A Subgeneric Classification of the Genus Uranotaenia Lynch Arribalzaga, with a Historical Review and Notes on Other Categories

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ABSTRACT. The subgenus Pseudoficalbia is resurrected from synonymy with Uranotaenia s. str. Keys are provided for the recognition of these two subgenera and for proposed sections within the subgenus Pseudoficalbia. Discussion of additional characteristics and probable affinities of other categories are presented. Special treatment is given those species within the subgenus Pseudoficalbia which are considered annectant. A list assigning all currently recognized species and subspecies to subgenera is appended. Varieties as recognized in Stone, Knight and Starke (1959) are also included.

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INTRODUCTION. In the course of studying Southeast Asian Uranotaenia, a number of significant decisions concerning higher categories of the genus were made. Since some of these decisions would have world-wide implications, it was decided to present a report, apart from the Southeast Asian study, so that it might receive the widest possible dissemination. For an understanding of the classification problems which have existed to date, a full review is presented. New interpretations and state of present knowledge of the genus will be discussed and, for cataloging purposes, an annotated list of world species is provided.

Of the 32 genera of mosquitoes recognized (Mattingly 1971), Uranotaenia ranks fourth in number of species following Aedes, Culex and Anopheles. At least 191 species and subspecies are now known (several new species are known but not yet described), and there is little doubt that many more await discovery. Oddly enough, the genus with its great assemblage of species is without recognized subgenera or other categories beyond a regional level. Although Theobald (1905, 1911 and 1912) created three separate genera for a number of species, all are now considered synonyms of Uranotaenia. Only one of these, "Pseudoficalbia," has ever been treated as a subgenus.

HISTORICAL REVIEW. The name Uranotaenia was first applied by Lynch Arribalzaga in 1891. It was derived from the Greek and Latin combinations of urano (heaven) and taenia (band or stripe) in reference to the brilliantly colored bands or stripes of broad scales on the adult thorax. This characteristic has indirectly contributed to confusion of species within the genus since the original description. A number of subsequently recognized species without such bands were assigned to Ficalbia Theobald or Pseudoficalbia Theobald. In 1911, Theobald created the genus Pseudoficalbia and transferred the single species Ficalbia inornata (Theobald) to it. In 1912, he again applied the name as new and included three species in addition to inornata. In the same year, Edwards (1912) suggested that Pseudoficalbia "should not be considered even as a subgenus," because he could find no important structural characteristics to distinguish these species from the rest. However, in the same paragraph, he conceded that the four species of Theobald and two additional species had the first fork cell somewhat longer than in most Uranotaenia and further stated that "it is noticeable that these six species are also abnormal in having no blue flat scales on the mesonotum." From these remarks and observations, it is obvious he was not completely convinced that two distinct phyletic lines did not in fact exist. In the same article, Edwards compounded the problem by considering Pseudoficalbia Theobald 1911 as a nomen nudum apparently because Theobald's 1911 article was not considered a definitive publication. Howard, Dyar and Knab (1917) later designated Pseudoficalbia pandani Theobald (1912) as the type species. This designation was followed until Stone, Knight and Starke (1959) listed Ficalbia inornata as the Haplotype of Pseudoficalbia.

In a footnote comparing the larvae of annulata Theobald and nigripes (Theobald), Edwards (1916 in Macfie and Ingram) suggested the validity of the "Pseudoficalbia group" and further suggested that it could "apparently be defined on the characters of the larval head

as well as on the scale characters of the adults." Apparently, he was satisfied with this interpretation because Edwards (1927 in Schwetz) listed species of the Ethiopian Region under the subgenera Uranotaenia and Pseudoficalbia. He made no further reference to structural differences, but it is clear from the species listed that he was influenced by the presence or absence of bands of broad scales on the adult thorax.

The whole effort to recognize subgenera was abandoned when Philip (1931) pointed out that the separation proposed by Edwards (1916) did not hold in the case of two newly described larvae of mashonaensis Theobald and bilineata var. fraseri Edwards. On the basis of these alleged discrepancies, Edwards gave up the idea of two subgenera, but he could not abandon the concept of two distinct groups; in his classic catalog of 1932, he relegated the two subgenera to group rank and listed all of the then known world species. Again, this division was based upon the presence or absence of bands of broad scales but modified to include in the"Uranotaenia group" those species which did not have broad scutal scales in front of wing root but did have, at least, bright blue scales on the head and patches of blue scales on the pleuron. He also added that the frontal setae of the larva were usually thick and spine-like and that for the "Pseudoficalbia group" they were usually slender. Finally, in 1941, he abandoned this arrangement because "it was not very natural, especially as it did not take sufficient account of the considerable diversity in the Pseudoficalbia group." It was apparently the species in groups B and D (discussed below) which prompted this reappraisal of the two-group concept. In its place, he suggested dividing the Ethiopian species into four groups which he designated A, B, C and D and characterized them as follows:

"A. Scutal scales mostly narrow but a supra-alar stripe of broad scales; apn scaly; wings usually with some white scales in lines. Terminalia (where known) with IXth tergite bare, its lateral corners produced into pointed processes or rounded knobs; style short and rather stout; lp with strong spines: U. pallidocephala, philonuxia, caeruleocephala, alboabdominalis, alba, mayeri, bilineata and var's. caliginosa, balfouri."

