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## SYSTEMATICS AND EVOLUTION OF THE PANTOPHTHALMIDAE (DIPTERA, BRACHYCERA)

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### ABSTRACT

*This work is a review of the systematics of the family Pantophthalmidae (Diptera, Brachycera) and an attempt to interpret the evolutionary patterns inherent in this group. Keys for the identification of species and of genera are presented. Short descriptions of the species with emphasis on characters used in species comparisons are included. Besides the conventional morphological structures, four metric characters are also analyzed.*

*The geographical distribution of each species is presented and a phylogenetic sketch is proposed.*

### INTRODUCTION

This is a study of evolutionary patterns in a small family of Diptera, the Pantophthalmidae (suborder Brachycera), found exclusively in Neotropical forests, where the larvae live in galleries which they excavate in trunks of trees, dead or living.

These flies are relatively rare in collections. In order to see all described species, types and series, it was necessary to study materials of 23 museums. It was possible to examine at one time, the most important collections from the Brazilian and American museums, and also of 5 European museums. Other European collections, however, were examined in loco, which prevented the simultaneous comparison of all the materials.

Thirty nine types of the forty five nominal species listed in "A Catalogue of the Diptera of the Americas South of the United States" (Papavero, 1967), were examined. Five types were not located: *P. tabaninus* Thunberg, 1819; *A. picta* Wiedemann, 1821; *R. planiventris* Wiedemann, 1821; *A. frauenfeldi* Schiner, 1868; *A. teretruncum* Fiebrig, 1906. It was not possible to borrow the type of *P. fastuosus* Knob, 1914, from the United States National Museum, but some paratypes were examined. There is no doubt about the identification of the species whose types were not seen.

In the study of the species, morphological characters that showed differences between species and were thought to indicate phylogenetic tendencies within the group, were selected. Male and female genitalia of all species were studied. Based on previous experience (Val, 1972) four body proportion characters were also investigated.

All characters were analyzed from a comparative point of view, with observation of intraspecific variation. Illustrations of the principal characters studied are presented in plates 1 to 30 and graphs 1 to 16.

Twenty species are accepted as valid and placed in two genera: *Opetiops*, with only one species, and *Pantophthalmus* with nineteen species.

Not all species were thoroughly redescribed, but all are analyzed from the view point of the characters used.

The geographical distribution of the species is shown in maps 1 to 6. Inaccurate localities or those which were not located are recorded only in lists of materials.

The main results were the following:

i. Morphological characters, such as the color pattern of the mesonotum, of the wing and of the abdomen proved to be of great value in species characterization, while the genitalia permit only the characterization of species groups.

ii. Through the analysis of body proportions it is also possible to separate groups of species and, in some cases, species.

iii. *O. alienus* is the most primitive species of the family; it is smaller than other species and has pilose eyes.

In *Pantophthalmus*, species groups are recognized; some are better characterized than others. Due to the presence of intermediates, no genera or subgenera are recognized.

iv. The history of the Pantophthalmidae seems to have been the following: initially *O. alienus* became differentiated in South America. A second branch gave origin, on one side, to *roseni*, *rothschildi*, *zoos*, *splendidus* and *subsignatus*, and on the other, to *comptus*, *kertesziianus* and *pictus*. From this last branch came 2 others: one giving initially

*chuni*, *engeli* and *facetus*, and afterwards the group of *argyropastus*, *batesi*, *punctiger*, *frauenfeldi* and *planiventris*; another giving *vittatus*, *tabaninus* and *bellardii*.

v. Species formation in this family, at least in the two better known groups, can be explained by the orthodox model of geographic speciation, and is probably related to the cycles of expansion and retraction of the tropical forests.

#### MATERIALS

In the preparation of the present work I studied the collection of the Museu de Zoologia da Universidade de São Paulo, as well as those of the following museums, to whose curators I am indebted:

- AMNH American Museum of Natural History, New York (Dr. P. Wygodzinsky).
- BM British Museum (Natural History), London (Mr. B. M. Cogan and Mr. H. Oldroyd).
- CAS California Academy of Sciences, San Francisco (Dr. P. H. Arnaud).
- DEI Deutsches Entomologisches Institut, Eberswalde (Dr. G. Morge).
- EAUU Entomologisk Avdelningen, University of Uppsala, Uppsala (Dr. Lars Hedström).
- HDE Hope Department of Entomology, Oxford University, Oxford (Mr. E. Taylor).
- IMT Istituto e Museo di Zoologia Sistemica, Università di Torino (Dr. M. Zunino).
- IOC Instituto Oswaldo Cruz, Rio de Janeiro (Dr. Hugo Souza Lopes).
- IPEACS Instituto de Pesquisas Agrônomicas Centro Sul, Campo Grande, RJ.
- IZP Instytut Zoologiczny Polskiej Akademii Nauk, Warszawa (Dr. Regina Pisarska).
- MABR Museo Argentino de Ciencias Naturales "Bernadino Rivadavia", Buenos Aires (Mr. M. J. Viana).
- MB Museum für Naturkunde der Humboldt-Universität zu Berlin, Berlin (Dr. H. Schumann).
- MG Museu Paraense Emilio Goeldi, Belém (Dr. R. Arlé).
- MGA Museu Anchieta, Porto Alegre (material examined by Dr. G. Lamas M.).
- MNRJ Museu Nacional do Rio de Janeiro, Rio de Janeiro (Dr. Dalcly de Oliveira Albuquerque).
- MP Muséum National d'Histoire Naturelle, Paris (Dr. L. Matile).
- NMB Naturhistorisches Museum Basel, Basel (Dr. C. Baroni Urbani).

NMIS	Natur-Museum und Forschungs Institut Senckenberg, Frankfurt A. M. (Dr. W. Tobias).
RNHL	Rijksmuseum van Natuurlijke Historie, Leiden (Dr. P. J. van Helsdingen).
SMD	Staatliches Museum für Tierkunde, Dresden (Dr. R. Krause).
USNM	United States National Museum, Washington, D.C. (Dr. W. W. Wirth).
ZSM	Zoologische Sammlung des Bayerischen Staates, München (Dr. F. Kühorn and Mr. W. Schacht).

For the purpose of this research, I received, on loan, materials from the most important Brazilian Museums, as well as the materials of the two U. S. Museums mentioned above, and of the Museums of Basel, Berlin, Dresden, Eberswalde and Leiden. The other collections were examined in the respective museums, and as already mentioned, this hindered a simultaneous comparison of the materials as a whole.

About 620 specimens were examined, including 39 of the 45 types described.

#### METHODS

##### FIGURES

Except for those of wings and femoral spines (13-16), all figures of the same organ are on the same scale.

Hairs were omitted in drawings of thorax, abdomen and male genitalia.

##### STATISTICS

Four characters were analyzed by means of regression analysis (Ostle, 1966): wing shape, mesonotum shape, head shape and the relation between the first and the third femora.

Two of these characters (shapes of the wing and thorax), were previously used successfully (Val, 1972). At first sight, head shape, seemed to differ among species. The relation between the femora was supposed to be important in the equilibrium and posture of these flies, and in some way related to the behavior of the species.

Sexual dimorphism within species and interspecific differentiation were investigated for each morphometric character. When sexual dimorphism was not significant, samples of males and females were assembled.

For wing and thorax shape, length was taken as the independent variable. For head shape, width was taken as the independent variable and the height of the eyes as the dependent. For the relation between the femora, the length of the first femur was taken as the independent variable and the length of the third as the dependent.

Regression lines were compared by means of analysis of variance. When heterogeneity was found among the regression coefficients, an extension of the Kramer test (1959) by Duncan (1970), for samples with different numbers, was used. For comparison of the regression constants another extension was used of the same test, by Vanzolini (personal communication).

The results of these simultaneous comparisons were not satisfactory, due to the degree of intergradation between lines, and therefore they will not be presented. The comparisons mentioned were made graphically.

Results are discussed in chapter IV and illustrated in graphs 1 to 16 and tables 1 to 4.

In each table are shown:

N number of specimens in the sample  
 $R_x$  range of the independent variable  
 b regression coefficient  $\pm$  its standard deviation  
 a regression constant  $\pm$  its standard deviation  
 $r^2$  coefficient of determination (square of the coefficient of correlation).

$y'_{x_1}$  and  $y'_{x_2}$  values of the dependent variable for given values ( $x_1$  and  $x_2$ ) of the independent variable.

The following abbreviations are used in the graphs:

A	<i>P. argyropastus</i>	P	<i>P. planiventris</i>
B	<i>P. batesi</i>	$\pi$	<i>P. pictus</i>
C	<i>P. chuni</i>	Q	<i>P. roseni</i>
E	<i>P. engeli</i>	R	<i>P. rothschildi</i>
F	<i>P. frauenfeldi</i>	S	<i>P. subsignatus</i>
I	<i>P. bellardii</i>	T	<i>P. tabaninus</i>
J	<i>P. facetus</i>	U	<i>P. punctiger</i>
K	<i>P. kerteszi</i>	V	<i>P. vittatus</i>
M	<i>P. comptus</i>	X	<i>P. splendidus</i>
O	<i>O. alienus</i>	Z	<i>P. zoos</i>

The Pantophthalmidae are flies too large to be measured under a dissecting scope with a micrometric eyepiece. All the measurements, therefore, were taken with a compass, and read on a rule, to the nearest tenth of a millimeter. The results of this method were satisfactory as demonstrated by the high values of the coefficient of determination.

The points of reference used for the measurements were the following:

Width of the head — maximum width at the level of the half height of the eyes.

Height of the head — maximum height of eye.

Length of the wing — from the beginning of the radial branch to the apex of the wing.

Width of the wing — maximum width perpendicular to the Costa.

Length of the thorax — the distance between the posterior limit of the humeral calli and an imaginary line between the scutum and the scutellum.

Width of the thorax — maximum width of the pre-scutum near the transverse suture.

Length of the femora — laterally taken between the basal articulation and the apical end of the segment; in the case of the posterior femur, not including the apical spine.

From the 620 specimens examined, about 320 were used for statistical purposes.

The numbers of specimens per sample in the list below is the total number used. Not all specimens, however, could be used for all the measurements.

Samples	♀	♂	Samples	♀	♂
<i>alienus</i>	14	—	<i>planiventris</i>	25	10
<i>rothschildi</i>	—	9	<i>tabaninus</i>	40	24
<i>comptus</i>	10	1	<i>bellardii</i>	25	8
<i>kerteszi</i>	13	2	<i>engeli</i>	—	2
<i>pictus</i>	15	12	<i>facetus</i>	1	—
<i>chuni</i>	14	6	<i>roseni</i>	1	2
<i>batesi</i>	10	5	<i>splendidus</i>	1	—
<i>punctiger</i>	8	1	<i>subsignatus</i>	—	2
<i>argyropastus</i>	3	3	<i>zoos</i>	—	1
<i>frauenfeldi</i>	17	2			

## I. SYSTEMATIC POSITION AND CHARACTERISTICS OF THE FAMILY

### Position of the group

There is no doubt that the Pantophthalmidae constitute a natural group, but up to now, it has not been definitely decided whether is a true family, or only a subfamily or even genus of another family.

Initially, the Pantophthalmidae were included within the Tabanidae, but in 1838 Macquart proposed a separated group for these flies: the tribe Acanthomeridae, in the family Notacanthes. Macquart considered the Acanthomeridae a transitional group between Tabanidae and Notacanthes, the latter including Xylophagidae, Coenomyidae and Stratiomyidae.

Bigot (1881) also believed that the Pantophthalmidae could be a link between Tabanidae and Xylophagidae. He was the first to suggest the name Pantophthalmidae, since *Pantophthalmus* had priority over *Acanthomera*.

Several other authors, such as Schiner (1868), Osten Sacken (1886), Aldrich (1905), and Kertész (1908), considered the Pantophthalmidae close to the Xylophagidae, Coenomyidae, Stratiomyidae, Tabanidae and Rhagionidae. Williston (1908) stated that the Pantophthalmidae should even be united to the Stratiomyidae.

Enderlein (1912) considered the affinities between Pantophthalmidae, Coenomyidae and Xylophagidae so important that he suggested these groups be united into a single family, with 3 subfamilies.

Austen (1923) commented on Williston's, Kertész's, Enderlein's and Hermann's opinions. He agreed with the two last named with respect to the great affinity between the Pantophthalmidae and the Xylophagidae and the Coenomyidae. However he concluded his comments saying that it would be well to remember that although the larvae of the latter families were also associated with dead or decaying trees, they were carnivorous and lived under bark. Austen believed that the larvae of Pantophthalmidae had a unique habit among the Diptera (discussion below).

Carrera & D'Andretta (1957) considered the Pantophthalmidae a very well characterized group in the Neotropical fauna, and not so closely related to the Xylophagidae as Enderlein and other authors supposed. Carrera & D'Andretta believed that the affinities between Pantophthalmidae and Xylophagidae were equivalent to those between Stratiomyidae and Tabanidae or even between Tabanidae and Rhagionidae. Therefore they believed that the Pantophthalmidae constituted a completely independent family.

In my opinion, this question will only be satisfactorily solved when the families of Brachycera, to which the Pantophthalmidae are supposed to be related, are properly studied.

#### Characterization of the adult flies

An adult of Pantophthalmidae can be described as follows:

Large robust flies; body without bristles; hairy or bare eyes; females dichoptic and males holoptic; with ocelli; face with a conic or round projection (beak); antennae with two short basal joints and third 8-segmented (with sexual dimorphism); short proboscis finishing in large labellae; palpi 2-segmented (with sexual dimorphism); small calyptera; wing with short prefurca;  $R_4$  and  $R_5$  divergent enclosing wing tip; fourth posterior cell closed; anal cell closed; legs slender with apical spurs in middle tibiae; male genitalia with a simple aedeagus, with double apodeme; hypandrium total or partially fused to the gonopodium; segment 10 vestigial or absent; females with telescoped ovipositor.

### Characterization of larvae

Almost everything known about the biology and morphology of the immature stages of the Pantophthalmidae is due to the works of Brauer (1883, *frauenfeldi*), Fiebrig (1906, *pictus* as *teretruncum*), Hempel (1911, 1912, *pictus*), Andrade (1929, 1930, *pictus*), Greene & Urich (1931, *tabaninus*), and Bondar (1938, *vittatus*).

In general works, such as Hennig's (1952), only superficial comparisons between the larvae of Pantophthalmidae and larvae of the nearer groups are presented.

The larvae of Pantophthalmidae already studied can be characterized as follows:

Body 12-segmented; 1 cephalic or pseudocephalic segment, 3 thoracic and 8 abdominal; first segment of thorax and last of abdomen strongly chitinized; 1 pair of thoracic spiracles and 1 pair of spiracles in the last abdominal segments (amphipneustic larvae); except when newborn the larvae have flabelliform "finger like organs", in the ventral posterior part of the abdomen (the function of these organs is not clear); lack of one pair of mouth-parts (according to Greene & Urich, the maxillae, according to Thorpe the mandible); the cephalic plate inside the prothorax (as in Rhagionidae).

According to Hennig (1952), except for some characteristics, the larvae of Pantophthalmidae are very similar to those of the Xylophagidae.

I examined only larvae of *P. pictus*, but a comparison of the puparia of *chuni* (figs. a, b, i), *pictus* (figs. c, d, h), *batesi* (figs. e, f, g) and two other unidentified species shows some specific differences, mainly in the spines and sculpture of the plate of chitin in the cephalic extremity.

### Biology

As Thorpe had already done (1934), Carrera & D'Andretta (1957) presented a good summary of the literature on the biology of *pictus* and *tabaninus*; it is not necessary to repeat it here. I will present only some of the most interesting points as general information.

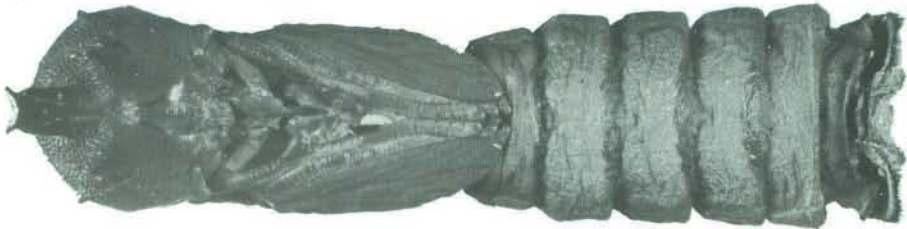
The Pantophthalmidae have wood-boring larvae, which is unusual among the Diptera, though not unique as Austen believed. Greene & Urich (1931) mentioned other examples of larvae of flies with similar habits: *Temnostoma* (Syrphidae) and *Dasyllis* (Asilidae). The latter, however, is a secondary borer, because it lives in galleries already open by Cerambycidae and only sometimes excavates connections between 2 galleries.

Anyway, as correctly pointed out by Austen, the Pantophthalmidae are very different from the Xylophagidae, Coenomyidae and other related families, concerning the habits of the larvae.





a



b



c



d

Plate 1. Puparia of *Pantophthalmus*, in lateral and ventral views: a, b, *P. chuni*;  
c, d, *P. pictus*.



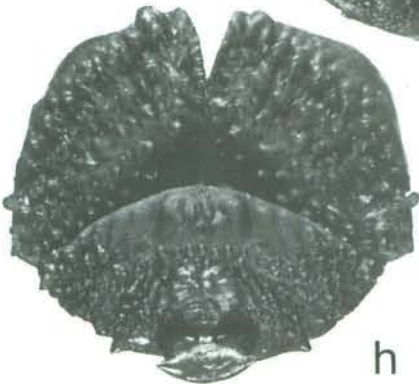
e



f



g



h



i

Plate 2. Puparia of *Pantophthalmus*. *P. batesi*: e, lateral view; f, ventral view; g, frontal view; h, *P. pictus*, frontal view; i, *P. chuni*, frontal view.

Concerning the beginning of the galleries, larvae of first stage of *tabaninus* use some orifice already present and begin to excavate (Greene & Urich, 1931). In *pictus* the larvae themselves begin the galleries (Andrade, 1930).

The larvae dig horizontal galleries in the trunk of various types of trees (Andrade, 1930). *Pictus* is found in live trees (Fiebrig, 1906 and Andrade, 1930), and *tabaninus* in decaying or fallen trees, but never in healthy ones (Greene & Urich, 1931).

As to the feeding habits of the imago and larvae, the several authors have not reached agreement. Andrade (1930) believed that the larvae were xylophagous; Thorpe did not disagree but preferred to believe that the larvae had, as chief food, fermenting sap. Greene & Urich (1931) had the opinion that the adult did not feed. Thorpe stated that, since the adult has mouthparts and well developed digestive system, it probably eats.

The life cycle seems to be longer in *pictus* that has a pupal period varying from 25 to 50 days, and a larval period of 20 to 26 months (Andrade, 1930). *Tabaninus* seems to have a larval period of five and a half to twelve and a half months.

The eclosion of the adult occurs at the entrance of the gallery, half the body remaining inside it.

Little information is available on the behavior of the adult. Copulation was never observed; egg laying was, many times. Adults were found sitting on tree trunks and caught in light traps.

Austen (1923) observed pseudo-parasites (phoretics), which were frequently found on specimens of several species of Pantophthalmidae. They were found in *tabaninus*, *frauenfeldi*, *chuni*, *vittatus*, *bellardii*, *splendidus*, *punctiger* and *rothschildi* and identified by Hirst as nymphs of one species of *Trachytes* (Acarina). An adult female of one species of *Macrocheles* (Acarina) was found, on the head of one specimen of *bellardii*.

## II. HISTORY OF THE CONCEPTS OF GENUS AND SPECIES WITHIN THE FAMILY

In 1819, Thunberg described the first fly of this group: a male of *Pantophthalmus tabaninus*. Since then, till 1934, several authors described new species of Pantophthalmidae without examining the types of the already known species.

Without study of series and without direct knowledge of a reasonable number of species, individuals of a same species showing color variation, or even the different sexes of the same species, were described as different species.

Concerning generic criteria, the different weight that each author attributed to the several characters seems to have often depended on the number of species and specimens available.

In 1821, Wiedemann described 2 genera: *Rhaphiorhynchus* and *Acanthomera*, for respectively *planiventris* and *picta*. Wiedemann himself commented, in 1828, that the genus *Rhaphiorhynchus* was based on a single specimen and that, one of the differential characters, shape and size of the facial beak, could be only a specific difference. On the other hand, the intumescence of the apical segment of the palpus in *planiventris* seemed to be a good reason against the inclusion of this species in the genus *Acanthomera*. He also commented on the necessity of the examination of further specimens.

In *Acanthomera*, Wiedemann included *picta*, with a small ventral spine in the posterior femora; *vittata* Wiedemann and *tabaninus* Thunberg, both without this spine; *seticornis* Wiedemann, a synonym of *P. taninus* Thunberg (male); *heydenii* Wiedemann, a female of *tabaninus* with dark abdomen; *immanis* Wiedemann, a female of *tabaninus* with red abdomen.

Wiedemann's diagnoses of *Acanthomera* and *Rhaphiorhynchus* were transcribed by Macquart, in 1834. In these diagnoses Wiedemann stated that *Acanthomera* had ventral spine on the posterior femur. In 1838, Macquart wrote that the species of *Acanthomera*, despite the name, did not have spines on the femur. He believed that Wiedemann had made a mistake about *Rhaphiorhynchus*. However, the inclusion of *picta*, with the spine, in *Acanthomera*, was accepted by Macquart, meaning that he did not know this species, having available, at most, *tabaninus* and *vittatus*, species without that spine.

On the same occasion Macquart included, in his key to the genera, a difference in the opening of the second posterior cell, a character whose variation within the species he himself had already observed. He also included in his key the degree of prominence of the facial beak.

Macquart was thus the first to consider the presence or absence of the ventral spine of the femur as a generic character. His concepts were based on personal knowledge of a few species, exactly how many it cannot be estimated from his work.

The inconsistency of Macquart's concepts becomes clearer upon consideration of his description of *A. flavipes* (a synonym of *A. picta*), a species with spine that he included in a genus considered by himself to be spineless. He also included *planiventris* in *Rhaphiorhynchus* and the same species, under the name *crassipalpis* in the genus *Acanthomera*.

Walker (1854) adopted Macquart's mistakes, including *planiventris* in *Rhaphiorhynchus* and *crassipalpis* in *Acanthomera*.

Schiner (1868) believed that *Acanthomera* and probably *Rhaphiorhynchus* were similar to *Pantophthalmus*, because the difference in the palpi did not seem to be consistent. However, he accepted *Rhaphiorhynchus* as valid, due to the very prominent facial projection, shown by no other species known at the time.

Bigot (1881) believed that *Rhaphiorhynchus* and *Acanthomera* were the same genus but did not synonymize them, creating instead a third one, *Megalemyia*, based on the shape of the antennae of one male of *seticornis* (= *tabaninus*). He described a female of the same species (*tabaninus*) as a new species, *rubriventris*, included in *Acanthomera*.

Bigot's concepts of genera and species had the same faults previously mentioned. He was not able to associate the sexes of the same species, and included in his keys synonyms of the same species in different genera.

Osten Sacken (1886) pointed out the absence of a consistent basis for the extant genera of Pantophthalmidae. He had the right idea about sexual dimorphism in antennal shape, and about the facial projection. He was able to foresee that antennae intermediate between the extreme types would be discovered. He doubted the validity of the presence or absence of femoral spines and the differences in the palpi as generic characters. He saw two natural groups of species: i. A group without spines in the femora, with attenuated facial projection and sides of the abdomen with sharp edges; ii. Another group, without spines, with marked projection of the face and sides of the abdomen blunt or rounded.

He wrote that if a generic subdivision should be attempted, the name *Acanthomera* should be retained for the group with rounded edges and femoral spines, and *Pantophthalmus*, the older name, for the species with sharp edges. However, Osten Sacken described the species *Acanthomera championi* (= *bellardii*), which according to his own logic, should have been included in *Pantophthalmus*. This species has all the characters of the first group. Osten Sacken believed that a thorough revision could only be carried out by a reviewer assembling materials from all European collections.

Finally, in 1908, Kertész synonymized *Acanthomera* and *Megalemyia* with *Pantophthalmus*. He included all the described species in this genus, except *planiventris* and its synonyms *bigoti* and *crassipalpis*, placed in *Rhaphiorhynchus*. Kertész did not work the group; his observations are contained in a general catalogue of Diptera and seem to be based only on the literature or on a superficial study of specimens in collections.

Williston (1908), skeptical about the validity of *Rhaphiorhynchus*, a genus based on a difference in the palpi, could not understand why the name *Acanthomera* was still used when *Pantophthalmus* had priority. Therefore he believed that all the species of Pantophthalmidae belonged to a single genus.

In the history of the group, Enderlein has an outstanding position as the most radical "splitter". He published several papers on the Pantophthalmidae (1912, 1914, 1921, 1931, 1934) and accepted 7 genera as valid.

In his first publication, he accepted 3 genera: *Pantophthalmus*, that included species without ventral spines on the femora, with projec-

tion of the face attenuated and the 8th segment of the flagellum aristiform; *Rhaphiorhynchus* and *Acanthomera*, both with medium or large spine in the femora, prominent facial projection and the 8th segment of the flagellum not aristiform.

The difference between the two would be in the apical segment of the palpi, normal in *Acanthomera* and swollen in *Rhaphiorhynchus*. He continued to include in different genera, synonyms of a single species.

In 1921 Enderlein established the genus *Opetiops* for the species *alienus* Hermann, 1916. According to Enderlein, *alienus* had at the same time characters of *Rhaphiorhynchus* and *Acanthomera*, such as the prominent beak, and characters of *Pantophthalmus*, such as the absence of the femoral spines.

In 1931, Enderlein described a further genus, *Lycops*, for the new species *zoos*. This genus was based on a difference in the nervation of the single known specimen. In the same paper he also accepted as valid the genus *Atopomyia* Austen, 1923, in which he included one of his new species, *roseni*.

Finally Enderlein (1934) described the genus *Meraca* for the species *A. sigma* Enderlein, 1931 (= *P. comptus* Enderlein, 1912) and *P. batesi* Austen, 1923. In 1931 he had included the latter in *Opetiops*. He preferred to place the 2 species in a separate genus because, although showing the same combination of characters of *Opetiops*, they differed from this genus by bearing apical spines on femora.

For each combination of characters Enderlein accepted or established a new genus. He could not see gradations. His main fault seems to have been a lack of a general comparison of all the materials he studied.

As to the concept of species Enderlein committed the mistakes of other authors: he described males and females as different species, and synonyms of his own species.

Austen (1923) again synonymized *Acanthomera* with *Pantophthalmus* but maintained the genus *Rhaphiorhynchus*, because he believed that the difference in the palpi was very important. He erected the genus *Atopomyia*, based on the shape of the body, the form of the third segment of the antennae, the pilosity of the palpi and the absence of small rounded, warty tubercles. Despite having at hand good materials and having examined several types, he also committed some mistakes, but properly synonymized many species.

Finally Carrera & D'Andretta (1957) the last reviewers of the family, with a good collection at hand and having examined some types, proposed a new classification, with 3 genera and 23 species. For these authors the genera could be characterized by the following combinations of characters: *Rhaphiorhynchus* with ventral spines in the posterior femora (15 species); *Opetiops* without spines, with a conic projection of the face and eyes distinctly pilose (2 species); *Pantophthalmus* without spines, with a round projection of the face and bare eyes (6 species). Like previous authors, they included species that they did not know in genera inadequate according to their own concepts.

## III. ANALYTIC SYSTEMATICS

The following systematic scheme is proposed:

Genus *Opetiops* Enderlein, 1921

1. *alienus* (Hermann, 1916)

Genus *Pantophthalmus* Thunberg, 1819

1. *argyropastus* (Bigot, 1880)
2. *batesi* Austen, 1923
3. *bellardii* (Bigot) in Bellardi, 1862
4. *chuni* (Enderlein, 1912)
5. *comptus* Enderlein, 1912
6. *engeli* (Enderlein, 1921)
7. *facetus* (Enderlein, 1931)
8. *frauenfeldi* (Schiner, 1868)
9. *kertesziianus* (Enderlein, 1914)
10. *pictus* (Wiedemann, 1821)
11. *planiventris* (Wiedemann, 1821)
12. *punctiger* (Enderlein, 1921)
13. *roseni* (Enderlein, 1931)
14. *rothschildi* (Austen, 1909)
15. *splendidus* Austen, 1923
16. *subsignatus* (Enderlein, 1931)
17. *tabanus* Thunberg, 1819
18. *vittatus* (Wiedemann, 1828)
19. *zoos* (Enderlein, 1931)

#### Concept of genera

The genera accepted as valid in the present paper can be identified with the following key:

1. Eyes clearly pilose; external apex of the posterior femora rounded, without spine; lateral stripes of the mesonotum interrupted at the sutural level ..... *Opetiops*
- Bare eyes; spine in the external apex of the posterior femora .....  
..... *Pantophthalmus*

The genus *Pantophthalmus*, as considered in the present revision, is composed of several groups of species. These groups could not be separated in subgenera or other genera due to the great intergradation of characters. They were only considered as "species groups" representing different evolutive trends within the genus.

I believe that the absence of the ventral spine in the posterior femora, in several species, except *alienus*, is a secondary character. Therefore I included species with and without the spine in the same genus.

I accept *Opetiops* as valid. There are very significant differences between *alienus* and the other species and those that induced me to maintain *alienus* in a separate genus were the following: pilosity of eyes and antennae; color pattern of thorax and abdomen; absence of the apical spine in the posterior femora. The combination of the absence of the ventral spine in the posterior femora with the presence of a conic projection of the face does not seem to me to have the relevance supposed by Enderlein (1921) when he erected the genus and which later was accepted by Carrera & D'Andretta (1957).

#### Species concept

The concept of species adopted in the present paper is exclusively based on the comparative external morphology and on the distribution on the species. At present, there are no data for a more refined consideration of "biological species".

These flies are very rare, so far only accidentally collected. Therefore, the raw materials available for this analysis were in the best cases, reasonable samples of dead and dried specimens.

#### Types not seen

*Pantophthalmus tabaninus* Thunberg, 1819: there is no doubt about the illustrated description of this species.

*Acanthomera picta* Wiedemann 1821: the description is clear and this species is the only one with bicolored tibiae.

*Rhaphiorhynchus planiventris* Wiedemann, 1821: is one of the most characteristic species, due to the shape of the palpi and of the facial beak. Wiedemann's description, figures and comments leave no doubt about it.

*Acanthomera teretruncum* Fiebrig, 1906 (= *A. picta* Wiedemann): the description is very good, illustrated and with biological data.

*Acanthomera frauenfeldi* Schiner, 1868: has a very characteristic yellow spot on the mesonotum, and Schiner mentions this in his description.

*Pantophthalmus fastuosus* Knab, 1914 (= *P. tabaninus* Thunberg): topotypes were examined, and the description is also clear.

The designation of lectotypes can be found after the diagnosis of the respective species.

#### New synonymies

Based on the examination of the types I can say that:



*P. conspicuus* Austen, 1923 is the same species as *P. comptus* Enderlein, 1912. *P. comptus* was erroneously synonymized with *P. tabaninus* by Carrera & D'Andretta (1957).

*P. leuckarti* Enderlein, 1931 (♂) and *A. helleriana* Enderlein, 1914 (♂) are synonyms of *A. chuni* Enderlein, 1912 (♀).

Except for the above mentioned cases the types examined showed that the synonymies of previous authors were correct.

Other notes

It must be said concerning *P. batesi*, that specimens from Argentina (♀ and ♂ in the Paris Museum) have small ventral spines on the posterior femora, while the specimens from Amazonia have only an intumescence on this region. As for other morphological characters, specimens from both regions are similar and therefore were considered to be same species. They probably are isolated populations, but it was not possible to determine whether these are biological species or not.

Besides *chuni*, already commented upon, the females of *batesi*, *argyropastus* and *roseni* were associated to the respective males.

Of some species, only one sex is known: *O. alienus* (♀); *P. rothschildi* (♂); *P. splendidus* (♀); *P. subsignatus* (♂); *P. engeli* (♂) and *P. facetus* (♀).

*Engeli* (♂) and *facetus* (♀) are related species, but they differ in the coloration of the abdomen and of the tarsi. The few specimens available make it difficult to evaluate these differences.

*Splendidus* (♀) and *subsignatus* (♂) could also be the two sexes of the same species, but they differ in the color of the tarsi, besides having a very distinct general aspect. Despite this, Enderlein (1931), in the same work in which he described *subsignatus*, identified another male, from the München collection, as *splendidus*. The comparison of this specimen with the type of *subsignatus*, shows that both belong to the same species.

In the following pages are presented keys for males and females of the species: following the keys, there are diagnoses and references to the species.

Key to the females of Pantophthalmidae (females dichoptic; posterior segment of the abdomen elongated, resulting in a telescoped ovipositor).

1. Hairy eyes; stripes on the mesonotum interrupted at the sutural level; posterior femora without apical or ventral spines (genus *Opetiops*) ..... *alienus*
- Bare eyes; posterior femora with apical spine (genus *Pantophthalmus*) ..... 2

2. Mesonotum surface without small rounded shining vesicles ... 3  
 Mesonotum surface with small vesicles or tubercles ..... 4
3. Abdomen elongated and completely dark; central region of the scutum and prescutum orange; palpi with dense black pilosity ..... *roseni*  
 Abdomen with lateral edges of tergites dark, contrasting with the ferruginous central region (shiny); palpi not so pilose as above; first segment of posterior tarsi yellow ..... *splendidus*
4. Wings with basal region yellow; lateral margins of prescutum and scutum light, clearly contrasting with the dorsal region ... 5  
 Wings with basal region dark; mesonotum without contrast ... 7
5. Posterior femora without ventral spine; lateral margins of the abdominal tergites dark, contrasting with the orange central region ..... *comptus*  
 Posterior femora with ventral spine; abdomen completely dark 6
6. Tibiae with basal portion dark and apical portion yellow; white spots on the lateral posterior edges of sternites 2 and 3 ..... *pictus*  
 Tibiae completely dark; facial beak very prominent; sternites without spots ..... *kertesziianus*
7. Lateral stripes of mesonotum with a small light spot (hard to see) at the level of the transverse suture; region between the stripes darker than laterally to them; abdomen dark polinose ...  
 ..... *chuni*  
 Lateral stripes of mesonotum with well marked light or dark spot: dark round spot on prealar callus area; or lateral stripes of mesonotum approximately parallel and posterior femora without ventral spines ..... 8
8. Lateral stripes of mesonotum with spot at the suture level ... 9  
 Lateral stripes without spot; posterior femora without spine 14
9. Scutum without a dark round spot at the prealar callus ..... 10  
 Scutum with a spot on the prealar callus, sometimes not readily visible ..... 12
10. Abdomen dark; lateral stripes of mesonotum with light spots ...  
 ..... *facetus*  
 Lateral edges of abdominal tergites dark, clearly contrasting with the ferruginous central region ..... 11
11. Apical segment of the palpi swollen, approximately reniform; dark smoky wings without contrasting yellow spots ... *planiventris*  
 Apical segment of the palpi not swollen; a yellow and easily visible spot on the lateral stripe of the mesonotum .... *frauenfeldi*

- 12. Spot on prealar callus not very distinct ..... *argyrospastus*  
 Spot on prealar callus rounded and very distinct ..... 13
- 13. Posterior femora always with a strong ventral spine; antennae  
 yellow; apical segment of palpi clavate with rounded apex ...  
 ..... *punctiger*  
 Spine absent or very thin and small; antennae dark; apical segment  
 of palpi with a sharp apex ..... *batesi*
- 14. Prealar callus with a round dark spot; lateral stripes of mesonotum  
 with a characteristic sinuosity, mainly due to a constriction  
 behind the transverse suture ..... *vittatus*  
 Prealar callus without spot ..... 15
- 15. Mesonotum completely dark; abdomen also dark, with central region  
 of tergites without pollinosity ..... *bellardii*  
 Mesonotum with the region between the stripes lighter than late-  
 rally to them; abdomen completely pollinose, dark and ferrugi-  
 neous with dark edges ..... *tabaninus*

Key to males of Pantophthalmidae (males holoptic, abdominal segments 5-8 short)

- 1. Mesonotum with or without small shining rounded vesicles on the  
 surface; apex of aedeagus expanded (generally visible without  
 preparation) ..... 2  
 Mesonotum surface with vesicles; apex of aedeagus not expanded 5
- 2. Lateral edges of abdominal tergites dark brown, contrasting with  
 the reddish brown central region ..... *subsignatus*  
 Abdomen dark brown or black, elongate; palpi with dense black  
 pilosity ..... 3
- 3. Wings with large and very contrasting yellow and brown spots;  
 mesonotum with lateral stripes easily visible ..... *zoos*  
 Wings without yellow spots, wing spots may be orange, reddish or  
 brown; stripes on the mesonotum not very distinct from the  
 ground color ..... 4
- 4. Scutum and prescutum with central region orange or ferruginous;  
 wings with dark stripe on the posterior edge, including the  
 apex ..... *roseni*  
 Mesonotum completely dark, or with posterior areas of the scutum  
 yellowish ..... *rothschildi*

5. Mesonotum completely pollinose, whitish or silvery or pollinose with some small contrasting dark spots ..... 6  
 Mesonotum without this pollinosity and with stripes very visible 12
6. Mesonotum with dark or smoky spots on the prealar callus or the lateral stripes at the transverse suture level ..... 9  
 Mesonotum without these spots ..... 7
7. Abdomen with lateral edges of tergites dark, clearly contrasting with the orange yellow central region ..... *comptus*  
 Abdomen completely dark ..... 8
8. Tibiae with basal portion dark, and apical region yellow; sternites 2 and 3 with lateral posterior white spots ..... *pictus*  
 Tibiae completely dark; sternite without white spots *kerteszianus*
9. Mesonotum with silvery pollinosity with dark brown approximately triangular spots on the lateral stripes of the prescutum; sternites 2 and 3 with latero-posterior light spots ..... *engeli*  
 Without this combination of characters ..... 10
10. Lateral stripes of mesonotum with a small and hardly visible v-shaped or triangular spot at the transverse suture level *chuni*  
 Mesonotum with small rounded spots on the lateral stripes at the suture level, or on the prealar callus ..... 11
11. Mesonotum with silvery pollinosity, with 4 small dark spots, 2 on the prealar callus and 2 on the lateral stripes at the transverse suture level (the latter less visible) ..... *punctiger*  
 Mesonotum with silvery pollinosity with small dark spots only on the lateral stripes at the transverse suture level ..... 12
12. Wings with small yellow spots; facial projection with rounded apex ..... *punctiger*  
 Wings with large yellow spots: apex of facial beak very sharp ..... *batesi*
13. Posterior femora with ventral spine; mesonotum with spot on prealar callus; abdomen with edges of tergites dark brown, forming a regular lateral stripe contrasting with the reddish central region ..... 14  
 Posterior femora without ventral spine, mesonotum with or without spot on prealar callus; color pattern of the abdomen not as above ..... 15

14. Wings smoky, without distinct spots; distal segment of palpi basally inflated and with a pointed apex; facial beak bent downwards  
 ..... *planiventris*
- Wings with distinct small yellow spots; apical segment of palpi elongated, not swollen; a distinct yellow spot on each lateral stripe of mesonotum at the transverse suture level .....  
 ..... *frauenfeldi*
15. Mesonotum with rounded spots on prealar callus; abdomen with oval or rounded dark spots on the lateral edges and also ventral region of tergites ..... *vittatus*
- Without this combination of characters ..... 16
16. Mesonotum reddish brown; coloration between lateral stripes and laterally to these not contrasting; abdomen with tergites completely ferruginous ..... *bellardii*
- Region between lateral stripes of mesonotum lighter than laterally to them; abdomen with dark lateral edges (not forming regular stripes) contrasting with the ferruginous central region ...  
 ..... *tabaninus*

### Genus *Opetiops*

*Opetiops* Enderlein, 1921: 231. Type species, *Pantophthalmus alienus* Hermann (orig. des.).

#### *Opetiops alienus* (Hermann, 1916)

*Pantophthalmus alienus* Hermann, 1916: 43, 2 figs. (♀, type-locality: Colônia Hansa, Santa Catarina, Brazil).

*Opetiops aliena*; Enderlein, 1921: 231; 1931: 361, 372; 1934: 182; Rapp & Snow, 1945: 253; Carrera & D'Andretta, 1957: 385, figs. 5, 23, 36, 47.

