because the head in this species has undergone both vertical enlargement of the ocellar triangle and forward projection of the lower facial margin.

Examples from other dipterous families are included, by way of comparison and are distributed in all biogeographic regions. Abbreviations for the biogeographic region of origin are given as: AFR = Afrotropical; AUS = Australasia and Oceania; NEA = Nearctic; NTR = Neotropical; ORI = Oriental; PAL = Palaearctic. All Plastotephritinae species were described and illustrated in Whittington (2000, 2003) and are listed below as only the initials AEW, the year and the figure.

TYPE 1

FORWARD EXTENSION OF THE FRONS (Tab. 3)

Extremus: *Cornutrypeta nigrifemur* (Tephritidae; Trypetinae) is perhaps the most bizarrely developed for this character, with *Stemonocera cornuta* (Tephritidae; Trypetinae) a close second. In both these species there is an unusual elaboration of setae, coupled with the extreme scleritic development. Note that the sequence of the above Tephritidae are not a linear progression (see Han, 1999, Fig. 11.3).

TAB. 3. Examples of Type 1 head modification in acalyptrate Diptera: forward extension of the frons.

Plastystomatidae			
Plastotephritinae	<i>Venacalva virga</i> Whittington, 2003	AFR	AEW (2003), Fig. 589
	<i>Stellapterys stellata</i> Whittington, 2003	AFR	AEW (2003), Fig. 549
	<i>Mesanopin adamanta</i> Whittington, 2003	AFR	AEW (2003), Fig. 321
	<i>Furcamyia pallida</i> Whittington, 2003	AFR	AEW (2003), Fig. 312
	<i>Agrochira bifocalis</i> Whittington, 2003	AFR	AEW (2003), Fig. 42
Tephritidae			
Trypetinae:	<i>Cornutrypeta nigrifemur</i> Han & Wang, 1993	PAL	Han (1999), Fig. 11.4D
	<i>Cornutrypeta superciliata</i> Frey, 1935	PAL	Han (1999), Fig. 11.4E
	<i>Stemonocera cornuta</i> Scopoli, 1772	PAL	Han (1999), Fig. 11.4K
	<i>Strauzia intermedia</i> (Loew, 1873)	NEA	Han (1999), Fig. 11.4N
	<i>Paramyiolia takeuchii</i> Shiraki, 1933	PAL	Han (1999), Fig. 11.4S

INTERMEDIATE TYPE 1 & 2

FORWARD EXTENSION OF THE FRONS COUPLED WITH VERTICAL DEVELOPMENT OF THE OCELLAR TRIANGLE (Tab. 4)

TAB. 4. An example of Intermediate Type 1 & 2 head modification in acalyprate Diptera: forward extension of the frons coupled with vertical development of the ocellar triangle.

Platystomatidae		
Plastotephritinae:	<i>Cladoderris ornata</i> Whittington, 2003	AFR AEW (2003, Fig. 120)

TYPE 2

VERTICAL ENLARGEMENT OF THE OCELLAR TRIANGLE (Tab. 5)

Extremus: Paramycodrosophila nephelea Wheeler, 1968 (Drosophilidae) from Jamaica has the ocellar triangle projecting above the vertex by as much as the length of the first antenna.

TAB. 5. Examples of Type 2 head modification in acalyprate Diptera: vertical enlargement of the ocellar triangle.

Platystomatidae		
Plastotephritinae	<i>Conopariella picipennis</i> (Enderlein, 1922)	AFR AEW (2003), Fig. 216
	<i>Rhegmatosaga latiuscula</i> (Walker, 1856)	ORI AEW (2000), Fig. 18
	<i>Agadasys hexablepharis</i> Whittington, 2000	ORI AEW (2000), Fig. 2
	<i>Cladoderris convexa</i> Whittington, 2003	AFR AEW (2003), Fig. 107
Drosophilidae:	<i>Paramycodrosophila nephelea</i> Wheeler, 1968	NTR Wheeler (1968), Fig. 3a

TYPE 3

FORWARD PROJECTION OF THE LOWER FACIAL MARGIN (Tab. 6)

Extremus: Prosoconoconus fuscigenus Enderlein, 1922 from Equatorial Guinea represents the extreme in Plastotephritinae, but even more extended lower facial margins exist in other taxa, such as the Syrphidae *Rhingia* Scopoli, 1763, although the evolutionary reasons for development of such a “beak” may be different. Dodson (1999) observed that species with extended lower facial margins used them as points of contact in pushing contests. This has not been observed in *Rhingia* and seems unlikely. A more likely scenario here is the need to hinge elongated mouthparts so that they rest in a backward facing position. Behaviour of any sort has not been recorded for *Prosoconoconus*, but I propose that pushing contests are most likely in this extreme example. Unfortunately, the unique type specimen lacks mouthparts, so it is not possible to determine if they are backwardly hinged as in *Rhingia*, but the form of the cavity suggests that these were centrally placed.

It should be noted that this character is frequently observed in Plastotephritinae, but to a lesser degree than in *Prosoconoconus*. Unlike in *Prosoconoconus*, in which the lower facial margin is lower than the level of the genae, nearly all the other examples have the lower facial margin raised above the genae (see figures for Types 1, 2 & 8 for example).

TAB. 6. Examples of Type 3 head modification in acalyprate Diptera: forward projection of the lower facial margin.