"B. Scutal scales all narrow (except montana) but apn scaly; wing scales dark. Terminalia (where known) with IXth tergite bare, neither middle nor corners produced; style short but less stout than in group A; lp with very small hooks: U. chorleyi, neireti, hopkinsi, montana, annulata, candidipes."

"C. Scutal scales all narrow. apn devoid of scales. Terminalia with IXth tergite bare, more or less produced in middle but not at corners; style long and slender; lp with small spines: U. ornata, nigripes, nepenthes, fusca, mashonaensis, nigromaculata."

"D. Scutal scales all broad; apn and pleurae also with broad scales. Terminalia with IXth tergite hairy, without processes: U. shillitonis, henrardi."

Edwards concluded by saying, "I do not consider that any of these groups are worthy of rank as subgenera, all the species exhibiting all the important generic characters in the adult stage." This was the first time male terminalia characters had been used, but there were, at that time, too few known to make much of these characters. Through an obvious oversight, Edwards did not assign micromelas to one of the above groups even though he included it in the key and described it on page 61. It would have assigned to group C. Since this date, several workers have suggested that various species from other parts of the world would assign to one or more of these groups. In many cases, these species did not fit in the strictest sense, for the groups are not natural as defined.

It is interesting to note that while Theobald had created at least two new genera, Leicester (1908) in his "Culicidae of Malaya" disregarded this and treated all 18 Malayan species as Uranotaenia. He pointed out, however, that "the species fall into two natural groups, the first containing all those shewing azure-blue lines on head, thorax and pleura, the second the dull-colored species usually clad with brown scales and of larger size."

Significantly, while there was much debate about species within the genus, it was not until 1921 that the genus was more or less adequately characterized in the adult stage by Edwards. In this paper he said, "Most writers have distinguished this genus mainly by the short upper fork-cell (cell R_2) but while this is a sufficient distinction in the majority of cases, there are a few species (e.g., unguiculata) in which the shortening of this cell is not very noticeable, and, on the other hand, some species of the Aedes group have the cell so short that they have been mistaken for species of Uranotaenia. A more absolutely diagnostic character, though requiring a high magnification for its detection, is the absence in all known species of the genus of microtrichia of the wing-membrane. This distinguishes Uranotaenia sharply from all other CULICIDAE. The short anal vein, ending before the base of radial sector, is shown also by the tropical genera Hodgesia and Harpagomyia." Barraud (1926) added to the definition of the genus and clarified Edwards' statement about the absence of microtrichia of the wing. Barraud reported that the minute setae could be seen with a 4 mm. objective and a 6 X eye piece, and under a 16 mm. objective the wing membrane in Uranotaenia has a minutely dotted appearance. We now know that this is apparently the only truly unique adult character of the genus. Sasa et al. (1971) demonstrated with the electron scan microscope at X5400 that the microtrichia of bimaculata Leicester are simple, curved and apically rounded setae arising directly from the wing membrane, with a length of about 6 microns. There are a few species with microtrichia much more obvious than this but still apparently less than in other groups. The genus was not adequately characterized in the larval stage until Belkin (1953), when, along with other characters, he pointed out the complete absence of a maxillary suture. I have seen no exceptions to this character. I have also found that head seta 1-C is always set on a rather prominent projection, thereby leaving the labrum with a conspicuous, often deep median emargination. Unfortunately, I have not examined all species of other genera, but the character appears to be more obvious in

Uranotaenia than in any other genus. Occasionally, the character is difficult to interpret in slide-mounted specimens because of the tendency of the head to turn downward anteriorly. The pupa was not adequately characterized until Mattingly (1971) pointed out the consistent deep inner basal excavation of the paddles. While the previously used characters of the width of the inner portion of paddle beyond mid rib and marginal serrations were sufficient to distinguish most species, there are several notable exceptions.

Numerous recent references have been made to Pseudoficalbia as a subgenus or group, but most of these have been merely listings of species with the terms loosely applied to groups in a broad, general sense, without any attempt to characterize the subgenus or group. Others have used the general terms "ornamented" and "unornamented" in referring to members of each group. An exception was Penn (1949) who provided a key to separate pupae of two species of the subgenus Uranotaenia and three species of Pseudoficalbia from New Guinea. While he was correct in his assignment of species, the characters, though they will separate a number of species, do not separate a sufficient number to be of primary value. Mattingly (1957) proposed that "Uranotaenia s. str. and Pseudoficalbia ought almost certainly be treated as distinct subgenera," but postponed a discussion of the point for a later paper. Stone, Knight and Starke (1959) and Stone (1961, 1963, 1967 and 1970) did not recognize subgenera.