*Opetiops alienus*; Papavero, 1967: 3.

Male unknown.

Female. Eyes distinctly pilose; antennae yellow with short pilosity (fig. 1); facial beak protruding with sharp apex (fig. 65). Mesonotum with lateral stripes interrupted at the transverse suture level and anteriorly united to the more lateral stripes, characteristic for this species (fig. 98); elongated rectangular spot on the prealar callus; surface without

shining vesicles or tubercles. Legs brown with tarsi lighter; posterior basitarsi yellow; ventral and apical spines of posterior femora absent (fig. 151). Wings with basal region yellow and with many distinct yellow spots on the remaining regions (fig. 131). Posterior margins of tergites 1-4 yellow or greenish, contrasting with the dark remainder of the tergites. Apical margin of sternite 8 with a shallow rounded indentation; cerci not distinctly divided into two pieces (basicerci and disticerci) (fig. 178).

*Material examined.* Sixteen specimens were examined and among them the type and paratypes of Hermann, in München.

BRAZIL. *Santa Catarina*: no other data (7 ♀, ZSM; 1 ♀, MB); Corupá (under the name of Colônia Hansa) (2 ♀, ZSM; 1 ♀, MZUSP). COLOMBIA. *Boyacá*: Muzo (1 ♀, IOC). PERU. *Huanuco*: Tingo Maria (1 ♀, CAS). *Loreto*: Aguaytia (1 ♀, AMNH). Without locality (2 ♀, DEI).

### Genus *Pantophthalmus*

*Pantophthalmus* Thunberg, 1819: 7. Type species, *tabaninus* Thunberg (mon.).

*Rhaphiorhynchus* Wiedemann, 1821: 59. Type species, *planiventris* Wiedemann (mon.).

*Acanthomera* Wiedemann, 1821: 60. Type species, *picta* Wiedemann (mon.).

*Megalomyia* Bigot, 1880: V. Type species, *Acanthomera seticornis* Wiedemann (orig. des.) = *tabaninus* Thunberg.

*Megalemyia* Bigot, 1881: 455 (lapsus).

*Atopomyia* Austen, 1923: 596. Type species, *Rhaphiorhynchus rothschildi* Austen (orig. des.).

*Lycops* Enderlein, 1931: 367. Type species, *zoos* Enderlein (orig. des.).

*Meraca* Enderlein, 1934: 181. Type species, *Opetiops sigma* Enderlein (orig. des.) = *comptus* Enderlein.

### *Pantophthalmus argyropastus* (Bigot, 1880)

*Megalomyia argyropasta* Bigot, 1880: v (♂, type-locality Panama).

*Megalemyia argyropasta*; Bigot, 1881: 455, 458.

*Acanthomera argyropasta*; Hunter, 1901: 147; Aldrich, 1905: 210; Enderlein, 1931: 362, 365.

*Pantophthalmus argyropasta*; Kertész, 1908: 294; Enderlein, 1912: 108; 1914: 583.

*Pantophthalmus argyropastus*; Austen, 1923: 571; Rapp & Snow, 1945: 253.

*Rhaphiorhynchus argyropastus*; Carrera & D'Andretta, 1957: 303, fig. 15; Papavero, 1967: 3.

Female previously unknown. Antennae light brown (fig. 8); frons dark brown; facial projection protruding, with rounded apex (fig. 72); apical segment of palpi swollen, with a slight median ventral concavity (fig. 41). Lateral stripes of mesonotum thinning away abruptly and irregularly, behind the transverse suture (fig. 105); median stripe clearly visible, ending in a triangular spot on the posterior part of the scutum; indistinct rounded spots on prealar callus. Legs brown with yellow basitarsi; ventral spine of posterior femora medium sized (fig. 162). Wings with some distinct small yellow spots (fig. 147). Abdomen with lateral margins of tergites black contrasting with ferruginous central regions; white spots on tergites 1-3. Apical margin of sternite 8 with indentation only indicated (fig. 185).

Male. Flagellum with 7 basal segments not much shortened and 8th aristiform (fig. 26); facial projection not very protruding, with rounded shining apex (fig. 91); palpi with pointed and elongated apical segment (fig. 57). Mesonotum with silvery polinosity (fig. 125), stripes poorly distinct; a clearly visible rounded spot on each of lateral stripes at the suture level; dark brown spot with characteristic shape (not triangular), on the posterior region of the scutum. Legs brown with yellow basitarsi; ventral spine of the posterior femora very small and thin (fig. 162). Wings similar to those of females, with few yellow spots (fig. 147a). Abdomen with reddish brown tergites with small black spots on margins of tergites 3-5; white spots on tergites 2 and 3. Aedeagus not apically expanded (figs. 205, 222, 239, 254, 271).

*Material examined.* Two females and three males were examined and among them the type, in the British Museum.

COSTA RICA. San Carlos (1 ♀, USNM). PANAMA. Chiriqui (1 ♀, MB; 1 ♂, BM; 1 ♀, 1 ♂, ZSM); Potrerillos (1 ♀, CAS).

### ***Pantophthalmus batesi* Austen, 1923 .**

*Pantophthalmus batesi* Austen, 1923: 566, fig. 2 (♂, type-locality: Villa Nova, R. Amazonas, Brazil).

*Opetiops batesi*; Enderlein, 1931: 371; Rapp & Snow, 1945: 253; Carrera & D'Andretta, 1957: 287; Papavero, 1967: 3.

*Meraca batesi*; Enderlein, 1934: 182.

Female previously unknown. Antennae dark brown (fig. 9a); frons ochre; facial beak very pointed (fig. 73); apical segment of palpi slightly swollen with pointed apex (fig. 40). Lateral stripes of mesonotum broad and converging on the scutellum (fig. 106); a punctiform or triangular dark spot on each of the lateral stripes of the mesonotum, at the transverse suture level; a distinct dark rounded spot on the prealar callus. Legs dark brown with yellow basitarsi; ventral spine of posterior femora absent in specimens from Amazonia (fig. 163, a, b, d), and small ones in specimens from Argentina (fig. 163c). Wings with yellow spot on the branching  $R_4 + R_5$  often united to the subapical yellow spot on  $R_{2+3}$  (fig. 146); yellow spot on the anal vein broader than in any other species; general coloration almost black. Lateral margins of the abdominal tergites 1-5 black, contrasting with the central regions; segments 6-8 completely dark; white spots on tergites 2 and 3 sometimes also on tergite 1. Apical margin of sternite 8 with a median fissure only indicated (fig. 186).

Male. Seven basal segments of flagellum not shortened and segment 8 aristiform (fig. 27); face with a very prominent and pointed beak (fig. 92); apical segment of palpi thin and elongated (fig. 58). Mesonotum with silvery yellowish pollinosity (fig. 126); oval dark spot on the posterior region of the scutum; one rounded spot on each lateral stripe at the transverse suture level; lateral stripes poorly marked. Wings similar to those of females (fig. 146a). Genitalia (figs. 207, 240, 255, 272).

*Material examined.* Twelve females and five males were examined and among them the type of *P. batesi*, in the British Museum.

The females in several collections had been put together, or identified as, *P. punctiger* (Enderlein).

ARGENTINA. *Misiones*: San Ignacio (1♀, 1♂, MP). BRAZIL. *Acre*: Marmelo (5♀, MZUSP). *Amazonas*: Benjamin Constant (1♂ AMNH); Parintins (under the name of Villa Nova) (1♂, BM); Tabatinga (2♀, IOC); Tefé (1♀, BM). FRENCH GUIANA. Alicoto, Oyapock (1♀, MP); Gourdonville (not located) (1♀, MP); Maroni (1♂, MP). GUYANA. Moraballi Creek, Essequibo River (1♂, BM). PERU. *Huancayo*: Monson Valley, Tingo Maria (1♀, CAS).

#### ***Pantophthalmus bellardii* (Bigot in Bellardi, 1862)**

*Acanthomera picta* Wiedemann of Bellardi, 1859: 76 (specimen misidentified).

*Acanthomera bellardii* Bigot in Bellardi, 1862: 16, pl. 3, fig. 11 (1♀, type locality: Mexico); Bigot, 1881: 459; Osten Sacken, 1886: 68; Aldrich, 1905: 210.



*Acanthomera championi* Osten Sacken, 1886: 67, pl. 3, fig. 16 (♀, type locality: Mexico; Chontales, Nicaragua; Bugaba, Panama); Townsend, 1895: 595; Aldrich, 1905: 210.

*Acanthomera* sp.; Osten Sacken, 1886: 68; Williston, 1908: fig., 61.

*Pantophthalmus bellardii*; Kertész, 1908: 294; Enderlein, 1912: 107, 114; 1914: 582; 1931: 373, 375; Austen, 1923: 587 (syn. *A. championi* Osten Sacken); Rapp & Snow, 1945: 253; Campos, 1952: 105; Carrera & D'Andretta, 1957: 281, figs. 3, 19, 20, 45, 46 (syn. *P. helleri* Enderlein, *P. versicolor* Austen, *P. latifrons* Enderlein); Papavero, 1967: 2.

*Pantophthalmus championi*; Kertész, 1908: 294; Enderlein, 1912: 108; 1914: 583; 1921: 231.

*Pantophthalmus helleri* Enderlein, 1912: 108, 110, figs. 8, 9 (1♀, type locality: Yungas de Coroico, Bolivia; 1♀, type locality: Depto. Chanchamayo, Peru); 1931: 373, 374; Rapp & Snow, 1945: 253.

*Pantophthalmus versicolor* Austen, 1923: 572, fig. 4 (1♂, type locality: Pancina, Vera Paz, Guatemala); Enderlein, 1931: 374; Rapp & Snow, 1945: 254.

*Pantophthalmus latifrons* Enderlein, 1931: 374 (1♀, type locality Chanchamayo, Peru); Rapp & Snow, 1945: 254.

Female. Antennae dark brown (fig. 14); apical segment of palpi cylindrical and elongated (fig. 46); face with a small rounded tubercle, with a slight depression in the median region (fig. 79). Mesonotum with lateral stripes almost parallel; shining spots on the lateral regions of the scutum (fig. 112). Legs dark brown; posterior femora without ventral spine (fig. 169). Wings without a yellow spot following the posterior vein of the discal cell or, this spot interrupted. Abdomen completely dark brown with lateral margins of tergites polinose and central region shiny (without polinosity). Apical margin of sternite 8 with a marked median split sided by salient lobules (fig. 192).

Male. Flagellum with 7 basal segments very shortened and segment 8 aristiform (fig. 30); apical segment of palpi thin (fig. 63); face with a small projection similar to that of females (fig. 96). Mesonotum with lateral stripes slightly darker than the central stripe; shiny spots on the sides of the scutum (fig. 129). Legs reddish brown with tarsi a little lighter. Wings without a yellow spot following the posterior vein of the discal cell (fig. 148). Abdomen reddish brown with narrow dark spot on margins of tergites 1 and 2; white spots lacking. Aedeagus subapically expanded (figs. 209, 226, 243, 260, 278).

*Material examined.* Sixty six specimens were examined; nine males and fifty seven females. Among them, the types of *A. bellardii* Bigot; *A. championi* Osten Sacken; *P. versicolor* Austen, all in the British Mu-

seum; *P. helleri* Enderlein, kindly sent to me from Dresden; *P. latifrons* Enderlein, in Berlin.

BOLIVIA. *La Paz*: Yungas de Coroico (1 ♀, SMD). BRAZIL. No other data (6 ♀, BM) (probably wrongly labelled). COLOMBIA. Buena Vista (not located) (1 ♀, USNM). *Valle*: Dagua River (1 ♀, BM). COSTA RICA. No other data (1 ♀, MB; 1 ♀, 1 ♂, BM); Higuito, San Mateo (1 ♀, USNM); Las Mercedes (1 ♀, 1 ♂, BM); San Carlos (1 ♀, USNM); San José (1 ♀, USNM). ECUADOR. *Los Rios*: Babahoyo (1 ♀, AMNH). *Pichincha*: San Rafael (1 ♀, USNM); Santo Domingo de los Colorados (1 ♀, MP); Yarugui (1 ♀, MZUSP). EL SALVADOR. Sta. Tecla (not located) (1 ♀, USNM). GUATEMALA. No other data (1 ♀, NMIS); Cayuga (1 ♀, USNM); Panima, Vera Cruz (4 ♀, BM); Panzós (2 ♀, 2 ♂, IOC; 1 ♀, MB). MEXICO. No other data (1 ♀, IMT; 2 ♀, BM). *Chiapas*: Finca Refugio (1 ♀, CAS); San José (not located) (1 ♀, CAS). *Vera Cruz*: Cuetá de Misantla (1 ♂, AMNH); El Palmar (not located) (1 ♀, USNM); Orizaba (1 ♀, BM). NICARAGUA. No other data (2 ♀, BM); Chontales (1 ♀, BM; 1 ♀, HDE). PANAMA. Barro Colorado (1 ♀, USNM); Bugaba (1 ♀, BM); Chiriqui (1 ♀, MZUSP; 1 ♀, ZSM; 1 ♀, DEI). PERU. No other data (1 ♀, HDE). *Cuzco*: Marcapata (1 ♀, ZSM); Quiroz. Paucartambo River (2 ♀, AMNH). *Junin*: Chanchamayo (1 ♀, MB). *Loreto*: Tapiche River (1 ♀, AMNH). VENEZUELA. *Aragua*: Rancho Grande (1 ♀, BM). Without locality: 1 ♀, AMNH; 1 ♀, BM; 2 ♀, MB; 2 ♀ MB; 1 ♀, ZSM; 1 ♀, IZP).

#### ***Pantophthalmus chuni* (Enderlein, 1912)**

*Acanthomera chuni* Enderlein, 1912: 102, 103, fig. 4 (2 ♀, type locality: Chanchamayo, Peru); 1914: 578; 1921: 229, 230; 1931: 362, 367; Hermann, 1916: 49.

*Pantophthalmus leuckarti* Enderlein, 1912: 107, 113, fig. 10 (1 ♂, type locality: Tefé, Amazonas, Brazil); 1914: 582; 1931: 373; Hermann, 1916: 49; Rapp & Snow, 1945: 254; Carrera & D'Andretta, 1957: 280; Papavero, 1967: 2. *Syn. n.*

*Acanthomera helleriana* Enderlein, 1914: 578, 581 (1 ♂, type locality: Santa Inéz, Peru); 1921: 228; 1931: 362. *Syn. n.*

*Pantophthalmus chuni*; Austen, 1923: 576; Rapp & Snow, 1945: 253.

*Pantophthalmus hellerianus*; Austen, 1923: 569, fig. 3; Rapp & Snow, 1945: 253.

*Rhaphiorhynchus chuni*; Carrera & D'Andretta, 1957: 300, figs. 7, 33; Papavero, 1967: 3.

*Rhaphiorhynchus hellerianus*; Carrera & D'Andretta, 1957: 306; Papavero, 1967: 3.

Female. Antennae (fig. 7) and frons dark brown; face with a protruding and sharp beak (fig. 71); apical segment of palpi variable (fig. 37). Mesonotum with small light spots poorly marked, on the lateral stripes at the transverse suture level (fig. 104); lateral stripes sharply convergent backward and united posteriorly; coloration between lateral stripes darker than outside. Legs dark brown with yellow basitarsi; posterior femora with a medium-sized to very small ventral spine. Wings with brown base and several yellow spots (fig. 135). Abdomen dark brown, pollinose; white spots on tergites 2 and 3, in some specimens also tergite 1. Apical margin of sternite 8 with a marked split (fig. 184).

Male. Flagellum with 7 basal segments not very shortened, segment 8 aristiform (fig. 24a); apical segment of palpi elongated (fig. 55). Mesonotum with silvery pollinosity, stripes poorly marked (figs. 121, a); spots on lateral stripes at the transverse suture level poorly visible; dark triangular spot on the posterior region of the scutum very elongated. Legs similar to those of females (figs. 160, a, b). Wings smoked and almost hyaline; spots hard to see (figs. 135, a, b). Abdomen reddish brown with silvery polinosity; smoky dark spots on lateral margins of tergites (fig. 174); white spots on posterior edges of tergites 2 and 3. Aedeagus not apically expanded (figs. 202, a, 219, a, 236, 248, a, 265, a).

*Material examined.* Nineteen females and seven males were examined. The types of *A. chuni* Enderlein, *P. leuckarti* Enderlein and *A. helleriana* Enderlein, were examined, in Warsaw.

*Lectotype designation.* Enderlein described 2 syntypes, in the Stettin collection. One of them is now in Warsaw, and is here made a lectotype. The other specimen has not been found.

ARGENTINA. *Misiones*: San Ignacio (1♀, MP). BOLIVIA. *Cochabamba*: San Antonio (1♀, IOC). BRAZIL. Amazonas River (1♀, 1♂, BM). *Amazonas*: Manicoré (1♀, 1♂, BM); Maués River (1♂, MB); Serra da Neblina, Tucano River (1♀, MZUSP); Tabatinga (2♀, IOC); Tapuruquara (1♂, IOC); Tefé (1♂, IZP). ECUADOR. *Morona*: Macas (1♀, DEI). *Pichincha*: Santa Inés (1♂, IZP). FRENCH GUIANA. Cayenne (1♀, MP); Maroni (1♀, MP). PERU. No other data (1♀, MB; 1♀, ZSM). *Cusco*: Quiroz, Paucartambo River (2♀, AMNH). *Huanuco*: Monzón Valley, Tingo Maria (1♂, CAS). *Junin*: Chanchamayo (1♀, IZP). *Loreto*: Jumbatis, Huallaga River (1♀, DEI); Iquitos (2♀, AMNH). *Ucayali*: Boquerón, Abadía (1♂, MZUSP).

### ***Pantophthalmus comptus* Enderlein, 1912**

*Pantophthalmus comptus* Enderlein, 1912: 107, 117 (1♀, type locality: South America); 1914: 582; 1931: 373; Hermann, 1916: 49; Rapp & Snow, 1945: 253.

*Pantophthalmus conspicuus* Austen, 1923: 581, fig. 67 (1♀, type locality: Corozal, Belize); Enderlein, 1931: 373-375; Curran, 1934: 323, 324; Rapp & Snow, 1945: 253; Carrera & D'Andretta, 1957: 278, figs. 1, 24, 50 (syn. *O. sigma* Enderlein); Papavero, 1967: 2. *Syn. n.*

*Opetiops sigma* Enderlein, 1931: 372 (1♀, type locality: Juanjui, Peru); Rapp & Snow, 1945: 253.

*Meraca sigma*; Enderlein, 1934: 181.

Female. Antennae yellow with a characteristic 8th segment, (fig. 2; only one specimen with one complete antenna was examined); face with a not very protruding beak (fig. 66); frons ochre; apical segment of palpi not swollen (fig. 33). Mesonotum coloration between the lateral stripes ochre and outside them brown, contrasting with the lateral regions of the scutum and prescutum that have white pollinosity (fig. 101). Legs with yellow tarsi; ventral spine of posterior femora lacking, but the region of the spine swollen and slightly darker than surrounding areas (fig. 152). Wing base yellow (fig. 132). Lateral margin of tergites with a dark stripe contrasting with the central region that is yellow or orange (fig. 175); sternites also yellowish; white spots on tergites 2 and 3 and sometimes on tergite 1. Apical margin of sternite 8 with a marked fissure (fig. 182).

Male. Antennae with basal segments of flagellum more or less shortened and 8th segment aristiform (fig. 16); face with a very small projection (figs. 81, a); palpus thin (fig. 48). Mesonotum with silvery pollinosity (fig. 114); stripes poorly marked, without spot at the suture level. Legs and wings similar to those of female. Abdomen similar to that of the female. Aedeagus not apically expanded (figs. 194, 211, 229, 245, 262).

*Material examined.* Two males and nine females were examined; among them the type of *P. comptus* Enderlein, kindly sent to me by the Dresden Museum; the type of *P. conspicuus* Austen, in the British Museum; the type of *O. sigma* Enderlein, in München:

BELIZE. Corozal (1♀, BM). BRAZIL. Amazonas: Tefé (1♂, ZSM). Pará: Óbidos, Colônia Rio Branco (1♀, IOC). FRENCH GUIANA. Maroni (1♀, MP). GUYANA. Kartabo, Bartica (1♀, AMNH). PERU. *San Martin*: Juanjui (1♀, ZSM). SURINAM. Butenvijk (not located) (1♀, RNHL). Without locality: 1♀, MZUSP; 1♀, SMD; 1♀, MP; 1♂, IZP.

### ***Pantophthalmus engeli* (Enderlein, 1931)**

*Acanthomera engeli* Enderlein, 1931: 362 (1♂, type locality: Chiriqui).

*Pantophthalmus engeli*; Rapp & Snow, 1945: 253.

*Rhaphiorhynchus engeli*; Carrera & D'Andretta, 1957: 305, figs. 16, 26, 55; Papavero, 1967: 3.

Female unknown.

Male. Antennae with 7 basal segments of flagellum shortened, but not markedly so, and segment 8 aristiform and very elongated (fig. 25); face with a small projection (fig. 89); palpus thin (fig. 56). Mesonotum with yellow or silvery polinosity; lateral stripes poorly marked behind the suture, but very marked anteriorly; a dark characteristic spot on the posterior region of the scutum (fig. 122). Legs brown with tarsi completely yellow; ventral spine in posterior femora (fig. 161). Abdomen reddish brown or ochre; lateral margin of tergites with dark spots: white spots on tergites 2, 3 and 4 and on sternites 2 and 3. Genitalia with aedeagus not apically expanded (fig. 201, a; 218, 235, 249, 266).

*Material examined.* Two specimens examined, the type, in München and one specimen without locality label, in the Instituto Oswaldo Cruz.

#### ***Pantophthalmus facetus* (Enderlein, 1931)**

*Acanthomera faceta* Enderlein, 1931: 362, 363, (1 ♀, type locality: Chiriqui, Panama).

*Pantophthalmus faceta*; Rapp & Snow, 1945: 253.

*Rhaphiorhynchus facetus*; Carrera & D'Andretta, 1957: 297, figs. 11, 30; Papavero, 1967: 3.

Male unknown.

Female. Antennae lacking the flagellum in the only specimen seen; face with a pointed beak (fig. 77); apical segment of palpi swollen and characteristically curved (fig. 39). Lateral stripes of mesonotum slightly wider at the transverse suture level (fig. 108); a reddish spot on each lateral stripe at the same level; median stripe very marked though thin; a dark triangular spot on the posterior region of the scutum uniting the lateral stripes. Wings with dark yellow spots (fig. 143). Abdomen without polinosity, with metallic reflections; rectangular white spots on tergites 2 and 3. Apical margin of sternite 8 with an apparently deep fissure (genitalia not dissected) (fig. 119).

*Material examined.* Only the type, in München, was examined.

#### ***Pantophthalmus frauenfeldi* (Schiner, 1868)**

*Acanthomera frauenfeldi* Schiner, 1868: 78 (1 ♀, type locality: Colombia); Bigot, 1881: 454, 459; Brauer, 1883: 25, pl. ii, figs. 25a, 25c;

Roeder, 1896: 261; Osten Sacken, 1886: 65; Hunter, 1901: 147; Enderlein, 1912: 101; 1914: 578, 580; 1921: 228, 230; 1931: 362, 366.

*Pantophthalmus frauenfeldi*; Kertész, 1908: 294; Austen, 1923: 565; Rapp & Snow, 1945: 253; Campos, 1952: 105.

*Rhaphiorhynchus frauenfeldi*; Carrera & D'Andretta, 1957: 301, figs. 6, 25, 31, 52; Papavero, 1967: 3.

Female. Frons dark brown with ocular margins golden and one golden spot just above the antennae (fig. 11); facial tubercle variable, but always very prominent (fig. 75, a, b); apical segment of palpi not swollen (fig. 43). Lateral stripes of mesonotum with elongate yellow spot at the suture level (fig. 109); dark posterior spot of scutum (just before the scutellum), in some specimens with a yellow margin. Legs brown with tibiae slightly darker; tarsi completely yellow; ventral spine of posterior femora variable (figs. 166, a, b). Light spots on wings not very contrasting with the dark general coloration (fig. 144). Abdomen reddish brown with lateral margin of tergites dark brown; white spots on tergites 1-3. Apical margin of sternite 8 lobulate with a median cleft (fig. 190).

Male. Flagellum with basal segments slightly shortened and segment 8 aristiform (fig. 23); facial projection protruding and with a small shining area (fig. 90); palpus (fig. 60). Mesonotum similar to that of the females but with white pollinosity. Aedeagus without apical expansion (figs. 203, 220, 238, 257, 275).

*Material examined.* Twenty seven females and two males were examined. The type of *A. frauenfeldi* Schiner was not found; it may be in Wien, perhaps in the public exhibits (N. Papavero personal communication). BOLIVIA. Yungas del Palmar (not located) (1 ♀, NMB). COLOMBIA. No other data (4 ♀, AMNH; 2 ♀, MB). *Antioquia*: Medellín (1 ♀, MP); Mesopotamia (1 ♀, AMNH). *Boyaca*: Muzo (1 ♀, MZUSP). *Cundinamarca*: Bogotá (1 ♀, BM; 1 ♀, MP). ECUADOR. No other data (1 ♀, DEI); Los Llanos (not located) (1 ♀, DEI; 1 ♀, MB). *Bolívar*: Balzapamba (1 ♀, MP). *Morona*: Macas (1 ♀, HDE). *Pichincha*: Santa Inéz (1 ♀, IZP); Yaruqui (1 ♂, MZUSP; 1 ♀, 1 ♂, IOC). PERU. No other data (1 ♀, MP; 1 ♀, BM). *Junin*: Chanchamayo (1 ♀, DEI). *Lima*: Lima (1 ♀, MB). VENEZUELA. *Aragua*: Rancho Grande (2 ♂, AMNH). Without locality: (1 ♀, MB).

#### ***Pantophthalmus kerteszi* (Enderlein, 1914)**

*Acanthomera kerteszi* Enderlein, 1914: 578 (2 ♀, type locality: Peru, Juanjui); 1921: 229, 230; 1931: 262, 366.

*Pantophthalmus conspicabilis* Austen, 1923: 577, fig. 5 (♀, type-locality: Colombia).

*Acanthomera conspicabilis*; Enderlein, 1931: 362.

*Pantophthalmus kertesziانا*; Rapp & Snow, 1945: 253.

*Rhaphiorhynchus kerteszianus*; Carrera & D'Andretta, 1957: 295; figs. 8, 27, 54 (syn. *P. conspicabilis* Austen); Papavero, 1967: 3.

Female. Antennae as in fig. 4, a; frons ochre; face with a very protruding beak basally wrinkled (fig. 68); apical segment of palpi not swollen (fig. 34). Lateral stripes of mesonotum almost parallel; lateral region of prescutum and scutum whitish, clearly contrasting with the brown dorsal regions; a dark triangular spot on the posterior region of the scutum (fig. 102). Legs dark brown with yellow basitarsi; ventral spine of posterior femora medium sized (fig. 154, a). Wings with yellow base and many yellow spots on the remainder (fig. 133). Abdomen completely dark; white spots on tergites 2 and 3, and, in some specimens, on tergite 1. Apical margins of sternite 8 with a median cleft (fig. 181).

Male. Flagellum with basal segments not shortened and segment 8 elongated (fig. 17); face with a pointed protruding beak (fig. 83); palpus as in fig. 49. Mesonotum with whitish polinosity; pattern similar to that of females but indistinct (fig. 115). Legs and wings similar to those of females. Abdomen as in female. Aedeagus without apical expansion (figs. 195, 212, 229, 246, 263).

*Material examined.* Fourteen females and two males were studied. Among the females, the type of *A. kertesziانا* Enderlein, in Berlin, and the type of *P. conspicabilis* Austen, in the British Museum.

*Lectotype designation:* Enderlein described *A. kertesziانا* from two females from Juanjui, Peru; the types should be in the museums of Stettin (Szczecin) and Budapest. In the Stettin collection (now in Warsaw), I could not find specimens of this species, under any name, but in Berlin there is a female of *kertesziانا*, from Juanjui, labelled as the type. This specimen is here designated as lectotype.

BOLIVIA. *Cochabamba*: San Antonio (1♂, IOC). *Santa Cruz*: Provincia del Sara (1♂, MB). BRAZIL. *Amazonas*: Manaus (2♀, MB). *Mato Grosso*: Corumbá (1♀, MZUSP). *Pará*: Óbidos (1♀, 1♂, IOC). COLOMBIA. No other data (1♀, BM). PANAMA. Barro Colorado (1♀, USNM). PERU. *Amazonas*: Santiago River (2♂, AMNH). *San Martin*: Juanjui (2♀, ZSM; 1♀, MB); Tarapoto Region (1♀, AMNH). Without locality: 1♀, MB.

### ***Pantophthalmus pictus* (Wiedemann, 1821)**

*Acanthomera picta* Wiedemann, 1821: 61 (♂, type locality: Brazil); St. Fargeau & Serville, 1825: 541; Wiedemann, 1828: 108; Mac-

quart, 1834: 218; Macquart, 1838: 167; Walker, 1848: 209; 1854: 301; Bigot, 1881: 458; Osten Sacken, 1886: 64; Hunter, 1901: 148; Aldrich, 1905: 210; Hempel, 1911: 613; 1912: 92, figs.; Enderlein, 1912: 102, 104 (syn. *A. teretruncum*); 1914: 578, 579; 1921: 229; 1931: 362, 366; Bondar, 1915: 27, figs.; Ribeiro, 1924: 65, figs.

*Acanthomera flavipes* Macquart, 1847: 26, pl. 1, fig. 2 (♀, type locality: Brazil); Walker, 1854: 301; Bigot, 1881: 459; Hunter, 1901: 147; Enderlein, 1912: 101; 1914: 578; 1921: 228.

*Acanthomera magnifica* Walker, 1850: 74, pl. 1, fig. 1 (♀, type locality: South America); 1854: 300; Schiner, 1868: 78; Bigot, 1881: 454, 459; Osten Sacken, 1886: 65; Hunter, 1901: 148; Enderlein, 1912: 101; 1914: 578; 1921: 228.

*Acanthomera teretruncum* Fiebrig, 1906: 316-323, 344-347, 19 figs. (♀, type locality: Paraguay); Brèthes, 1908: 285; Bezzi, 1912: 2; Bondar, 1915: 31.

*Pantophthalmus pictus*; Kertész, 1908: 295; Austen, 1923: 575 (syn. *A. flavipes* and *A. magnifica*); Andrade, 1927: 69; 1929: 595, 2 figs.; 1930: 253, pl. 29-36, figs. 1-40; 1930: 436; Anonimous, 1935: 777; Lima, 1936: 370; Bondar, 1938: 20; 1938a: 762; 1954: 33, figs. 1-4; Rapp & Snow, 1945: 254; Carvalho, 1950: 217; Fonseca, 1950: 191, 1 fig.; Mariconi, 1963: 518.

*Pantophthalmus flavipes*; Kertész, 1908: 294.

*Pantophthalmus magnificus*; Kertész, 1908: 295.

*Rhaphiorhynchus pictus*; Carrera & D'Andretta, 1957: 293, figs. 12, 28, 29, 43, 44, 56-59, 75-78; Carrera, 1957: 817, fig. 1, 4-7; Papavero, 1967: 303; Silva, 1968: 587.

Female. Antennae (as in fig. 3); palpus (fig. 35); face with a characteristic protruding beak (fig. 67). Lateral areas of prescutum and scutum whitish, contrasting with the brown dorsal region (fig. 103). Tibiae bicolored, base yellow and apex brown; tarsi completely yellow; ventral spine of posterior femora of medium size (fig. 153). Wing base yellow, many yellow spots on the remainder (fig. 134). Abdomen completely dark (fig. 170) with shiny spots (without polinosity) on the median region of the tergites; white spots on tergites 2 and 3 and also on sternites 2 and 3 (absent in some specimens). Apical margin of sternite 8 with a deep median cleft (fig. 183, a), sometimes enlarged.

Male. Flagellum with basal segments not shortened, and segment 8 elongated (fig. 18); face with a small beak, similar to that of the female (fig. 82); apical segment of palpus thin (fig. 50). Mesonotum with silvery polinosity; pattern under this polinosity similar to that of female (fig. 116). Legs and wings similar to those of female. Aedeagus not apically expanded (figs. 196, 213, 230, 247, 264).



*Material examined.* Sixty five females and twenty six males were examined; among the females the types of *A. flavipes* Macquart and *A. magnifica* Walker, both in the British Museum. The type of *A. picta* Wiedemann and of *A. teretruncum* Fiebrig were not found.

ARGENTINA. *Misiones*: no other data (1 ♀, MABR); Puerto Bem-berg (not located) (1 ♀, 1 ♂, MABR); San Antonio (1 ♀, IOC); San Ignacio (1 ♂, MABR). BRAZIL. No other data (1 ♂, MB; 1 ♂, DEI; 1 ♀, 1 ♂, BM). *Espírito Santo*: Sooretama (National Park) (1 ♀, IOC). *Guanabara*: Rio de Janeiro (1 ♀, IOC; 1 ♀, AMNH; 2 ♂, MP). *Minas Gerais*: Uberaba (1 ♀, 1 ♂, BM). *Paraná*: Matelândia (1 ♀, IOC); Rolândia (1 ♂, IOC; 1 ♂, AMNH). *Rio de Janeiro*: Barreiras, Magé (1 ♀, MNRJ); Muri, Nova Friburgo (1 ♀, MZUSP); Paineiras (2 ♀, MP); Petrópolis (1 ♀, IOC). *Rio Grande do Sul*: Cerro Largo (1 ♀, MGA); Itapiranga (not located) (4 ♀, MGA); São Salvador (1 ♀, MGA). *Santa Catarina*: Corupá (2 ♀, IOC); Mafra (1 ♀, IOC); Nova Teutônia (1 ♀, MZUSP); Rio Natal (1 ♀, AMNH); Rio Vermelho (1 ♀, IOC). *São Paulo*: Cássia dos Coqueiros (1 ♂, MZUSP); Cotia, Morro Grande (1 ♀, MZUSP); Limeira (1 ♀, IOC); Piracicaba (2 ♀, 3 ♂, MB); Rio Claro (3 ♀, 4 ♂, MZUSP; 3 ♀, IOC; 1 ♀, MNRJ; 2 ♀, 1 ♂, IPEACS; 1 ♀, DEI; 3 ♀, 1 ♂, BM); São Paulo (2 ♀, 1 ♂, MZUSP; 1 ♀, IOC; 1 ♀, ZSM; 1 ♀, DEI). PARAGUAY. No other data (1 ♀, BM). Concepción (1 ♀, AMNH). *Paraguay*: Sapucaí (1 ♀, BM). *Guaira*: Villarrica (1 ♀, DEI).

Specimens without locality label: 3 ♀, MZUSP; 2 ♀, 1 ♂, IOC; 1 ♀, MB; 1 ♀, DEI; 3 ♀, BM; 2 ♀, HDE. Probably wrongly labelled: 1 ♀, DEI: "Amazonas Gebiet, Brasilien".

***Pantophthalmus planiventris* (Wiedemann, 1821), comb. n.**

*Rhaphiorhynchus planiventris* Wiedemann, 1821: 60 (♀, type locality: Brazil); 1929: 106, pl. 1, fig. 4; 1830: 622; St. Fargeau & Serville, 1828: 545; Macquart, 1834: 217; 1838: 170, pl. 20, figs. 3, a, b; Guérin Meneville, 1835: 544, pl. 98, fig. 3; Cuvier, 1849: pl. 172 bis, fig. 2; Walker, 1854: 299; Schiner, 1868: 77; Bigot, 1881: 454; Osten Sacken, 1886: 65, 66; Hunter, 1901: 148 (syn. *A. bigoti* and *A. crassipalpis*); Aldrich, 1905: 210; Kertész, 1908: 296; Enderlein, 1912: 105, fig. 5; 1914: 582; 1921: 230; 1931: 362, 371; Hermann, 1916: 47; Austen, 1923: 596, fig. 10; Curran, 1934: 323; Rapp & Snow, 1945: 254; Carrera & D'Andretta: 1957: 291, figs. 32, 37, 38, 41, 42, 66-74, 84, 85; Papavero, 1967: 3.

*Acanthomera crassipalpis* Macquart, 1847: 27, pl. 1, fig. 3 (♀, type-locality: Guatemala); Walker, 1854: 302; Schiner, 1868: 78; Bigot, 1881: 454; Aldrich, 1905: 210.

*Acanthomera bigoti* Bellardi, 1862: 16, fig. 10 (♂, type-locality: Mexico, Chinantla near Oaxaca); Schiner, 1868: 78; Bigot, 1881: 349; Aldrich, 1905: 210.

*Rhaphiorhynchus crassipalpis*; Bigot, 1881: 458.

Female. Antennae (fig. 12); Face with a very protruding beak, bent downward (fig. 76); apical segment of palpi very swollen, almost reniform (fig. 44). Lateral stripes of mesonotum converging toward the scutellum and meeting the median stripe (fig. 110); a light brown and elongated spot on each of the lateral stripes at the transverse suture level. Legs brown with yellow tarsi; ventral spine of posterior femora large and strong (figs. 165, a). Wings without distinct spots, with only some smoky dark spots (fig. 142). Abdomen reddish brown with lateral margins of tergites dark, contrasting with the central region (fig. 176); very small white spots on tergites 2 and 3. Apical margin of sternite 8 lobulated and cleft (fig. 188).

Male. Basal segments of flagellum not shortened, the apical segment more elongated (fig. 22); apical segment of palpi basally swollen and apically pointed (fig. 61); face with beak similar to that of female (fig. 94). Mesonotum (fig. 124), legs and wings similar to those of female. Abdomen reddish-brown with dark lateral margins often indistinct; white spots on tergites 2 and 3. Aedeagus not apically expanded (figs. 204, 221, 237, 258, 274).

*Material examined.* Eighty nine specimens were examined; 22 males and 67 females. The types of: *A. crassipalpis* Macquart, in the British Museum and *A. bigoti* Bellardi, in Torino, were seen. In Berlin was found a specimen labelled as type; being a male from Cordua (Surinam), it is certainly not the specimen described by Wiedemann (1821), a female from Brazil. It is instead probably one of the specimens later referred to by Wiedemann (1828).

BOLIVIA. *Cochabamba*: Provincia Chaparé, S. Francisco del Chipiriri (2 ♀, MZUSP). *Santa Cruz*: Provincia del Sara (1 ♀, BM). BRAZIL. No other data (1 ♀, DEI). *Acre*: Rio Branco (1 ♂, IOC). *Amazonas*: Tefé (1 ♂, BM). *Goiás*: Anápolis (1 ♀, IOC); Leopoldo Bulhões (1 ♂, MZUSP). *Maranhão*: Maracaçume River (1 ♀, MZUSP). *Pará*: no other data (1 ♀, 1 ♂, IOC: 4 ♀, 1 ♂, BM); Coraci, Gurupi River (1 ♀, MZUSP); Óbidos (2 ♀, MZUSP; 4 ♀, 1 ♂, IOC). *Rondônia*: São Carlos, km 48 of the Madeira-Mamoré railway (1 ♀, IOC). COLOMBIA. *Cundinamarca*: Bogotá (1 ♂, MP). *Santander*: Suarez River (1 ♀, AMNH). COSTA RICA. No other data (1 ♀, MB); Carillo (1 ♀, USNM); Higuito, San Mateo (1 ♂, USNM). ECUADOR. *Manabi*: Palmar (1 ♀, RNHL). *Pastaza*: Canelos (1 ♀, MB). FRENCH GUIANA. Nouveau Chantier (1 ♂, MB); St. Jean du Maroni (1 ♀, MP). GUATEMALA. No other data (1 ♀, BM); Cayuga (1 ♂, USNM); Qiriguá (1 ♀, USNM); San Sebastian (not located) (1 ♂, USNM). GUYANA. Kartabo, Bartica District (3 ♀, AMNH; 1 ♀, BM; 1 ♀, CAS). MEXICO. *Puebla*: Chinantla (1 ♂, IMT). NICARAGUA. Chontales (3 ♀, BM). PANAMA. Bugaba (1 ♂, BM); Cerro Campana (not located) (1 ♀, CAS); Chiriqui (1 ♂, BM; 1 ♂, BM; 1 ♂, ZSM). PERU. *Huanuco*: Monzón Valley (5 ♀, CAS);

Tingo Maria (3 ♀, AMNH; 1 ♀, 1 ♂, CAS). *Junin*: Chanchamayo (1 ♀, USNM; 1 ♀, IZP); Satipo (1 ♀, MZUSP; 1 ♀, IOC). *Loreto*: Pebas (1 ♀, IZP); Pucallpa (2 ♀, IOC). *Ucayali*: Boquerón, Abadia (1 ♀, IOC). SURINAM. No other data (1 ♀, RNHL; 1 ♀, MB); Charlesburg (not located), Paramaribo (1 ♂, AMNH; 1 ♀, RNHL). TRINIDAD. Arima Valley (3 ♀, AMNH); Maracas Valley (1 ♀, USNM); Santa Cruz (1 ♀, USNM). VENEZUELA. No other data (1 ♀, ZSM). *Monagas*: Caripito (1 ♂, AMNH). Specimens without locality label: 1 ♂, IOC; 1 ♀, ZSM; 2 ♀, 2 ♂, MP.