Platystomatidae		
Plastotephritinae	<i>Conopariella picipennis</i> (Enderlein, 1922)	AFR AEW (2003), Fig. 216
	<i>Prosoconoconus fuscigenus</i> Enderlein, 1922	AFR AEW (2003), Fig. 528

A further development along this trend may be members of the platystomatid genus *Mesoctenia* Enderlein, 1924 from Australasia (McAlpine, 1975) and illustrated by McAlpine (1982), Fig 9 and McAlpine (2001), Fig 9.

TYPE 4

BACKWARD DEEPENING OF THE POSTGENA (Tab. 7)

Extremus: this type reaches an extreme in platystomatine genera and is noticeably developed in *Mezonia* Speiser, 1910.

TAB. 7. Examples of Type 4 head modification in acalyprate Diptera: backward deepening of the postgena.

Platystomatidae		
Plastotephritinae	<i>Oectotopa parallelomma</i> Hendel, 1914	AFR AEW (2003), Fig. 461
	<i>Micronesomyia hemihyalina</i> Whittington, 2003	AFR AEW (2003), Fig. 436
Platystomatinae:	<i>Mezonia proxenus</i> Speiser, 1910	AFR Hendel (1914), Pl. 8 Fig. 143

TYPE 5

DORSAL DEVELOPMENT OF ORBITAL LOBES AND SUNKEN VERTEX (Tab. 8)

Extremus: *Eudasys ophrys* Whittington, 2003 from West and Central Africa represents the most bizarre form of this type, supplemented by extreme hairiness.

TAB. 8. Examples of Type 5 head modification in acalyprate Diptera: dorsal development of orbital lobes and sunken vertex.

Platystomatidae		
Plastotephritinae	<i>Oectotopa parallelomma</i> Hendel, 1914	AFR AEW (2003), Fig. 460
	<i>Eudasys ophrys</i> Whittington, 2003	AFR AEW (2003), Fig. 257

TYPE 6

ANTERO-POSTERIOR COMPRESSION OF HEAD; LATERAL DEVELOPMENT AND VENTRAL DEEPENING OF THE FRONS, FACE AND GENA (Tab. 9)

Extremus: *Plastotephritis compta* Enderlein, 1922 and *Plastotephritis limbata* Enderlein, 1922 from West Africa represent the most extreme in this type, with the head being compressed to less than a third of its width.

TAB. 9. Examples of Type 6 head modification in acalyprate Diptera: antero-posterior compression of head; lateral development and ventral deepening of the frons, face and gena.

Platystomatidae		
Plastotephritinae	<i>Plastotephritis nosphidia</i> Whittington, 2003	AFR AEW (2003), Fig. 502, 503
	<i>Plastotephritis patagiata</i> Enderlein, 1922	AFR AEW (2003), Fig. 511, 512
	<i>Plastotephritis sica</i> Whittington, 2003	AFR AEW (2003), Fig. 519, 520
	<i>Plastotephritis compta</i> Enderlein, 1922	AFR AEW (2003), Fig. 487, 488
	<i>Plastotephritis limbata</i> Enderlein, 1922	AFR AEW (2003), Fig. 493, 494
Scholastinae:	<i>Pterogenia singularis</i> Bigot, 1859	AUS Hendel (1914), Pl. 13 Fig. 236
	<i>Zygaenula paradoxa</i> Doleschall, 1858	AUS Hendel (1914), Pl. 9 Fig. 160

Unplaced subfamily: <i>Atopognathus goniceps</i> (Hendel, 1914)	AUS	McAlpine (1982), Fig. 4; McAlpine (2001), Fig. 4
Ulidiidae: <i>Dasymetopa lutulenta</i> Loew, 1868	NTR	Kameneva (2004a), Fig. 31 & 32
<i>Paragorgopis medusa</i> Kameneva, 2004	NTR	Kameneva (2004a), Fig. 55

TYPE 7

ANTERO-POSTERIOR COMPRESSION OF HEAD; LATERAL DEVELOPMENT OF THE GENA AND VENTRAL DEEPENING OF THE FACE AND GENA; FORWARD EXTENSION OF THE APEX OF THE GENA; DISTORTION OF THE EYE INTO A KIDNEY SHAPE; AND OVERALL DEVELOPMENT OF THE HEAD INTO A TRIANGULAR SHAPE (Tab. 10)

Extremus: in *Conopariella cidara* Whittington, 2003 from West and Central Africa the forward projection of the eye is level with the base of the third flagellomere.

TAB. 10. Examples of Type 7 head modification in acalyptrate Diptera: antero-posterior compression of head with lateral development of the gena (see text for explanation).

Platystomatidae		
Plastotephritinae: <i>Conopariella togoensis</i> Enderlein, 1922	AFR	AEW (2003), Fig. 241, 242
<i>Conopariella conspicua</i> Frey, 1932	AFR	AEW (2003), Fig. 182, 183
<i>Conopariella cidara</i> Whittington, 2003	AFR	AEW (2003), Fig. 169–171
<i>Pterogenomyia picta</i> (Bigot, 1891)	AFR	Hendel (1914), Pl. 3 Fig. 48, AEW (2003), Fig. 533

TYPE 8

ANTERO-POSTERIOR COMPRESSION OF HEAD; LATERAL DEVELOPMENT OF THE GENA WITHOUT VENTRAL DEEPENING OF THE FACE AND GENA; FORWARD EXTENSION OF THE APEX OF THE GENA; DISTORTION OF THE EYE INTO A KIDNEY SHAPE; AND OVERALL DEVELOPMENT OF THE HEAD INTO A TRIANGULAR SHAPE (Tab. 11)

Extremus: The outward extensions on the genae of *Phytalmodes africanus* Bezzi, 1908 are sharply pointed and resemble, to some extent, the lower extreme of “antlers” described in Type 11 i.e. they are similar to *Giraffomyia* sp. from Australasia (illustrated by McAlpine (1982), Fig 6 and McAlpine (2001), Fig 6).