BASIS AND SCOPE OF PRESENT ANALYSIS. The following analysis is based primarily upon the genus as it occurs in Southeast Asia and secondarily on species from the rest of the world. There are no final answers offered on a number of questions, for I have been limited by two major factors: time and availability of material. Since my primary objective was the review of the genus in Southeast Asia, a thorough review of world species would have been an unreasonable and time-consuming departure from the project and contract objectives. In addition, material of many species has been extremely difficult to obtain, and some available material was in too poor condition to be of much help. Nevertheless, I have made a special effort at least to examine those species which have presented problems in the past or those which have been considered aberrant or unique and of special significance to the diagnosis of the genus. I have made an examination of all other descriptions, illustrations and specimens that became available. I have recognized a number of supraspecific and infraspecific groups in various parts of the world and especially the close affinities of Southeast Asia and Ethiopian species groups. Although I have recognized the existence of a number of these, I have made no attempt to characterize them if not represented in Southeast Asia; I have merely made note of them. In addition, I have noted a few species and varieties which, in my opinion, are either synonyms or full species and a few unrecognized new species, especially in the Indian and African material. I have made no attempt to correct these errors, except in the Southeast Asian fauna. In a few cases, I have brought them to the attention of specialists in the areas concerned. Also, in very recent times, at least 10 new species from the Malagasy and Ethiopian Regions have been described from larvae only, while the larvae of a number of long established species of the Ethiopian Region remain unknown or very poorly

described and illustrated. Mattingly (1954) placed at least one of these in the synonymy of one of the earliest known Pseudoficalbia. In view of this, the listing of specific names in this paper does not necessarily imply recognition of the validity of such names. I am including new synonymies for Southeast Asian species only, for these are a result of a thorough examination of types and other material in the SEAMP collection and will be discussed in the soon to be published revision of Southeast Asian Uranotaenia. Obviously, the genus is in need of a thorough world-wide review. It is hoped this initial step in recognizing subgenera will ultimately lead to a solution of a number of problems and to a much better understanding of the genus. Certainly, all the answers to the complexities of the genus cannot be offered here.

VALIDATION OF THE SUBGENUS PSEUDOFICALBIA. In this paper I am revalidating the subgenus Pseudoficalbia and will attempt to characterize it in all stages. What will probably come as a surprise to many is that I am recognizing, for the first time, the presence of members of this subgenus in the New World. A number of annectant and aberrant species are recognized and their position is briefly discussed.

Species within the subgenus Uranotaenia are quite homogeneous, and I do not, at present, recognize any major, well defined sections. There is some suggestion that possibly most of the New World species may be set apart from the rest, though I am not prepared to make such a proposal at this time. Most species within the subgenus can be divided into series or species groups based primarily upon superficial similarities in adult ornamentation and, to a lesser extent, upon other stages. The Pseudoficalbia are quite complex, and the diversity within the subgenus is considerable. I recognize two major sections to which all presently known species are assignable. In addition, several rather well marked series within each section are recognized. Several of these require much further study, for a number of the immature stages are insufficiently known. The treatment of series in this paper is on the same level as series treated in Galindo, Blanton and Peyton (1954) and as sections in Belkin (1962); the choice is primarily based on personal preference, and no firm stand is taken on this issue. Belkin (1962) stated that "it appears that Uranotaenia may be almost as complex as Aedes and that several subgenera will have to be recognized contrary to the current practice of lumping everything into one supposedly homogeneous genus." While the statement may ultimately prove correct, I prefer to consider at this time only two subgenera. The division works very well, with rare exceptions, in all stages, and I believe it is a natural assemblage of species. There are a number of recognizable groups within each subgenus, but few can be easily characterized in all stages at this time; unless this later proves possible, I think they are best treated as sections or series. If additional subgenera are to be recognized in the future, it should be done with great caution and certainly not until many more of the males and immature stages are better known.

I am proposing no new names here. Rather, for the Pseudoficalbia, I am designating the two major groups as Sections A and B. Section A contains all the species of Edwards' groups C and D,

including the type species and the majority of remaining species of the subgenus. Section B contains only three of Edwards' group B and five related species with two subspecies. The other three species of Edwards' group B (neireti, chorleyi and hopkinsi) are assigned to the subgenus Uranotaenia. Series will bear the earliest available name of a species within each series, limited to the geographic region in which they are being treated. Too many species are insufficiently known in one or more stages to make many assignments beyond well known limits at this time. However, where extralimital members are recognized, they will be cited under the discussion of a series even though the name cited may predate the name being applied.