### ***Pantophthalmus punctiger* (Enderlein, 1921)**

*Acanthomera punctigera* Enderlein, 1921: 228, 229 (1 ♀, type locality: Espirito Santo, Brazil); 1931: 362, 365 (syn. *P. variegatus*).

*Pantophthalmus variegatus* Austen, 1923: 592, fig. 9 (1 ♀, type locality: Brazil); Rapp & Snow, 1945: 254.

*Pantophthalmus punctigera*; Rapp & Snow, 1945: 254.

*Rhaphiorhynchus punctiger*; Carrera & D'Andretta, 1957: 298, figs. 9, 34, 39, 51, 53 (with description of male); Papavero, 1967: 4.

Female. Antennae yellow (fig. 10); frons ochre; face with a protruding but not pointed projection (fig. 74); apical segment of palpi swollen, with rounded apex (fig. 42). Lateral stripes of mesonotum (fig. 107) very wide, anteriorly converging backward; a dark rounded spot on each of the lateral stripes at the transverse suture level; dark rounded spots on prealar callus. Legs brown with yellow basitarsi; a strong ventral spine on posterior femora (fig. 164). Wings with a yellow spot on the branching of  $R_4 + R_5$ , united or almost united to the yellow spot on  $R_{2+3}$ ; an elongated yellow spot on the anal vein (fig. 145). Abdomen with lateral margins of tergites dark, contrasting with the ferruginous color of the remainder; tergites 6-8 completely dark; white spots on tergites 1-4. Apical margin of sternite 8 with a shallow rounded cleft (fig. 187); the sides of the split are also rounded.

Male. Flagellum with basal segments not shortened, 8th segment elongated (fig. 28); apical segment of palpi short with rounded apex (fig. 59). Mesonotum with silvery pollinosity (fig. 127); stripes not clearly visible; dark punctiform spots present at the transverse suture level on the region of the lateral stripes, and also on the prealar calus. Legs, and wings similar to those of the female (fig. 145a). Abdomen with white polinosity, tergites 1-5 orange or yellow, dark spots on lateral anterior margins and white spots on the posterior edges of tergites 1-4. Aedeagus not apically expanded (figs. 206, 224, 241, 256, 273).

*Material examined.* One male and eight females were studied, including the types of *A. punctigera* Enderlein, in Berlin, and of *P. variegatus* Austen, in the British Museum.

BRAZIL. No other data (1 ♀, MB; 2 ♀, BM). *Espírito Santo*: no other data (1 ♀, MB); Farm Jerusalém, Alegre (1 ♀, MZUSP; 1 ♀, IOC). *Paraná*: no other data (1 ♀, BM). *Rio de Janeiro*: Itatiaia (1 ♂, IPEACS); Teresópolis (1 ♀, IOC).

***Pantophthalmus roseni*** (Enderlein, 1931), comb. n.

*Atopomyia roseni* Enderlein, 1931: 370, fig. 3 (♂, type locality: Panama, Chiriqui).

*Rhaphiorhynchus roseni*; Carrera & D'Andretta, 1957: 308, fig. 14, 35; Papavero, 1967: 4.

Female previously unknown. Similar to male. Antennae orange (fig. 5); apical segment of palpi swollen, fusiform (fig. 36); head as in fig. 70. Mesonotum orange; light lateral stripes with red spots anteriorly and at the transverse suture level; a dark transversal stripe on the posterior margin of the scutum. Wings (fig. 139a). Apical margin of sternite 8 without a clear cleft; cerci, short without a clear division between basicerci and disticerci (fig. 179).

Male. Antennae orange, flagellum without short segments (sexual dimorphism not marked) (fig. 21); face with a very protruding and swollen beak, basally wrinkled (fig. 86); apical segment of palpi fusiform, with dense black pilosity on the basal and median regions (fig. 51). Mesonotum with reddish lateral stripes and central stripe brown (fig. 117); red spot on lateral stripes at the suture level, indistinct in males; posterior margin of the scutum with a dark transversal stripe uniting the spots on the posalar calli; mesonotum surface without shining vesicles. Legs dark brown or black; strong ventral spine on posterior femora (fig. 156). Wing spots orange or reddish, a black stripe following the posterior of the wing and including the apex (fig. 139). Abdomen elongated, dark brown, with a shiny longitudinal stripe (without pollinosity) on the median region of the tergites; distinct white spots on tergite 1 and very small ones on tergite 3. Aedeagus with square apex (figs. 197, 214, 231, 251, 268).

*Material examined*. One female and two males, one of the latter the type of *A. roseni* Enderlein, in München.

GUATEMALA. Panzós (1 ♀, MB). MEXICO. *Vera Cruz*: El Palmar (not located) (1 ♂, USNM). PANAMA. Chiriqui (1 ♂, ZSM).

***Pantophthalmus rothschildi*** (Austen, 1923)

*Rhaphiorhynchus rothschildi* Austen, 1909: 129 (♂, type locality: Buena Vista, Bolivia); Hermann, 1916: 47; Bezzi, 1917: 210; Carrera & D'Andretta, 1957: 307, fig. 40; Papavero, 1967: 4.

*Acanthomera rothschildi*; Enderlein, 1921: 228, 230.

*Atopomyia rothschildi*; Austen, 1923: 597, fig. 11; Enderlein, 1931: 369, fig. 4.

*Atopomyia rothschildi* var. *ocellata* Enderlein, 1931: 370 (1♂ type locality: Prov. Sara, Santa Cruz, Bolivia).

Female unknown.

Male. Antennae dark, flagellum with basal segments not shortened, 9th segment not very long (fig. 20); face with a strong protruding beak, basally wrinkled (fig. 85); apical segment of palpi fusiform with dense black pilosity (fig. 52). Mesonotum completely black (fig. 118) or with yellowish spots on latero-posterior region of scutum; lateral stripes indistinct; surface with rare vesicles anterior to the prealar callus. Legs black; ventral spine of posterior femora very strong (fig. 157). Wing coloration variable, from completely smoky to a pattern very similar to that of *roseni*, with posterior margin and apex darker than the remainder (fig. 140, a, b). Abdomen dark brown, elongated, with a median dorsal stripe without pollinosity; white spots on tergites 1-3 variable, generally larger on tergite 1, sometimes lacking on tergite 2 (fig. 170). Genitalia with aedeagus with a squarish dilation at the apex (figs. 198, 215, 232, 257, 269).

*Material examined.* Ten specimens of *P. rothschildi* were examined including Austen's type, in the British Museum, and that of the variety *ocellata* of Enderlein, in Berlin.

BOLIVIA. *La Paz*: Mapiri (1♂, ZSM). *Santa Cruz*: Buenavista (1♂, BM; 1♂, NMB); Provincia del Sara (2♂, MB); Santa Cruz (1♂, DEI). BRAZIL. *Amazonas*: Benjamin Constant (1♂, AMNH); Caiari River, Uaupés (1♂, AMNH). COLOMBIA. *Meta*: Huape River, Orinoco region (1♂, MB). ECUADOR. No other data (1♂, BM).

### ***Pantophthalmus splendidus* Austen, 1923**

*Pantophthalmus splendidus* Austen, 1923: 589, fig. 8 (1♀, type locality: Panama, Chiriqui); Rapp & Snow, 1945: 254.

*Acanthomera splendida*; Enderlein, 1931: 362.

*Rhaphiorhynchus splendidus*; Carrera & D'Andretta, 1957: 310; Papavero, 1967: 4.

Male unknown.

Female. Eighth segment of flagellum with a concavity on the outer side of the apex (fig. 6); face with a strongly protruding beak,

whose dorsal margin is convex and the ventral one straight (fig. 69); apical segment of palpi slightly swollen and with straight and long apical bristles (fig. 38). Lateral stripes of mesonotum very broad anteriorly, tapering backward, and characteristically broadened at the transverse suture level (fig. 99); shiny spots (without pollinosity) lateral to the stripes on the scutum and prescutum; mesonotum surface without shiny vesicles or tubercles. Anterior and median legs completely black; posterior legs with yellow basitarsi (remaining tarsal segments lacking in the only specimen known); ventral spine of posterior femora small and blunt, not well defined (fig. 159). Wings dark brown with very contrasting yellow spots (fig. 137). Abdomen with tergite 1 pollinose, tergites 2-4 with dark lateral margins (irregular spots) and central region light brown without pollinosity; white spots on tergites 1-3. Apical margin of sternite 8 with a small cleft (genitalia not dissected) (fig. 180).

*Material examined.* Only the type of this species was examined, in the British Museum.

#### ***Pantophthalmus subsignatus* (Enderlein, 1931)**

*Acanthomera subsignata* Enderlein, 1931: 362, 364, fig. 1 (1♂, type locality: Chiriqui, Panama).

*Acanthomera splendida*; Enderlein, 1931: 366 (descript. 1♂, misident.).

*Pantophthalmus subsignata*; Rapp & Snow, 1945: 254.

*Rhaphiorhynchus subsignatus*; Carrera & D'Andretta, 1957: 309; Papaverro, 1967: 4.

Female unknown.

Male. Flagellum with seven basal segments not shortened, segment 8 elongated (fig. 19); apical segment of palpi slightly swollen (fig. 54). Inner edge of stripes of mesonotum reddish (fig. 120), lateral region of prescutum and scutum ochre moderately contrasting with the brown dorsal region; surface with small shiny tubercles. Legs brown with yellow basitarsi; ventral spine of posterior femora thin and long (fig. 155). Wings without contrasting spots (fig. 138). Abdomen light brown, lateral margins of tergites with brown spots resulting in a regular longitudinal dark stripe; white spots on tergites 1-3. Apex of aedeagus with a squarish dilation (figs. 200, 217, 234, 267).

*Material examined.* Two specimens were examined, the type in Berlin, and one specimen in München, mis-identified as *A. splendida* Austen, by Enderlein, and also collected in Chiriqui.

**Pantophthalmus tabaninus** Thunberg, 1819

- Pantophthalmus tabaninus* Thunberg, 1819: VII, pl. 7, fig. 2 (♂, type locality: St. Barthélemi); Osten Sacken, 1886: 66; Williston, 1908: 175; Kertész, 1908: 296; Enderlein, 1912: 108, 109, fig. 6; 1914: 583; 1931: 373, 374; Austen, 1923: 552, 555, 556, 562, fig. 1 (new synonymies: *A. seticornis* Wiedemann, *A. heydenii* Wiedemann, *A. immanis* Wiedemann, *A. rubriventris* Bigot, *P. fastuosus* Knab); Greene & Ulrich, 1931: 277, pl. VII-IX, figs. 1-4 (larvae, pupae, biology); Curran, 1934a: 323, 324; Thorpe, 1934: 5-21 (anatomy, biology); Bondar, 1938a: 20; Rapp & Snow, 1945: 254; Greene, 1956: 24; Carrera & D'Andretta, 1957: 259, 275, figs. 2, 21, 22, 48, 79-83; Carrera 1957: 817, fig. 2; Papavero, 1967: 2.
- Acanthomera tabanina*; Wiedemann, 1828: 110; Walker, 1854: 300; Bigot, 1881: 459.
- Acanthomera seticornis* Wiedemann, 1828: 108 (1♂, type locality: "Brazil"); Macquart, 1838: 168, pl. 20, fig. 1; 1847: 27; Walker, 1848: 210; 1854: 301; Bigot, 1881: 454, 455 (*setiformis lapsus*); Hunter, 1901: 148; Aldrich, 1905: 210.
- Acanthomera heydenii* Wiedemann, 1828: 555 (1♀, type locality: "Brazil"); Walker, 1848: 209; 1854: 301; Bigot, 1881: 458; Hunter, 1901: 147; Enderlein, 1912: 102.
- Acanthomera immanis* Wiedemann, 1830: 623 (1♀, type locality: "Surinam"); Guérin Méneville, 1835: 544; Westwood in Duncan 1840: 331, pl. 35, fig. 2; Walker, 1848: 209; 1854: 301; D'Orbigny, 1849: pl. 2, fig. 3; Bigot, 1881: 456, 459; Hunter, 1901: 147.
- Acanthomera picta*; several authors in Cuvier, 1849: pl. 172 bis, fig. 1.
- Acanthomera rubriventris* Bigot, 1880: v (4♀, type locality: "Guatemala"); 1881: 456, 460; Osten Sacken, 1886: 64 (female of *M. seticornis*); Hunter, 1901: 148; Aldrich, 1905: 210.
- Megalomyia seticornis*; Bigot, 1880: v; 1881: 458 (*Megalemyia, lapsus*); Osten Sacken, 1886: 64.
- Acanthomera tabaninus*; Aldrich, 1905: 210.
- Acanthomera* sp.; Williston, 1908: fig. 2.
- Pantophthalmus heydenii*; Kertész, 1908: 294; Enderlein, 1914: 583; 1921: 23; Carrera & D'Andretta, 1957: 277, figs. 18, 49, 60-65; Papavero, 1967: 2; Silva, 1968: 587.
- Pantophthalmus immanis*; Kertész, 1908: 295; Enderlein, 1912: 107, 116; 1914: 583; 1921: 231.
- Pantophthalmus magnificus*; Kertész, 1908: 295.
- Pantophthalmus rubriventris*; Kertész, 1908: 295; Enderlein, 1912: 108; 1914: 583.

*Pantophthalmus seticornis*; Kertész, 1908: 295; Enderlein, 1912: 108, 114, figs. 12-15; 1914: 583, 585; 1921: 231 (*reticornis*, *lapsus*).

*Pantophthalmus gigas* Enderlein, 1912: 109, 110, fig. 7 (2 ♀, type locality, "South America"); 1914: 583; 1931: 373; Hermann, 1916: 49; Bezzi, 1917: 287 (*gigans*, *lapsus*); Anonymous, 1935: 777; Bondar, 1938a: 22, fig. 19; Silva, 1939: 93; Rapp & Snow, 1945: 253; Barbiellini, 1954: 617, 2 figs.

*Pantophthalmida* (unnamed); Bezzi, 1912: 1-4, figs.

*Pantophthalmus fastuosus* Knab, 1914: 27 (type locality: Trinidad; French Guiana, St. Jean; Panama, Canal Zone, Ancon).

*Pantophthalmus tabaninus* var. *immanis*; Enderlein, 1931: 374, 375.

*Pantophthalmus* sp.; Curran, 1934: fig. p. 155.

Female. Flagellum filiform, the 3 basal segments wider than the others (fig. 15); face with a small rounded tubercle, which has a small central depression at the top (fig. 80); palpi with apical segment apically rounded (fig. 47). Lateral stripes of mesonotum more or less parallel, with a characteristic sinuosity; median stripe poorly defined; posterior region of the scutum without dark triangular spot (fig. 113); color between lateral stripes ochre, lateral to them brown. Legs reddish brown with yellow or light brown tarsi; posterior femora without ventral spine. Wings with contrasting yellow spots. Abdomen completely dark, or tergite with dark and irregular margins and the central region reddish brown (fig. 177); white spots on tergites 2 and 3 sometimes on tergite 1. Apical margin of sternite 8 lobulated and cleft (fig. 193).

Male. Flagellum with 7 basal segments short and 8th segment aristiform (fig. 31); apical segment of palpi thin (fig. 64); without rounded apex; face without a protruding beak, as in the female (fig. 97). Mesonotum wings and legs similar to those of female (figs. 130, 149). Lateral edges of tergites dark, contrasting with central region ferruginous; sternites brown, the sixth lighter; white spots on tergites 1-3. Genitalia with hypandrium well marked, aedeagus with a rounded apical dilation (figs. 210, 227, 244, 261, 277).

*Material examined.* Fifty four males and ninety four females were examined, among these, the type of *A. seticornis* Wiedemann, in Leiden; *A. heydenii* Wiedemann, in Frankfurt; *A. immanis* Wiedemann, in Berlin; *A. rubriventris* Bigot, in London; *P. gigas* Enderlein, in Warsaw; and one male in Thunberg's collection, in Uppsala, but not labelled as type. Thunberg's type was also a male, but was said to come from St. Barthélemy and the specimen examined in Uppsala is labelled as coming from Brazil. I know of no other record of *Pantophthalmidae* in the West Indies or in any other island but Trinidad.

*Lectotype designation:* Wiedemann described *A. seticornis* based on a male from Brazil, in the Leiden Museum. I found in the Leiden collec-



tion, two specimens that might be the types. The specimen whose label reads "Calkoen, Brazil" (Calkoen is the collector), is here designated as the lectotype, while the other specimen, without locality label, is here designated as paralectotype.

ARGENTINA. *Buenos Aires*: Buenos Aires (1 ♀, MP). *Misiones*: San Ignacio (1 ♀, MP). BOLIVIA. *Cochabamba*: Cristal Mayo River (1 ♀, CAS); Provincia Chaparé, Chipiriri River (4 ♀, and 1 ♂, ZSM). *Santa Cruz*: Buenavista (2 ♀, NMB). BRAZIL. No other data (2 ♀, IOC; 5 ♀, ZSM; 1 ♂, MB; 1 ♂, IZP; 1 ♂, EAU: 1 ♀, MP; 1 ♂, RNHL); Amazonas River (1 ♂, BM). *Amapá*: Macapá (1 ♂, BM). *Bahia*: no other data (2 ♀, BM). *Espírito Santo*: Córrego do Itá (1 ♀, IOC); Jerusalém Farm, Alegre (2 ♀, MZUSP); Santa Leopoldina (1 ♀, MZUSP, 1 ♀, DEI). *Minas Gerais*: Mar de Espanha (1 ♂, MZUSP; 1 ♀, IOC); Matipó River, Floresta farm (1 ♀, 1 ♂, MZUSP). *Pará*: no other data (1 ♂, HDE); Belém (5 ♀, 2 ♂, MG); Mangabeira, Mocajuba River (1 ♀, IOC); Óbidos (2 ♀, IOC); *Rio de Janeiro*: Angra dos Reis (1 ♀, MZUSP; 1 ♀, IOC; 1 ♀, DEI; 2 ♀, IPEACS); Itaguaí (1 ♀, IOC). *Santa Catarina*: no other data (2 ♀, 1 ♂, ZSM; 1 ♀, MB); Corupá (1 ♀, 1 ♂, IOC; 1 ♀, BM); Santa Luzia (1 ♀, MNRJ). *São Paulo*: Jacutinga (not located) (1 ♀, IOC). COLOMBIA. *Meta*: Villavicencio (1 ♀, MP). FRENCH GUIANA. No other data (1 ♀, MP); Alicoto, Oyapock (1 ♀, MP); Cayenne (1 ♀, MB; 2 ♂, MP); St. Jean du Maroni (1 ♂, MP; 1 ♂, USNM). GUATEMALA. No other data (4 ♀, BM). GUYANA. Kartabo, Bartica (1 ♂, BM). NICARAGUA. No other data (1 ♀, BM). PANAMA. Barro Colorado (1 ♀, USNM); Canal Zone (1 ♂, CAS); El Cermeño (1 ♂, USNM); Gatun Lake, Canal Zone (1 ♂, AMNH). PERU. No other data (1 ♀, MP). *Cuzco*: Quirós, Paucartambo River (1 ♀, AMNH; 1 ♀, USNM). *Huanuco*: Monzón valley, Tingo Maria (1 ♂, CAS); Tingo Maria (1 ♀, MZUSP; 1 ♀, AMNH; 1 ♀, USNM). *Junín*: Satipo (1 ♀, MZUSP). *Loreto*: Iquitos (1 ♀, AMNH; 1 ♀, USNM); Pucallpa (3 ♀, CAS). SURINAM. No other data (1 ♀, IZP; 1 ♀, BM; 1 ♂, USNM; 1 ♀, NMIS; 1 ♀, MB); Oelemarie (1 ♀, AMNH; 1 ♀, USNM); Paramaribo (1 ♀, AMNH; 2 ♀, 3 ♂, RNHL); Zanderij (1 ♂, RNHL). TRINIDAD. No other data (2 ♀, 5 ♂, BM; 1 ♀, 3 ♂, USNM); Arima Valley (2 ♀, AMNH); Mayaró State (1 ♀, 1 ♂, BM); Port of Spain (1 ♂, USNM); Sangre Grande (1 ♂, USNM); Tusure Forest, Sangre Grande (1 ♂, USNM). VENEZUELA. No other data (1 ♂, MB; 1 ♂, BM). *Amazonas*: Duida Mt. (1 ♂, AMNH). *Aragua*: Maracay (2 ♀, 1 ♂, ZSM). *Delta Amacuro*: no other data (1 ♀, MP). *Falcón*: no other data (1 ♂, NMB). *Monagas*: Caripito (1 ♂, AMNH). Without locality: 1 ♀, AMNH; 4 ♂, BM; 3 ♀, MB; 1 ♀, RNHL; 2 ♀, 1 ♂, HDE; 2 ♀, 1 ♂ HDE; 2 ♀, 2 ♂, MP.

### *Pantophthalmus vittatus* (Wiedemann, 1828)

*Acanthomera vittata* Wiedemann, 1828: 109, pl. 2, fig. 2 (♀ and ♂, type locality: Brazil); Macquart, 1838: 168, pl. 20, fig. 2; Walker 1848: 210; Walker, 1854: 302; Schiner, 1868: 78; Bigot, 1881: 454;

Osten Sacken, 1886: 64; Hunter, 1901: 148.

*Acanthomera servillei* Guérin Méneville, 1835: 543, pl. 98, fig. 2 (type locality: Brazil); Bigot, 1881: 454 (syn. *A. vittata*).

*Acanthomera fulvida* Bigot, 1880: v (♀, type-locality: Guiana); 1881: 456, 460; Osten Sacken, 1886: 68; Hunter, 1901: 147.

*Pantophthalmus vittatus*; Kertész, 1908: 296; Enderlein, 1912: 107, 114, fig. 11; 1914: 583, 585; 1921: 231; 1931: 374, 376; Austen, 1923: 586 (new syn. *A. fulvida*); Curran 1934a: 323, 324; Bondar, 1938: 762 figs.; 1938a: 20, fig. 10; Rapp & Snow 1945: 254; Carrera & D'Andretta 1957: 283, fig. 4, 17; Carrera, 1957: 817, fig. 3; Papavero, 1967: 2; Silva, 1968: 587.

*Pantophthalmus fulvidus*; Kertész, 1908: 294; Enderlein, 1912: 107; 1914: 583.

Female. Flagellum or antenna with 8th segment, in some specimens, almost divided in two (fig. 13); frons ferruginous with a dark brown spot (fig. 72); face with a sharp but not very protruding beak; apical segment of palpi variable, sometimes slightly swollen apically (fig. 45). Lateral stripes of mesonotum almost parallel, with a characteristic sinuosity (fig. 111); median stripe well defined; dark rounded spots on prealar callus and also on postalar callus. Legs reddish brown with yellowish tarsi; posterior femora without ventral spine, but with region slightly darker and swollen (fig. 168). Wings with a characteristic yellow spot on the base of the discal cell, following vein "M" toward the wing base (fig. 150). Abdomen with oval or irregular dark spots on the lateral margins and median region of tergites; white spots on tergites 1-3. Apical margin of sternite 8 lobulated with a cleft of variable depth (fig. 191).

Male. Flagellum with 7 basal segments very short and 8th segment aristiform (fig. 29); in some specimens there is no clear segmentation; face with beak similar to that of the female but less protruding (fig. 95); apical segment of palpi thin and with chisel-like apex (fig. 95). Mesonotum similar to that of female (fig. 128). Wings almost hyaline in some specimens. Spots on the median region of tergites sometimes poorly defined (fig. 173). Genitalia with well defined hypandrium; aedeagus slightly expanded subapically (figs. 208, 225, 242, 259, 276).

*Material examined.* Fifty eight females and twelve males were examined, among them the two syntypes of *A. vittata* Wiedemann, in Berlin and Frankfurt, *A. fulvida* Bigot, in the British Museum, *A. servillei* Guérin Méneville, in Paris.

*Lectotype designation:* Wiedemann described *A. vittata* probably from 2 syntypes, one male and one female; both from Brazil. These specimens should be in his collection, in the Berlin Museum. However, in the Berlin collection there is only one male, labelled as type; in the

Frankfurt collection I found a female from Brazil, also labelled as type. The male in the Berlin Museum is here designated as a lectotype, and the female, in Frankfurt, as paralectotype.

BOLIVIA. *Cochabamba*: Prov. Chaparé, S. Francisco del Chipiriri (1 ♀, MZUSP). *Santa Cruz*: Provincia del Sara (1 ♂, MB). BRAZIL. No other data (1 ♀, MB; 1 ♀, NMIS; 1 ♀, 1 ♂, MP; 1 ♀, HDE); Amazons River (1 ♂, BM). *Acre*: Rio Branco (2 ♀, IOC). *Amapá*: Porto Santana (1 ♀, MNRJ). *Amazonas*: no other data (1 ♀, IOC). Manaus (2 ♀, MNRJ); Tabatinga (3 ♀, IOC). *Bahia*: no other data (1 ♀, IOC; 2 ♀, 2 ♂, BM). *Espírito Santo*: Córrego do Itá (1 ♀, IOC); Itabapoana River (1 ♂, IOC); Sooretama (National Park) (1 ♀, MNRJ). *Mato Grosso*: Barra do Tapirapés (1 ♂, CAS); Cuiabá (4 ♀, IZP). *Minas Gerais*: no other data (2 ♀, ZSM). *Pará*: no other data (1 ♀, IOC; 1 ♀, BM); Belém (1 ♂, MG); Óbidos (1 ♀, MZUSP; 2 ♀, 1 ♂, IOC). *São Paulo*: Piratininga (1 ♀, IOC). COLOMBIA. *Meta*: Villavicencio (1 ♀, MZUSP). FRENCH GUIANA. Cayenne (2 ♀, AMNH); Massiriri, Oyapock (not located) (1 ♀, MP); Nouveau Chantier (1 ♀, MP); Pariacabo, Kourou River (1 ♀, MP); Passoura (not located) (1 ♀, MP); Roches de Kourou (1 ♀, MP); St. Jean du Maroni (1 ♀, MP). GUIANA. No other data (2 ♀, BM). PERU. *Loreto*: Iquitos (1 ♂, NMIS). SURINAM. No other data (1 ♀, ZSM). TRINIDAD. Arima District (1 ♀, BM); Arima valley (1 ♀, AMNH). VENEZUELA. *Monagas*: Caripito (1 ♀, AMNH). Without locality: (1 ♀, 1 ♂, MZUSP; 1 ♀, 1 ♂, IOC; 3 ♀, MP; 2 ♀, BM; 5 ♀, HDE).

#### ***Pantophthalmus zoos* (Enderlein, 1931)**

*Lycops zoos* Enderlein, 1931: 367, fig. 2 (♂, type locality: Mexico, Oaxaca).

*Rhaphiorhynchus zoos*; Carrera & D'Andretta, 1957: 311; Papavero, 1967: 4.

Female unknown.

Male. Antennae with basal segments (1-2) light brown; flagellum lacking in the only known specimen; face with a very protruding beak, basally swollen and wrinkled (fig. 87); apical segment of palpi swollen and with dense dark pilosity (fig. 53). Mesonotum with lateral stripes and median stripe well defined (fig. 119); surface without small shiny tubercles. Legs dark brown; ventral spine large and strong on posterior femora (fig. 158). Wings with large yellow spots contrasting with the dark posterior margin and apex (fig. 141). Abdomen elongated, dark brown, with a median dorsal stripe without pollinosity (fig. 172). Genitalia with aedeagus square at the apex (figs. 189, 216, 253, 270).

*Material examined.* Only the type specimen, belonging to the Deutsches Entomologisches Institut, was examined.

#### IV. BODY PROPORTIONS

##### Head

*Sexual dimorphism.* As females are dichoptic and male holoptic, the measurement of the width of the head includes, in females, but not in the male, the width of the frons. Thus, for the same height of eyes, females have wider heads.

*Interspecific differentiation.* Among females (graph 1), *P. vittatus* and *P. tabaninus* are outstanding for having narrower heads.

The other species show smooth intergradation between extremes. *P. bellardii*, *O. alienus* and *P. chuni* are nearer to *P. vittatus* and *P. tabaninus*.

The lines for *P. kerteszi* and *P. pictus* are coincident, with a small difference in range; *P. kerteszi* has the smaller specimens. *P. batesi* is almost coincident with them.

The line for *P. punctiger* crosses those for *P. kerteszi* and *P. pictus*.

*P. planiventris* and *P. frauenfeldi* are almost coincident; the same is true respectively of *P. comptus* and *P. chuni* and also of *O. alienus* — *P. bellardii* which have very different ranges, with a small area of overlap.

As for the (graph 2), the situation is similar: *P. tabaninus* and *P. vittatus* are separated from the remaining line. *P. argyropastus*, *P. chuni*, *P. pictus*, *P. frauenfeldi*, *P. comptus*, *P. batesi*, *P. punctiger* and *P. subsignatus* are close lines or points and these are nearer to *P. tabaninus* and *P. vittatus* than *P. planiventris*, *P. rothschildi*, *P. roseni* and *P. zoos*.

In summary, males and females of *P. vittatus* and *P. tabaninus* have narrower heads than the other species.

Females of *P. frauenfeldi* — *P. planiventris*, *P. pictus* — *P. kerteszi*, *P. chuni* — *P. comptus* have approximately the same head shape while males of these species differ more.

##### Thorax

*Sexual dimorphism.* There are no significant differences between males and females.

In general, the smaller thoraces belong to males and the larger to females. Sometimes the range of the males is included in that of the females.

Males and females were assembled and these mixed samples were compared with samples containing only females (*O. alienus*) or only males (*P. rothschildi*); this verified the legitimacy of the procedure.

*Interspecific differentiation.* *P. rothschildi* and *P. roseni* are separated from other species by having narrower thoraces.

As shown in graph 3, lines for the other species are bunched so that a joint consideration is difficult. When small groups are analyzed the results are the following:

*P. comptus*, *P. kerteszi* and *P. pictus* (graph 4) have almost coincident lines. *P. vittatus* crosses these three lines and the *P. batesi* line. The latter is near to *P. comptus*, *P. kerteszi* and *P. pictus* and is the nearest line to *P. rothschildi*.

*P. frauenfeldi* and *P. planiventris* (graph 5) are coincident, with a small difference in range; *P. argyropastus* and *P. punctiger* are close to them.

*P. chuni* and *P. bellardii* (graph 4) have almost coincident lines, near *P. tabaninus*, which in the general assemblage has the furthest line from *P. rothschildi*.

Among all species, *O. alienus* (graph 6) has the smallest specimens. The respective line is approximately complementary to those of the group near *P. frauenfeldi*.

*Comments.* Despite the great amount of intergradation it is possible to say that:

i. Some species that are closely related to others in external morphology, such as *P. frauenfeldi* and *P. planiventris*, are also closely similar in the shape of the mesonotum (lines almost coincident).

ii. Other species similar in external morphology, such as *P. vittatus* — *P. tabaninus*, or *P. punctiger* — *P. batesi*, show relatively large differences in the shape of the mesonotum. However it is possible to see that *P. vittatus* (graph 4), although differing from *P. tabaninus* and *P. bellardii* with regard to the regression constants, agrees in slope.

## Wing

*Sexual dimorphism.* There is no significant sexual dimorphism in wing shape among the studied species.

*Interspecific differentiation:* As seen in graph 7, all the regression lines are bunched up, and the points representing small samples fit well in the ensemble.

Two groups, more or less well characterized, may be perceived, one with narrower, one with broader wings.

The first group is composed of *P. comptus*, *P. kerteszi*, *P. pictus* and *P. rothschildi* (lines) and also of *P. zoos*, *P. roseni*, *P. subsignatus* and *P. facetus* (points). *P. splendidus* might also be brought into this group.

In the second group are *P. chuni*, *P. argyropastus*, *P. frauenfeldi*, *P. planiventris*, *P. batesi*, *P. punctiger*, *O. alienus*, *P. tabaninus*, *P. vittatus* and *P. bellardii*. *P. engeli*, not in complete agreement, might also be included in this group.

Within the first group (graph 8), *P. rothschildi* and *P. kerteszi* are coincident, although differing in range. *P. rothschildi* has larger wings.

Within the second group, *P. chuni* has the line furthest away from the first group (graph 8). *P. argyropastus* is close to *P. chuni* and near to these two are *P. batesi* and *P. punctiger*, almost coincident (graph 9). Following these are *P. frauenfeldi* and *P. bellardii* and next *P. planiventris* and *P. vittatus*. *P. frauenfeldi* and *P. planiventris* differ (graph 10): *P. frauenfeldi* is almost coincident with *P. tabaninus* and *P. vittatus*. The two latter are coincident but *P. vittatus* has smaller wings (graph 11). *O. alienus* has the smallest wings and its regression line is more or less aligned with *P. planiventris* and *P. tabaninus*.

#### Femur

*Sexual dimorphism.* There is no significant sexual dimorphism in the regression of the length of the first femur on the length of the third femur.

*Interspecific differentiation.* Two groups of lines may be perceived (graph 12):

In the first, the posterior femora are longer (graph 13): it includes *P. comptus*, *P. kerteszi*, *P. pictus* and *P. rothschildi* (lines), and *P. roseni*, *P. subsignatus*, *P. splendidus* and *P. zoos* (points).

In the second group, the posterior femora are proportionally shorter: within it is possible to distinguish two subgroups:

i. (graph 14) *P. argyropastus*, *P. batesi*, *P. punctiger*, *P. frauenfeldi* and *P. planiventris*, that more or less approach the group of *P. comptus* (the first group described above).

ii. (graph 15) *P. chuni*, *P. tabaninus*, *P. vittatus* and *P. bellardii*, *P. facetus*.

*P. engeli* (points) could have been included in either of these subgroups.

*O. alienus* is displaced when compared with any other species.

*Comments.* When these two groups and subgroups are analyzed, one must try to discern two kinds of phenomena: convergence and real affinity.

In the first group, *P. comptus*, *P. kerteszius* and *P. pictus* are closely related species with regard to other characters. The same may be said about *P. rothschildi*, *P. roseni*, *P. subsignatus*, *P. splendidus* and *P. zoos*.

As to the relationships between the two species groups, there is no way yet to decide whether they are related or convergent.

In graph 15, *P. chuni* is close to *P. tabaninus*, *P. vittatus* and *P. bellardii*, which are similar species with regard to other external characters. However the line for *P. chuni* has a slope in relation to that of those species and is parallel to the lines for *P. comptus* and related species.

#### V. GEOGRAPHIC DISTRIBUTION (SHORT DESCRIPTIONS)

The family Pantophthalmidae is exclusively Neotropical, occurring from southern Mexico to northern Argentina. However, within this area the family is neither known from Chile nor from the Brazilian northeast.

It is extremely peculiar that 4 species have so far been reported only from Chiriquí in Panama. These species (*splendidus*, *subsignatus*, *engeli* and *facetus*) belong to two distinct groups.

*Opetiops alienus* seems to have a marginal distribution. Specimens of this species are known from Muzo (Colombia), Aguaitia and Huanuco (Peru) and from Corupá (Santa Catarina, Brazil).

As for the species of *Pantophthalmus*:

*zoos* is known exclusively from the type collected in Oaxaca (southern Mexico).

*roseni* seems to range from southern Mexico to Panama.

*rothschildi* occurs in Bolivia, Ecuador, Colombia and the extreme west of Brazilian Amazonia. *rothschildi* and *roseni* are closely related species with complementary distributions.

*comptus* is known from Corozal (Belize), from the coast of the Guianas, from Juanjui (Peru) and from the main course of the Amazon (Óbidos and Tefé).

*kerteszius* occurs in Panama, the main course of the Amazon, in Peruvian Amazonia and in Bolivia.

*pictus* occurs in southeastern Brazil, in Misiones (Argentina) and in Paraguay. *kerteszi* and *pictus* are closely related species with complementary distributions.

*chuni* ranges from the Guianas to northern Argentina and has been collected in Brazilian and Peruvian Amazonia, in Ecuador and Bolivia.

*argyropastus* seems to occur only in Costa Rica and Panama.

*batesi* is known from the Guianas and Amazonia and also from the northeast of Argentina.

*punctiger* occurs in southern Brazil.

*frauenfeldi* is restricted to northeastern Colombia, northern Venezuela, Ecuador (also in the Pacific slope of the Andes), southwestern Peru and Bolivia.

*planiventris* is largely distributed and occurs in southern Mexico, northwestern Colombia, northern Venezuela, Trinidad, Guianas, Peru, Bolivia and Brazil (Amazonia, Maranhão, Goiás).

*bellardii* occurs in all Central America; in South America it is restricted to the so called arch of northwest (Vanzolini, 1968), reaching Bolivia.

*vittatus* is widespread, known from Brazil, Bolivia, Peru, Colombia, Venezuela, Trinidad and Guianas.

*tabaninus*, also broadly distributed, occurs in Brazil, Argentina, Bolivia, Peru, Colombia, Guianas and Panama.

## VI. EVOLUTIONARY SYSTEMATICS

The discussion that follows is based initially on 2 items:

i. *alienus* is isolated from the remaining species, that are closely related among themselves.

ii. *alienus* is considered the most primitive species of the group.

*alienus* is maintained in the genus *Opetiops*, while all other species are assembled in *Pantophthalmus*. Within *Pantophthalmus*, there are 4 groups of species representing different evolutionary trends:

1. *roseni*, *rothschildi* and *zoos*
2. *comptus*, *kerteszi* and *pictus*
3. *argyropastus*, *batesi*, *punctiger* plus *planiventris* and *frauenfeldi*
4. *vittatus*, *tabaninus* and *bellardii*



*P. splendidus* and *subsignatus* are intermediate between groups 1 and 2.

*P. chuni*, *engeli*, and *facetus* are intermediate between groups 2 and 3.

Therefore there are 3 levels of relationships that will be discussed in the following order:

i. relationship between *alienus* and the remaining species, that is, the relationship between *Opetiops* and *Pantophthalmus*.

ii. relationships of the species of *Pantophthalmus*.

iii. relationships of the species groups within *Pantophthalmus*.

i. Relationships between *Opetiops* and *Pantophthalmus*

I believe that *alienus* is more primitive than the other species because it is the smallest species, morphologically very isolated from the others and with a disjunct geographical distribution.

I believe that the species of *Pantophthalmidae* with the smallest size (normal size) can be more easily related to species of other groups or families. Therefore *alienus* could be nearer to the origin of the *Pantophthalmidae* than the giant species of this family and gigantism, in this case, would be a secondary character.

*O. alienus* could also be considered the most primitive species on account of its hairy eyes. Hairy eyes seem to appear more frequently in more primitive genera of *Tabanidae*. Mackerras (1954) commented that among the *Pangoninae*, the hairiness of the eyes constitutes a trustworthy character, while among the *Chrysopsinae* and *Tabaninae* (less primitive subfamilies) this character has no phylogenetic value, but tends to be associated with life in cold climates.

If *alienus* is really the most primitive species of the group it does not mean that all characters of *alienus* are necessarily the most primitive ones.

The characters that are in the same state in *alienus* and some other species, are the characters that can point out to the relationships between *Opetiops* and *Pantophthalmus*.

Mainly 4 characters can be discussed in this respect: the absence of small vesicles on the mesonotum surface; the absence of a ventral spine in the posterior femora; color pattern of the wing; female genitalia.

The species of *Pantophthalmus* that, as *alienus*, do not bear shiny vesicles on the mesonotum surface are: *roseni*, *rothschildi* (partial absence), *zoos* and *splendidus*.