Comment: There are similarities between Type 8 and Type 11, in that both are outward development of the genal sclerite. The main difference lies in the head capsule itself: in Type 8, extreme compression of the head capsule results in a narrow profile, while in Type 11, the profile remains rounded.

TAB. 11. Examples of Type 8 head modification in acalyptrate Diptera: antero-posterior compression of head and lateral development of the gena (see text for explanation).

Clusiidae: <i>Clusoides latifrons</i> (McAlpine, 1960)	AUS	Marshall (2000), Fig. 5-12
Platystomatidae		
Plastotephritinae: <i>Furcamyia contra</i> Whittington, 2003	AFR	AEW (2003), Fig. 282
<i>Xyrogena gratiosa</i> (Enderlein, 1922)	AFR	AEW (2003), Fig. 502, 503
<i>Cladoderris cnephosa</i> Whittington, 2003	AFR	AEW (2003), Fig. 99, 100
<i>Cladoderris silvestrii</i> Bezzi, 1914	AFR	AEW (2003), Fig. 130
<i>Cladoderris convexa</i> Whittington, 2003	AFR	AEW (2003), Fig. 108-110
Platystomatinae: <i>Phytalmodes africanus</i> Bezzi, 1908	AFR	personal observation

TYPE 9

LATERAL DEVELOPMENT OF THE PARAFACIAL SCLERITE RESULTING IN OVERALL DEVELOPMENT OF EYESTALKS NOT BEARING ANTENNAE (ANTENNAE REMAIN ADJACENT EITHER SIDE OF MIDLINE); COUPLED WITH MODERATE VENTRAL DEEPENING OF THE FACE AND GENA (Tab. 12)

Extremus: The Papua New Guinean species *Achias rothschildi* Austen, 1910, has the widest separation of the eyes in Diptera, with the greatest span measuring 55mm (Arnaud, 1994).

Comment: Besides general development from a slight broadening of the head to peduncular eye-stalks, there are species in which some development of the orbit also occurs, eg. *Asyntona tetyroides* Walker, 1859, which is, to some extent, intermediate between Type 9 and Type 12.

TAB. 12. Examples of Type 9 head modification in acalyptrate Diptera: lateral development of the parafacial sclerite resulting in overall development of eyestalks (see text for explanation).

Clusiidae:	<i>Clusiodes gladiator</i> McAlpine, 1960	AUS	Marshall (2000), Fig. 1-3
	<i>Clusoides latifrons</i> (McAlpine, 1960)	AUS	Marshall (2000), Fig. 5-12
Platystomatidae			
Plastotephritinae	<i>Mesanopin ametromastax</i> Whittington, 2003	AFR	AEW (2003), Fig. 326, 327
	<i>Mesanopin laticeps</i> (Enderlein, 1922)	AFR	AEW (2003), Fig. 373, 374
	<i>Mesanopin tephritinum</i> Enderlein, 1912	AFR	Hendel (1914), Pl. 4 Fig. 68
	<i>Agrochira achoides</i> Enderlein, 1911	AFR	AEW (2003), Fig. 24 – 26
	<i>Agrochira parallaxis</i> Whittington, 2003	AFR	AEW (2003), Fig. 59 – 61
Platystomatinae:	<i>Achias</i> spp.	AUS	McAlpine (1982), Fig. 7 & 8, McAlpine (1994), Figures; McAlpine (2001), Fig. 7 & 8
	<i>Laglaizia</i> sp.	AUS	McAlpine (1982), Fig. 5, McAlpine (2001), Fig. 5
	<i>Laglaizia caloptera</i> Bigot, 1878	AUS	Hendel (1914), Pl. 3 Fig. 139, 141
Scholastinae:	<i>Asyntona</i> sp.	AUS	McAlpine (1982), Fig. 3; McAlpine (2001), Fig. 3
	<i>Asyntona tetyroides</i> Walker, 1859	ORI	Hendel (1914), Pl. 13 Fig. 246 & 247; Séguy (1951), Fig. 647
Tephritidae			
Phytalmiinae:	<i>Acanthonevra fuscipennis</i> Macquart, 1843	PAL, ORI, AUS	personal observation
	<i>Acanthonevroides basalis</i> Walker, 1853	AUS	personal observation
Trypetinae:	<i>Pelmatops ichneumonea</i> (Westwood, 1850)	PAL, ORI	personal observation
	<i>Pseudopelmatops nigricostalis</i> Shiraki, 1933	PAL	Shiraki (1913), Fig. 1A, 2A, Pl. 1 Fig. 3
	<i>Themarictera flaveolata</i> Fabricius, 1861	AFR	
Ulidiidae:	<i>Paragorgopsis mallea</i> Hendel, 1909	NTR	Kmeneva (2004a), Fig. 41
	<i>Plagiocephalus intermedia</i> Kameneva, 2004	NTR	Kameneva (2004b), Fig. 1,3, 2,3 & 2,5
	<i>Plagiocephalus latifrons</i> (Hendel, 1909)	NTR	Kameneva (2004b), Fig. 1,1, 2,1 & 2,4
	<i>Plagiocephalus lobularis</i> Wiedemann, 1830	NTR	Kameneva (2004b), Fig. 1,2 & 2,2

Separation of the antennae (i.e. by lateral expansion of the frontal plate) is noticeable in *Paragorgopsis mallea* Hendel, 1909 (Ulidiidae), but the antennae remain separated from the extremes of the eye-stalk by the ptilinal suture.