Both Edwards (1916, 1932 and 1941) and Belkin (1962) provided the basic keys for the recognition of the Pseudoficalbia. Edwards (1916 and 1932) was correct in assuming that the two groups could be characterized on the basis of larval head seta development. He was incorrect in assuming that the shape of the head was of significance and that adult scale patterns could be correlated with these differences. It is worth noting, however, that of the 53 "Group A" (Uranotaenia) and 28 "Group B" (Pseudoficalbia) listed in 1932, only one species of the subgenus Uranotaenia and four Pseudoficalbia were incorrectly assigned. Of added interest, all four Pseudoficalbia belong to Section B by present definition. Edwards (1941) made a most significant observation when characterizing the genus by the following: "Pre-alar area separated from sternopleura by a distinct furrow or suture (more obvious than in any other Culicine genus)." It is unfortunate he did not observe this character more carefully and attempt to correlate it more closely with other known group characters, for herein was the long sought character for a natural division of the genus. Yet it is easy to understand why he did not, when one considers that the one species of the subgenus Uranotaenia which he assigned to the "Pseudoficalbia group" in 1932 was metatarsata Edwards, a Southeast Asian species. This species is aberrant in lacking lines or patches of broad colored scales on head, thorax or wing and bears little resemblance to any member of the subgenus Uranotaenia. Superficially, it looks very much like a Pseudoficalbia. This species probably demonstrates best of all the limitations of the use of scale and color patterns in determining affinities, for it is a member of a series of highly ornamented species in the Oriental and Australasian areas. On the other hand, Edwards included the two North American Pseudoficalbia, anhydor Dyar and subspecies syntheta Dyar and Shannon under the "Uranotaenia group." This species complex is unquestionably a member of the Pseudoficalbia by present definition and is here reported for the first time. Galindo, Blanton and Peyton (1954) recognized the anhydor complex as distinct from other American species and placed them in a separate series. Belkin and Macdonald (1956) concurred with this interpretation. The nominate species and its subspecies syntheta have very well developed lines of broad blue-white scales on head, scutum and pleuron, and are as ornamented as most species of the subgenus Uranotaenia, excepting those with pictured wings and a few with brilliant metallic scales. Apparently, Edwards could not reconcile the striking differences in the above species with the presence or absence of a suture separating the prealar area from the sternopleuron. Belkin (1962) hesitated to recognize the Pseudoficalbia, preferring instead to wait until many

species (especially annectant forms) were better known and until a greater number of immature stages were known. He also acknowledged that he had not studied carefully the Ethiopian Uranotaenia. He also accurately predicted that many of the answers to problems would be found in the Indomalayan Region. His very thorough method of treatment of the nine South Pacific species came very close to characterizing the two subgenera, though he did not suggest a connection. Of the nine species treated, only three Pseudoficalbia were represented. Belkin also noted the separation of the prealar area from the sternopleuron. Under the definition of the genus he says, " pra usually separated by a distinct suture from upper edge of stp." For the nine species he expressed it as either "pra distinctly separated from stp," or "pra not distinctly separated from stp." What proved to be somewhat perplexing was the failure to show the separation in the illustration of barnesi Belkin, which was supposed to have a distinct suture. Reexamination of barnesi revealed this to be apparently an illustrator's error. Galindo, Blanton and Peyton (1954) pointed out that the suture between the sternopleuron and prealar area was quite marked in all American species but failed to note the absence in the small series of anhydor-syntheta examined.

Adults from as many areas as possible were examined for this character, and a representative of most was cleared, stained and slide mounted. With the confirmation of this character in a number of Ethiopian and South American species late in the study, a number of species which I had heretofore considered questionable were placed in proper perspective.

All Uranotaenia have the upper edge of the sternopleuron rounded and raised above the prealar area and usually give the appearance of a shallow groove or furrow across the extreme upper edge. However, members of the subgenus Uranotaenia have a distinct suture between the two sclerites. It is usually exhibited as a distinct, narrow, darkly pigmented, curved line from anterior edge, and on examination of cleared, stained, moderately pigmented specimens it can be seen as extending internally as a thin ridge or shelf. In the Pseudoficalbia no such line or internal extension can be seen, the sclerites apparently being wholly continuous with each other. In most species these are easily seen on dry, pinned specimens. Although absolutely diagnostic, a few species are deceptive and require close examination of prepared specimens. Occasional dry mounted specimens of a few species of the subgenus Uranotaenia do not readily exhibit a distinct suture, and only a prepared specimen will reveal it. On the other hand, a few Pseudoficalbia have the upper one fourth or more of the sternopleuron darkly pigmented and the prealar area light. In some of these the contrast is so sharp along the rounded, raised upper edge of the sternopleuron that even a prepared specimen can give the false impression of a suture, and only manipulation or removal of the two sclerites will reveal its true nature. Usually manipulation so as to enable one to view the two areas from an angle at the lowest point, rather than down on the raised dark edge of the sternopleuron, is sufficient. In considering the significance of such a distinct morphological difference, I must admit having debated the possibility of