I believe that the absence of vesicles in these species of *Pantophthalmus* is a primitive character uniting them to *alienus*. The other hypo-

thesis to be considered is that the absence of vesicles in those species of *Pantophthalmus* is a secondary character. Accepting the latter, one could better explain why *subsignatus*, a species related to the group of species without vesicles, has vesicles, and why there are a few vesicles in the anterior region of the prealar callus in *rothschildi*.

As for the female genitalia, there are some similarities between *alienus* and the known females of group 1 (*roseni* and *splendidus*). There is no clear division between basicerci and disticerci, in any of these 3 species: therefore they have short cerci. However *alienus* has the smallest genitalia, and for this reason it has an outstanding position within the Pantophthalmidae.

As for the ventral spine of the posterior femora, the species that do not have it, besides *alienus* are: *batesi* (specimens from Amazonia), *comptus*, *vittatus*, *tabaninus* and *bellardii*.

Any hypothesis that tries to unite *batesi* to *alienus* due to the lack of the ventral femoral spine, will be immediately discarded because the specimens of *batesi* from Argentina do have spines, and this indicates that the absence is a secondary character. On the other hand, as will be discussed, *batesi* is closely related to *punctiger*, a species with a strong ventral spine.

In *comptus* and *vittatus* the region on the ventral spine is swollen and in some specimens darker than the remainder of the posterior femur. This leads me to believe that here also, the absence of the spine is a secondary character.

*Tabaninus* and *bellardii* have a slight depression in the region of the spine and therefore one could relate these species to *alienus*. However these 2 species show certain characters in an extreme state and could not be considered as intermediate. In a phylogeny based on the affinity between *alienus* and these 2 species one would have to accept the spine appearing several times in the evolution of the group, and this does not seem to be true. Because it seems easier, I prefer to believe that the spine disappeared in some species. In this way, *vittatus*, related to *tabaninus* and *bellardii*, shows still a vestige of the spine, while in *tabaninus* and *bellardii*, this has completely disappeared.

The conclusion is that in *comptus*, *batesi*, *bellardii*, *tabaninus* and *vittatus*, the absence of the spine is probably a secondary character and it is not possible to establish a relationship between those species and *alienus* based on this character.

Among the Pantophthalmidae, 6 species have a yellow wing base: *alienus*, *zoos*, *comptus*, *kertesziianus*, *pictus* and *facetus*. The *zoos* and *facetus* patterns are very characteristic, while *comptus*, *kertesziianus* and *pictus* have almost the same pattern, with abundant small yellow spots, very similar to that of *alienus*. I believe that this pattern of coloration is a primitive one and it has persisted in *comptus*, *kertesziianus* and *pictus*.

It is possible then to say that, with regard to the pattern of wing coloration, *comptus*, *kertesziianus* and *pictus* are related to *alienus*. As to the absence of vesicles on the surface of the mesonotum *roseni*, *rothschildi*, *zoos* and *splendidus* are related to *alienus*. As for the female terminalia there is a similarity among *splendidus*, *roseni* and *alienus*. As for the absence of the ventral spine of the posterior femora, it is not possible to relate *alienus* to any other species of the group.

As will be discussed in the following pages, the *comptus* group (2) is related to that of *roseni* (1) and as these 2 groups present some relationships with *alienus* they are considered to be more primitive than the remaining groups of *Pantophthalmus*.

## ii. Relationships among species of *Pantophthalmus*.

Group 1. *P. roseni* (♀ and ♂), *rothschildi* (♂), *zoos* (♂); not so closely related (intermediate with group 2): *splendidus* (♀) and *subsignatus* (♂).

Males of *roseni*, *rothschildi*, *zoos* and *subsignatus* have the aedeagus with an approximately square expansion (figs. 250-253) and ejaculatory apodemes with almost the same shape (figs. 267-270).

Females of *roseni* and *splendidus* do not have a well defined cleft at the apical margin of sternite 8 and bear short cerci, without clear division between basicerci and disticerci (figs. 179-180).

*Roseni*, *rothschildi*, *splendidus* and *zoos* lack shiny vesicles on the mesonotum surface.

In body proportions such as wing and shape relations between first and third femora, the species of this group (1), and those of group 2 are relatively isolated from the remainder. As for the shape of the mesonotum, *roseni* and *rothschildi* are set apart from other species with regard to head shape, *rothschildi* and *zoos* (males) and *roseni* and *rothschildi* (females) are also different from the other species.

*Roseni* and *rothschildi* are closely related species. They have antennae, palpi, beak, shape of head, mesonotum and abdomen, genitalia and therefore the general aspects very similar, but very different from the other species of *Pantophthalmus* with the exception of *zoos*. Austen proposed the genus *Atopomyia* for *rothschildi* and Enderlein included *roseni* in the same genus but erected a new one for *zoos*, *Lycops*.

*Zoos* is very similar to *roseni* and *rothschildi* in the shape and coloration of the abdomen, the beak, the shape and pilosity of the palpi, characters that are in the same state exclusively in these 3 species. However the pattern of coloration of the wing and the insertion point of M<sub>2</sub> after the discal cell, in the single specimen examined, are unique among the Pantophthalmidae. The wing coloration pattern somewhat

resembles that of *pictus*. The coloration pattern of the mesonotum differs from those of *roseni* and *rothschildi* mainly because the lateral stripes are well visible.

The position of *splendidus* is difficult to evaluate, as this species (known only from the type specimen) has little resemblance to any other. The coloration pattern of wing, mesonotum and abdomen and the antennae are peculiar to this species. The genitalia was not dissected but, as already mentioned, it seems to be similar to that of *roseni* (♀). *Splendidus* was associated to group 1, mainly due to the absence of vesicles on the mesonotum.

*Subsignatus* (♂) was associated to this group, due to characters of the genitalia which could hardly be convergent. The lateral stripes of the mesonotum are easily visible, as in *zoos*, and the lateral portions of the scutum and prescutum are light, as happens in *comptus*, *kertesziianus* and *pictus*. *Subsignatus* has vesicles on the mesonotum as all other species of *Pantophthalmus*, except those from this group 1.

Summarizing: *roseni* and *rothschildi* are extreme species, and very closely related. *Zoos* is closely related to both of them, but shows some affinities with other species. *Subsignatus* is an intermediate species, for it has genitalia similar to species of group 1, and vesicles on the mesonotum and other characters similar to species of other groups, mainly species of group 2. *Splendidus*, very different from all other species, was associated to this group due to the lack of vesicles on the mesonotum.

Group 2. *comptus*, *kertesziianus* and *pictus*.

*Comptus*, *kertesziianus* and *pictus* were initially assembled due to the great similarity in the coloration pattern of the wing and mesonotum, in males and females. *Comptus*, *kertesziianus* and *pictus* present sexual dimorphism as for the pattern of the mesonotum; the males are silverish pollinose. The male genitalia of these species are very similar: the aedeagus has no apical expansion; the shape of the compressor apodeme is almost the same. Among females, there is a deep cleft in the apical edge of the 8th sternite. The palpi are not swollen; the antennae of the 3 species are similar in both sexes.

In body proportions, such as wing shape and relationships between first and third femur, the species of group 2 and 1 constitute an assemblage, separated from the remaining species. As for the shape of the mesonotum, *comptus*, *kertesziianus* and *pictus* have a marginal position among the species.

*Kertesziianus* and *pictus* are closely related species but can be easily recognized due to the different coloration of the tibiae. Both have a completely dark abdomen and this is one of the main differences between *comptus* and them.

*Comptus* shows the same color pattern of the abdomen as *subsignatus*, and the species of group 3 (*argyropastus*, *batesi*, *punctiger* plus *planiventris*, *frauenfeldi*). This more complex pattern (fig. 175) was considered to be the most primitive one, or the basic pattern in *Pantophthalmus*. As it seems to be demonstrated by the females of *tabaninus*, *facetus* and some anomalous specimens of *pictus* and *bellardii*, this complex pattern can be disguised when the tergites are completely dark brown or black.

*Comptus* also differs from *kertesziianus* and *pictus* due to the lack of ventral spine on the posterior femora.

With regard to genitalic characters *chuni* (♀ and ♂), *engeli* (♂) and *facetus* (♀) can be included among the species of group 2. However the color pattern of the mesonotum unites them to group 3. *Chuni* and *facetus* have completely dark abdomen, while in *engeli* the abdomen is similar to that of *comptus* and of the species of group 3.

*Facetus* has a yellow wing base, as do *comptus*, *kertesziianus*, *pictus*, *zoos* and *alienus*. The light spot on the lateral stripes of the mesonotum, in *facetus*, is similar to those of *frauenfeldi* and *planiventris*.

Group 3. *argyropastus*, *batesi*, *punctiger*, plus *planiventris* and *frauenfeldi*.

These 5 species are grouped because they have a spot on the lateral stripe of the mesonotum, the same color pattern of abdomen, and the aedeagus is not expanded apically.

In body proportions, such as shape of wing and mesonotum and relationship between first and third femur and shape of mesonotum, the ensemble of these lines is relatively isolated from that of *vittatus*, *tabaninus* and *bellardii*. As to wing shape, the lines of the 3 latter ones intersect those of group 3.

Within group 3, *planiventris* and *frauenfeldi* are closely related, and the same is true for *batesi* and *punctiger*. *Argyropastus* is related to both pairs but mainly to *batesi* and *punctiger*. In this way, group 3 can be divided into 2 subgroups, one containing *frauenfeldi* and *planiventris* and the other, with *argyropastus*, *batesi* and *punctiger*.

*Argyropastus* and *frauenfeldi* have a non-characteristic apical segment of palpi. *Batesi*, *punctiger* and *planiventris* have characteristic palpi, that of *planiventris* being exceptionally swollen.

In males, the flagellum of *planiventris* is more elongated than in the other species of the group.

*Argyropastus*, *batesi* and *punctiger* exhibit sexual dimorphism in the color pattern of the mesonotum, due to the silvery pollinosity of males. In male *frauenfeldi*, there are vestiges of this pollinosity and in *planiventris* it is completely absent. *Argyropastus*, *batesi* and *punctiger* have dark rounded spots on the lateral stripes of mesonotum, at the

level of the transverse suture. In *frauenfeldi* and *planiventris*, the spot is light and elongated; in *frauenfeldi* the spot is yellow.

In *batesi* and *punctiger*, there is a conspicuous dark round spot on the prealar callus of the females. The same spot is visible in females of *argyropastus*, but, in this species, it is not well defined. Among males, this spot is found in *punctiger*. Some other species of *Pantophthalmus* have concentrations of dark pollinosity in this region, but only the 3 species above and *vittatus* have a defined rounded spot. In *Opetiops alienus*, the spot on the prealar callus is definite and forms a rectangular stripe. In *comptus*, *kertesziianus* and *pictus*, the concentration of dark pollinosity on the prealar callus is visible, but it does not form a definite spot or stripe.

With regard to wing coloration pattern, *planiventris* stands out among the Pantophthalmidae. This species lacks definite yellow spots on the wings; the wings are smoky brown. *Argyropastus* and *frauenfeldi* have very similar wings, with few but well defined yellow spots. *Batesi* and *punctiger* also have very similar wings but with more yellow spots than the latter ones.

As to the color pattern of the legs, the 5 species of group 3 present yellow basitarsi; *frauenfeldi* and *planiventris* have the whole tarsi yellow; *argyropastus*, *batesi* and *punctiger* have the remaining segments of the tarsi dark brown. *Planiventris* is the only species with all tibiae yellow.

The Amazonian specimens of *batesi* lack a ventral spine on the posterior femora and, in this way, differ from the remaining species of group 3.

As to the male genitalia, the shape of the compressor apodeme is peculiar to each species; *argyropastus*, *planiventris* and *frauenfeldi* are more or less similar; in *batesi* and *punctiger* the shapes are very characteristic.

Regarding the apical edge of the 8th sternite of the female, *argyropastus*, *batesi* and *punctiger* present a small median cleft; in *punctiger* the cleft is broader. In *frauenfeldi* and *planiventris*, it is deeper and the rounded edges form a lobule on each side. These lobules are similar to those found in females of *tabaninus*, *bellardii* and also in *vittatus*, where they are not so well developed.

Summarizing: *batesi* and *punctiger* are closely related species with few differential characters. They are closely related to *argyropastus*, mainly because they are the only species with dark spots on the lateral stripes of the mesonotum and also on the prealar callus. However, the compressor apodeme, wing and palpi of *batesi* and *punctiger* are very different from those of *argyropastus*. *Argyropastus* is, in some aspects such as shape of palpi or color pattern of the wing, similar to *frauenfeldi*. The compressor apodeme is very similar to those of *planiventris* and *frauenfeldi*.

Though showing peculiar characters, *planiventris* seems to be closely related to *frauenfeldi*, and these 2 species are separated from the remaining species of the group.

Group 4. *vittatus*, *tabaninus* and *bellardii*.

*Tabaninus* and *vittatus* are related species and *bellardii* was associated to them because it has some characters similar to those of *tabaninus*, as for instance, the genitalia.

In *tabaninus* and *vittatus*, the lateral stripes of the mesonotum have a characteristic sinuosity, only found in these 2 species. There is great similarity between *vittatus* and *tabaninus*, for example the shape of the palpi (especially among females), the wing color pattern, and the flagellum shape of males.

In body proportions *vittatus* and *tabaninus* are always together. On head shape, these species stand out among the Pantophthalmidae, and *bellardii* is near them, but belongs with the remaining lines. As to wing shape, *vittatus*, *tabaninus* and *bellardii* belong together and the ensemble of their lines intersects the lines of group 3; *tabaninus* — *vittatus* differ in range but have very close and almost parallel lines. Regarding the shape of the mesonotum, *bellardii* and *tabaninus* have a marginal position in the general assemblage of lines; *vittatus* has a line approximately parallel to these but relatively far from them, intersecting that of *comptus*, *kertesizianus* and *pictus*. On the relationship between first and third femur, *vittatus* and *tabaninus* are together, but have a slightly different slope.

*Vittatus* has fewer outstanding or extreme characters than *bellardii* and *tabaninus*. The beak of *vittatus* is not very protruding, but it is similar to that of the other species. Ventral spines on the posterior femora are absent, but the region is swollen and slightly darker than in the remaining femora. The apex of the aedeagus of *vittatus* is of the common type, not expanded as in *tabaninus* and *bellardii*. The median cleft of the apical edge of the 8th sternite of the females can be deep or not, and the lobules at the sides of the cleft are smaller than those of *tabaninus*, *bellardii*, *frauenfeldi* and *planiventris*. *Vittatus* also differs from *tabaninus* and *bellardii* because it bears a dark rounded spot on the prealar callus, similar to that of *batesi* and *punctiger*. The abdominal color pattern of *vittatus* looks like a variation of that of *comptus*, *subsignatus* and group 3 species. The abdomen of *bellardii* is completely dark. In *tabaninus* females, the abdomen can be completely dark or similar to that of the male, that is, with dark irregular margins and reddish central region. This latter pattern might also be considered as another variation of the *comptus* pattern, different from that of *vittatus*.

Some characters are in an exclusive state in *tabaninus* and *bellardii* but, despite this fact, *tabaninus* and *bellardii* differ significantly in other characters; for instance the coloration of the mesonotum, which in other

cases was a character decisive in weighing affinities among species. The mesonotum color pattern of *bellardii* could be related to that of *comptus* or *kertesziianus*. The complete absence of the ventral spine in the posterior femora, and the presence of a slight depression in that region are shown only by *tabaninus* and *bellardii*. Another exclusive character of these species is the attenuated facial projection. The rounded expanded apex of the aedeagus and the shape of the compressor apodeme also separate *tabaninus* and *bellardii* from any other species. The largest known specimens of Pantophthalmidae belong to *tabaninus* and *bellardii*. Austen commented that the only species capable of competing with *tabaninus* would be *bellardii*, due to its size.

### iii. Relationships among groups of species

The following discussion begins with the evidence that groups 1 and 2 are related to *alienus*, as previously analyzed.

The relationships between groups 1 and 2 in wings shape and relationship between first and third femora was commented on in the chapter dealing with body proportions.

The wing base of *zoos* is yellow as in *alienus* and species of group 2. *Zoos* and *subsignatus* have lateral regions of scutum and prescutum lighter than the dorsal region as in *comptus*, *kertesziianus* and *pictus*, but not so contrasting as in these species.

However, the critical species seems to be *subsignatus*, for it bears genitalic characters very similar to those of group 1 species and several other characters similar to other groups; for instance, small shiny tubercles on the mesonotum surface, found in groups 2, 3 and 4, and palpi and antennae similar to those of group 2 species.

Excluding the hypothesis of convergence between characters of *subsignatus* and those of the other species, the relationships between groups 1 and 2 can be explained by one of the following hypotheses:

1. The lack of tubercles on the mesonotum, in species of group 1 would be secondary; in this case, it is not important to decide which aedeagus type is the most primitive, simple or with expanded apex. The respective phylogeny would be: 2 groups were isolated from an ancestral with tubercles on mesonotum; one with aedeagus type 1 and another with aedeagus type 2. In group 1, the tubercles disappeared in all species but *subsignatus*. *Subsignatus* should also maintain other characters of the ancestral; characters maintained in species of group 2.

2. The lack of tubercles in species of group 1 would not be secondary, but a primitive character, also found in *alienus*; the aedeagus of group 1 should be more primitive than that of group 2. Then 2 groups would have appeared from an ancestral with aedeagus 1: one group maintaining the absence of tubercles on mesonotum and the other with



tubercles. From the latter, *subsignatus* would have evolved, maintaining aedeagus of type 1 and species of group 2 aedeagus of type 2.

It is not impossible for a character to have appeared and disappeared, but I believe that this would weaken considerably the first hypothesis. Therefore in the general scheme, hypothesis 2, will be adopted as more economical.

The relationships between groups 2 and 3 seems to be straight forward. The ancestral of group 3 would have evolved from the ancestral of group 2. *Chuni* preserves genitalic characters of 2 but has some other characters as in 3.

The origin and relationships of group 4 are more complicated and not clear to me. The difference between the mesonotum of *tabaninus* and *bellardii* makes it difficult to understand the relationships between these 2 species. The female genitalia unites *tabaninus*, *bellardii* and *vittatus* to *frauenfeldi* and *planiventris*. The general aspect of the male of *bellardii* could be associated to that of *frauenfeldi* but this resemblance is not evident between females. Therefore, the group might have originated from the same ancestral as group 3.

If one considers the hypothesis of a convergence of characters concerning the shape of the female 8th sternite, then one could see a similarity between aedeagus and compressor apodeme of groups 4 and 1. Lateral stripes of mesonotum non-convergent towards the scutum, could relate group 4 to group 2. The absence of a ventral spine on the posterior femora could still relate group 4 to *comptus*. The wings of group 4 species, with many well definite yellow spots, with brown basis, resemble more those of group 2 species than those of *frauenfeldi* and *planiventris*. In this way the ancestral of group 4 could also have derived from that of group 2.

There are thus 2 plausible hypothesis: origin from the branch that resulted in 3 or in 2.

Some facts speak against the first hypothesis: i. the aedeagus that had become simple secondarily, would have to become expanded again; ii. the lateral stripes of the mesonotum which tend to converge in 3, would have to become parallel again in 4; iii. the spots on the lateral stripes of mesonotum would have to disappear secondarily in *tabaninus*, *bellardii* and *vittatus*.

The main fact against the second hypothesis is the convergence concerning the shape of the female 8th sternite.

In the phylogenetic scheme I adopt the second hypothesis but I recognize that the position on these species is not completely satisfactory.

## GENERAL PHYLOGENETIC SCHEME

In a first step, the ancestrals of *Opetiops* and of *Pantophthalmus* evolved from a common ancestor.

Among *Pantophthalmus* a group remained without vesicles on the mesonotum and aedeagus with quadrangularly expanded apex. From this group evolved initially *zoos* in Mexico (Oaxaca) and *splendidus* in Panama (Chiriqui), and posteriorly *roseni* in Mexico and Central America, and *rothschildi* in Amazonia (northwest) and Bolivia.

In another branch tubercles appeared on the mesonotum and, in a first stage, evolved *subsignatus* or its ancestor, still with the apex of the aedeagus squarish.

The ancestors of group 4 also evolved from this branch, but with aedeagus smaller and with an apical rounded dilation. In this group with tubercles on the mesonotum, there was, posteriorly, a simplification of aedeagi, and 2 other branches evolved: one with a clear contrast between lateral and dorsal regions of the mesonotum (proto-2); another without this contrast (proto-3).

From proto-4 evolved *bellardii* in Mexico, Central America and the arch of northwest to Bolivia, and a group in South America that posteriorly branched into *vittatus* and *tabaninus*.

From proto-2, came *comptus* in Central America and Amazonia; *kertesziannus* in Panama, Amazonia, Bolivia and Paraguay and *pictus* in the Brazilian southeast, the northeast of Argentina and Paraguay.

From proto-3 evolved initially *chuni* in South America and *facetus* and *engeli* in Panama (Chiriqui). Another division separated a "proto-*frauenfeldi*" with light spots on the lateral stripes of the mesonotum, from a "proto-*argyropastus*" with dark spots on the stripes.

*Frauenfeldi* was isolated in the arch of northwest and *planiventris* initially in Central America, both from proto-*frauenfeldi*.

*Argyropastus* in Central America, *batesi* in Amazonia and northeast Argentina and *punctiger* in the Brazilian southeast all originated from proto-*argyropastus*.

## SPECIATION PATTERNS

Since the Pantophthalmidae are presumably an old family, closely related to tropical forests, one can expect their speciation pattern to be disguised, due to the forest retraction and expansion cycles (Haffer, 1969; Vanzolini, 1970; Vanzolini and Williams, 1970), and by extinctions due to competition in a narrow ecological niche. In this way, it is

only possible to examine eventual mechanisms of species multiplication, based on those groups whose degree of homogeneity induces us to believe that their diversification was recent.

Therefore, only 4 cases will be examined:

1. *comptus*, *kertesziianus* and *pictus*.
2. *argyropastus*, *batesi* and *punctiger*.
3. *zoos*, *rothschildi* and *roseni*.
4. *frauenfeldi* and *planiventris*.

In the first case, we have one species, *comptus*, distributed from Belize to the Guianas and Brazilian Amazonia; *kertesziianus* from Panama, through the main valley of the Amazon, to Bolivia and Mato Grosso; finally *pictus* in the Atlantic forest, reaching Paraguay and Misiones. This pattern seems to indicate differentiation in 3 refuges (Haffer, 1969). Two (*comptus* and *kertesziianus*) are peri-Amazonian; the third one (*pictus*) is in the Atlantic forest. The existence of a Central American record of *comptus* seems to indicate that one of the mentioned peri-Amazonia refugia would be that of Cordillera de la Costa in Venezuela (Haffer, 1969; Vanzolini & Williams, 1970). *Kertesziianus* could have originated in northern South America or south or southwest of the Hylaea.

The second case is a similar one. *Argyropastus* must have differentiated in the northwest of South America, or in Central America; *batesi* in southwestern Amazonia, as indicates its penetration through Bolivia (and not the Atlantic forest) to northern Argentina; finally, *punctiger*, in the Atlantic forest.

The group of *zoos*, *rothschildi* and *roseni* does not show penetration of the Atlantic forest; its history is entirely northern. *Zoos*, probably the most primitive species, is Mexican; concerning the 2 more evolved species, *roseni* is Central American and *rothschildi* is in western Amazonia. This pattern can be interpreted in two manners:

1. The origin of the group would be in northeastern Amazonia, *zoos* representing the first form to expand outside the area of origin, *roseni* the second and *rothschildi* the last and most successful branch of the group.

2. The group would be originally Central American, with an Amazonian isolate, *rothschildi*. I prefer this second hypothesis.

Finally we have *frauenfeldi* and *planiventris*: *frauenfeldi* in the arch of northwest and *planiventris* widely distributed, from the south of Mexico to Central Brazil. A distribution limited to the arch of northwest may represent either an invasion stopped by a filter zone (Simpson, 1967) or a relictual pattern (Vanzolini, 1968). The distribution of *planiventris* is suggestive, though. The fact that this species is in Central Brazil can be interpreted in 2 ways: it is a species that is invading a new ecology, or it is a species, that reached central Brazil in times of much more extensive forests than today, and that maintained itself in islands of favorable ecology. This is a question that can only be ans-

wered by field research. Nevertheless, considering that the Pantophthalmidae show, in known cases, an outstanding ecological fidelity to the tropical forest, I believe that *planiventris* is a species that got to Central Brazil during a wet episode (Vanzolini, 1970). In this way, *frauenfeldi* would be an old species, of Amazonian origin, but superseded by *planiventris* inside the hylaea, and maintaining itself relictual only in the arch of northwest.

So, of the 4 speciation patterns over which some conjectures can be made, 2 are orthodox ones, from the points of view of the peri-Amazonian refugia model (Haffer, 1969; Vanzolini & Williams, 1970; Vuilleumier, 1971); the other 2 are of not so sure an interpretation.

The pattern of the group of *zoos*, *roseni* and *rothschildi* remains undetermined, as far as I can see, and that of *planiventris* and *frauenfeldi* indicates that we are dealing with survivors of a more ancient episode.

In the systematic discussion it was said that *argyropastus*, *batesi*, *punctiger*, *frauenfeldi* and *planiventris* were considered as belonging to a same group 3. The above consideration of the geographical patterns indicates that *frauenfeldi* and *planiventris* represent an intermediate state of differentiation, previous to that of *argyropastus*, *batesi* and *punctiger*. Considering that the expansion and retraction cycles of tropical forests were very rapid, a pattern such as this is not impossible.

Actually, we do not have as yet any element to put the evolution of the Pantophthalmidae and of any other segment of the family in an absolute chronological scale. What is left is to suppose that the expansion of *frauenfeldi* and *planiventris* happened before the differentiation of *argyropastus*, *batesi* and *punctiger*.

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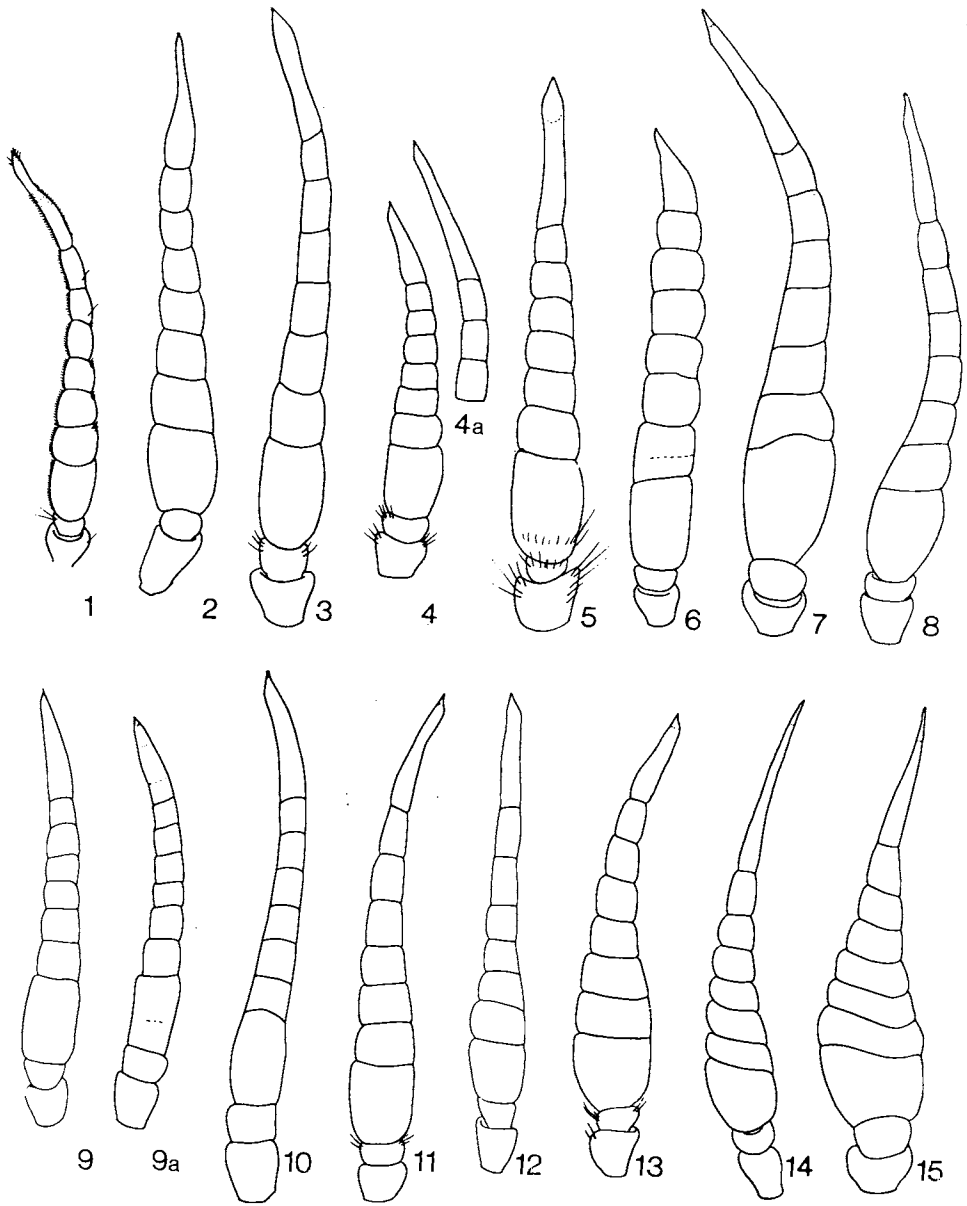
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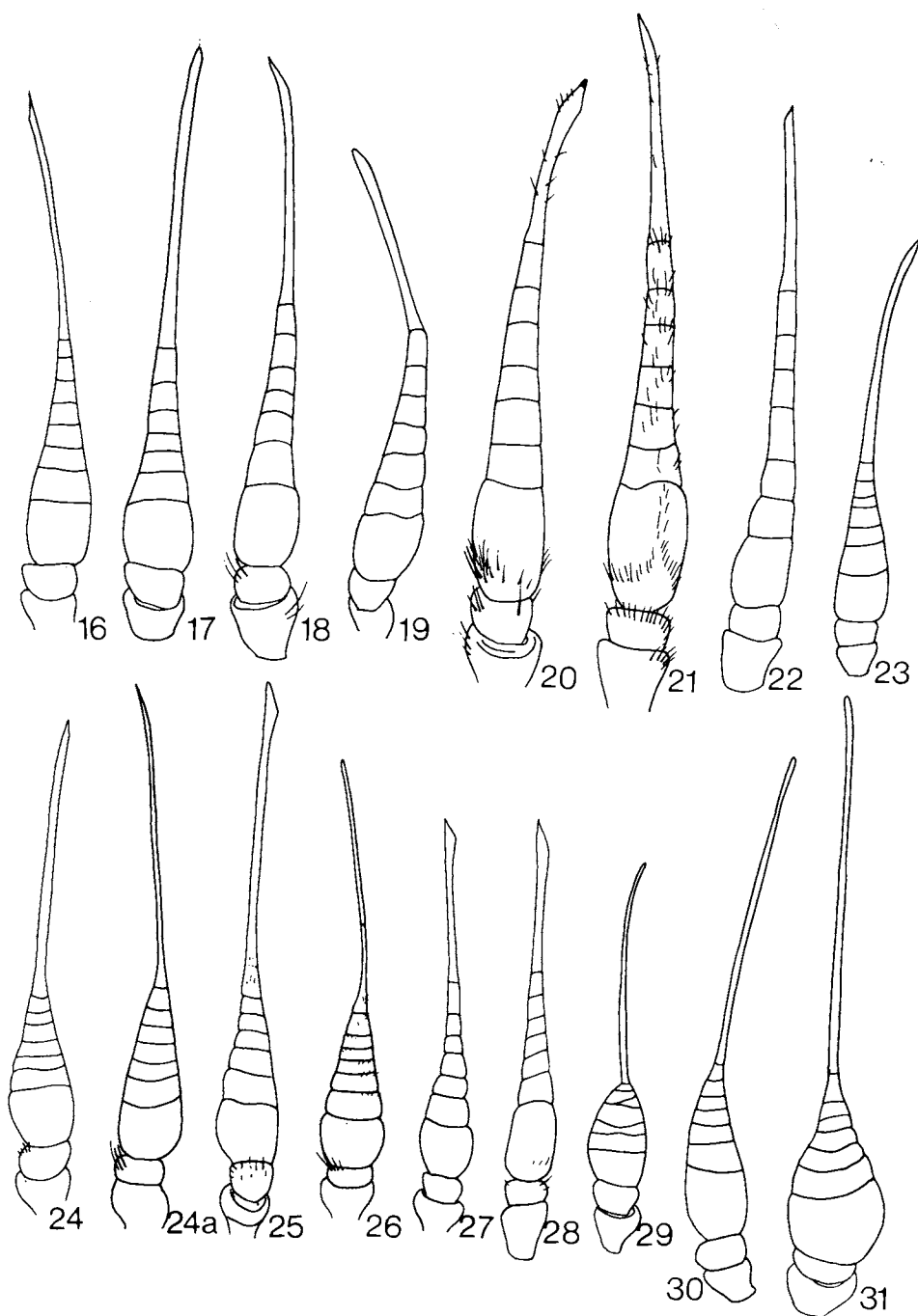
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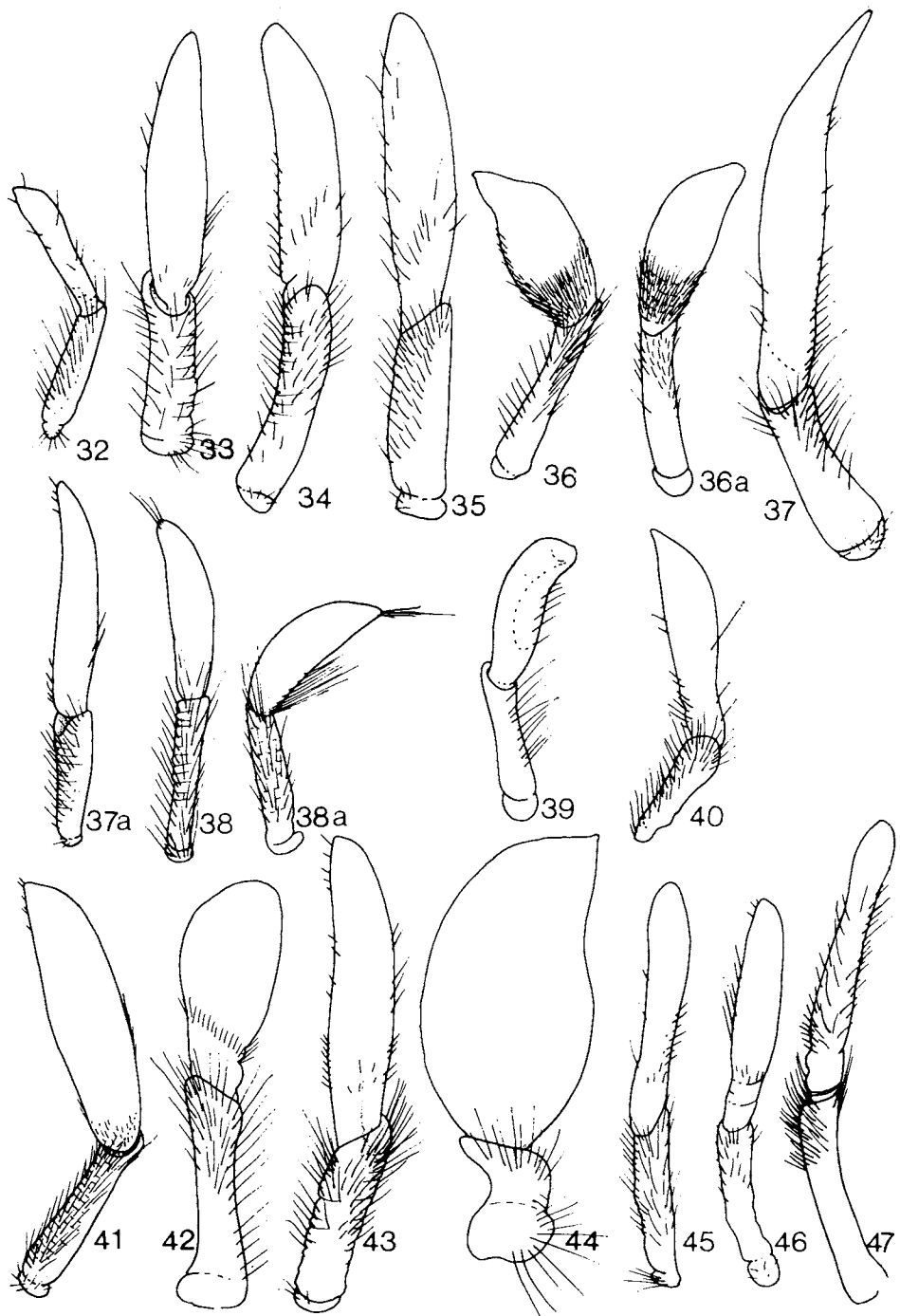
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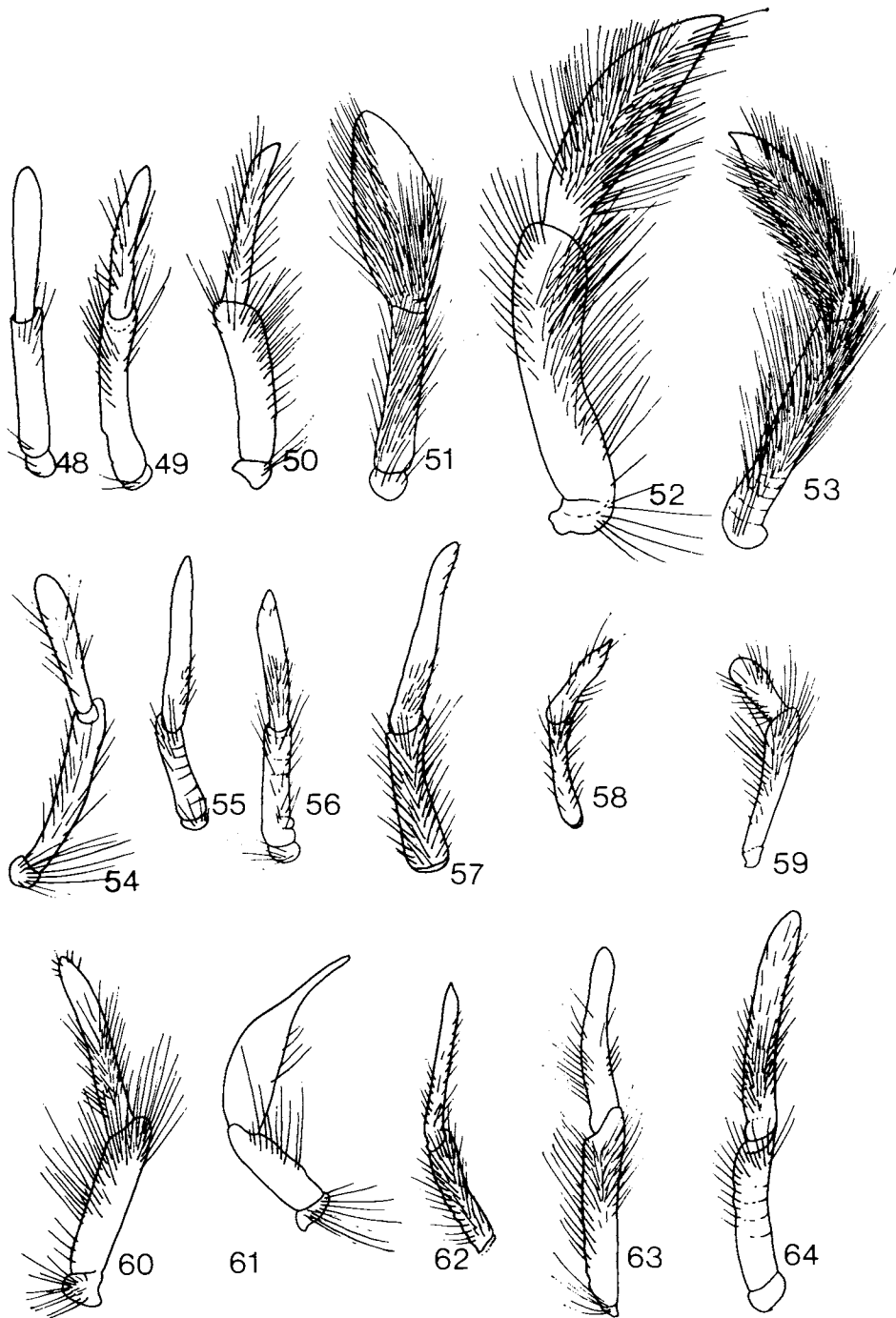
Antenna, females: 1, *Opetiops alienus* (Santa Catarina); 2, *Pantophthalmus comptus*; 3, *pictus*; 4, *kerteszianus* (Corumbá); 4a, *kerteszianus* (Pucallpa), detail; 5, *roseni*; 6, *splendidus*; 7, *chuni*; 8, *argyropastus*; 9, 9a, *batesi* (Marmelo); 10, *punctiger*; 11, *frauenfeldii*; 12, *planiventris*; 13, *vittatus*; 14, *bellardii*; 15, *tabaninus*.