TYPE 10

LATERAL DEVELOPMENT OF THE FRONTAL SCLERITE RESULTING IN OVERALL DEVELOPMENT OF EYESTALKS, BEARING ANTENNAE (Tab. 13)

TAB. 13. Examples of Type 10 head modification in acalyptrate Diptera: lateral development of the frontal sclerite resulting in overall development of eyestalks, bearing antennae.

Diopside	<i>Centrioncus prodiopsis</i> Speiser, 1910	AFR	Meier & Baker (2002), Fig. 1c
	<i>Cyrtodiopsis whitei</i> (Curran, 1936)	ORI	Moffett (1997)
	<i>Teleopsis boettcheri</i> Frey, 1928	ORI	Shillito (1971), Fig. 5c
	<i>Diasemopsis signata</i> (Dalman, 1817)	AFR	Dalman (1823), Tab. 1, Figs 1-3
	<i>Diopsis apicalis</i> Dalman, 1817	AFR	Dalman (1823), Tab. 1, Figs 1-4
	<i>Diopsis macrophthalma</i> Dalman, 1817	AFR	Dalman (1823), Tab. 1, Figs 1-3

TYPE 11

EXTREME DEVELOPMENT OF THE GENAL PLATE TO FORM “ANTLERS” (Tab. 14)

Extremus: Numerous members of the genus *Phytalmia* can be considered to be extreme, because the diversity of the elaborations is so varied. *Phytalmia alcornis* (Saunders, 1861) is perhaps the most bizarre of the lateral (or antler) extensions. Dodson (1999) reviewed the behaviour and phylogeny of known species of this genus.

Comment: There are similarities between Type 8 and Type 11, in that both are outward development of the genal sclerite. The main difference lies in the head capsule itself: in Type 8, extreme compression of the head capsule results in a narrow profile, while in Type 11, the profile remains rounded.

As is often seen in hypercephalic plastotephratine species with broadened heads (stalk eyes), such as in *Agrochira* and *Mesanopin*, males of various *Phytalmia* spp. also have armature on the fore femora (see for example *Phytalmia alcornis* illustrated in Moffett (1997) and *Phytalmia mouldsi* illustrated in Dodson (1999)).

TAB. 14. Examples of Type 11 head modification in acalyptrate Diptera: extreme development of the genal plate to form “antlers”.

Platystomatidae:	<i>Giraffomyia</i> sp.	AUS	McAlpine (1982), Fig. 6; McAlpine (2001), Fig. 6
Clustidae:	<i>Clitodoca fenestralis</i> (Macquart, 1843)	AFR	personal observation
	<i>Clustodes kinetrolicros</i> Caloren & Marshall, 1998	NTR	Caloren & Marshall (1998), Fig. 82
	<i>Clusoides mirabilis</i> (Frey, 1928)	NTR	Caloren & Marshall (1998), Fig. 85 & 86
	<i>Sobarocephaloides alini</i> Shatalkin, 1991	NTR	Shatalkin (1991), Fig. 1 & 2
Tephritidae			
Phyalmiinae:	<i>Diplochorda aneura</i> Malloch, 1939	AUS	Dodson (1999), Fig. 8.1F
	<i>Diplochorda australis</i> Permkam & Hancock, 1995	AUS	Dodson (1999), Fig. 8.1G

<i>Sessilina nigrilinea</i> (Walker, 1861)	AUS	McAlpine & Schneider (1978), Fig. 21; Dodson (1999), Fig. 8.1E
<i>Terastiomyia lobifera</i> Bigot, 1859	AUS	Dodson (1999), Fig. 8.1D
<i>Sophira limbata</i> Enderlein, 1911	ORI	Dodson (1999), Fig. 8.1O
<i>Phytalmia cervicornis</i> Gerstaecker, 1860	AUS	Moffett (1997), Wilkinson & Dodson (1996), Fig. 18-1b; Dodson (1999), Fig. 8.1J
<i>Phytalmia mouldsi</i> McAlpine & Schneider (1978)	AUS	McAlpine & Schneider (1978), Fig. 2; Schneider, 1978; Moffett, (1997); Dodson (1997), Fig. 1 & 2; Wilkinson & Dodson (1996), Fig. 18-1c; Dodson (1999), Fig. 8.1B & 8.2, Colour Figure 17
<i>Phytalmia megalotis</i> Gerstaecker, 1860	AUS	Dodson (1999), Fig. 8.1L
<i>Phytalmia robertsi</i> Schneider, 1993	AUS	Dodson (1999), Fig. 8.1M
<i>Phytalmia biarmata</i> Malloch, 1939	AUS	Dodson (1999), Fig. 8.1K
<i>Phytalmia antilocarpa</i> McAlpine & Schneider	AUS	McAlpine & Schneider (1978), Fig. 1; Schneider, 1978; McAlpine (1982), Fig. 2; Wilkinson & Dodson (1996), Fig. 18-1a
<i>Phytalmia alcicornis</i> (Saunders, 1861)	AUS	Moffett (1997); Wilkinson & Dodson (1996), Fig. 18-1d; Dodson (1999), Fig. 8.1C, Colour Figure 18
Ulidiidae: <i>Chondrometopum bifenestratum</i> Kertész, 1913	NTR	Kameneva (2004a), Fig. 5