elevating the Pseudoficalbia to generic rank. This character, in combination with characters of the male terminalia and immature stages, certainly deserved such a consideration, for a number of presently recognized genera rest upon much less significant morphological distinctions. However, after considering all the world's species, I did not feel that the recognition of two separate genera was justified, and I am satisfied with the present interpretation. The two subgenera share many generic characters in all stages. In my opinion, Section B of Pseudoficalbia is truly annectant and exhibits in one or more stages characters of both subgenera. More interestingly, it is only a single member of this section (unguiculata Edwards) which represents the genus from India west across the Eastern Mediterranean into Eastern Europe and Northern Africa. A single species (maxima Leicester) extends into Southeast Asia, and it is apparently the only section of Pseudoficalbia (anhydor-syntheta) represented in the New World. The only subspecies presently recognized in the subgenus belong in this section; these are anhydor syntheta and unguiculata pefflyi Stone. I consider the above species and subspecies as belonging to the same series which, for the present, I refer to as the maxima series of Section B. The five remaining species of this section, annulata Theobald, cavernicola Mattingly, lucyae Someren, montana Ingram and de Meillon and nivipous Theobald, belong to a separate series apparently confined to the Ethiopian Region and are referred to as the annulata series. These will be discussed further below.

KEYS TO THE SUBGENERA AND A DISCUSSION OF ADDITIONAL CHARACTERS FOR ADULTS, LARVAE AND PUPAE

ADULT

1. Prealar area separated from sternopleuron by a suture; alula bare; erect head scales usually absent or, when present, usually restricted to a few small stout ones on occiput or rarely a few long slender ones on vertex . . . . . .URANOTAENIA

2. Prealar area not separated from sternopleuron by a suture; alula with a few broad dorsomarginal scales (except Section B) or erect head scales with long slender basal stems and broadly expanded apices, numerous, and covering most of the vertex . .PSEUDOFICALBIA

MALE TERMINALIA

1. Lateral plates of aedeagus distinctly connected dorsally only; basal mesal lobe poorly developed or occasionally apparently absent; distimere very short and stout, usually with tergal subapical margin distended . . . . . .URANOTAENIA

2. Lateral plates of aedeagus distinctly connected dorsally and ventrally; basal mesal lobe well developed, usually produced tergoapically into a very distinct finger-like lobe; distimere moderately long to long, usually slender and tapered to narrow apex, occasionally (Section B) rather stout and distended on tergal subapical margin . . . . . .PSEUDOFICALBIA

PUPA

1. Trumpets set close together (nearer to mid dorsal line than to wing pad), (except wysockii), always (?) strongly tracheoid on basal 0.25 or more . . . . . .URANOTAENIA

2. Trumpets set far apart (nearer to wing pad than to mid dorsal line), (except anhydor-syntheta and montana), indistinctly tracheoid on anterior basal 0.3 or less (except Section B) . . . . . .PSEUDOFICALBIA

LARVA

1. Head setae 5 and 6-C very stout and spine- or spike-like, apex acute or often fringed (except wysockii Belkin), always set far back on head, with 6 on level with or posterior to antennal base and 5 approaching middle; grid of segment X always (?) distinctly joined midventrally to saddle . . . . . .URANOTAENIA

2. Head setae 5 (except maxima) and 6-C not stout, spine- or spike-like, apical one fourth or more strongly attenuate, usually set far forward on anterior third of head, rarely far back approaching middle; grid of segment X rarely joined (anhydor, painei, and two undescribed species) midventrally to saddle . . . . . .PSEUDOFICALBIA

There are a number of additional characters which help to recognize the two subgenera, and often these characters, when present, are diagnostic but do not appear frequently enough to be of primary consideration. The erect head scales of the two subgenera can be used to separate all species, but there are a few species in which a degree of interpretation is involved. For this reason I have reduced it to secondary consideration after determining the presence or absence of scales on the alula even though they do not occur in all species. All Pseudoficalbia have erect head scales with slender basal stems and broadly expanded apices. However, the number and length vary considerably among the species. Some are exceptionally long, large and very dense, while in some of the very small species they are greatly reduced in number and size and, at most, only very sparsely scattered over vertex. Rarely are they restricted to occiput but typical in development. In such cases, as in shillitonis Edwards, the patch of broad scales on the alula is quite conspicuous. In Section B, the alula is bare, but the erect scales are exceptionally large, numerous (as they are also in the majority of Section A) and cover most of the dorsal surface of head in all species. In the subgenus Uranotaenia, the erect scales, when present, are of a different type. The scales are usually extremely small, slender, inconspicuous and, in the few cases where there are scales on the vertex, they are long and slender or only very slightly expanded and arranged in a distinct paired line or patch near mid vertex rather than scattered over vertex as in the Pseudoficalbia. In two or three Ethiopian and New World species, we find rather short scales restricted to a line on occiput, but they are conspicuously expanded apically and differ only in being stout from base. The separation of the eyes in the adult is as significant as scales on the alula.