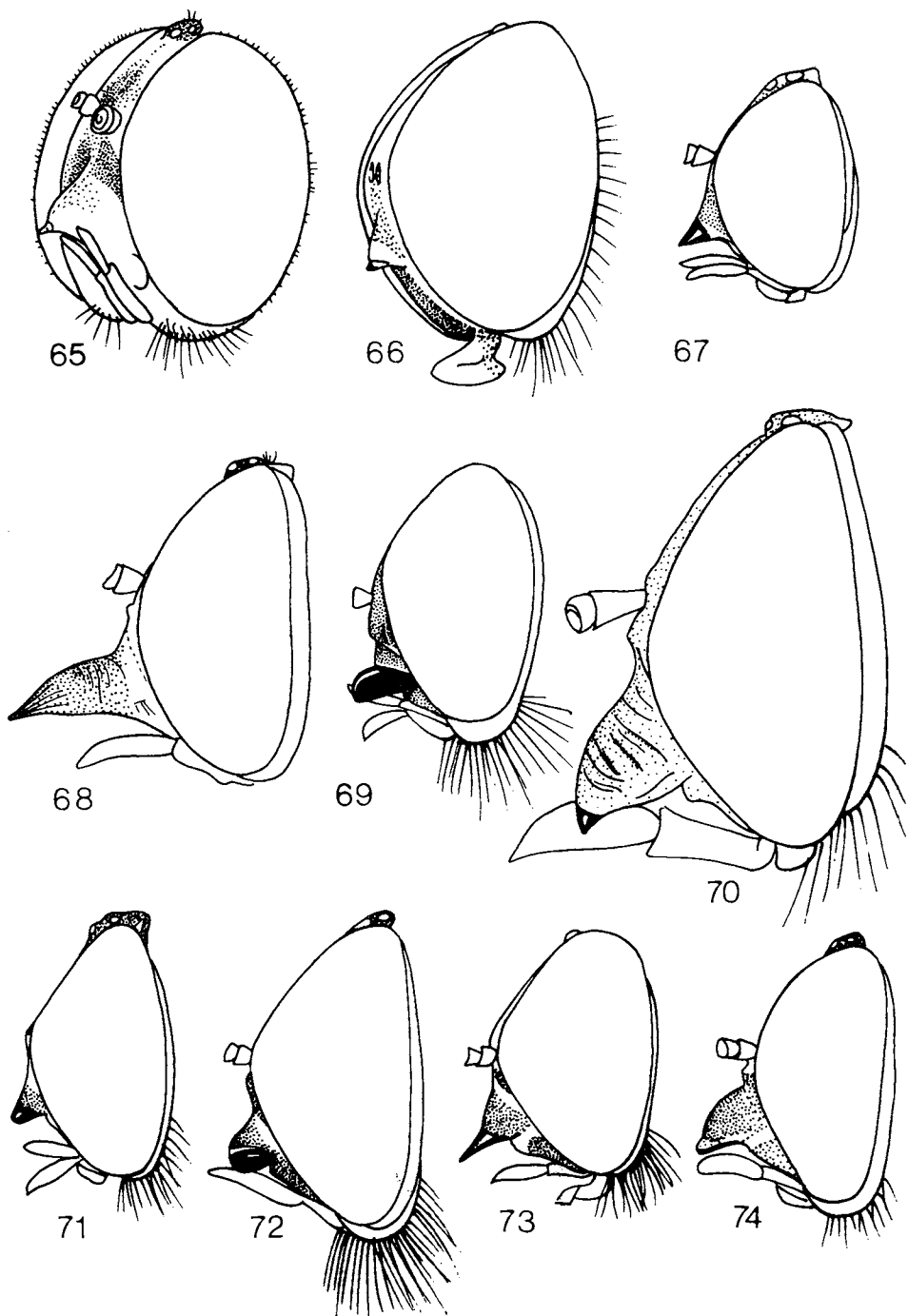
Antenna, males: 16, *Pantophthalmus comptus*; 17, *kerteszi*; 18, *pictus*; 19, *subsignatus*; 20, *rothschildi*; 21, *roseni*; 22, *planiventris*; 23, *frauenfeldi*; 24, *chuni* (type specimen of *P. leuckarti*); 24a, *chuni* (type specimen of *A. helleriana*); 25, *engeli* (type specimen); 26, *argyropastus*; 27, *batesi*; 28, *punctiger*; 29, *vittatus*; 30, *bellardii*; 31, *tabaninus*.



Palpus, females: 32, *Opetiops alienus*; 33, *Pantophthalmus comptus*; 34, *kerteszi*; 35, *pictus*; 36, 36a, *roseni* (right and left palpi); 37, *chuni* (S. Neblina); 37a, *chuni* (Tabatinga); 38, 38a, *splendidus* (right and left palpi); 39, *facetus*; 40, *batesi*; 41, *argyropastus*; 42, *punctiger*; 43, *frauenfeldi*; 44, *planiventris*; 45, *vittatus*; 46, *bellardii*; 47, *tabaninus*.

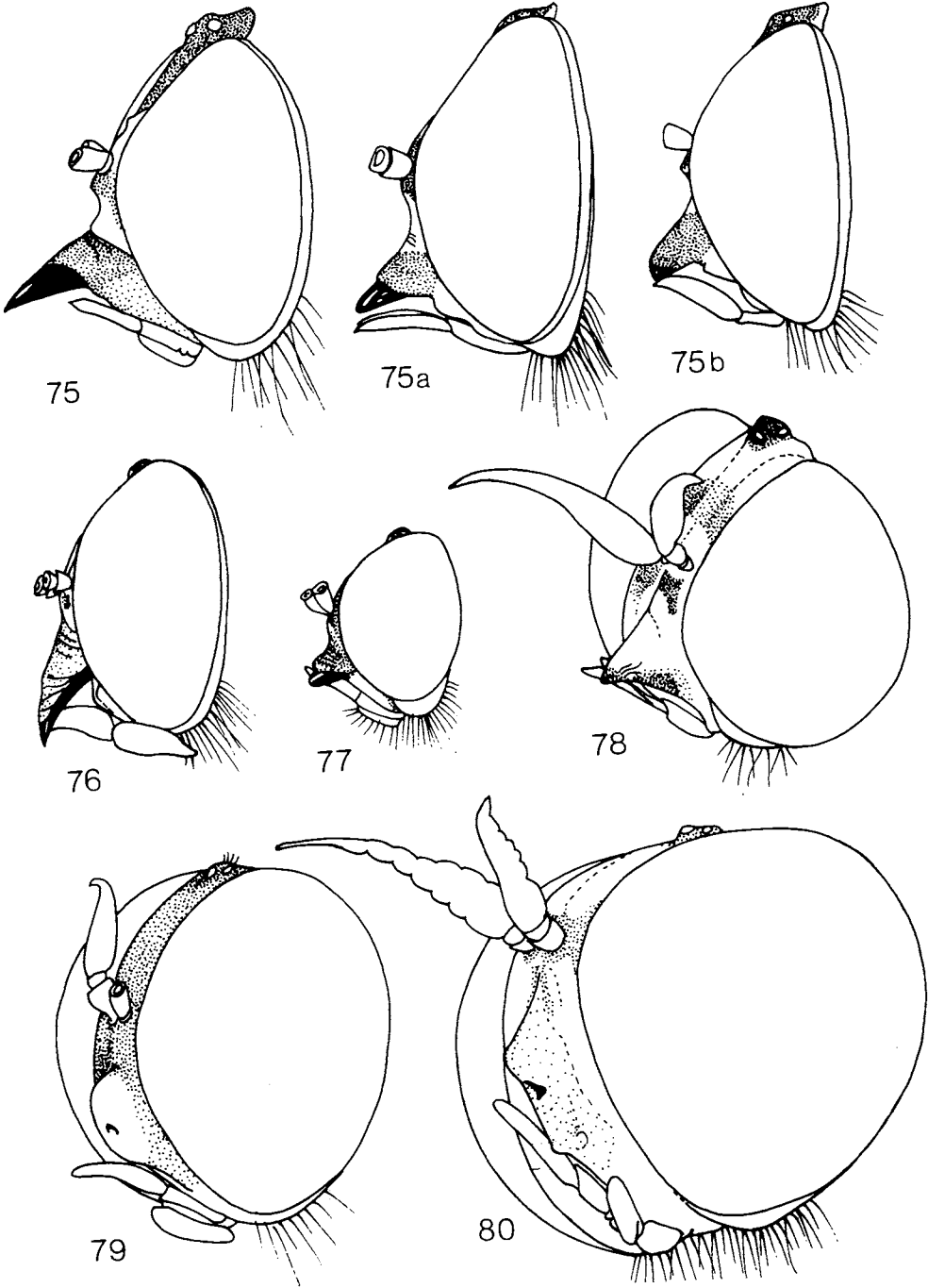


Palpus, males: 48, *Pantophthalmus comptus*; 49, *kerteszi*; 50, *pictus*; 51, *roseni*; 52, *rothschildi*; 53, *zoos*; 54, *subsignatus*; 55, *chuni*; 56, *engeli*; 57, *argyropastus*; 58, *batesi*; 59, *punctiger*; 60, *frauenfeldi*; 61, *planiventris*; 62, *vittatus*; 63, *bellardii*; 64, *tabaninus*.

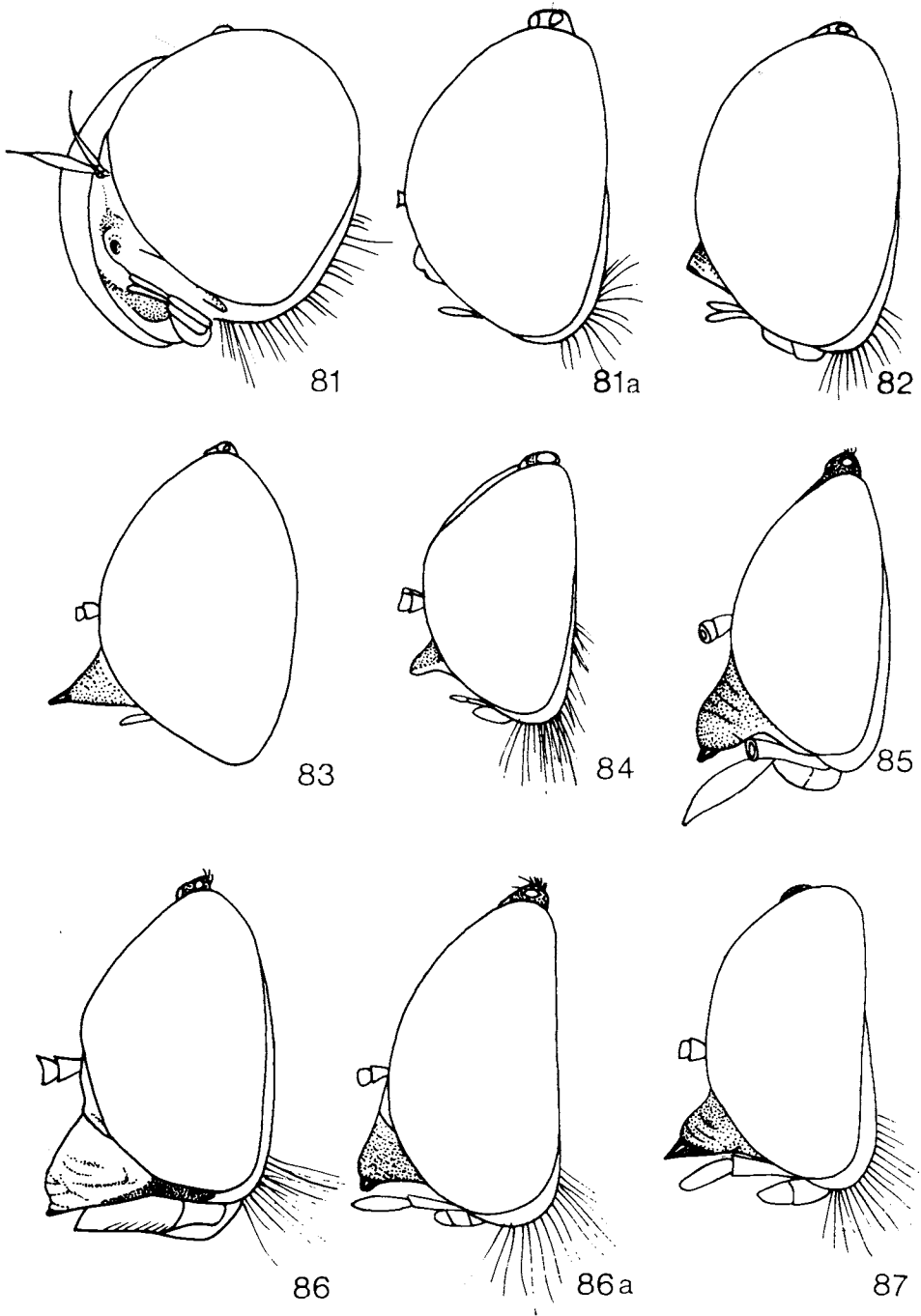


Head, females: 65, *Opetiops alienus*; 66, *Pantophthalmus comptus*; 67, *pictus*; 68, *kerteszianus*; 69, *splendidus*; 70, *roseni*; 71, *chuni*; 72, *argyropastus*; 73, *batesi*; 74, *punctiger*.

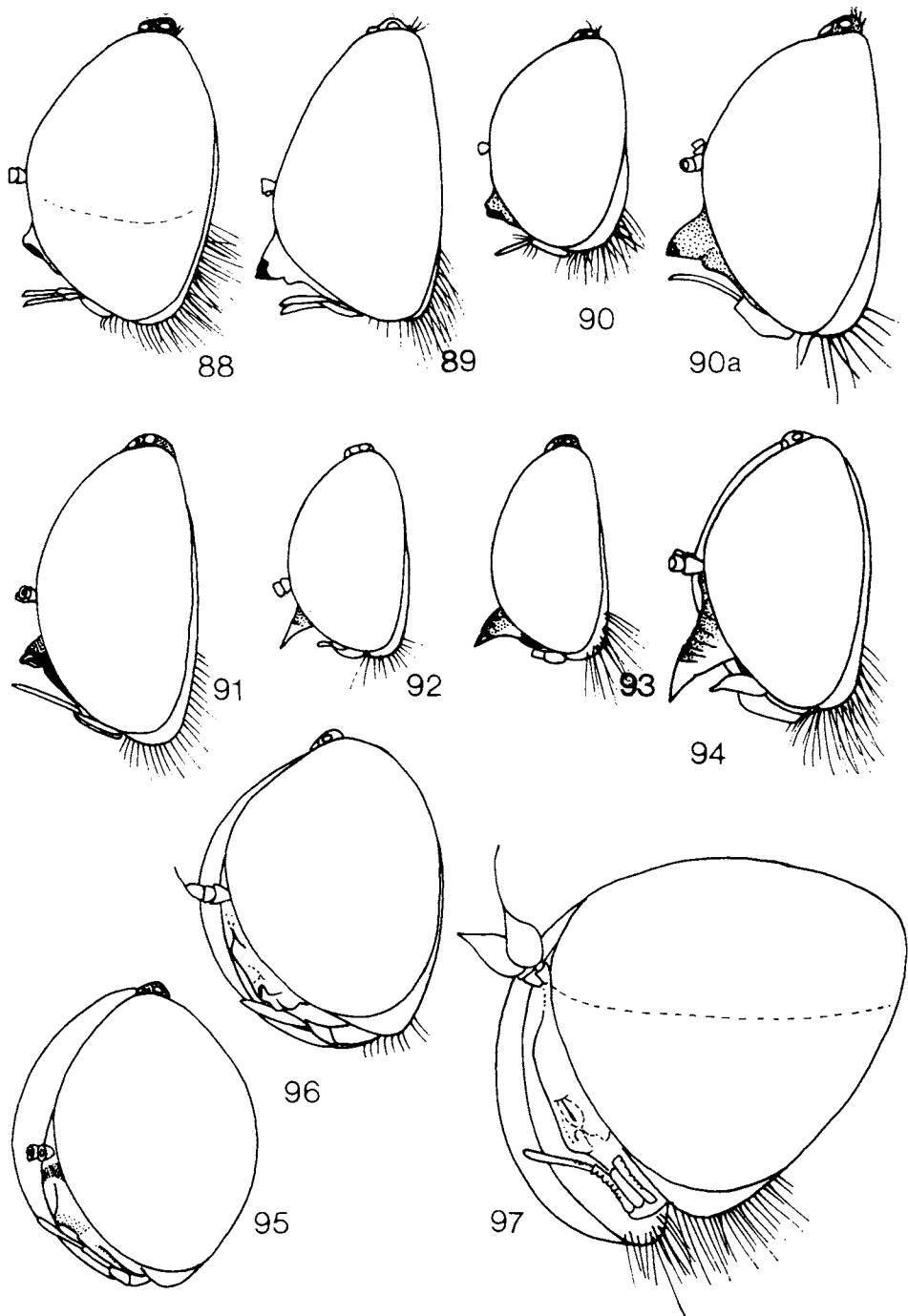




Head, females: 75, *Pantophthalmus frauenfeldi* (Yungas); 75a, *frauenfeldi* (Chan-chamayo); 75b, *frauenfeldi* (Muzo); 76, *planiventris*; 77, *facetus*; 78, *vittatus*; 79, *bellardii*; 80, *tabaninus*.



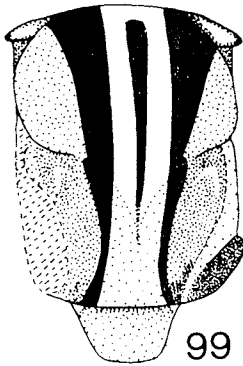
Head, males: 81, 81a, *Pantophthalmus comptus*; 82, *pictus*; 83, *kerteszi*; 84, *subsignatus*; 85, *rothschildi*; 86, *roseni* (type specimen, Chiriqui); 86a, *roseni* (El Palmar); 87, *zoos*.



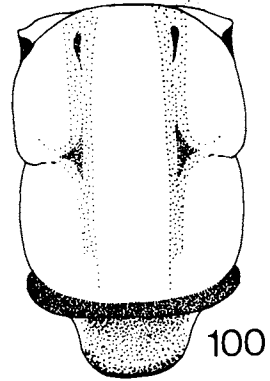
Head, males: 88, *Pantophthalmus chuni* (Santa Inés); 89, *engeli*; 90, 90a, *frauenfeldi* (Jarugui); 91, *argyropastus*; 92, *batesi*; 93, *punctiger*; 94, *planiventris*; 95, *vittatus*; 96, *bellardii*; 97, *tabaninus*.



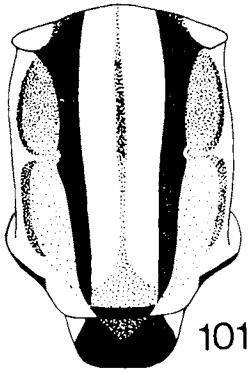
98



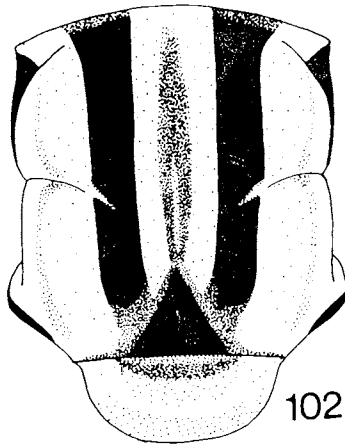
99



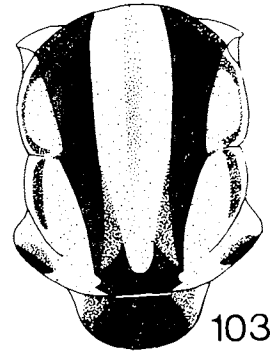
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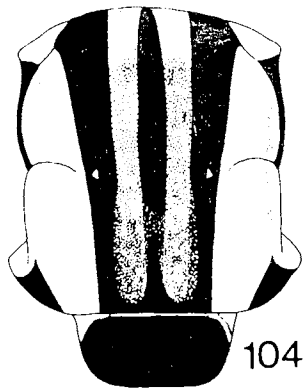
101



102

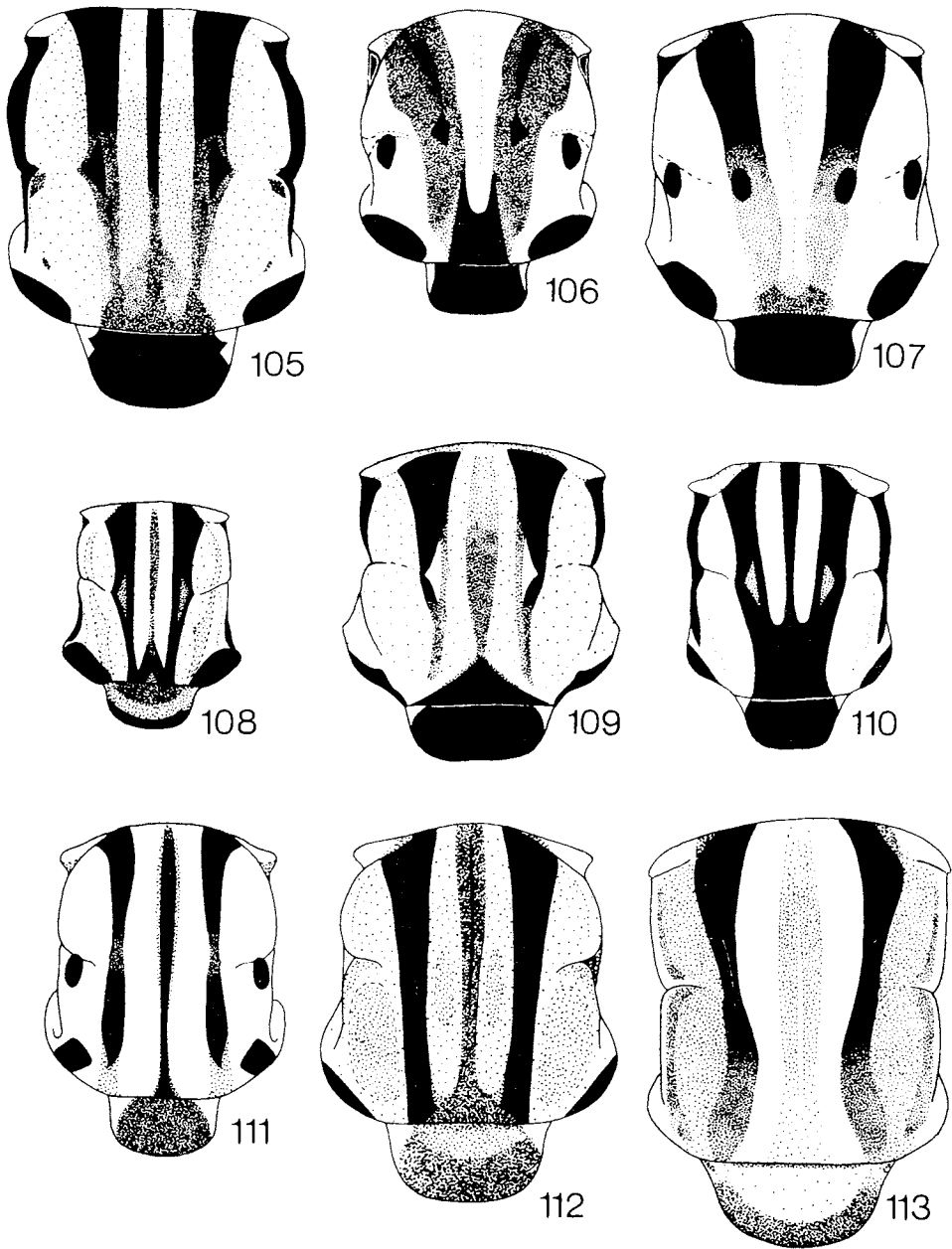


103

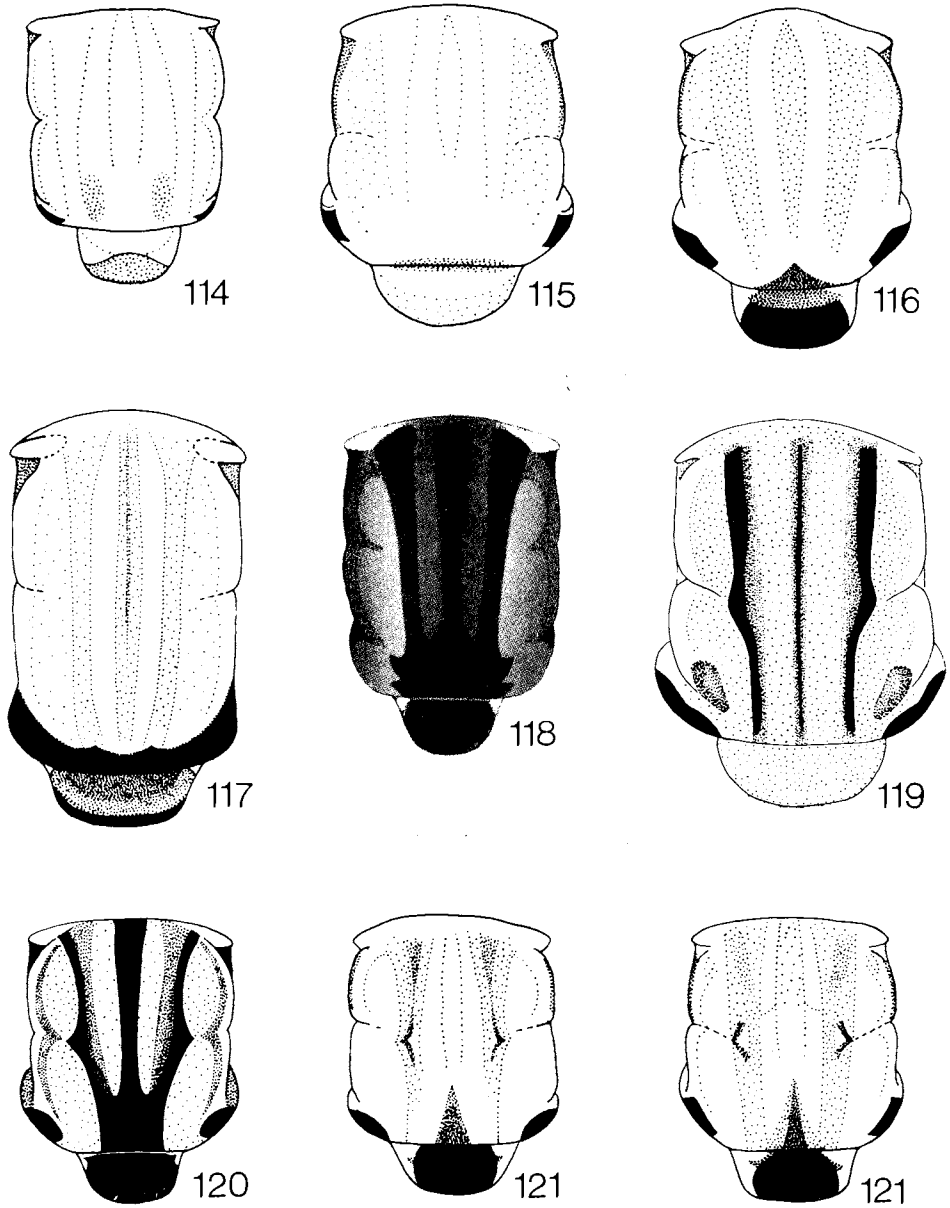


104

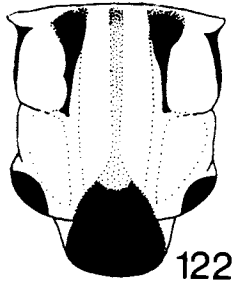
Mesonotum, females: 98, *Opetiops alienus*; 99, *Pantophthalmus splendidus*; 100, *roseni*; 101, *comptus*; 102, *kertesziannus*; 103, *pictus*; 104, *chuni*.



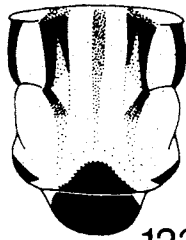
Mesonotum, females: 105, *Pantophthalmus argyropastus*; 106, *batesi*; 107, *punctiger*; 108, *facetus*; 109, *frauenfeldi*; 110, *planiventris*; 111, *vittatus*; 112, *bellardii*; 113, *tabaninus*.



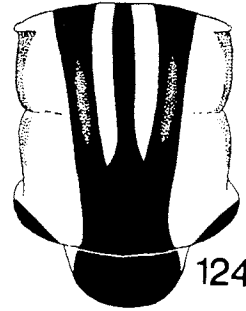
Mesonotum, males: 114, *Pantophthalmus comptus*; 115, *kerteszi*; 116, *pictus*; 117, *roseni*; 118, *rothschildi*; 119, *zoos*; 120, *subsignatus*; 121, *chuni* (type specimen of *P. leuckarti*); 121, *chuni* (type specimen of *A. helleriana*).



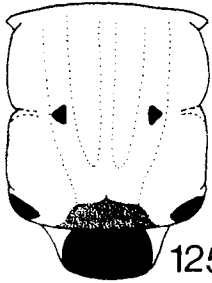
122



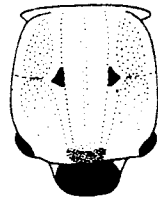
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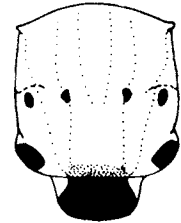
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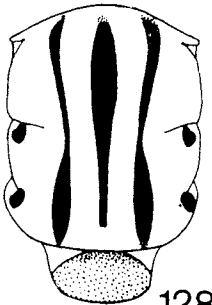
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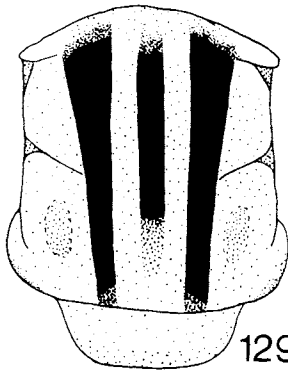
126



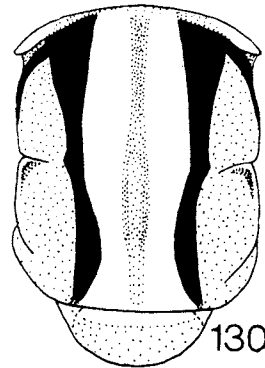
127



128

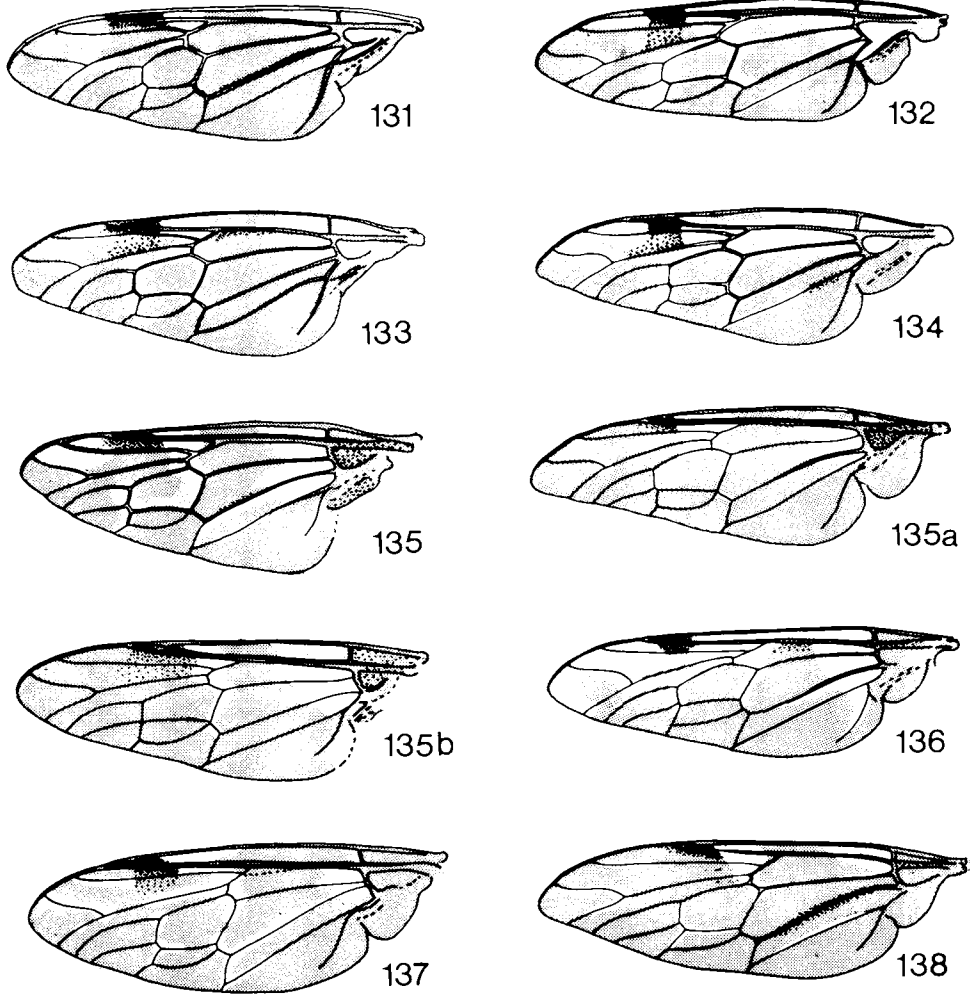


129



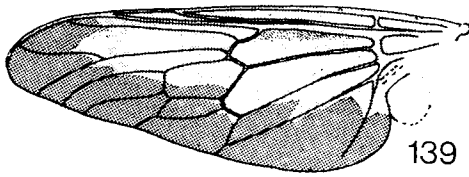
130

Mesonotum, males: 122, *Pantophthalmus engeli*; 123, *frauenfeldi*; 124, *planiventris*; 125, *argyropastus*; 126, *batesi*; 127, *punctiger*; 128, *vittatus*; 129, *bellardii*; 130, *tabaninus*.

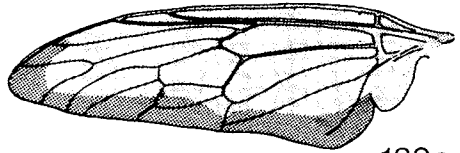


Wing: 131, *Opetiops alienus* (♀); 132, *Pantophthalmus comptus* (♀); 133, *kertes-zianus* (♀); 134, *pictus* (♀); 135, *chuni* (♀); 135a, *chuni* (♂, type specimen of *A. helleriana*); 135b, *chuni* (♂, type specimen of *P. leuckarti*); 136, *engeli* (♂); 137, *splendidus* (♀); 138, *subsignatus* (♂).