TYPE 12

EXTREME DEVELOPMENT OF THE ORBIT AND FRONTO-ORBITAL PLATES (Grimaldi, 1987) (Tab. 15)

Extremus: The Ecuadorian and Peruvian species *Zygothrica exuberans* (Wheeler, 1968), has the widest elaboration of the eyes in Type 12, and is also illustrated by Wheeler (1968).

TAB. 15. Examples of Type 12 head modification in acalyptrate Diptera: extreme development of the orbit and fronto-orbital plates.

Drosophilidae: various <i>Zygothrica</i> spp.	NTR	Grimaldi (1987)
<i>Zygothrica dispar</i> (Wiedemann, 1830)	NTR	Sturtevant (1920), Fig. 1; Séguy (1951), Fig. 679 & Grimaldi (1987), Fig. 212
<i>Zygothrica exuberans</i> (Wheeler, 1968)	NTR	Grimaldi (1987), Fig. 213

TYPE 13

HEAD WITH UNUSUAL PROJECTIONS OF, OR CHANGES TO, THE ANTENNA (Tab. 16)

This classification deals specifically with the head capsule, but could be broadened to include other modifications of the head, such as extensive development of the vibrissae and genal setation. This is found in Platystomatidae and Clusiidae e.g.

TAB. 16. Examples of Type 13 head modification in acalyptrate Diptera: head with unusual projections of, or changes to, the antenna.

Clustidae:	<i>Clusiodes gladiator</i> McAlpine, 1960	AUS	Marshall (2000), Figures
	<i>Clusoides latifrons</i> (McAlpine, 1960)	AUS	Marshall (2000), Figures
Platystomatidae			
Scholastinae	<i>Asyntona</i> sp.	AUS	McAlpine (1982), Fig. 3; McAlpine (2001), Fig. 3
	<i>Asyntona tetyroides</i> Walker, 1859	ORI	Hendel (1914), Pl. 13 Fig. 246-249, Séguy (1951), Fig. 647
Tephritidae			
Tephritinae	<i>Terellia cerutocera</i> (Hendel, 1913)	PAL	White (1988), Fig. 96

Atopognathus barbatus Hendel, 1914 (see Hendel (1914), Pl. 11 Fig. 211 & 213), *Pogonortalis doclea* Walker, 1849 (see Hendel (1914), Pl. 9 Fig. 156 and McAlpine (1975), figs. 1-3), *Clusiodes gladiator* McAlpine, 1960 and *Clusoides latifrons* (McAlpine, 1960) (see Marshall (2000), figs 1-12), and *Clusiodes gracilolobus* Caloren & Marshall (1998) and Caloren & Marshall (1998), Plate fig 5)), all of which (except the latter) also have slightly broadened head capsules (Type 9) and extended antennae (Type 13).

The existence of this additional (and perhaps other) categories, suggests that categorisation is more complex than outlined above and that in fact we may be dealing with groups of nested or linked character traits. The classification needs further development and ultimately, it is hoped, it will be incorporated into a much broader understanding of acalyptrate phylogeny.

Furthermore, the occurrence in most categories above of more than one generic (or above generic) taxon, suggests that the morphological character categorised in each case has evolved more than once, which concurs with the findings of Dodson (1999) for the development of “antlers” in the Phytalmiinae (Tephritidae). Contrary to Dodson’s (1999) suggestion that the character is biogeographically bound to Australasia, the existence of genal projections (Types 8 & 11), which in their extreme form produce “antlers” (Type 11), occurs in the Afrotropical and Neotropical regions as well. Nevertheless, the association does appear to be tropical at least, since so far I have come across no striking examples from temperate regions.

CONCLUSIONS

The presence of head capsule modifications in many genera of Plastotephritinae suggests that agonistic behaviour is present in the subfamily and that males of some genera defend rare or discrete resources (Sivinski, 1999), such as oviposition sites. It is clear that the biology behind these ornamentations, whether it be agonistic in nature or a matter of female choice, is really only the fringe of a much bigger biology of mate selection and subsequent natural selection. The lack of behavioural biology, as with breeding biology, of Plastotephritinae is a hindrance in the understanding of the inter-relationships and phylogeny of the subfamily.

ACKNOWLEDGEMENTS

It gives me great pleasure to acknowledge the permission given by Andreas Stark of Ampyx Verlag, for the reprinting here of figures previously used in Whittington (2003). Not only has this saved much repeated work, but it also provided consistency and furthermore extends the 2003 paper with new concepts. I am also grateful to the National Museums of Scotland for providing a stipend for travel and conference costs. Thank you to the anonymous external referee for suggested improvements to the manuscript of this paper. Lastly, but not least, I also gratefully acknowledge Bernhard Merz, for the huge amount of effort put into making firstly the conference & field work and latterly this volume, the success that they are.