In the subgenus Uranotaenia, the eyes are broadly and deeply V-shaped posterodorsally, and the pair of interocular setae are distinctly set down between the eyes. In Section A of Pseudoficalbia, the interocular space is long and narrow and the median pair of ocular setae (interoculars) are not distinctly set between the eyes. In Section B, the eye separation and insertion of interoculars are as in the subgenus Uranotaenia. The position of interocular setae is difficult to interpret when the bases are obscured by overlying scales and usually requires slide preparations. The majority of species in the subgenus Uranotaenia have a moderate to very well developed frontal tuft, and, when present, it is diagnostic. A frontal tuft in Pseudoficalbia is unknown. A number of species in the subgenus Uranotaenia have the wings extensively pale scaled (pictured) and some have lines or patches of broad, brilliantly colored silvery, golden or blue-green metallic scales; these are also diagnostic. All species of the subgenus Uranotaenia in the Southeast Asian, Australasian and South Pacific Regions have the anterior claws of all legs of females and fore and hind legs of male very broad, flat, falcate, much broader than posterior claws. All known species of the subgenus Pseudoficalbia are without such claws. Probably the most unusual and better known character of the genus is the peculiar secondary sexual modifications exhibited in the males of many species. These include numerous long setae on the proboscis, various and often complex modifications of tibiae and tarsi, including shortening, bends, excavations, and distinct arrangements of specialized setae and scales on tibiae or one or more tarsomeres, depending on species. Rarely, the antennae in some of these are sparsely plumose, approaching that of female, which misled some of the early workers to erroneously describe them as female. These peculiar characters occur only in the male, and, except for the sparsely plumose antennae, are known only in species of the subgenus Uranotaenia. The males of Pseudoficalbia exhibit only the usual sexual characters of plumose antennae, enlarged mid tarsal claws and, occasionally, fore tarsal claws. Species of Pseudoficalbia often exhibit distinct arrangements or groupings of setae or spines on femora, but these are always found in both sexes and often provide good specific characters.

The development of basotergal lobes of male proctiger of Peyton and Hochman (1970), hereafter referred to as tenth tergal lobes, following Knight and Laffoon (1971), are of no subgeneric value. They do, however, offer excellent group characters in most cases. The development of the basal mesal lobe of basimere is not always evident in mounted specimens and is often left to individual interpretation in specimens pressed with a cover slip. Usually the tergal and sternoapical border is more darkly pigmented and sharply defined in the Pseudoficalbia. However, in unmounted specimens or in those showing the lobe from a lateral or caudal view, the lobe is clearly distinct and projects well above the dorsal surface of the basimere. The shape and length of distimere is of limited value, for there is considerable diversity in this structure. The distimere in the Pseudoficalbia is generally stout at extreme base and tapered to narrow apex, but there is a whole range of lengths though usually always more slender and tapered apically than in the subgenus Uranotaenia. Those that appear somewhat broad on lateral view appear slender on tergal view.

This is just the opposite of what usually occurs in the subgenus Uranotaenia. The distimere is exceptionally short and stout in most species, usually differs little in basal and apical width, and is usually broad in tergal view. In Section B of Pseudoficalbia, the distimere is long but quite stout and somewhat intermediate between the very long and short ones; however, in true distended tergal view it is rather slender. Probably just as useful a character is the presence or absence of cercal setae on the proctiger. In many of the Pseudoficalbia, there is at least a single pair and often there is a distinct patch. No cercal setae have been seen in the subgenus Uranotaenia. Other secondary characters seen in Pseudoficalbia only are conspicuous setae at or near the apical margin of the ninth tergum and tenth tergum produced into a very conspicuous median lobe. These two characters, singly or in combination, are found in a great many species. The development of aedeagus is rather consistent throughout, but the number and size of teeth or spines on each lateral plate vary considerably among species and often exhibit good group characters, although they are of limited value in specific determinations. The ventral connection of the lateral plates in the Pseudoficalbia is usually a conspicuous, narrow, sclerotized subapical or median transverse bridge. Only in the Southeast Asian nivipleura Leicester is it very weak and inconspicuous. No teeth occur below this bridge.