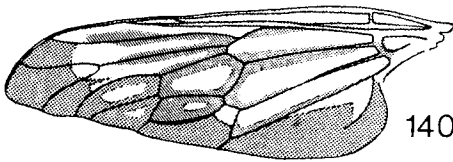




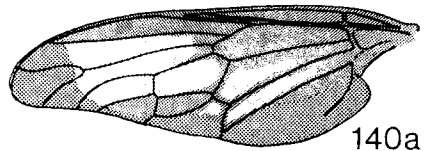
139



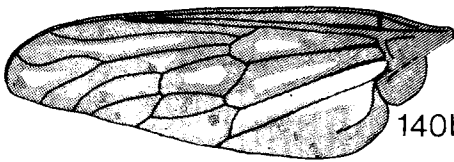
139a



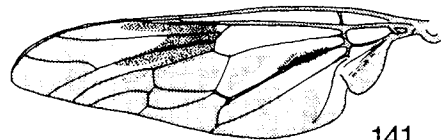
140



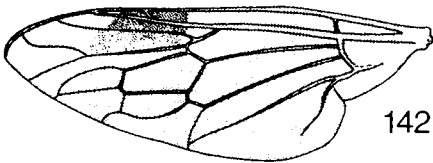
140a



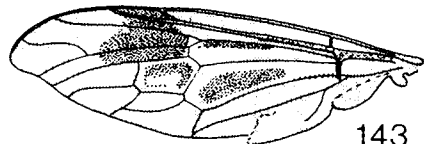
140b



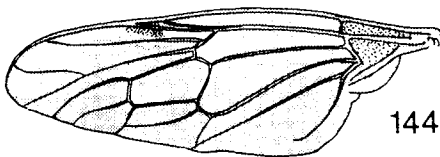
141



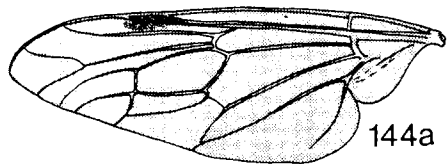
142



143

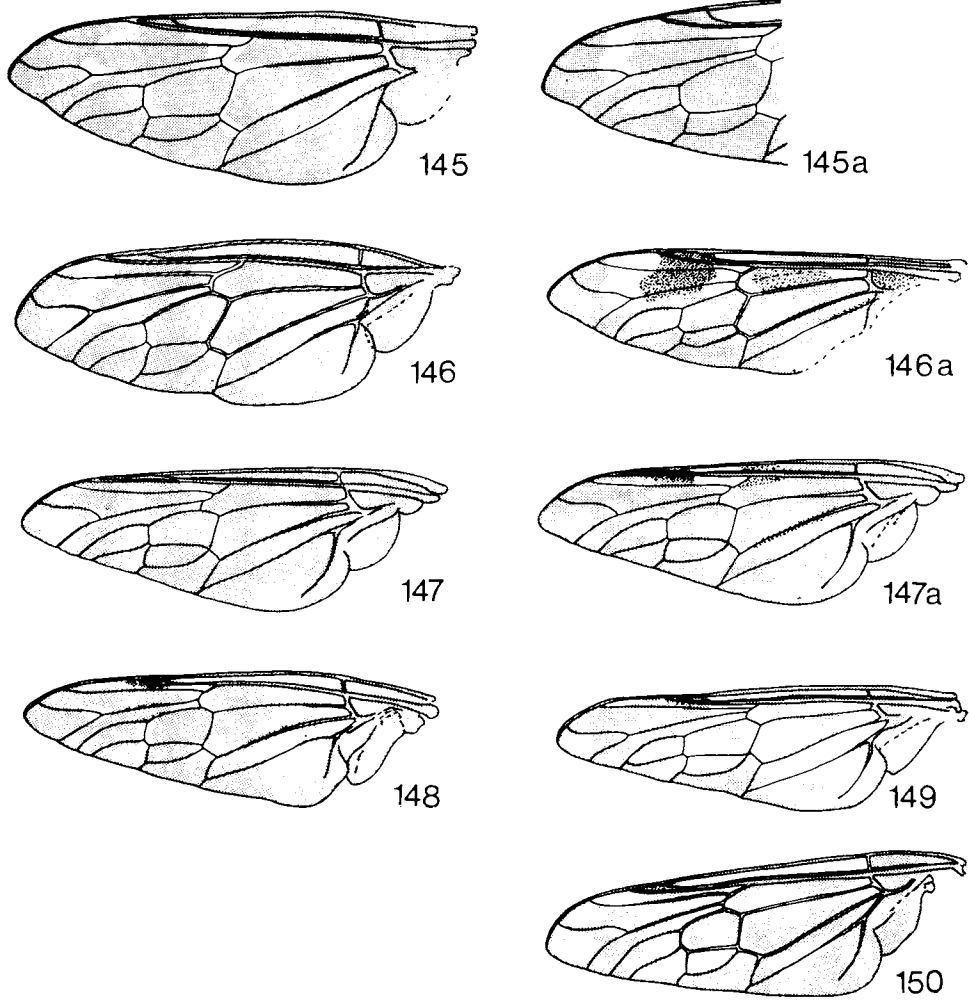


144

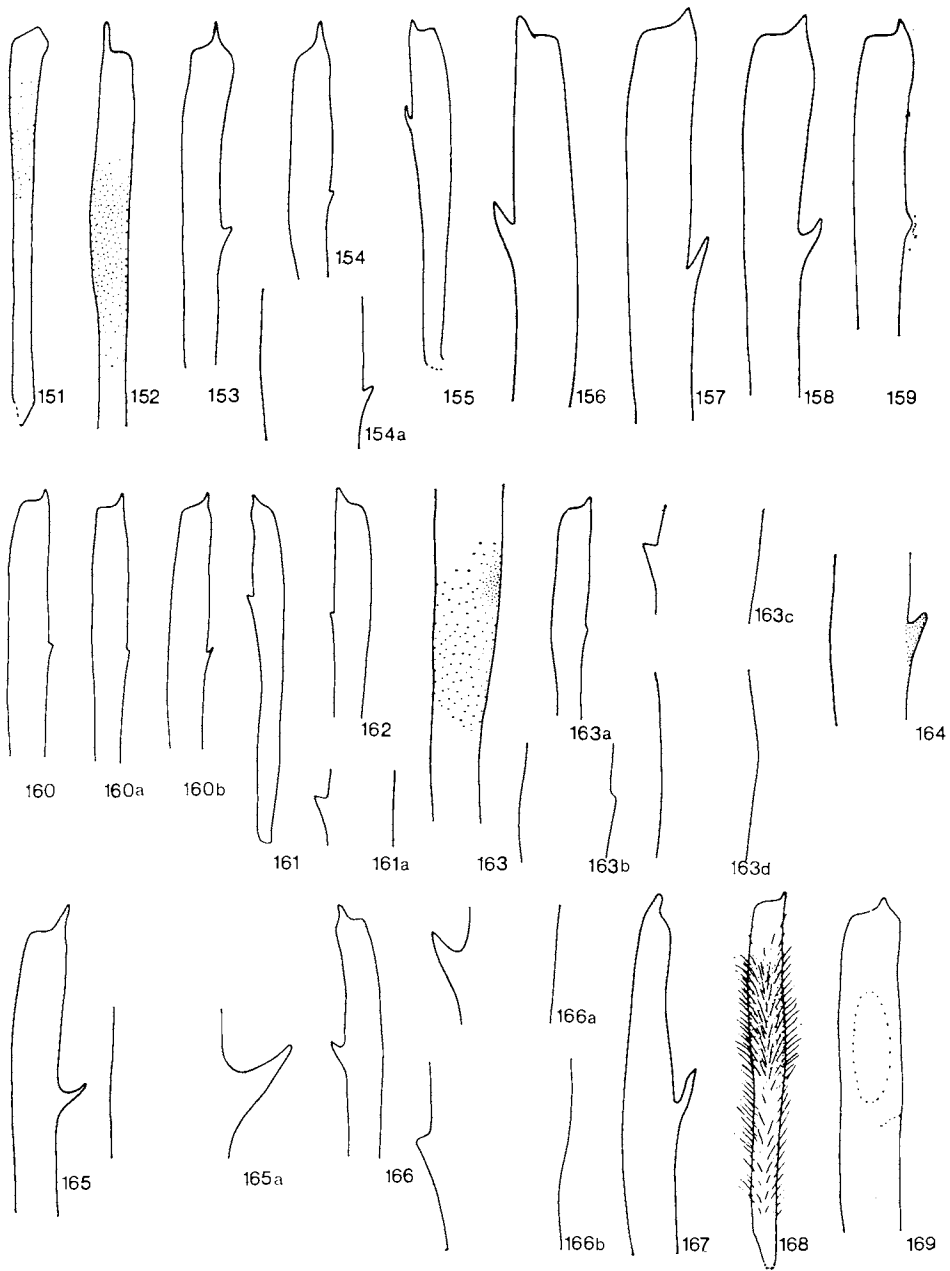


144a

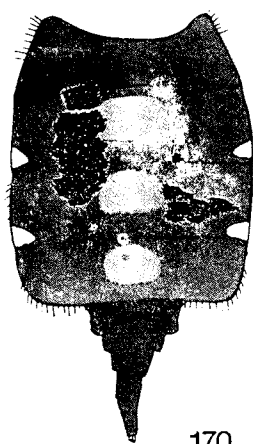
Wing: 139, *Pantophthalmus roseni* ( $\sigma$ ); 139a, *roseni* ( $\varphi$ ); 140, *rothschildi* (type specimen, Bolivia); 140a, *rothschildi* ( $\sigma$ , Mapiri); 140b, *rothschildi* var. *ocellata* ( $\sigma$ ); 141, *zoos* ( $\sigma$ ); 142, *planiventris* ( $\varphi$ ); 143, *facetus* ( $\varphi$ ); 144, *frauenfeldi* ( $\varphi$ ); 144a, *frauenfeldi* ( $\sigma$ ).



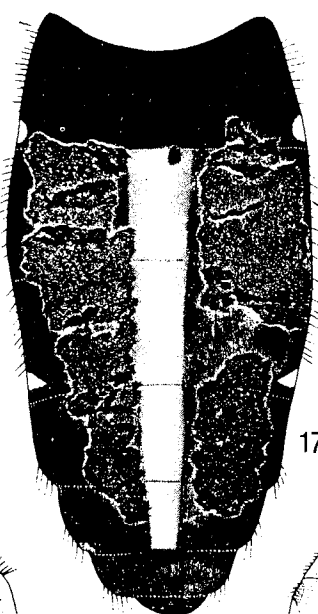
Wing: 145, *Pantophthalmus punctiger* (♀); 145a, *punctiger* (♂); 146, *batesi* (♀); 146a, *batesi* (♂); 147, *argyropastus* (♀); 147a, *argyropastus* (♂); 148, *bellardii* (♂); 149, *tabaninus* (♂); 150, *vittatus* (♀).



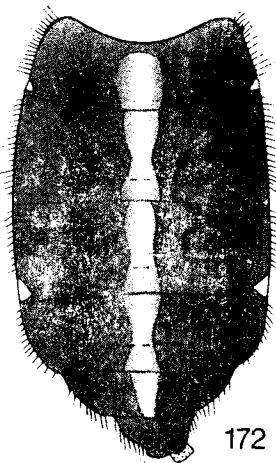
Ventral spine of posterior femora: 151, *Opetiops alienus* ( $\sigma$ ); 152, *Pantophthalmus comptus* ( $\rho$ ); 153, *pictus*; 154, *kerteszianus*; 154a, *kerteszianus* (higher magnification); 155, *subsignatus*; 156, *roseni*; 157, *rothschildi*; 158, *zoos*; 159, *splendidus*; 160, *chuni* ( $\sigma$ , Rio Amazonas); 160a, *chuni* ( $\sigma$ , type specimen of *P. leuckarti*); 160b, *chuni* ( $\sigma$ , type specimen of *A. helleriana*); 161, *engeli*; 161a, *engeli* (higher magnification); 162, *argyropastus*; 163, *batesi* ( $\sigma$ , Benjamin Constant); 163a, *batesi* ( $\sigma$ , Parintins); 163b, *batesi* ( $\sigma$ , Parintins, higher magnification); 163c, *batesi* ( $\rho$ , Argentina); 163d, *batesi* ( $\rho$ , Tabatinga); 164, *punctiger*; 165, *planiventris*; 166, *frauenfeldi* (Muzo); 166a, *frauenfeldi* (Muzo, higher magnification); 166b, *frauenfeldi* (Jarugui); 167, *facetus*; 168, *vittatus*; 169, *bellardii*.



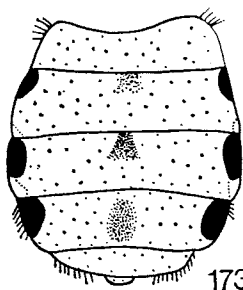
170



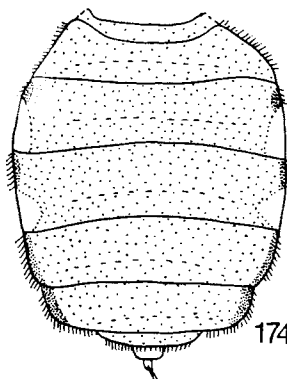
171



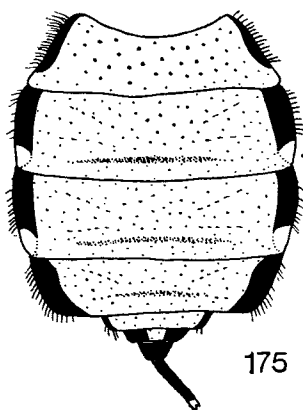
172



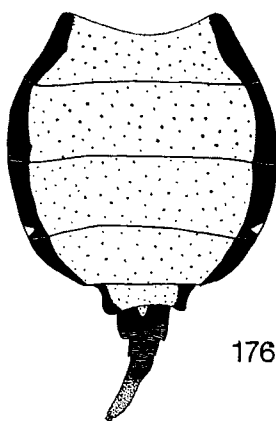
173



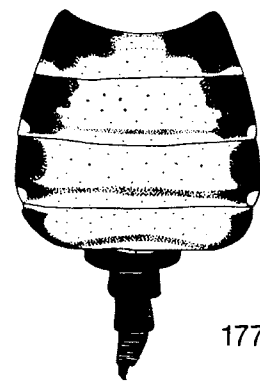
174



175

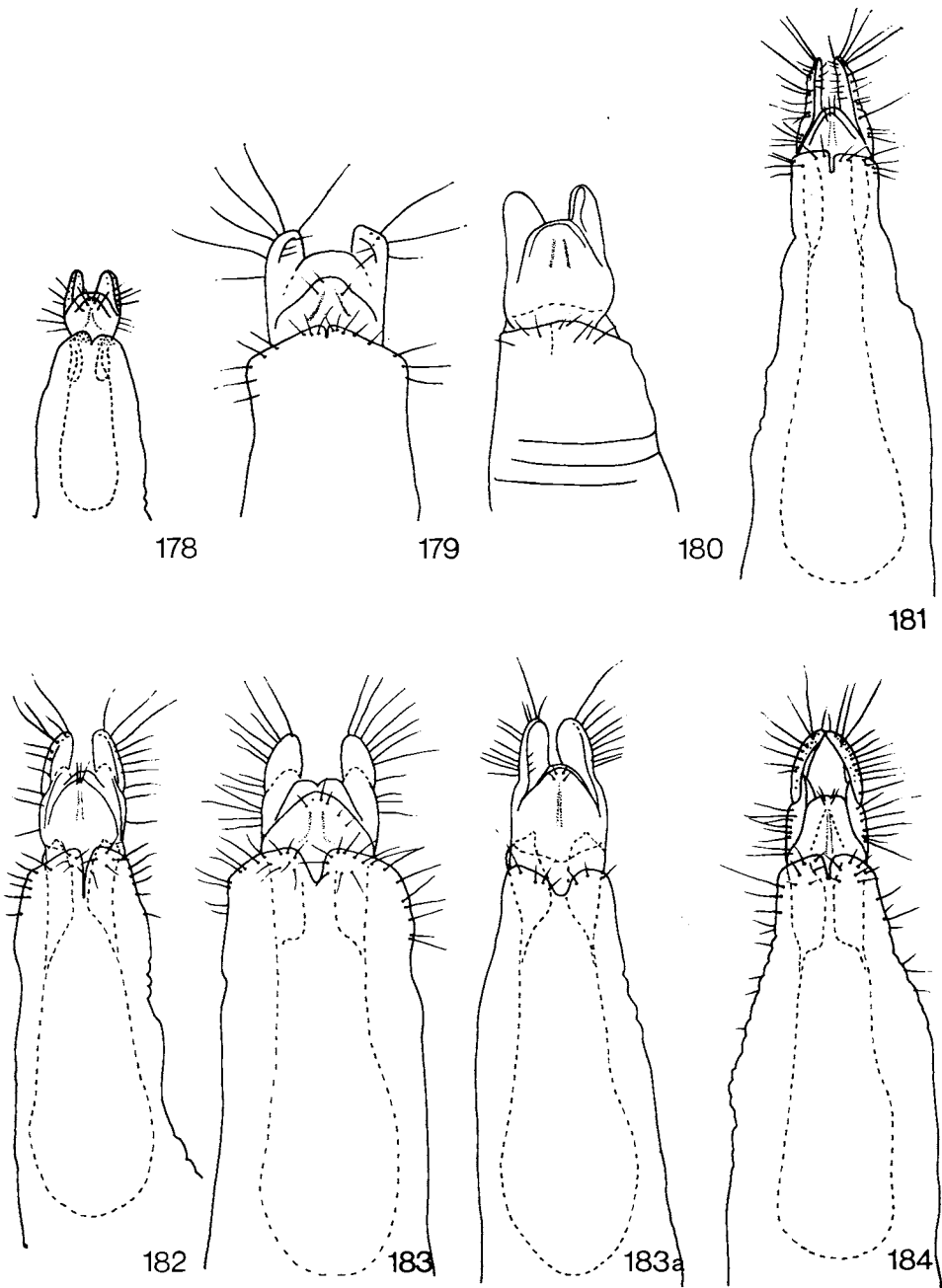


176

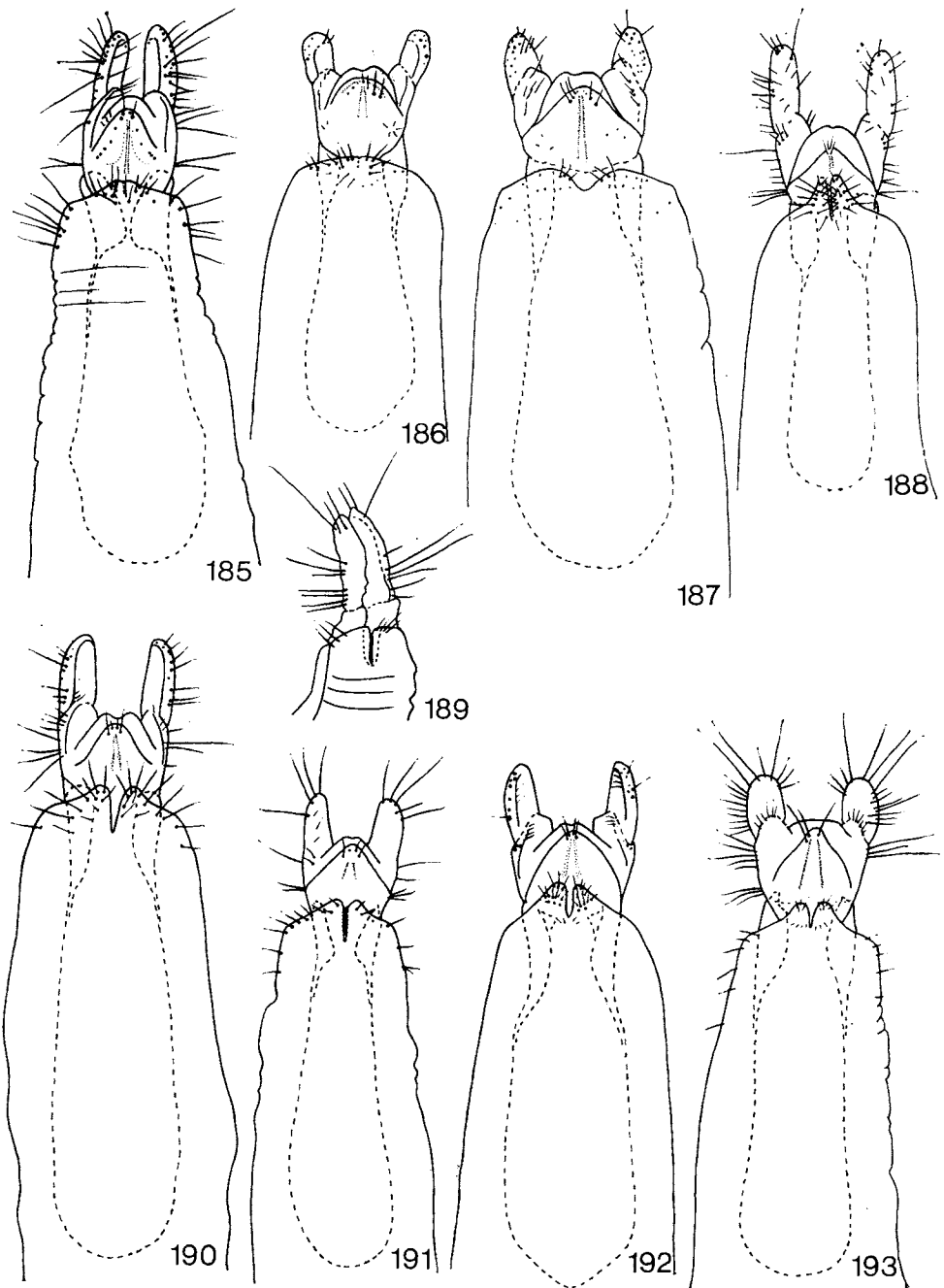


177

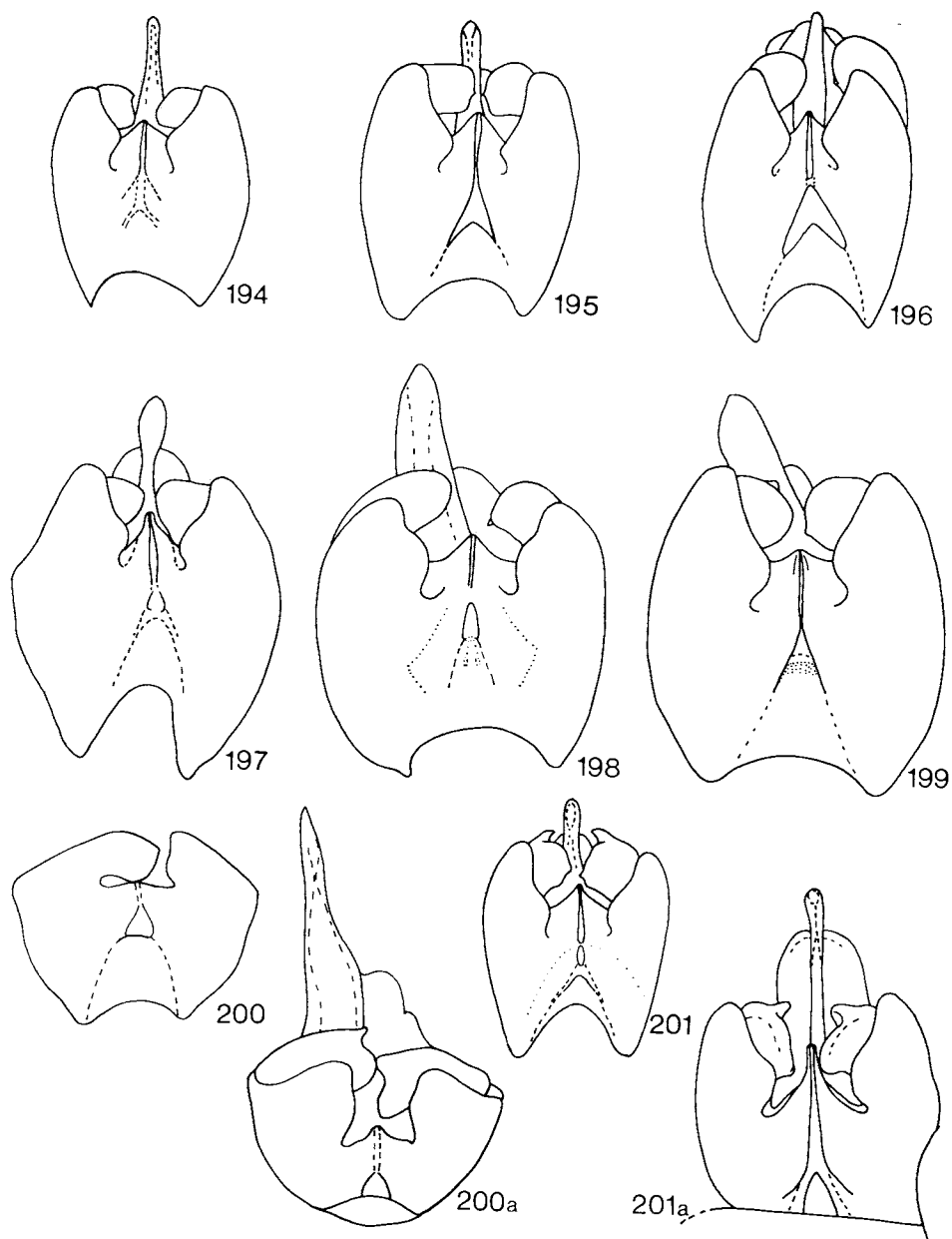
Abdomen: 170, *Pantophthalmus pictus* (♀); 171, *rothschildi* (♂); 172, *zoos* (♂); 173, *vittatus* (♂); 174, *chuni* (♂); 175, *comptus* (♀); 176, *planiventris* (♀); 177, *tabaninus* (♀).



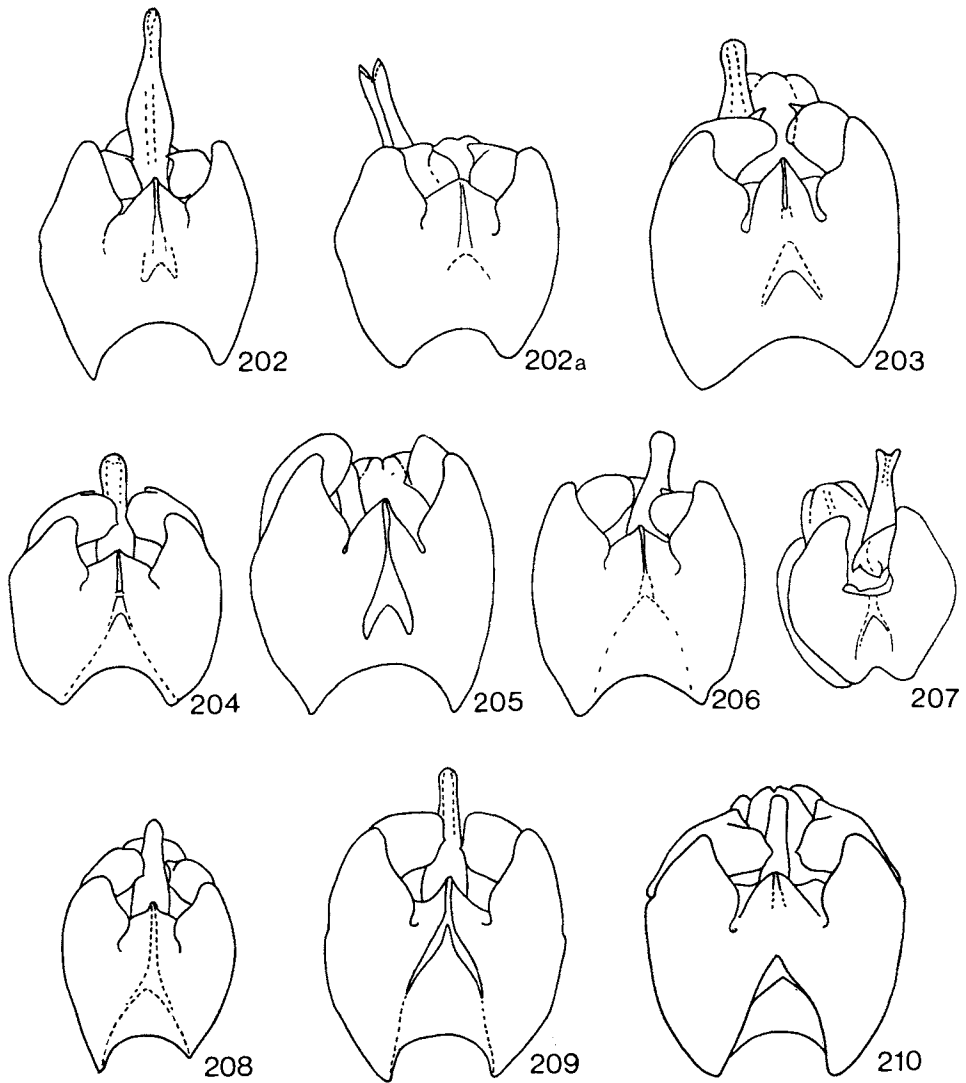
Genitalia, ventral view, females: 178, *Opetiops alienus*; 179, *roseni*; 180, *splendidus*; 181, *kerteszi*; 182, *comptus*; 183, *pictus* (Rio Claro); 183a, *pictus* (Argentina); 184, *chuni*.



Genitalia, ventral view, females: 185, *argyropastus*; 186, *batesi*; 187, *punctiger*; 188, *planiventris*; 189, *facetus*; 190, *frauenfeldi*; 191, *vittatus*; 192, *bellardii*; 193, *tabaninus*.

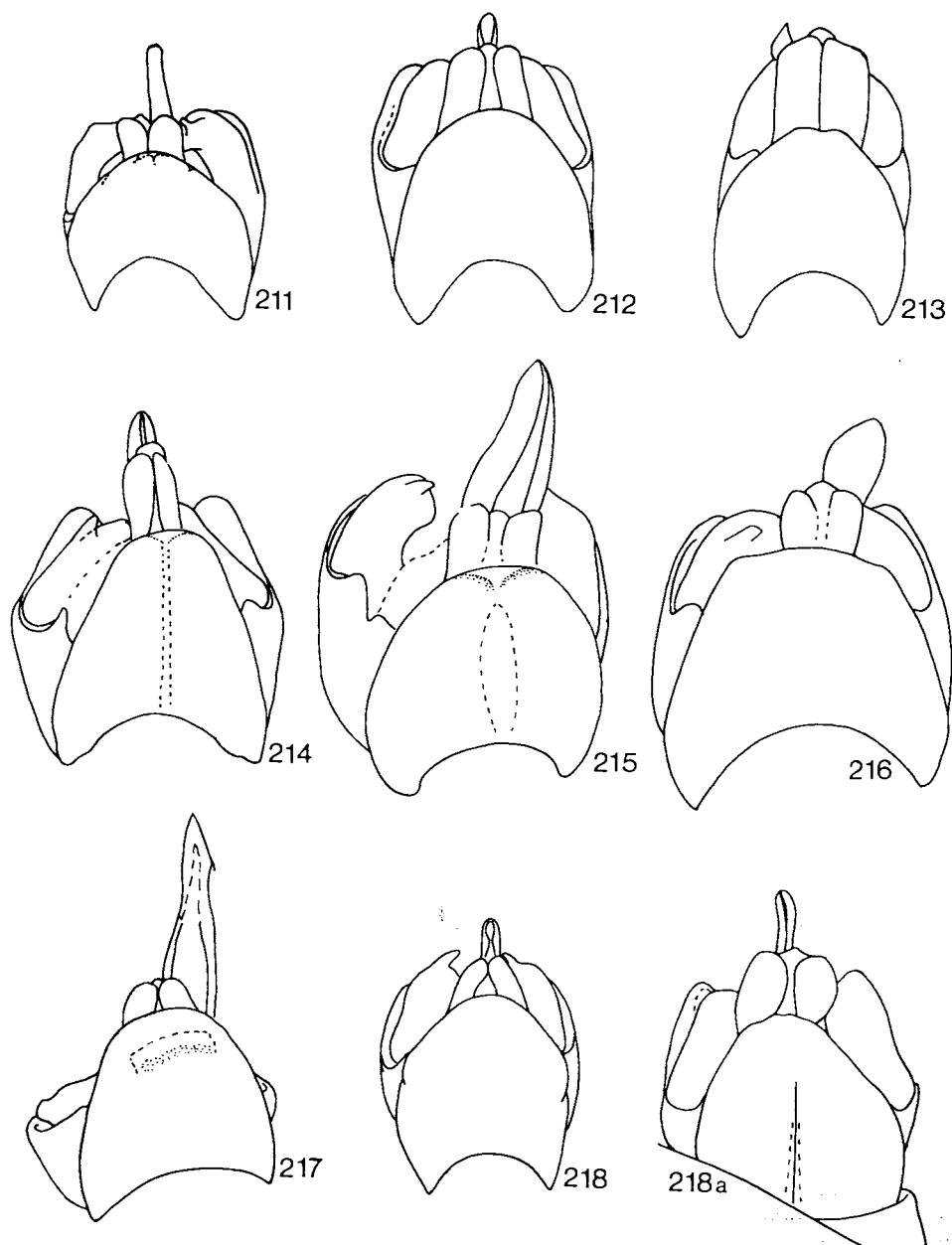


Genitalia, hypandrium, males: 194, *Pantophthalmus comptus*; 195, *kerteszi*; 196, *pictus*; 197, *roseni*; 198, *rothschildi*; 199, *zoos*; 200, *subsignatus*; 200a, *subsignatus* (other view); 201, *engeli* (no locality); 201a, *engeli* (type specimen).

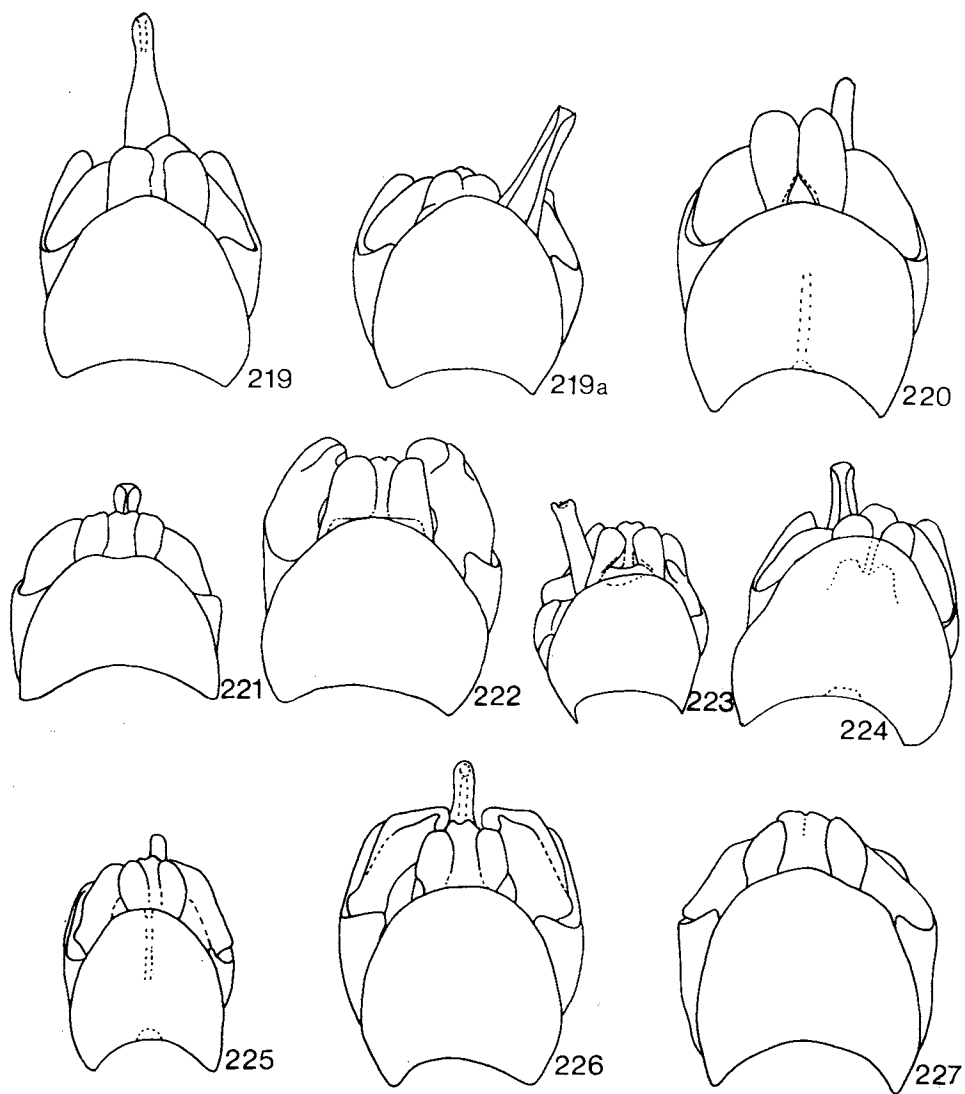


Genitalia, hypandrium, males: 202, *Pantophthalmus chuni* (type specimen of *P. helleriana*); 202a, *chuni* (type specimen of *P. leuckarti*); 203, *frauenfeldi*; 204, *plani-ventris*; 205, *argyropastus*; 206, *punctiger*; 207, *batesi*; 208, *vittatus*; 209, *bellardii*; 210, *tabaninus*.

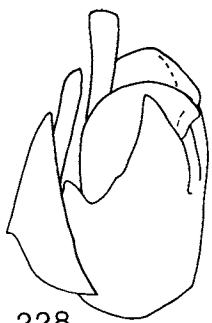




Genitalia, epanthidium, males: 211, *Pantophthalmus comptus*; 212, *kerteszi*; 213, *pictus*; 214, *roseni*; 215, *rothschildi*; 216, *zoos*; 217, *subsignatus*; 218, *engeli* (no locality); 218a, *engeli* (type specimen).



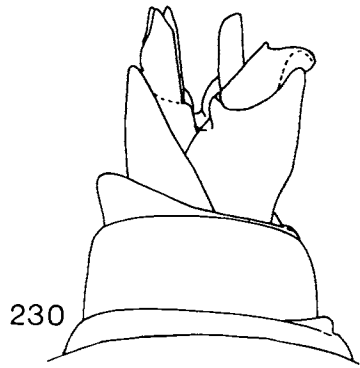
Genitalia, epandrium, males: 219, *Pantophthalmus chuni* (type specimen of *A. helleriana*); 219a, *chuni* (type specimen of *P. leuckarti*); 220, *frauenfeldi*; 221, *plani-ventris*; 222, *argyropastus*; 223, *batesi*; 224, *punctiger*; 225, *vittatus*; 226, *bellardii*; 227, *tabaninus*.



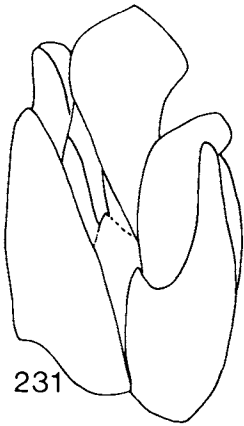
228



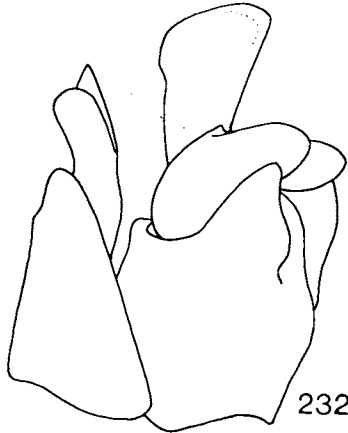
229



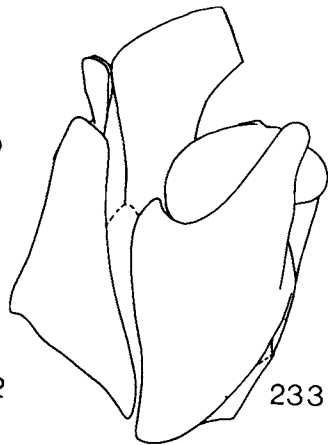
230



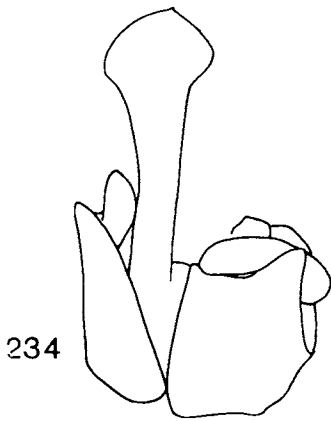
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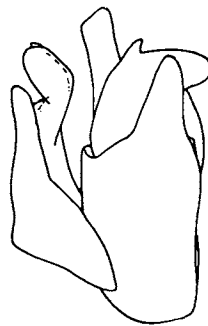
232



233

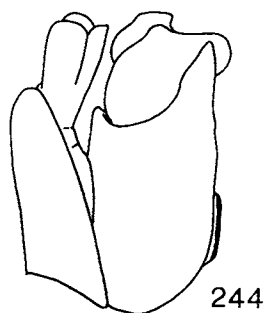
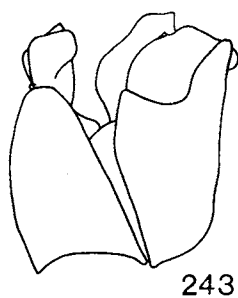
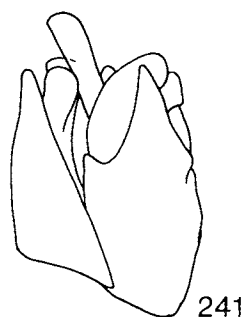
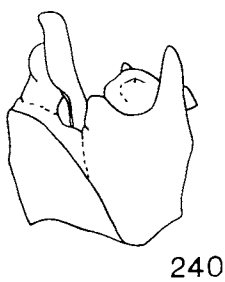
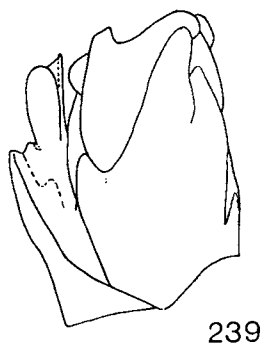
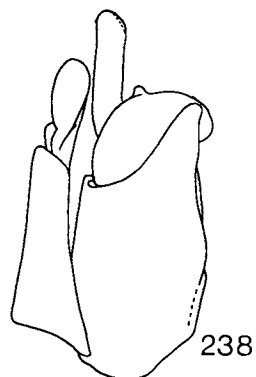
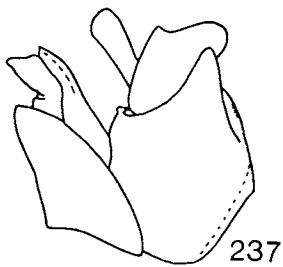
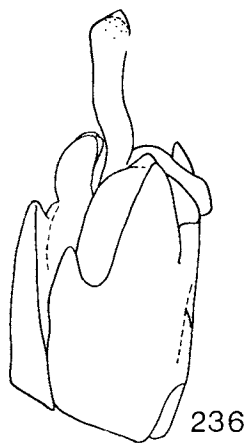


234

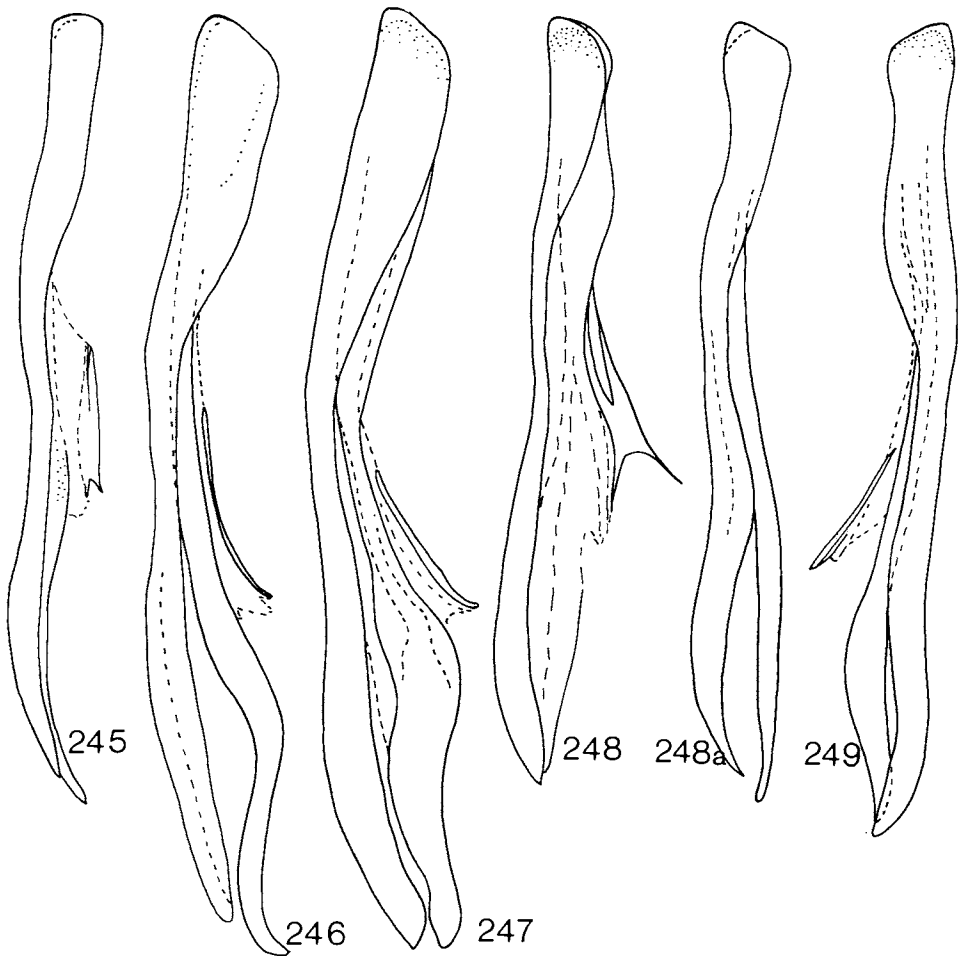


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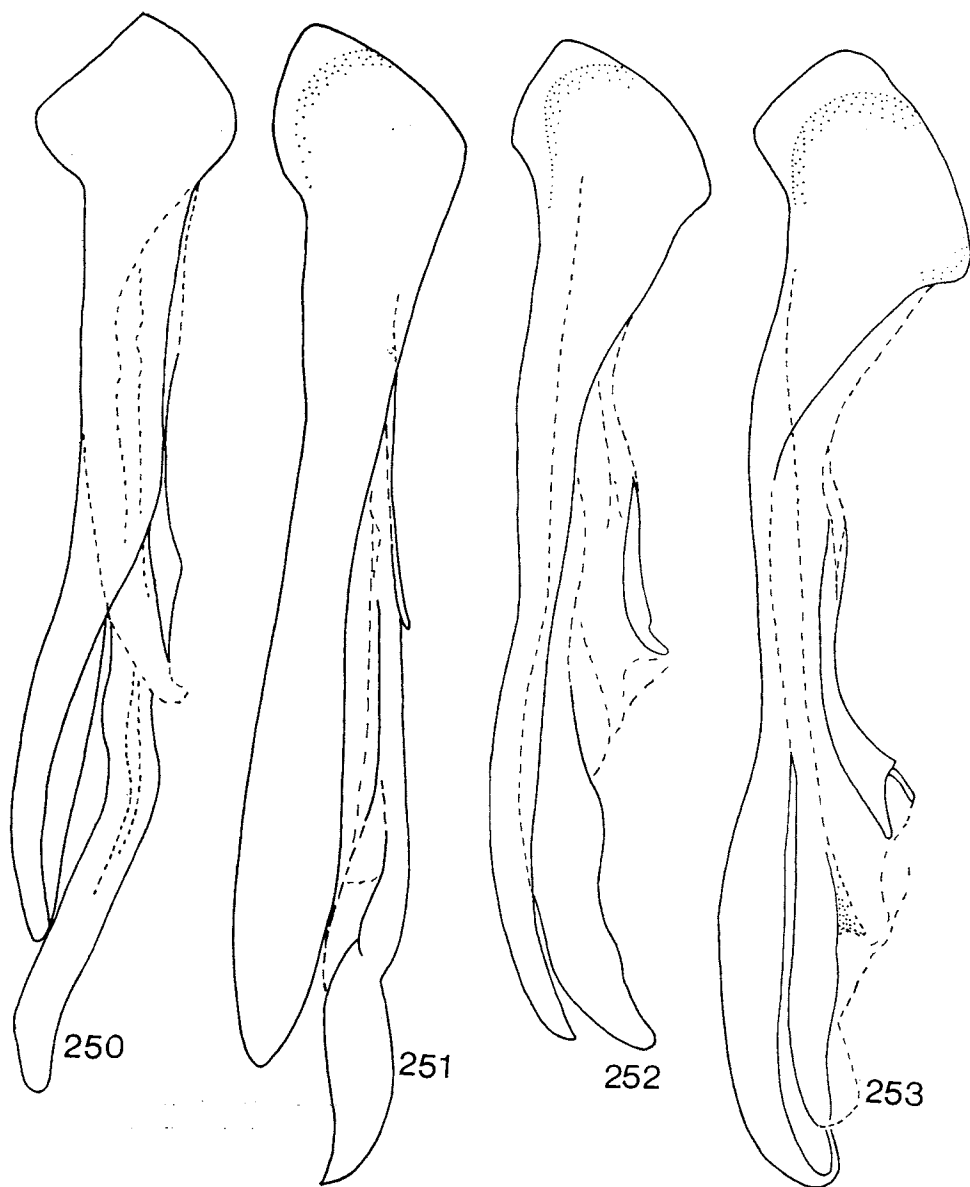
Genitalia, side view, males: 228, *Pantophthalmus comptus*; 229, *kertesziianus*; 230, *pictus* (not dissected); 231, *roseni*; 232, *rothschildi*; 233, *zoos*; 234, *subsignatus*; 235, *engeli*.