REFERENCES

- ARNAUD, P. H., JR. 1994. Frontispiece: *Achias rothschildi* (Austen) (Diptera: Platystomatidae). *Myia* 5: IV.
- BAKER, R. & WILKINSON, G. S. 2001. Phylogenetic analysis of sexual dimorphism and eye span allometry in stalk eyed flies (Diopsidae). *Evolution* 55: 1373-1385.
- BURKHARDT, D. & DE LA MOTTE, I. 1983. How stalk-eyed flies stalk: observations and measurements of the eyes of *Cyrtodiopsis whitei* (Diopsidae, Diptera). *Journal of Comparative Physiology* 151: 407-421.
- BURKHARDT, D. & DE LA MOTTE, I. 1988. Big 'antlers' are favoured: female choice in stalk-eyed flies (Diptera, Insecta), field collected harems and laboratory experiments. *Journal of Comparative Physiology* 162: 649-652.
- BURKHARDT, D., DE LA MOTTE, I. & LUNAU, K. 1994. Signalling fitness: larger males sire more offspring. Studies of the stalk-eyed fly *Cyrtodiopsis whitei* (Diopsidae, Diptera). *Journal of Comparative Physiology A* 1774: 61-64.
- CALOREN, D. C. & MARSHALL, S. A. 1998. A revision of the New World species of *Clusiodes* Coquillett (Diptera: Clusiidae). *Studia dipterologica* 5(2): 261-321.
- DALMAN, J. W. 1823. *Analecta Entomologica. Typis Lindhianis, Holmiae*, VI + 108pp. & 4 plates.
- DODSON, G. N. 1997. Resource defence mating system in Antlered Flies, *Phytalmia* spp. (Diptera: Tephritidae). *Annals of the Entomological Society of America* 90(4): 496-504.
- DODSON, G. N. 1999. Behavior of the Phytalmiinae and the evolution of antlers in Tephritid flies (pp. 175-184). In: ALUJA, M. & NORRBOOM, A. L. (eds). *Fruit flies (Tephritidae): Phylogeny and evolution of behavior*. CRC Press, Boca Raton, XVI + 944 pp.
- EBERHARD, W. G. 2001. The functional morphology of species specific clasping structures on the front legs of male *Archisepsis* and *Palaeosepsis* flies (Diptera, Sepsidae). *Zoological Journal of the Linnean Society* 133: 335-368.
- ELLIOT, J. M. 1983. Some methods for the statistical analysis of samples of benthic invertebrates. *Freshwater Biological Association* 25: 1-159.
- GRIMALDI, D. A. 1987. Phylogenetics and Taxonomy of *Zygothrica* (Diptera: Drosophilidae). *Bulletin of the American Museum of Natural History* 186: 103-268.
- HAN, H-Y. 1999. Phylogeny and behaviour of flies in the tribe Trypetini (Trypetinae) (pp. 253-297). In: ALUJA, M. & NORRBOOM, A. L. (eds). *Fruit flies (Tephritidae): Phylogeny and evolution of behavior*. CRC Press, Boca Raton, XVI + 944 pp.
- HENDEL, F. 1914. Diptera Fam. Muscaridae Subfam. Platystominae. *Genera Insectorum* 157: 1-179.
- HENNIG, W. 1965. Die Acalypterae des baltischen Bernsteins und ihre Bedeutung für die Erforschung der phylogenetischen Entwicklung dieser Dipteren Gruppe. *Stuttgarter Beiträge zur Naturkunde* 145: 1-215.
- KAWANO, K. 1998. How far can the Neo-Darwinism be extended? A consideration from the history of higher taxa in Coleoptera. *Rivista di Biologia / Biology Forum* 91: 31-56.