The development and position of larval head setae 5 and 6-C are very characteristic of the two subgenera, except for the aberrant South Pacific plant axil breeder wysockii. This most surely is a clear case of convergence in both the larva and pupa of this species, for the adult stages are very typical of other species of the subgenus Uranotaenia. Its nearest known relatives in Southeast Asia are ground pool breeders as are other presently known species of the subgenus. The majority of species in Pseudoficalbia utilize, almost exclusively, restricted natural container type habitats. A number of the Pseudoficalbia have one or both of 5, 6-C rather stout, but even in these cases they do not approach the least developed of the subgenus Uranotaenia (except wysockii), which is apparently represented in lateralis Ludlow. Only in U. (P.) maxima is there a true short stout spike-like seta 5-C. Seta 6-C in this species is a very typical Pseudoficalbia type of seta. Other species of the maxima series also have 5-C much stronger and shorter than 6-C, but in these they are not truly spine-like and the ends are attenuate. This is another of several examples in which I think this section exhibits a connecting link between the two subgenera. In the case of U. (P.) mashonaensis Theobald which, as Philip (1931) pointed out did not conform to Edwards' (1916) definition of slender hairs, setae 5 and 6-C are seen as exceptionally stout on basal one third to one half and then as abruptly reduced to long attenuate ends and not as illustrated by Hopkins (1936). In species of the subgenus Uranotaenia, 5 and 6-C are almost always single (5 double only in wysockii), and 6 is almost always posterior to antennal base. Rarely, anomalous splitting of one or more setae is observed on a specimen. In Pseudoficalbia, the setae are usually single, but a good number of species have either 5 or 6-C branched, sometimes multiple. In the majority of species, setae 5 and 6-C are placed well forward on the anterior third

of the head; usually 6 is anterior to and 5 is nearer to level of antennal base than to middle of head. When this is evident, it is absolutely diagnostic. Only a very few species have the two setae farther back on the head, approaching or equal to that of the subgenus Uranotaenia. When this occurs, prothoracic seta 3-P is long, well developed and nearly equal in development to 2, 4-P. In U. (U) wysockii, where 5 and 6-C are reduced, 3-P is a short, weak, multiple tuft. The majority of species in the subgenus Uranotaenia have siphonal seta 13-S as a well developed, basally twisted chitinous filament, and when present it is diagnostic. Siphonal seta 13-S is minute or inapparent in all Pseudoficalbia I have examined. Montschadsky (1930) figured a similar pair of chitinous filaments as apical external extensions of the tracheae in unguiculata. I have observed this same structure in a number of Pseudoficalbia and in at least one series of the subgenus Uranotaenia. Both of these structures are highly specialized and require a much more detailed study than I have been able to give them. Although the two filaments are not homologues, they probably serve very similar functions. A similar, highly specialized siphonal seta 13-S also occurs in species of the genera Hodgesia Theobald and Ficalbia Theobald. A fair number of Pseudoficalbia larvae have the saddle of segment X incomplete ventrally. All presently known species of the subgenus Uranotaenia have a complete saddle. The foregoing assertion is based on the examination of larval specimens or descriptions and illustrations of approximately 73 species of the subgenus Uranotaenia and 68 species of Pseudoficalbia.

The pupa is much more difficult to characterize than the larva and requires much further study. I have examined specimens of at least 105 species. I have also examined a number of descriptions and illustrations, but these had very little to offer in the way of group characters, for most of these dealt with salient, specific points only. In a few of the slide mounted specimens available, I was unable to accurately determine the position of the trumpet. The trumpet appears to offer the only reliable character for the separation of subgenera; however, as the pupae become better known, alternate or combination characters may become apparent. The relative position of trumpet appears to be the most reliable character for separating the two subgenera at this time. Of over 100 species examined, only three species did not conform. In the case of the pupa of anhydor-syntheta and montana, I cannot, at present, separate them from other species of the subgenus Uranotaenia, nor can I separate the pupa of wysockii from the Pseudoficalbia. Certainly the apparent aberrations noted in the pupae of the above and the larva of wysockii are not in themselves justification for abandoning an attempt to categorize species within the genus, as occurred in the early days with Philip (1931); rather, it should stimulate a search for alternate characters or for a combination of such characters. A few group pupal characters found in the Pseudoficalbia can serve to separate a great number of species from those of the subgenus Uranotaenia. These are as follows: paddle with filamentous fringe on one or both borders; paddle with an accessory seta 2-P: combination of trumpet index less than 6, indistinctly tracheoid on anterior basal side only, meatus without slit; or a combination of any single character above with the absence of abdominal seta I-IX. Although the

pupa presently presents a few problems at the subgeneric level, it offers many unique and useful characters at the specific level.

Since Sections A and B of Pseudoficalbia are an integral part of this report and considering the important position of Section B, characters for the recognition of both sections and the series within Section B are presented below. These are based on the groups as presently known. As new and more adequate material of Section B becomes available, additional characters may become apparent. The immature stages of the maxima series can be separated from the annulata series on at least one character, although the same character may be found in other species of Section A. I call attention to them here, for as only one species occurs in Southeast Asia, I will give no further attention to them. A complete analysis of recognized series within Section A will be presented at a later date.