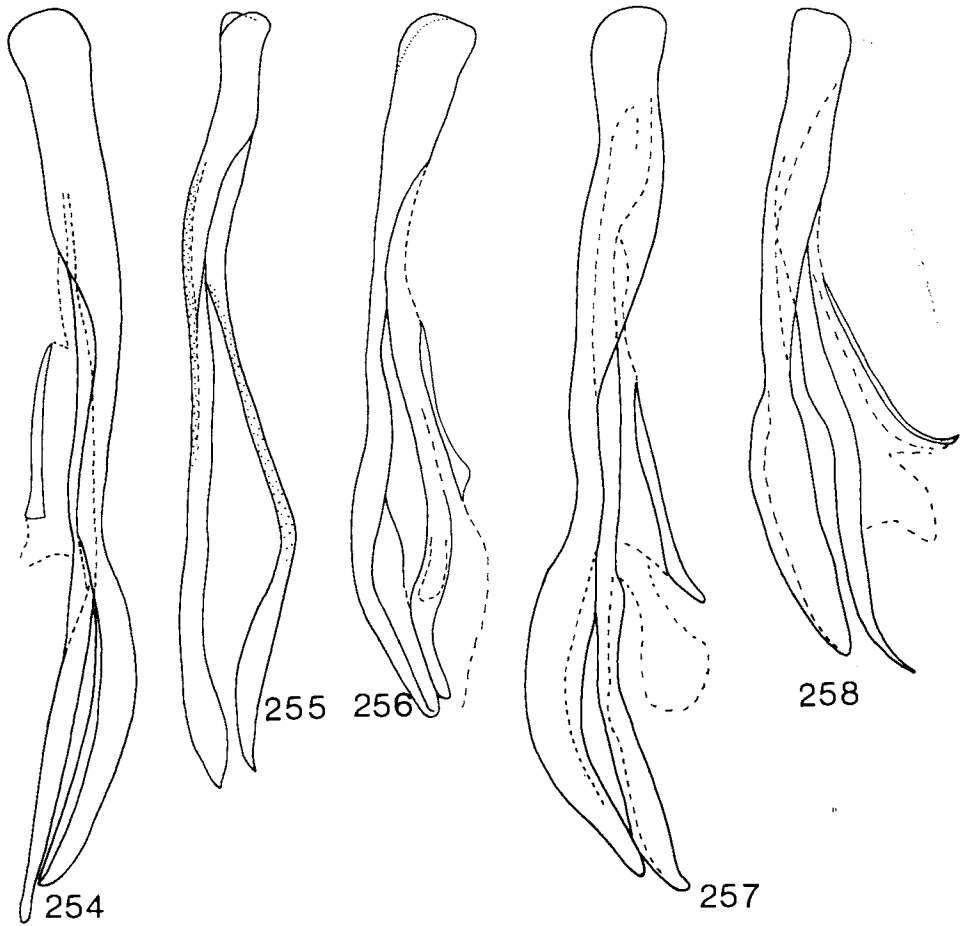
Genitalia, side view, males: 236, *Pantophthalmus chuni* (type specimen of *A. helleriana*); 237, *planiventris*; 238, *frauenfeldi*; 239, *argyropastus*; 240, *batesi*; 241, *punctiger*; 242, *vittatus*; 243, *bellardii*; 244, *tabaninus*.



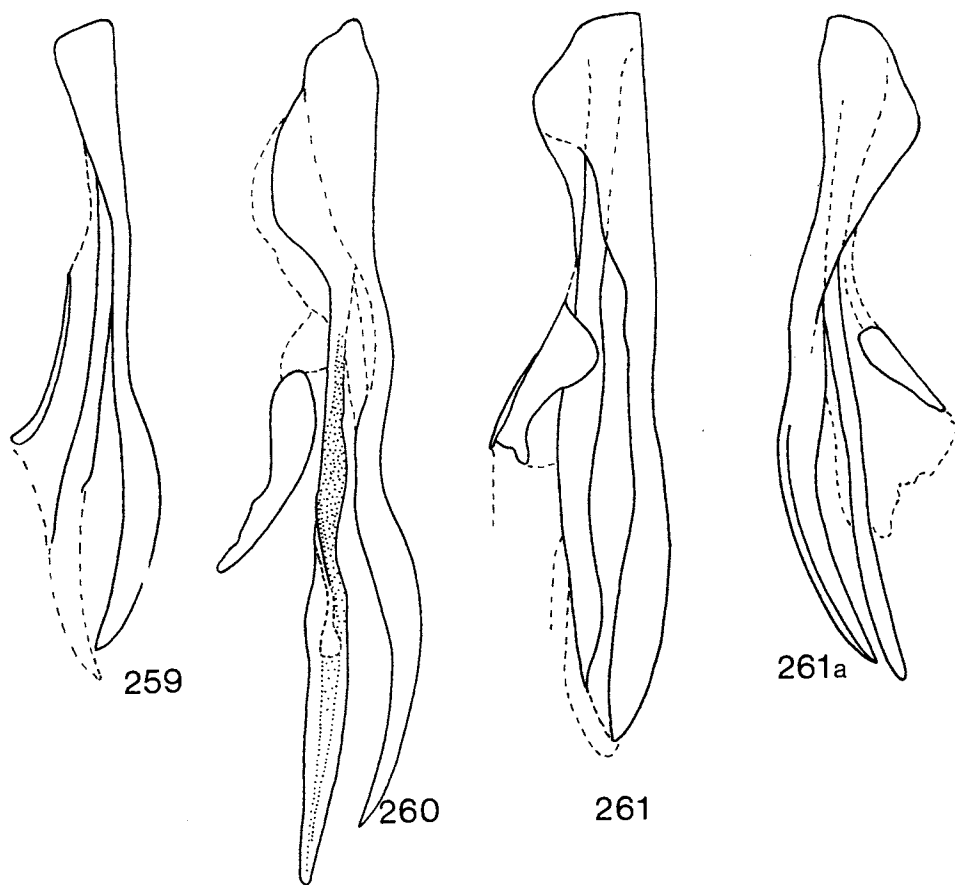
Genitalia, aedeagus, males: 245, *Pantophthalmus comptus*; 246, *kertcszianus*; 247, *pictus*; 248, *chuni* (type specimen of *P. leuckarti*); 248a, *chuni* (type specimen of *A. helleriana*); 249, *engeli*,



Genitalia, aedeagus, males: 250, *Pantophthalmus subsignatus*; 251, *roseni*; 252, *rothschildi*; 253, *zoos*,

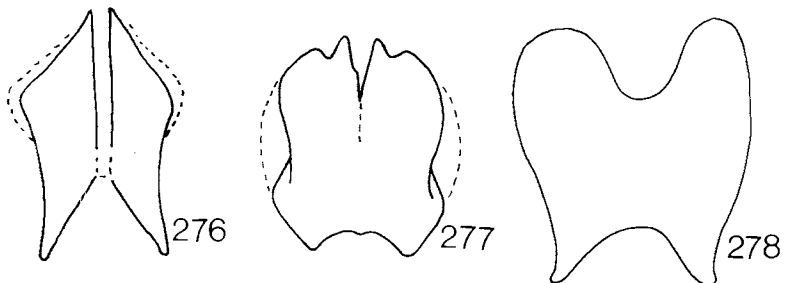
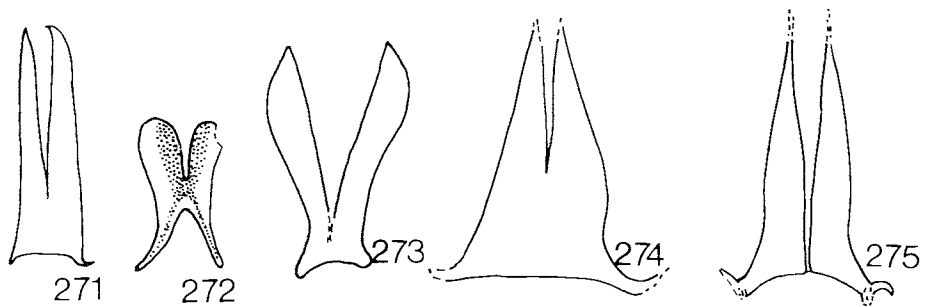
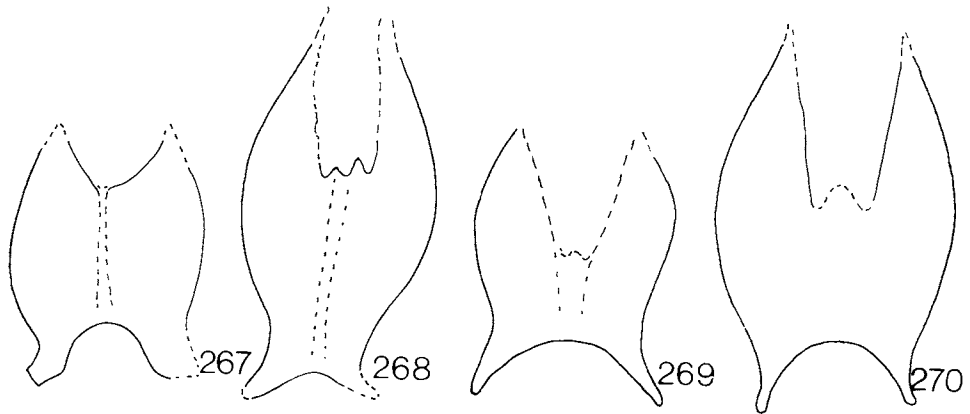
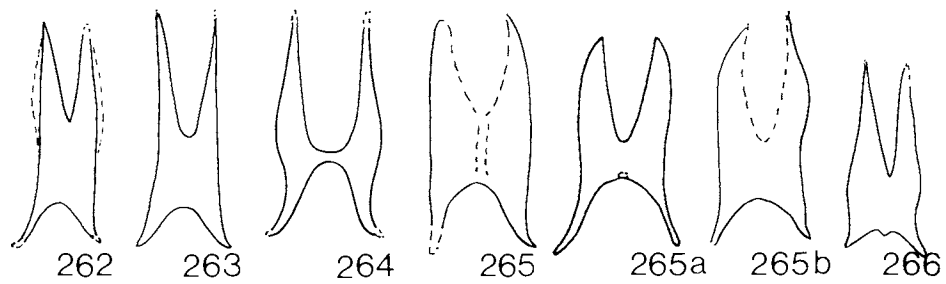


Genitalia, aedeagus, males: 254, *Pantophthalmus argyropastus*; 255, *batesi*; 256, *punctiger*; 257, *frauenfeldi*; 258, *planiventris*.

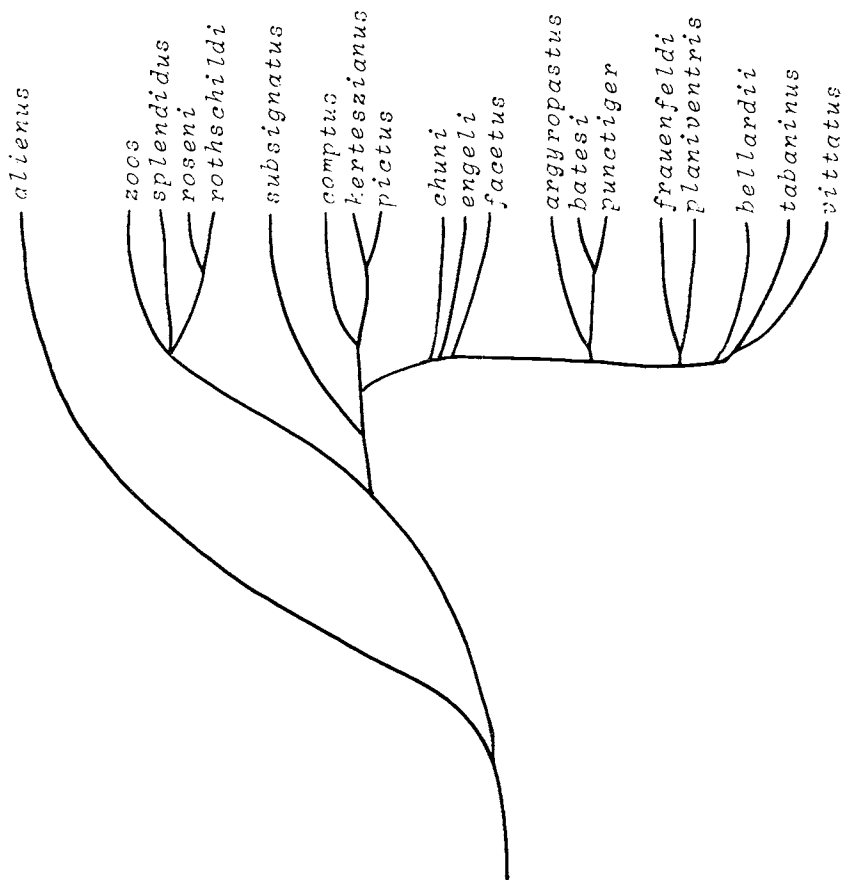


Genitalia, aedeagus, males: 259, *Pantophthalmus vittatus*; 260, *bellardii*; 261, *tabaninus* (Rio Matipó); 261a, *tabaninus* (Córrego do Itá).

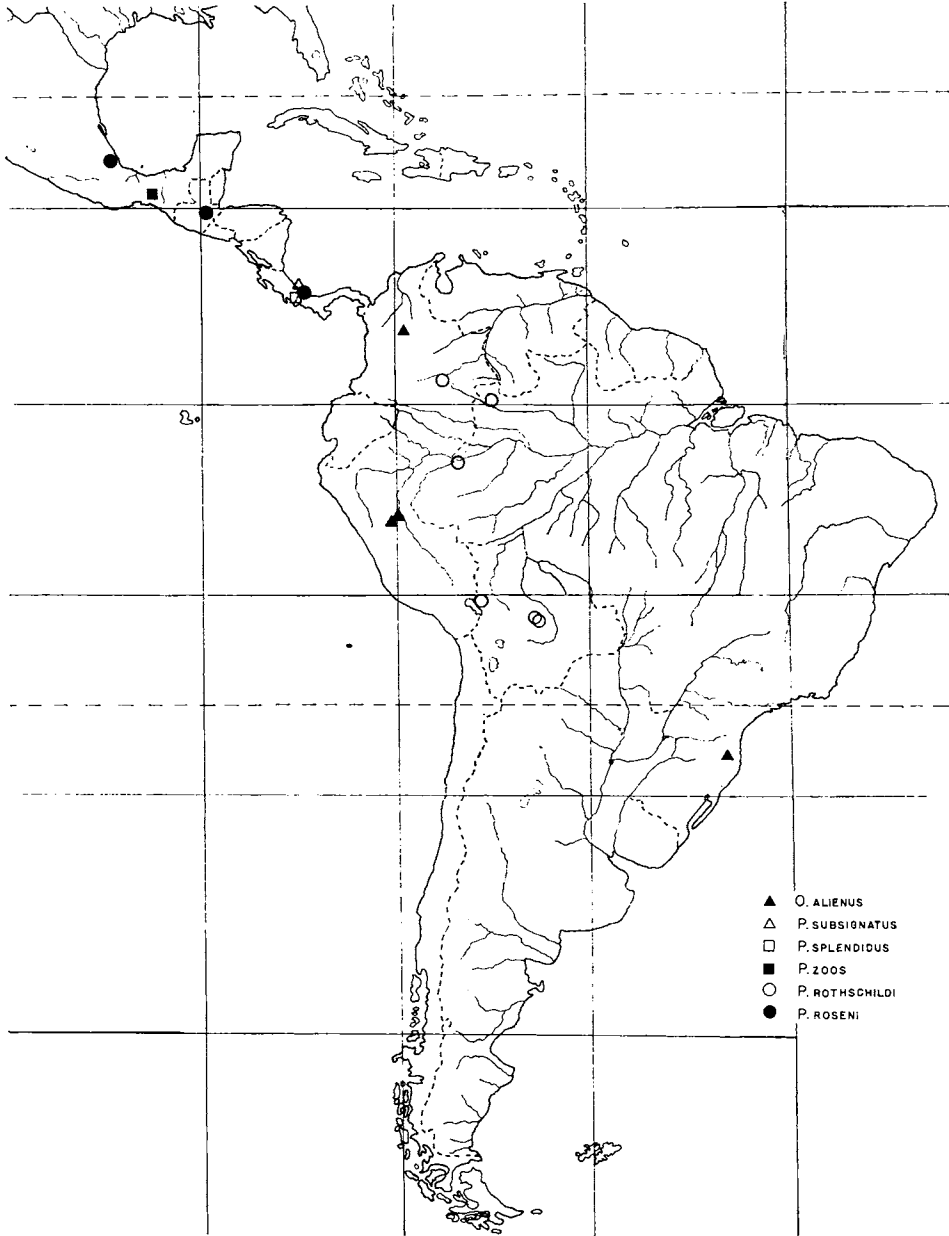




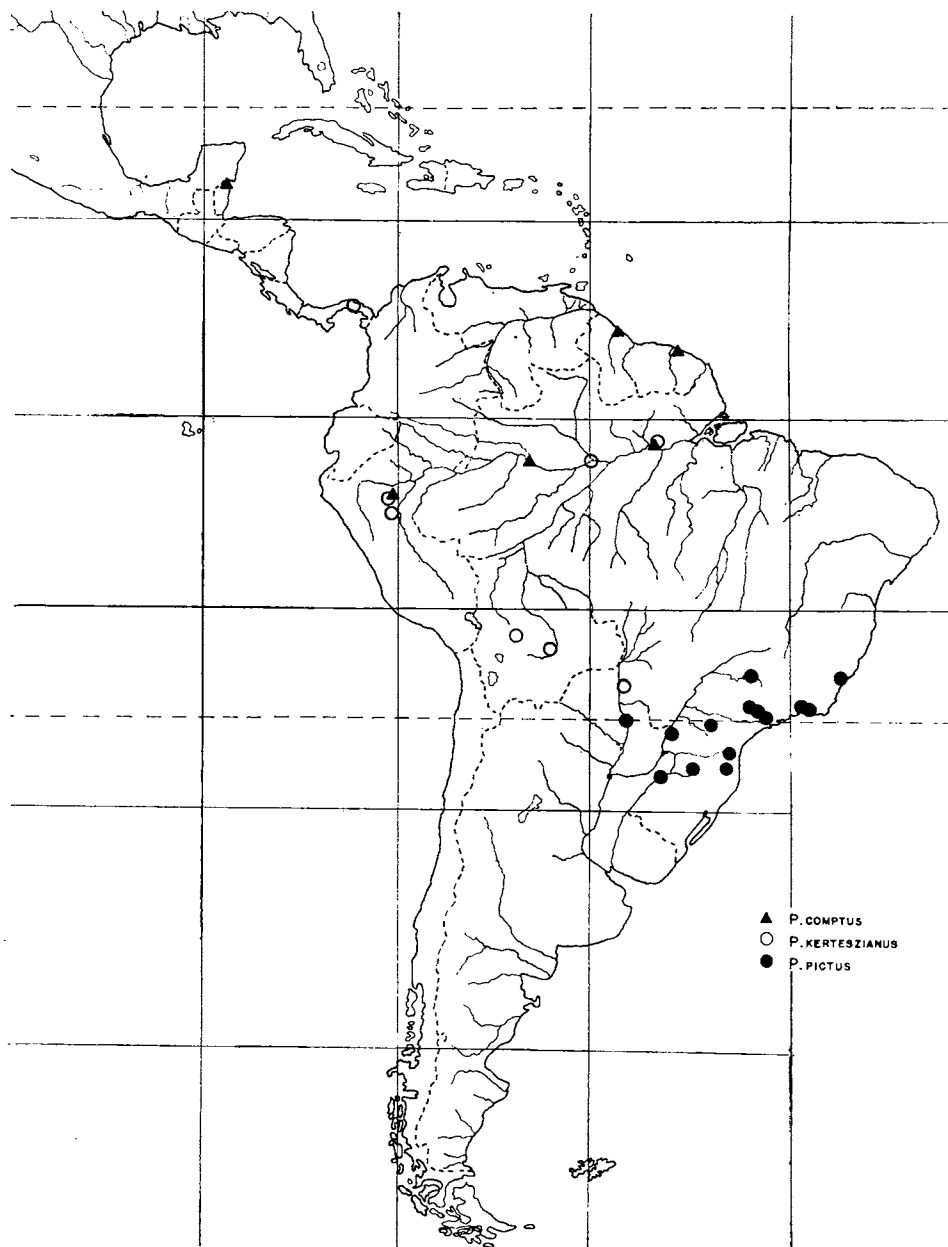
Genitalia, ejaculatory apodeme, males: 262, *Pantophthalmus comptus*; 263, *kerteszianus*; 264, *pictus*; 265, *chuni* (Boquerón); 265a, *chuni* (type specimen of *A. helleriana*); 265b, *chuni* (type specimen of *P. leuckarti*); 266, *engeli*; 267, *subsignatus*; 268, *roseni*; 269, *rothschildi*; 270, *zoos*; 271, *argyropastus*; 272, *batesi*; 273, *punctiger*; 274, *planiventris*; 275, *frauenfeldi*; 276, *vittatus*; 277, *tabaninus*; 278, *bellardii*.



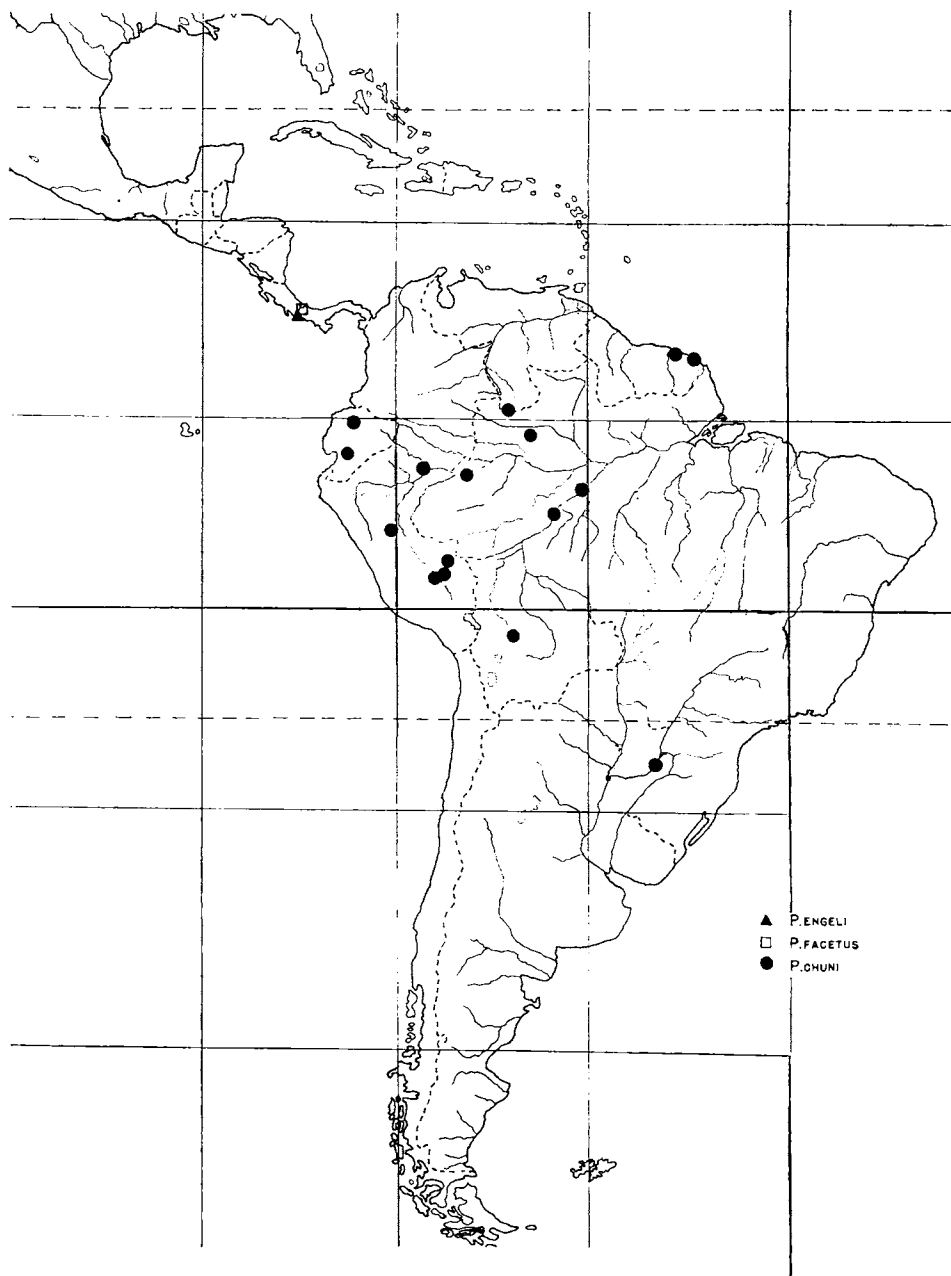
Phylogeny of the species of Pantophthalmidae.



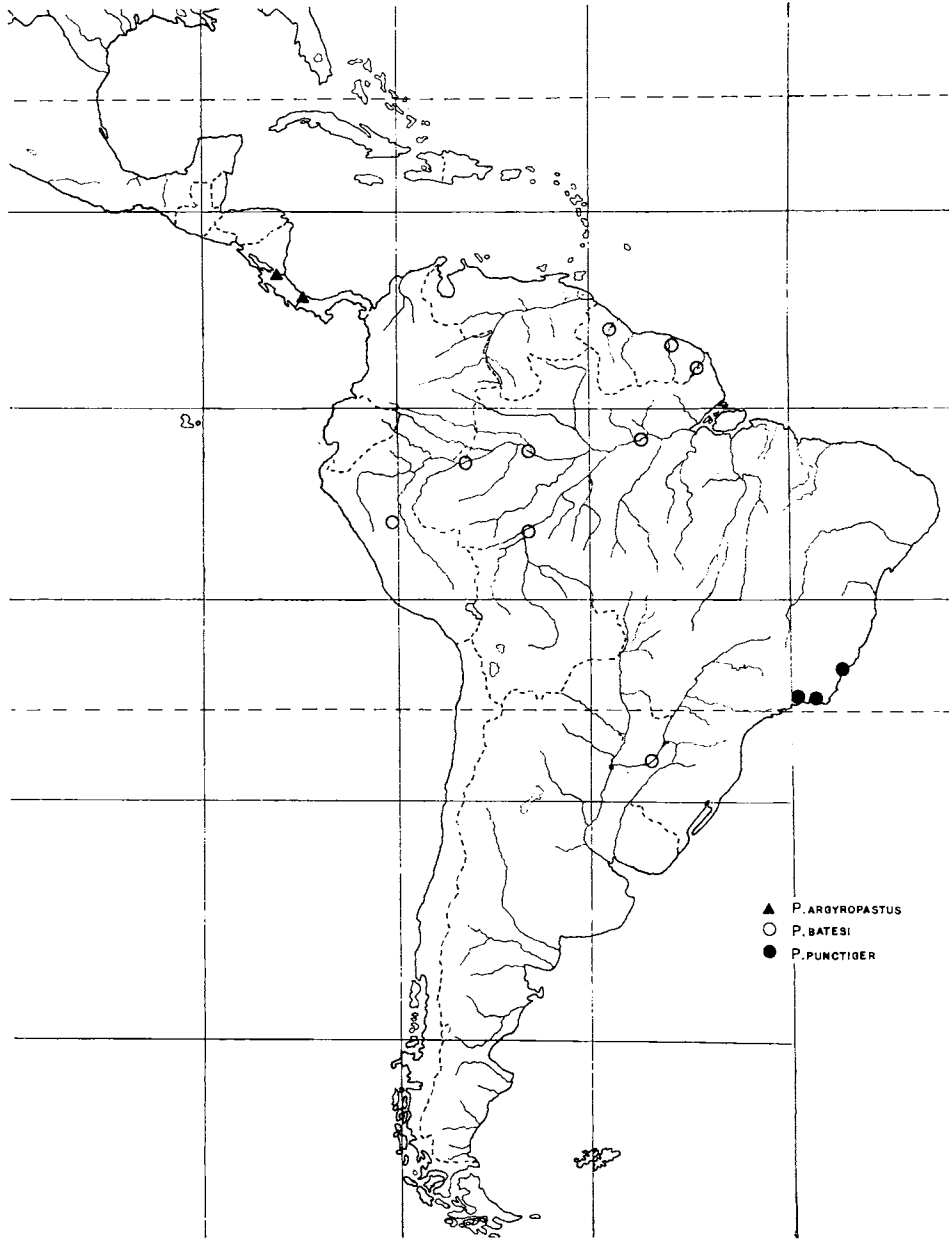
Map 1. Distribution of *Opetiops alienus* and species of *Pantophthalmus*.



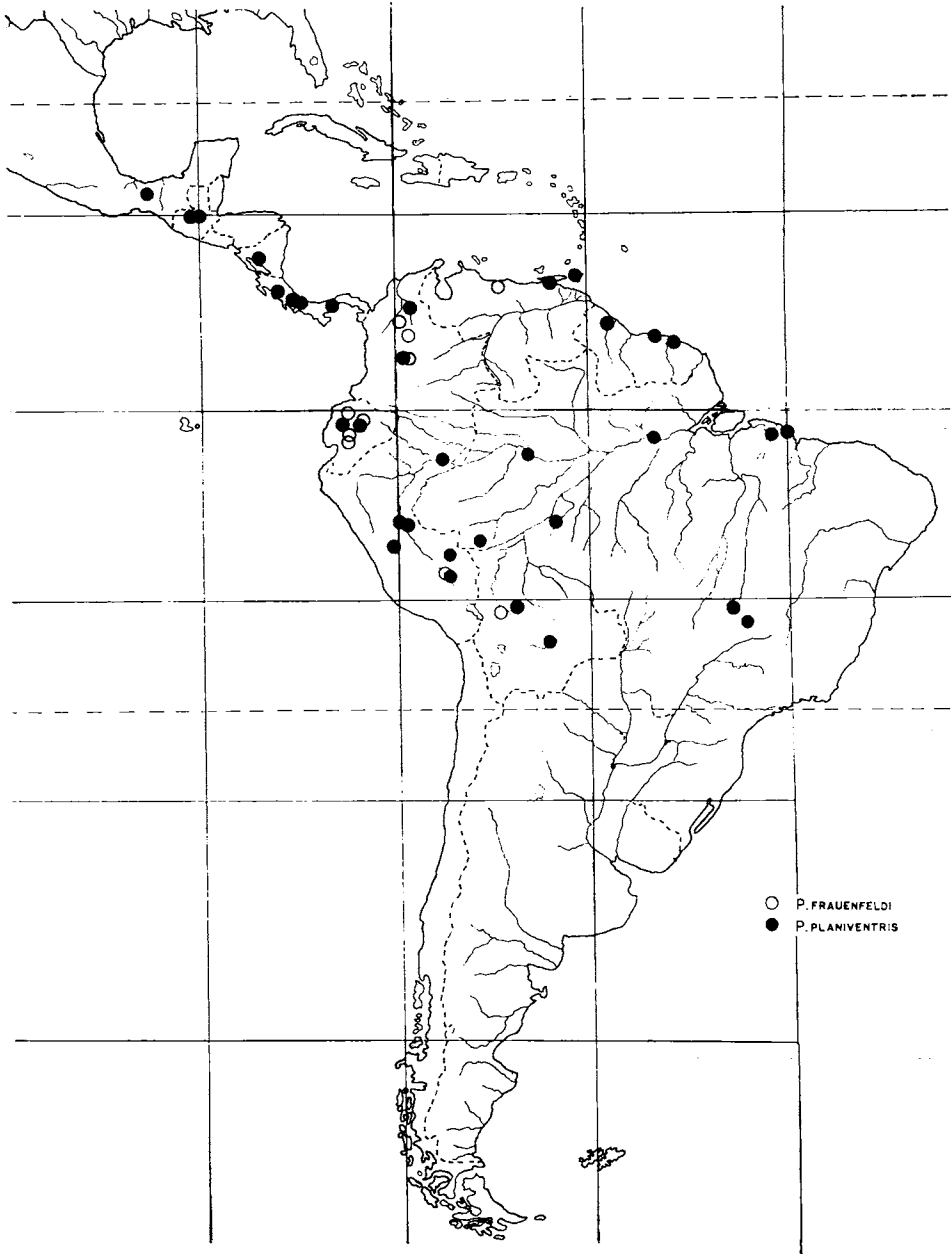
Map 2. Distribution of three species of *Pantophthalmus*.



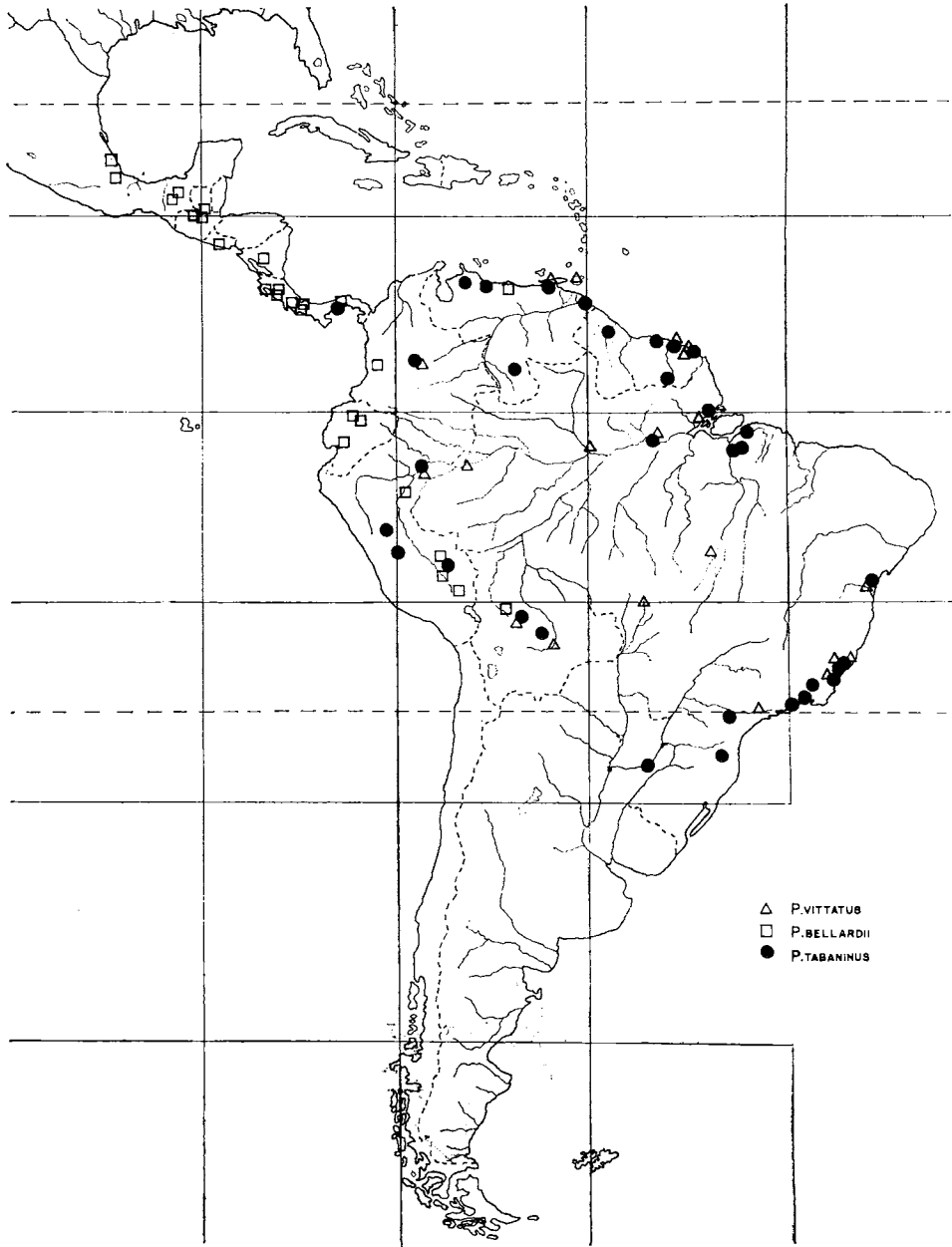
Map 3. Distribution of three species of *Pantophthalmus*.