- KAMENEVA, E. P. 2004a. New records of picture-winged flies (Diptera, Ulidiidae) of Central America, including the description of new taxa. *Studia dipterologica* 10(2): 609-652.
- KAMENEVA, E.P. 2004b. A new species of the genus *Plagiocephalus* (Diptera, Ulidiidae) from Central America. *Vestnik Zoologii* 38(4): 15-22.
- KNELL, R. J., FRUHAUF, N. & NORRIS, K. A. 1999. Conditional expression of sexually selected trait in the stalk-eyed fly *Diasemopsis aethiopica*. *Ecological Entomology* 24: 322-328.
- MARSHALL, S. A. 2000. Agonistic behaviour and generic synonymy in Australian Clusiidae (Diptera). *Studia dipterologica* 7(1): 3-9.
- MCALPINE, D. K. 1973. Observations on sexual behaviour in some Australian Platystomatidae (Diptera, Schizophora). *Records of the Australian Museum* 29(1): 1-10.
- MCALPINE, D. K. 1975. Combat between males of *Pogonortalis doclea* (Diptera, Platystomatidae) and its relation to structural modification. *Australian Entomological Magazine* 2(5): 104-107.
- MCALPINE, D. K. 1979. Agonistic behavior in *Achias australis* (Diptera, Platystomatidae) and the significance of eyestalks (pp. 221-230). In: BLUM, M. S. & BLUM, N. A. (eds). Sexual selection and reproductive competition in insects. *Academic Press, New York*, 463 pp.
- MCALPINE, D. K. 1982. The acalyptrate Diptera with special reference to Platystomatidae (pp. 659-673). In: GRESSITT, J. L. (ed.). Biogeography and ecology of New Guinea. *Monographiae Biologicae* 42, Dr W. Junk, The Hague, VII + 983 pp.
- MCALPINE, D. K. 1994. Review of the species of *Achias* (Diptera: Platystomatidae). *Invertebrate Taxonomy* 8: 117-281.
- MCALPINE, D. K. 1998. 64 Platystomatidae (Signal Flies) (pp. 147-174). In: Oosterbroek, P. (ed.). The families of Diptera of the Malay Archipelago. *Fauna Malesiana Handbooks* 1: 1-225.
- MCALPINE, D. K. 2000. Australian Signal Flies of the genus *Rhytidortalis* (Diptera: Platystomatidae). *Proceedings of the Linnaean Society of New South Wales* 121: 147-174.
- MCALPINE, D. K. 2001. Review of the Australian genera of Signal flies (Diptera: Platystomatidae). *Records of the Australian Museum* 53: 113-199.
- MCALPINE, D. K. & SCHNEIDER, M. A. 1978. A systematic study of *Phyrtalmia* (Diptera, Tephritidae) with description of a new genus. *Systematic Entomology* 3: 159-175.
- MCALPINE, J. F., PETERSON, B. V., SHEWELL, G. E., TESKEY, H. J., VOCKEROTH, J. R. & WOOD, D. M. (eds). Manual of Nearctic Diptera. Volume 2. *Research Branch, Agriculture Canada, Monograph* 28: 675-1332.
- MEIER, R. & BAKER, R. 2002. A cladistic analysis of Diopsidae (Diptera) based on morphological and DNA sequence data. *Insect Systematics and Evolution* 33: 325-336.
- MOFFETT, M. W. 1997. Flies that fight. *National Geographic* 192(5): 68-77.
- DE LA MOTTE, I. & BURKHARDT, D. 1983. Portrait of an Asian stalk-eyed fly. *Naturwissenschaften* 70: 452-461.
- PAPP, L. & DARVAS, B. (eds) 1998. Contributions to a Manual of Palaearctic Diptera (with special reference to flies of economic importance) Volume 3. *Science Herald, Budapest*, 880 pp.
- PAPP, L. & DARVAS, B. (eds) 2000. Contributions to a Manual of Palaearctic Diptera (with special reference to flies of economic importance) Appendix volume. *Science Herald, Budapest*, 604 pp.
- SÉGUY, E. 1951. Ordre des Diptères (Diptera Linné, 1758) (pp. 449-744). In: GRASSÉ, P-P. (ed). Traite de Zoologie Anatomie, Systématique, Biologie. Tome X, Insectes Supérieurs et Hémiptéroïdes (Premier Fascicule). *Masson et Cie Éditeurs Libraries de L'Académie de Médecine, Paris*, 975 pp.
- SHATALKIN, A. I. 1991. *Sobarocephaloides alini* sp.n. (Diptera, Clusiidae) a new species of clusiid flies from Brazil with a peculiar cheek process in male. *Entomologiceskoe Obozreniye* 70(4): 928-930 (in Russian, translated into English in 1992 in *Entomological Review* 71(6): 35-37).
- SHILLITO, J. F. 1971a. The genera of Diopsidae (Insecta: Diptera). *Zoological Journal of the Linnaean Society* 50: 287-295.