Map 4. Distribution of three species of *Pantophthalmus*.

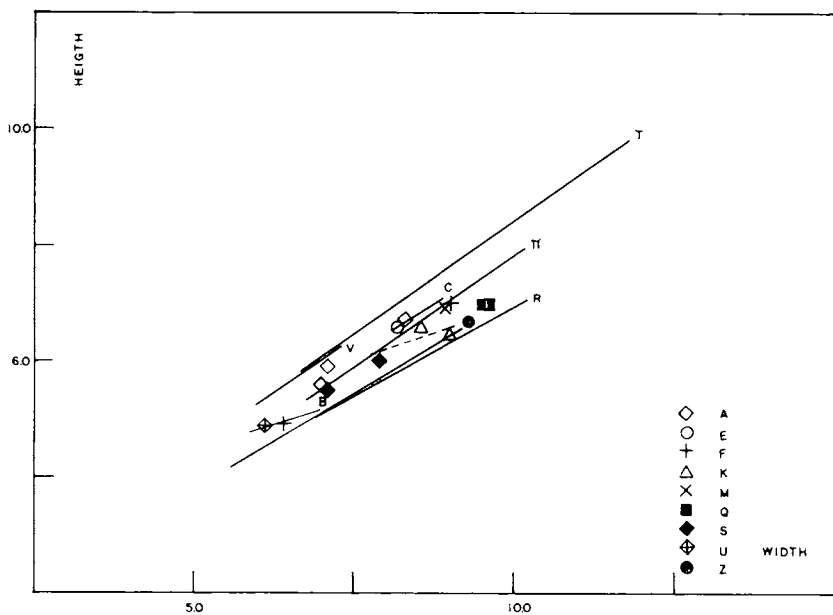
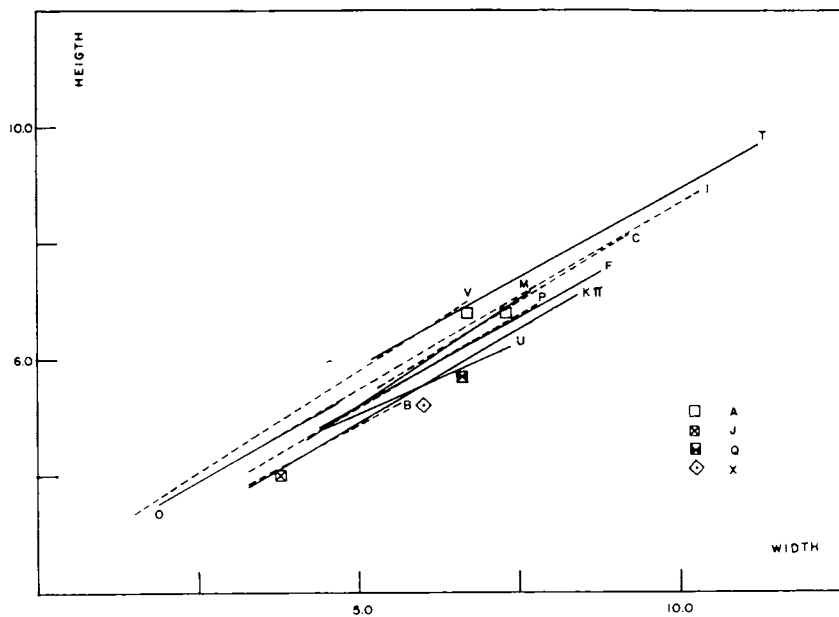


Map 5. Distribution of two species of *Pantophthalmus*.

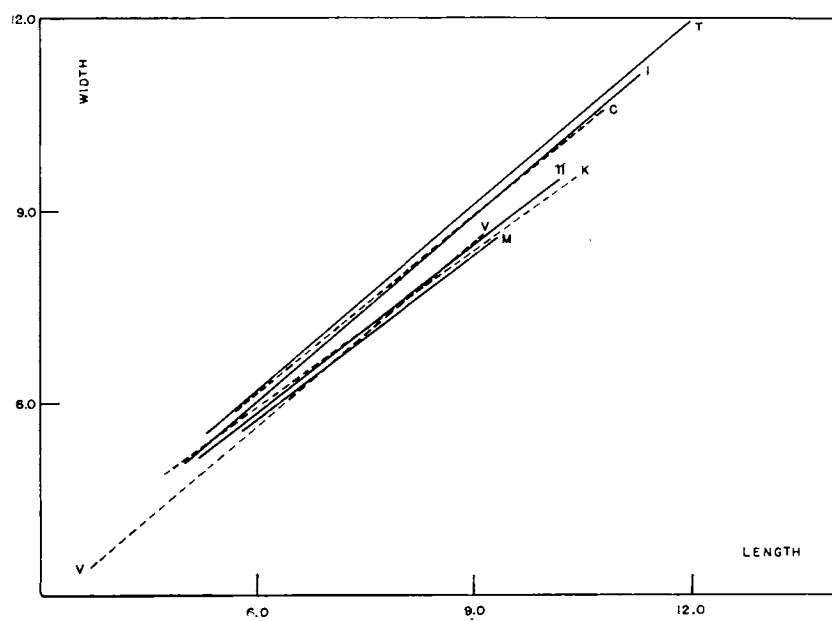
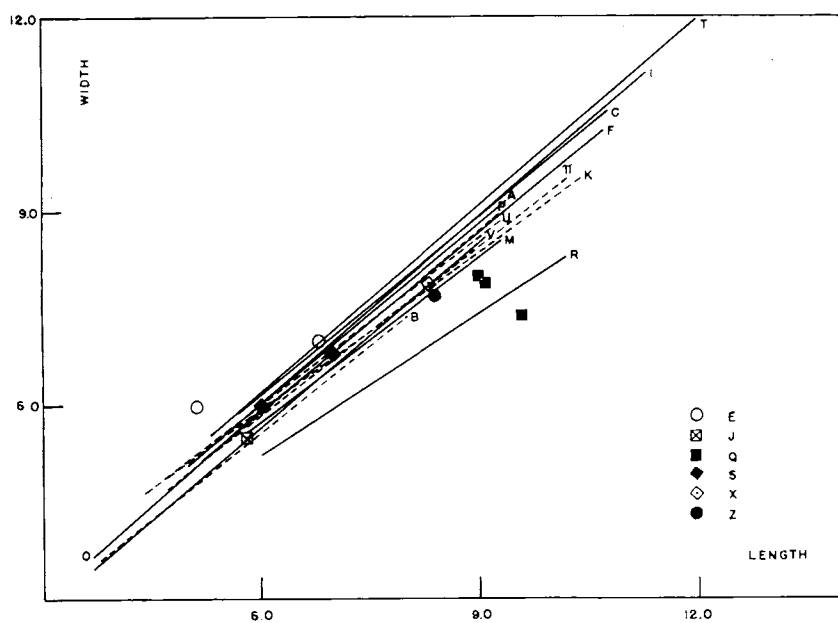


Map 6. Distribution of three species of *Pantophthalmus*.

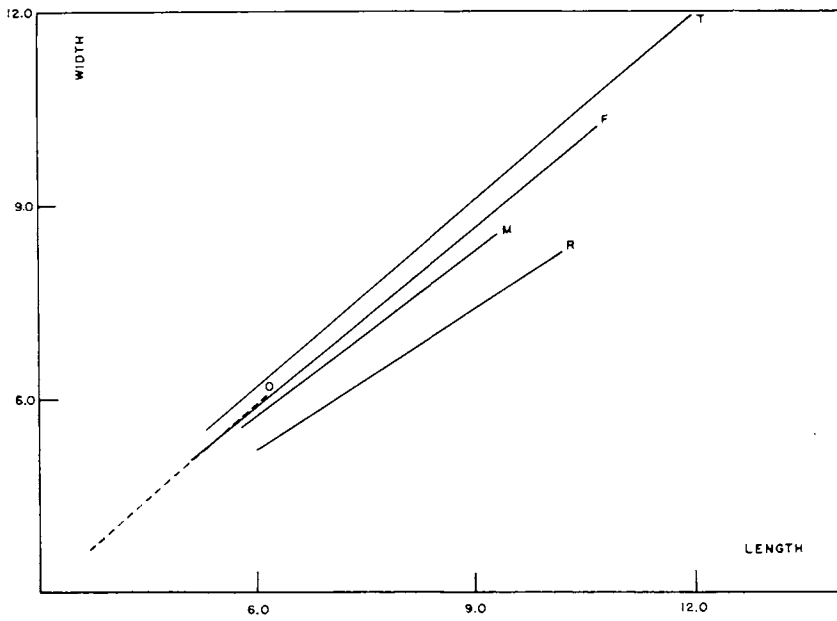
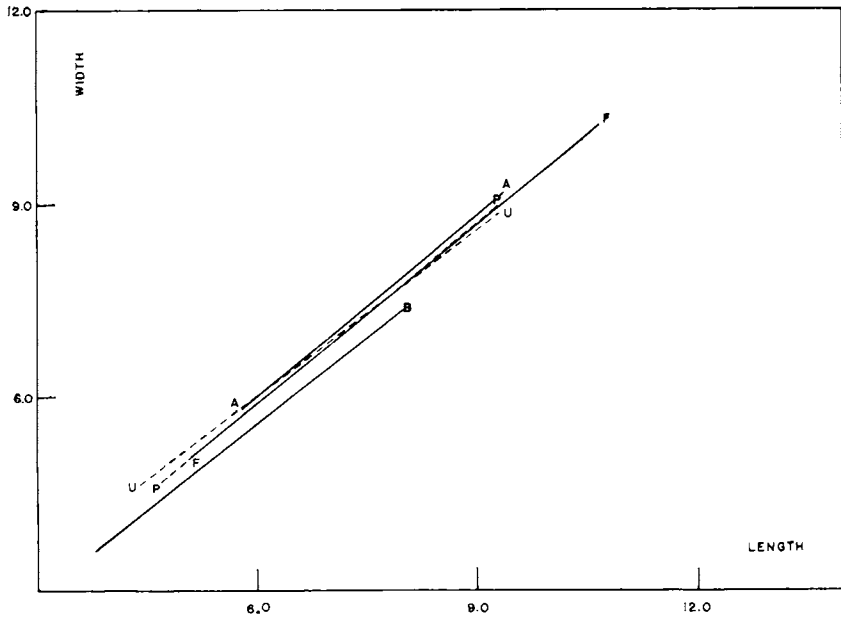




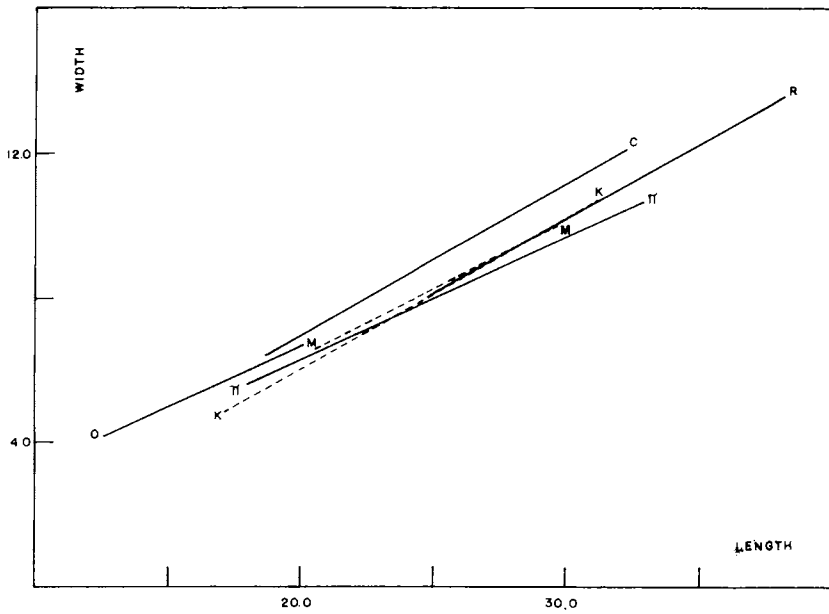
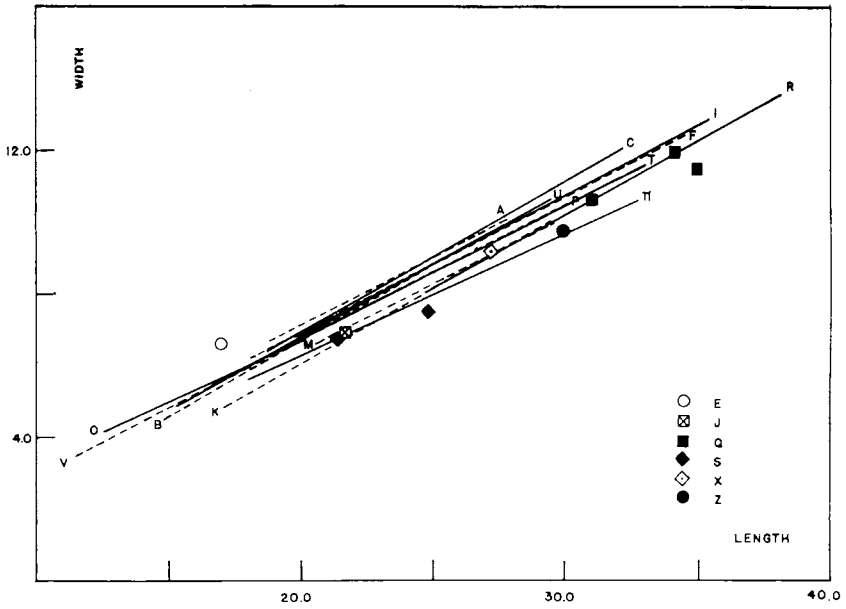
Graph 1. Pantophthalmidae, all species, females: regression of eye height on head width. Graph 2. *Idem*, males: regression of eye height on head width.



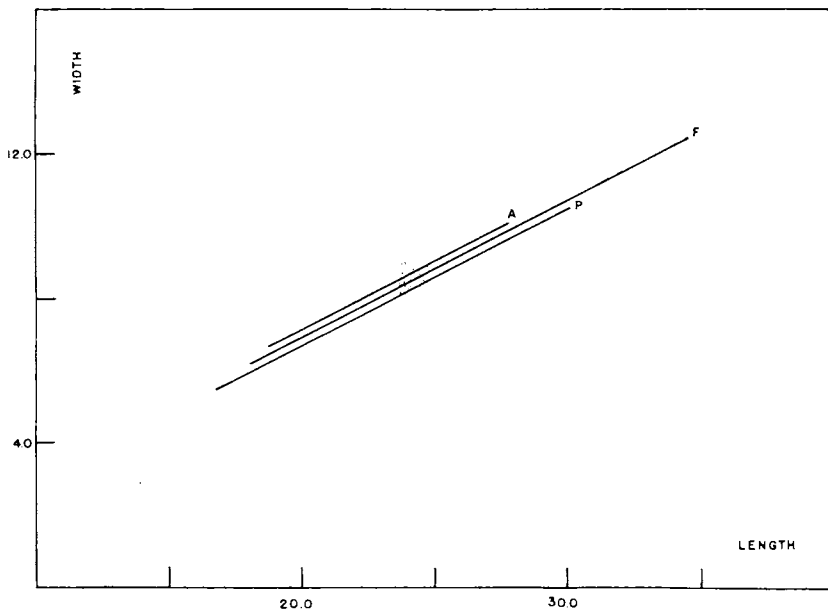
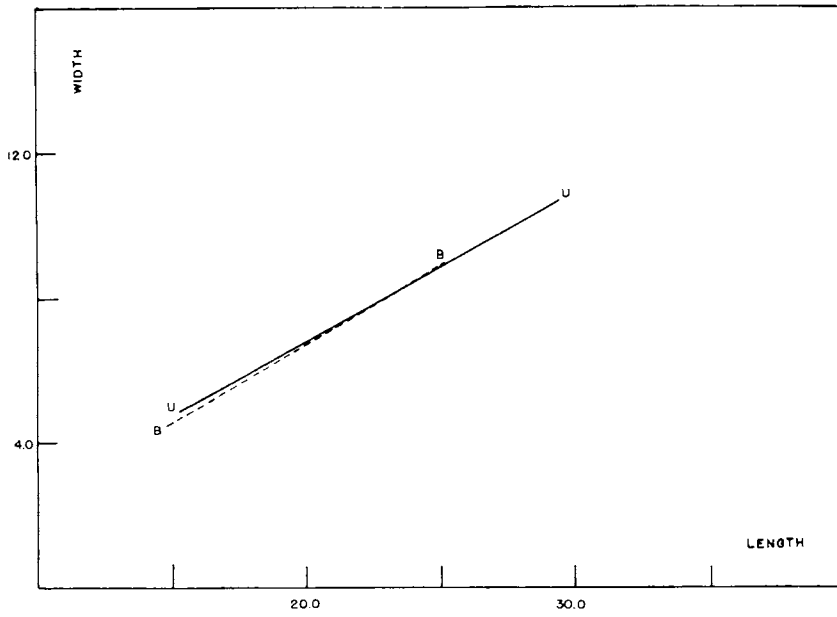
Graph 3. Pantophthalmidae, all species, samples with males and females: regression of thorax width on thorax length. Graph 4. *Pantophthalmus*, species of groups "b" and "d": regression of thorax width on thorax length.



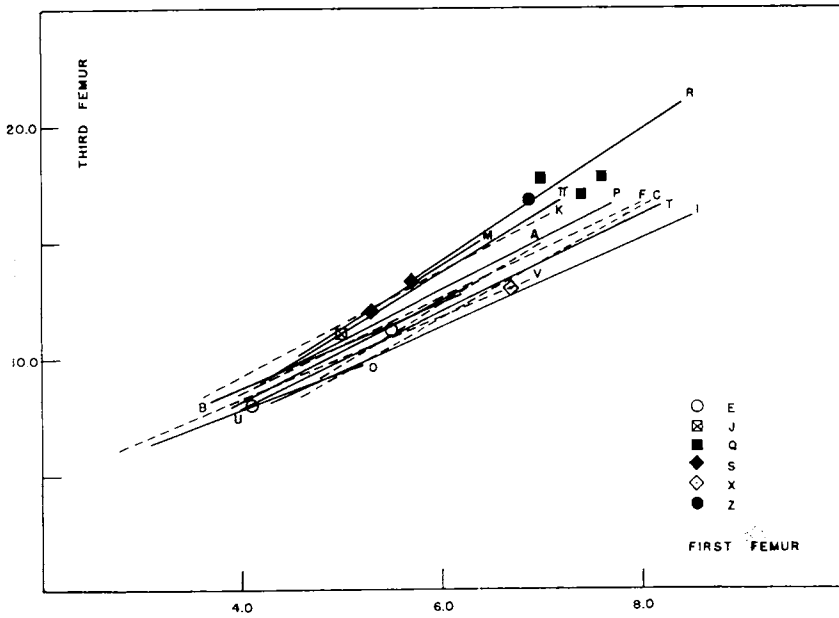
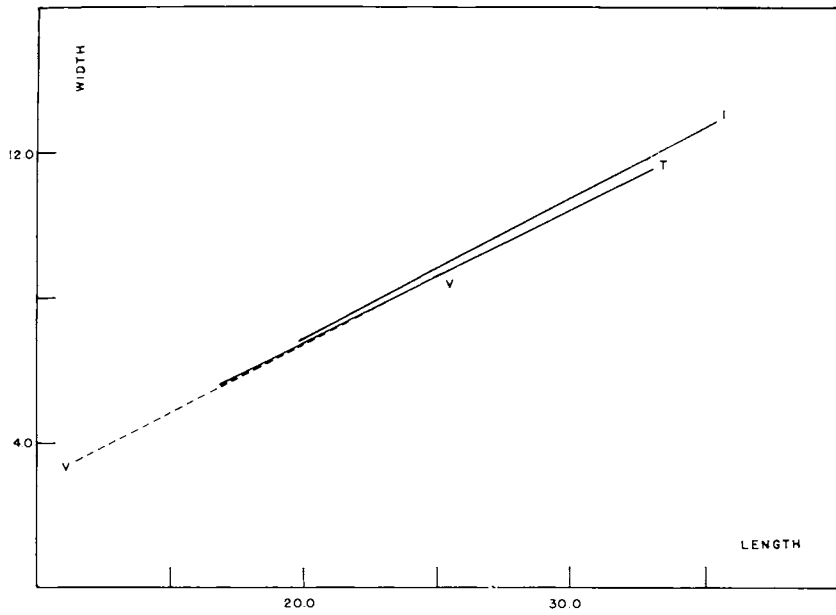
Graph 5. *Pantophthalmus*, species of group "c": regression of thorax width on thorax length. Graph 6. One species of each of *Pantophthalmus* and *Opetiops*: regression of thorax width on thorax length.



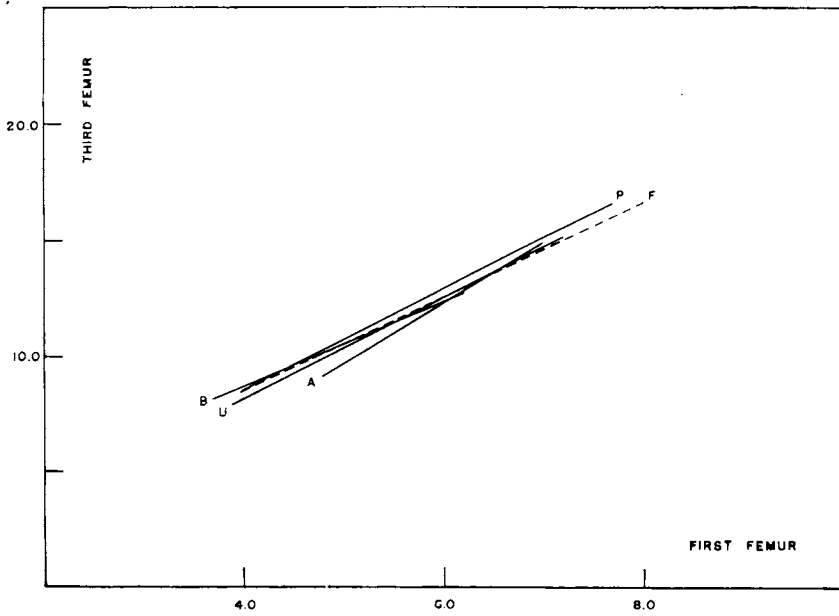
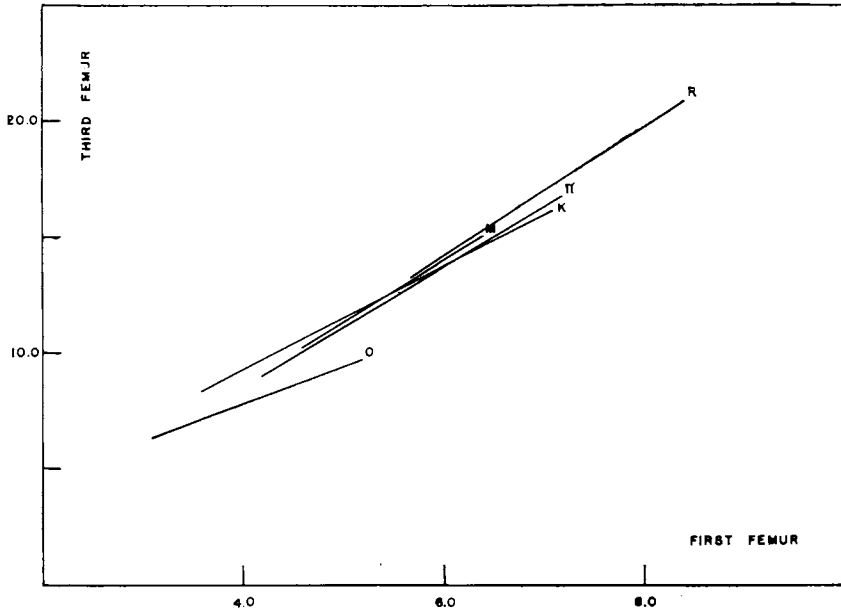
Graph 7. Pantophthalmidae, all species, samples with males and females: regression of wing width on wing length. Graph 8. *Pantophthalmus rothschildi*, *chuni*, species of group "b" and *Opetiops alienus*: regression of wing width on wing length.



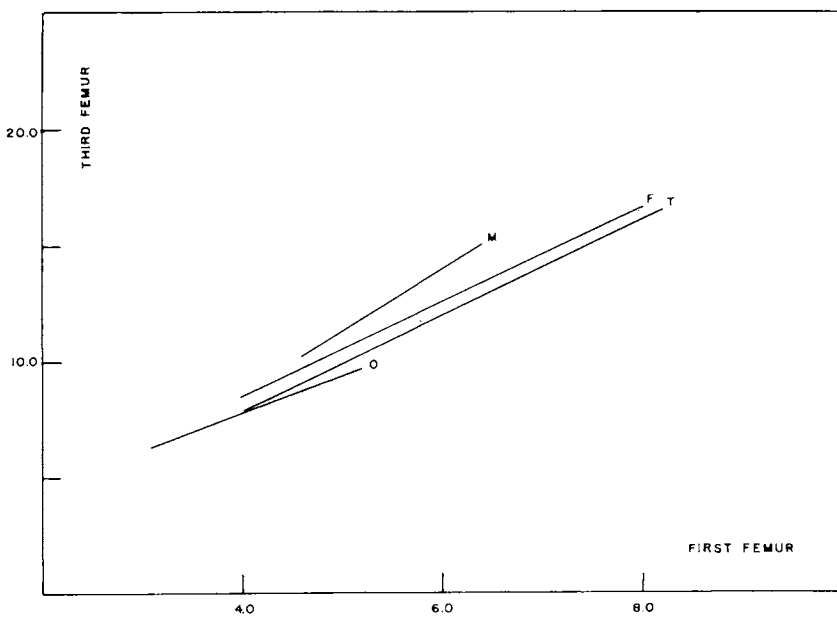
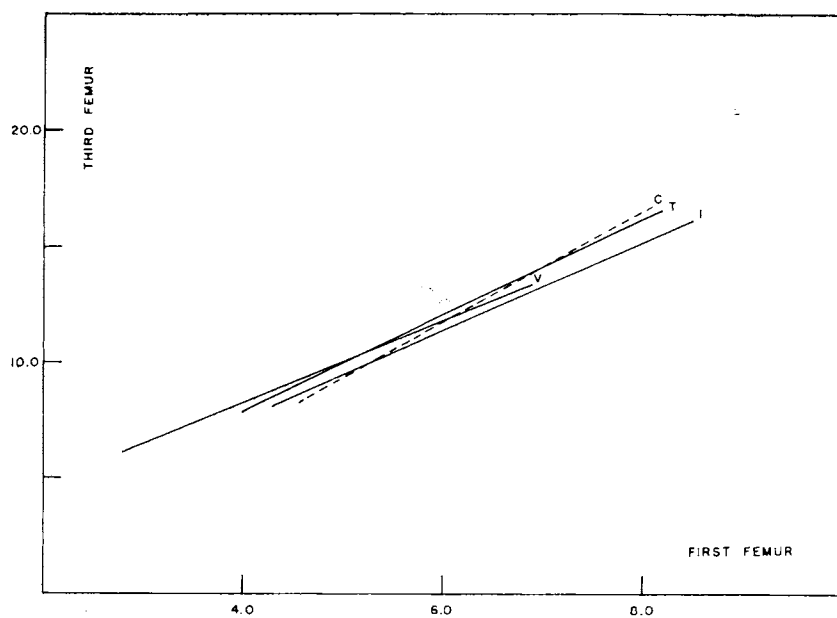
Graph 9. *Pantophthalmus batesi* and *punctiger*: regression of wing width on wing length. Graph 10. *Pantophthalmus argyropastus*, *frauenfeldi* and *planiventris*: regression of wing width on wing length.



Graph 11. *Pantophthalmus*, species of group "d": regression of wing width on wing length. Graph 12. Pantophthalmidae, all species, samples with males and females: regression of posterior femur length on anterior femur length.



Graph 13. *Opetiops alienus*, *Pantophthalmus rothschildi* and species of group "b": regression of third femur length on first femur length. Graph 14. *Pantophthalmus*, species of group "c": regression of third femur length on first femur length,



Graph 15. *Pantophthalmus chuni* and species of group "d": regression of third femur length on first femur length. Graph 16. One species of each group of *Pantophthalmus* and *Opetiops alienus*. Regression of third femur length on first femur length.



Table 1 : Regression of eye height on head width

Species	Sex	N	$R_x$	b	a	$r^2$	$\bar{y}_{5,0}$	$\bar{y}_{12,0}$
<i>alienus</i>	♀	14	4,6 - 7,0	$0,62 \pm 0,058$	$0,79 \pm 0,37$	0,90	3,9	8,2
<i>rothschildi</i>	♂	9	7,1 - 10,0	$0,62 \pm 0,072$	$0,73 \pm 0,66$	0,91	3,8	8,2
<i>comptus</i>	♀	10	6,9 - 10,0	$0,73 \pm 0,047$	$-0,27 \pm 0,41$	0,97	3,4	8,5
<i>kerteszianus</i>	♀	13	6,0 - 10,5	$0,65 \pm 0,036$	$0,04 \pm 0,34$	0,97	3,3	7,8
<i>pictus</i>	♀	15	7,1 - 10,7	$0,65 \pm 0,045$	$0,03 \pm 0,43$	0,94	3,3	7,8
"	♂	12	7,0 - 10,0	$0,77 \pm 0,043$	$0,11 \pm 0,39$	0,97	4,0	9,4
<i>ohuni</i>	♀	14	8,0 - 11,5	$0,68 \pm 0,044$	$0,18 \pm 0,43$	0,95	3,6	8,3
"	♂	5	8,3 - 8,7	$0,70 \pm 0,14$	$0,86 \pm 1,19$	0,89	4,4	9,3
<i>batesi</i>	♀	9	6,0 - 8,0	$0,59 \pm 0,057$	$0,42 \pm 0,41$	0,94	3,4	7,5
"	♂	5	6,1 - 6,8	$0,35 \pm 0,045$	$2,70 \pm 0,29$	0,95	4,5	6,0
<i>punctiger</i>	♀	8	7,1 - 9,7	$0,49 \pm 0,056$	$1,39 \pm 0,49$	0,93	3,8	7,3
<i>frauenfeldi</i>	♀	17	7,1 - 11,1	$0,62 \pm 0,028$	$0,54 \pm 0,25$	0,97	3,6	8,0
<i>planiventris</i>	♀	21	6,0 - 10,1	$0,64 \pm 0,025$	$0,37 \pm 0,21$	0,97	3,6	8,1
"	♂	16	5,8 - 9,0	$0,67 \pm 0,043$	$0,41 \pm 0,34$	0,95	3,8	8,5
<i>vittatus</i>	♀	21	4,2 - 9,0	$0,70 \pm 0,034$	$0,55 \pm 0,26$	0,96	4,1	9,0
"	♂	10	6,2 - 7,1	$0,77 \pm 0,066$	$0,62 \pm 0,44$	0,94	4,5	9,9
<i>tabaninus</i>	♀	39	7,9 - 13,7	$0,61 \pm 0,021$	$1,31 \pm 0,24$	0,96	4,4	8,6
"	♂	24	6,9 - 11,6	$0,78 \pm 0,31$	$0,62 \pm 0,32$	0,97	4,5	10,0
<i>bellardii</i>	♀	25	6,3 - 12,8	$0,64 \pm 0,021$	$0,68 \pm 0,22$	0,98	3,9	9,4
"	♂	8	8,0 - 9,0	$0,38 \pm 0,18$	$3,18 \pm 1,51$	0,42	5,1	7,7

Table 2 : Regression of thorax width on thorax length

Species	Sex	N	$R_x$	b	a	$r^2$	$\bar{y}_{4,5}$	$\bar{y}_{12,0}$
<i>alienus</i>	♀	14	3,9 - 5,9	$0,98 \pm 0,10$	$0,05 \pm 0,56$	0,88	4,5	11,8
<i>rothschildi</i>	♂	9	6,2 - 10,0	$0,73 \pm 0,081$	$0,84 \pm 0,74$	0,92	4,1	9,6
<i>comptus</i>	♀ ♂	9	6,0 - 9,1	$0,85 \pm 0,050$	$0,64 \pm 0,41$	0,98	4,5	10,9
<i>kerteszianus</i>	♀ ♂	15	4,9 - 10,2	$0,81 \pm 0,037$	$1,07 \pm 0,32$	0,97	4,7	10,8
<i>pictus</i>	♀ ♂	27	5,4 - 10,0	$0,87 \pm 0,050$	$0,61 \pm 0,42$	0,92	4,5	11,1
<i>ohuni</i>	♀ ♂	20	5,9 - 10,6	$0,92 \pm 0,035$	$0,63 \pm 0,29$	0,98	4,7	11,6
<i>batesi</i>	♀ ♂	15	4,0 - 7,3	$0,89 \pm 0,056$	$0,23 \pm 0,34$	0,95	4,2	10,9
<i>punctiger</i>	♀ ♂	9	4,6 - 9,1	$0,86 \pm 0,042$	$0,84 \pm 0,33$	0,98	4,7	11,2
<i>argyropastus</i>	♀ ♂	6	6,0 - 9,2	$0,93 \pm 0,067$	$0,43 \pm 0,51$	0,93	4,6	11,6
<i>frauenfeldi</i>	♀ ♂	17	5,3 - 10,5	$0,92 \pm 0,038$	$0,37 \pm 0,32$	0,98	4,5	11,4
<i>planiventris</i>	♀ ♂	37	4,9 - 9,1	$0,93 \pm 0,040$	$0,31 \pm 0,30$	0,94	4,5	11,4
<i>vittatus</i>	♀ ♂	33	3,9 - 8,9	$0,95 \pm 0,032$	$-0,05 \pm 0,23$	0,97	4,2	11,4
<i>tabaninus</i>	♀ ♂	61	5,5 - 11,8	$0,96 \pm 0,021$	$0,44 \pm 0,20$	0,97	4,7	11,9
<i>bellardii</i>	♀ ♂	31	5,2 - 11,1	$0,96 \pm 0,026$	$0,27 \pm 0,22$	0,98	4,6	11,8

Table 3 : Regression of wing width on wing length

Species	Sex	N	$R_x$	b	a	$r^2$	$\bar{Y}_{11,0}$	$\bar{Y}_{35,0}$
<i>alienus</i>	♀	13	12,0 - 19,9	$0,34 \pm 0,020$	$-0,13 \pm 0,34$	0,98	3,6	11,8
<i>rothschildi</i>	♂	9	25,1 - 38,0	$0,41 \pm 0,025$	$-2,09 \pm 0,88$	0,98	2,4	12,3
<i>comptus</i>	♀ ♂	10	20,8 - 29,4	$0,38 \pm 0,034$	$-1,24 \pm 0,86$	0,94	3,0	12,2
<i>kertesziianus</i>	♀ ♂	15	17,3 - 31,0	$0,42 \pm 0,021$	$-2,37 \pm 0,57$	0,97	2,2	12,3
<i>pictus</i>	♀ ♂	23	18,2 - 32,6	$0,34 \pm 0,013$	$-0,52 \pm 0,36$	0,97	3,3	11,5
<i>chuni</i>	♀ ♂	18	18,9 - 32,0	$0,42 \pm 0,021$	$-1,46 \pm 0,54$	0,96	3,1	13,1
<i>batesi</i>	♀ ♂	14	15,0 - 25,0	$0,43 \pm 0,023$	$-1,91 \pm 0,45$	0,97	2,8	13,2
<i>punctiger</i>	♀ ♂	7	15,5 - 29,3	$0,41 \pm 0,028$	$-1,42 \pm 0,70$	0,98	3,1	12,9
<i>argyropastus</i>	♀ ♂	6	19,0 - 27,6	$0,38 \pm 0,033$	$-0,48 \pm 0,74$	0,97	3,7	12,8
<i>frauenfeldi</i>	♀ ♂	17	18,3 - 34,3	$0,38 \pm 0,022$	$-0,66 \pm 0,57$	0,95	3,5	12,5
<i>planiventris</i>	♀ ♂	37	17,0 - 29,9	$0,36 \pm 0,012$	$-0,90 \pm 0,30$	0,97	3,3	12,5
<i>vittatus</i>	♀ ♂	26	11,7 - 24,9	$0,38 \pm 0,012$	$-0,89 \pm 0,29$	0,97	3,3	12,5
<i>tabaninus</i>	♀ ♂	40	17,0 - 32,8	$0,37 \pm 0,010$	$-0,65 \pm 0,27$	0,97	3,4	12,2
<i>bellardii</i>	♀ ♂	22	20,0 - 35,2	$0,39 \pm 0,015$	$-0,94 \pm 0,41$	0,97	3,4	12,8

Table 4 : Regression of third femur length on first femur length

Species	Sex	N	$R_x$	b	a	$r^2$	$\bar{Y}_{3,0}$	$\bar{Y}_{8,5}$
<i>alienus</i>	♀	13	3,3 - 5,0	$1,60 \pm 0,12$	$1,36 \pm 0,53$	0,95	6,2	15,0
<i>rothschildi</i>	♂	9	5,9 - 8,2	$2,82 \pm 0,37$	$-2,79 \pm 2,82$	0,89	5,7	21,2
<i>comptus</i>	♀ ♂	8	4,8 - 6,2	$2,70 \pm 0,55$	$-2,23 \pm 3,12$	0,80	5,9	20,7
<i>kertesziianus</i>	♀ ♂	14	3,6 - 6,9	$2,25 \pm 0,11$	$0,18 \pm 0,65$	0,97	6,9	19,3
<i>pictus</i>	♀ ♂	26	4,4 - 7,0	$2,60 \pm 0,15$	$-1,97 \pm 0,90$	0,93	5,8	20,1
<i>chuni</i>	♀ ♂	19	4,8 - 7,9	$2,40 \pm 0,19$	$-2,71 \pm 1,25$	0,90	4,5	17,6
<i>batesi</i>	♀ ♂	15	3,9 - 6,0	$1,84 \pm 0,15$	$1,34 \pm 0,72$	0,92	6,9	17,9
<i>punctiger</i>	♀ ♂	9	4,1 - 7,0	$2,17 \pm 0,14$	$-0,50 \pm 0,88$	0,97	5,9	17,9
<i>argyropastus</i>	♀ ♂	5	5,0 - 6,8	$2,62 \pm 0,41$	$-3,43 \pm 2,38$	0,93	4,4	18,8
<i>frauenfeldi</i>	♀ ♂	18	4,2 - 7,8	$2,05 \pm 0,15$	$0,26 \pm 0,90$	0,93	6,4	17,7
<i>planiventris</i>	♀ ♂	36	4,3 - 7,5	$2,18 \pm 0,10$	$-0,20 \pm 0,58$	0,94	6,3	16,3
<i>vittatus</i>	♀ ♂	32	3,0 - 6,7	$1,77 \pm 0,12$	$1,13 \pm 0,63$	0,87	6,4	16,1
<i>tabaninus</i>	♀ ♂	56	4,2 - 8,0	$2,08 \pm 0,070$	$-0,51 \pm 0,46$	0,94	5,7	17,2
<i>bellardii</i>	♀ ♂	33	4,5 - 8,3	$1,91 \pm 0,10$	$-0,14 \pm 0,64$	0,93	5,6	16,1