- SHILLITO, J. F. 1971b. Dimorphism in flies with stalked eyes. *Zoological Journal of the Linnaean Society* 50: 297-305.
- SHIRAKI, T. 1933. A systematic study of Trypetidae in the Japanese Empire. *Memoirs of the Faculty of Science and Agriculture Taihoku Imperial University* 8 (*Entomology* 2): 1-509.
- SIVINSKI, J. 1997. Ornaments in the Diptera. *Florida Entomologist* 80(2): 142-164.
- SIVINSKI, J. 1999. Breeding habits and sex in families closely related to the Tephritidae: Opportunities for comparative studies of evolution of fruit fly behaviour (pp. 23-37). *In*: ALUJA, M. & NORRBOM, A. L. (eds). *Fruit flies (Tephritidae): Phylogeny and evolution of behavior*. CRC Press, Boca Raton, XVI + 944 pp.
- SOÓS, Á. & PAPP, L. (eds) 1984a. Catalogue of Palaearctic Diptera, Volume 9, Micropezidae–Agromyzidae. *Akadémiai Kiadó, Budapest and Elsevier, Amsterdam*, 460 pp.
- SOÓS, Á. & PAPP, L. (eds) 1984b. Catalogue of Palaearctic Diptera, Volume 10, Clusiidae – Chloropidae. *Akadémiai Kiadó, Budapest and Elsevier, Amsterdam*, 402 pp.
- SOÓS, Á. & PAPP, L. (eds) 1988. Catalogue of Palaearctic Diptera, Volume 8, Syrphidae – Conopidae. *Akadémiai Kiadó, Budapest and Elsevier, Amsterdam*, 363 pp.
- STURTEVANT, A. H. 1920. The *Zygothrica* of Wiedemann. *Proceedings of the United States National Museum* 58: 155-158
- WHEELER, M. R. 1968. XXI. Some remarkable new species of Neotropical Drosophilidae. *The University of Texas Publication* 6818: 429-442.
- WHITE, I. M. 1988. Tephritid flies. Diptera: Tephritidae. *Handbooks for the Identification of British Insects* 10(5a): 1-134.
- WHITE, I. M. 1999. Morphological features of the tribe Dacini (Dacinae): Their significance to behaviour and classification (pp. 505-533). *In*: ALUJA, M. & NORRBOM, A. L. (eds). *Fruit flies (Tephritidae): Phylogeny and evolution of behavior*. CRC Press, Boca Raton, XVI + 944 pp.
- WHITE, I. M., HEADRICK, D. H., NORRBOM, A. L. & CARROLL, L. E. 1999. Glossary (pp. 881-924). *In*: ALUJA, M. & NORRBOM, A. L. (eds). *Fruit flies (Tephritidae): Phylogeny and evolution of behavior*. CRC Press, Boca Raton, XVI + 944 pp.
- WHITTINGTON, A. E. 1998. Progress report on a revision of the Plastotephritinae (Diptera, Schizophora, Platystomatidae) pp. 243-244. *In*: Ismay, J. W. (ed.). *Abstracts volume. Fourth International Congress of Dipterology, 6-13 September 1998, Oxford, UK*, 275 pp.
- WHITTINGTON, A. E. 2000. Revision of the Oriental genera of Plastotephritinae (Diptera; Platystomatidae). *Tijdschrift voor Entomologie* 142(2) (1999): 333-344.
- WHITTINGTON, A. E. 2003. Taxonomic Revision of the Afrotropical Plastotephritinae (Diptera; Platystomatidae). *Studia dipterologica, Supplement* 12: 1-300.
- WILKINSON, G. S. & DODSON, G. N. 1996. Function and evolution of antlers and eye stalks in flies (pp. 310-328). *In*: CHOE, J. C. & CRESPI, B. J. (eds). *The evolution of mating systems in insects and arachnids*. Cambridge University Press, Cambridge, UK, 387 pp.
- WILKINSON, G. S. PRESGRAVES, D. C. & CRYMES, L. 1998. Male eye span in stalk-eyed flies indicates genetic quality by meiotic drive suppression. *Nature* 391: 276-279.
- WILKINSON, G. S. & REILLO, P. R. 1994. Female choice response to artificial selection on an exaggerated male trait in a stalk-eyed fly. *Proceedings of the Royal Society, London B* 255: 1-6.

APPENDIX

Maximum and minimum ranges for body length in Acalyprate Diptera.

Pseudopomyzidae	1.70	Cremifaniidae	1.50	Carnidae	1.00
	5.50		2.60		3.00
Cypselosomatidae	2.00	Coelopidae	2.50	Tethinidae	1.50
	3.50		16.00		3.50
Neriidae	6.00	Helcomyzidae	4.00	Canacidae	1.60
	15.00		12.00		5.00
Micropezidae	3.50	Helosciomyzidae	?	Milichiidae	1.00
	20.00		?		6.00
Tanypezidae	5.00	Dryomyzidae	4.00	Risidae	2.00
	8.00		18.00		2.50
Strongylo- phthalmyiidae		Sciomyzidae	1.80	Cryptochetidae	2.00
	3.50		14.00		4.00
	4.00	Phaeomyiidae	3.00	Chloropidae	1.50
Psilidae	3.00		11.00		8.00
	8.00	Ropalomeridae	6.00	Heleomyzidae	1.20
Somatiidae	?		12.00		12.00
	?	Sepsidae	2.00	Trixoscelididae	1.50
Nothybidae	?		6.00		4.00
	?	Heterocheilidae	4.00	Rhinotoridae	6.00
Megamerinidae	?		12.00		6.00
	?	Clusiidae	1.80	Chyromyidae	0.50
Syringogastridae	?		7.50		8.00
	?	Acartophthalmidae	1.00	Sphaeroceridae	0.70
Diopsidae	4.00		3.00		5.50
	12.00	Odiniidae	2.00	Curtonotidae	3.00
Conopidae	2.50		5.00		11.00
	20.00	Agromyzidae	0.90	Camillidae	2.00
Lonchaeidae	3.00		6.50		4.00
	6.00	Opomyzidae	2.00	Drosophilidae	1.00
Ulidiidae	3.00		5.00		7.00
	12.00	Anthomyzidae	1.30	Diastatidae	2.00
Platystomatidae	1.70		4.50		4.00
	12.00	Aulacigastridae	2.00	Campichoetidae	2.50
Tephritidae	1.00		5.00		4.00
	20.00	Periscelididae	2.00	Ephydriidae	1.00
Pyrgotidae	6.00		5.00		11.00
	18.00	Neurochaetidae	2.50	Nannodastiidae	0.70
Richardiidae	3.25		5.00		1.25
	15.00	Teratomyzidae	1.30		
Palloppteridae	2.50		4.50		
	7.00	Xenasteiidae	1.30	Mean	5.12
Piophilidae	3.00		1.70	Range min.	0.50
	8.00	Asteiidae	1.00	Range max.	20.00
Lauxaniidae	2.50		3.00	n	122.00
	5.50	Australimyzidae	?	Stdev	4.58
Celyphidae	2.50		?	Confid	
	5.50	Braulidae	1.20	(95% i.e. 1.96)	0.28
Chamaemyiidae	1.00		3.30		
	5.00				