KEYS TO THE SECTIONS OF THE SUBGENUS PSEUDOFICALBIA AND TO THE SERIES OF SECTION B, WITH A DISCUSSION OF OTHER POINTS

ADULT

1. Alula with a few broad dorsomarginal scales; interocular space long and narrow, median pair of ocular setae (interoculars) not distinctly set between the eyes . . . . . SECTION A

   Alula bare; interocular space broadly and deeply V-shaped posterodorsally, interocular setae set distinctly between the eyes . . . . . SECTION B . . 2

2. Scutum with a distinct supra-alar and prescutal line of white or blue-white scales, at least some of the scales distinctly short, broad; wing vein R with at least a basal anterior row of pale scales extending beyond humeral cross vein (usually extensively pale); cell R_2 long, near equal to cell M_2; microtrichia more obvious than in any other Uranotaenia species; claws of male foreleg same as claws of midleg . . . . . MAXIMA SERIES

   Scutum with at most a short line or patch of long moderately broad, lanceolate white scales between wing root and scutal angle only; wing vein R with at most a posterior row of pale scales on remigium only; cell R_2 distinctly shorter than cell M_2; microtrichia typical; claws of male foreleg normal, much smaller than claws of midleg . . . . . ANNULATA SERIES

MALE TERMINALIA

1. Lateral plates of aedeagus with one or more large, conspicuous teeth or processes; distimere usually slender, slightly curved, broad at extreme base and tapered to narrow apex, never distended on tergal subapical margin . . . . . .SECTION A

   Lateral plates of aedeagus with, at most, a few small inconspicuous teeth or hooks; distimere rather straight, stout, at least slightly distended on tergal subapical margin . . . . . SECTION B . . 2

2. Tenth tergum well developed, produced laterally beyond ninth tergal margin into long finger-like lobes; plates of aedeagus with small apicolateral hooks . . . . . MAXIMA SERIES

Tenth tergum with basolateral bands only, not extending as lobes beyond apical margin of ninth tergum; plates of aedeagus with very small teeth or serrations on subapical sternal margin . . . . . ANNULATA SERIES

PUPA

1. Trumpet without slit in meatus, indistinctly tracheoid on anterior basal 0.3 or less (except one undescribed species with trumpet index of 3); index rarely 5 or more . . . . . SECTION A

Trumpet with slit in meatus, usually distinctly tracheoid on basal 0.3 or more; index 5 or more . . . . . SECTION B . . 2

2. Abdominal segment IX strongly developed, wrinkled only at basolateral corners, seta I-IX conspicuous; trumpets with weak inconspicuous denticals basally . . . . . MAXIMA SERIES

Abdominal segment IX small, weakly developed, strongly contracted and wrinkled, seta I-IX absent; trumpets with very strong conspicuous denticals basally . . . . . ANNULATA SERIES

LARVA

1. Abdominal seta 7-II very stout, usually single, occasionally 2 or more branched, near equal in degree of development to 7-I and 6-II; head setae 5, 6-C usually rather weak . . . . . SECTION A

Abdominal seta 7-II a tuft of 2-5 branches, distinctly shorter and weaker than 7-I and 6-II; head setae 5, 6-C conspicuously stout but not spine-like (except 5-C of maxima) . . . . . SECTION B . . 2

2. Head seta 1-C distinctly spine-like; seta 5-C distinctly shorter and stronger than 6-C . . . . . MAXIMA SERIES

Head seta 1-C foliform, with apical half transparent; seta 5-C near equal to 6-C in development . . . . . ANNULATA SERIES

Although a few of these characters are found in other Uranotaenia species, the peculiar larval head seta 1-C in the annulata series is unique to this group. Analysis of the annulata series is based on the examination of larvae of four species and pupal skins of three species. Adults of all species of Section B have been examined. The tenth tergum of the male is often produced into lobes beyond the apical margin of ninth tergum in a number of Pseudoficalbia, but the maxima series is the only one in which long, well developed finger-like lobes are found. In this respect it is similar to that found in many species of the subgenus Uranotaenia. The anhydor complex shows

its closest affinities to unguiculata in the adult stage. Characters which are apparently unique to these species in the Pseudoficalbia are as follows: decumbent head scales rather long, moderately broad; ppn with narrow scales; scutellum with narrow scales. In addition, the supra-alar and prescutal lines of white scales in unguiculata are continuous and very similar in composition and position to that found in subspecies syntheta. Both also have pale knee spots which are rather rare in the subgenus. The male aedeagus is also surprisingly similar in development in all species of this series. Considering the limited study of this group, I hesitate to go beyond the above evaluation at this time.

Some may feel that Section B should be accorded subgeneric rank. Based on the very distinctive adult differences and, to a lesser extent, differences in other stages from those of Section A, this could well be done if one were so inclined. For this reason I have given it a separate super group category above that of the usual series or sibling species group treatment, which it obviously is not. However, if it is viewed from the total aspect of morphology, biology and zoogeography, it properly belongs to the subgenus Pseudoficalbia. The immature stages, especially those of the annulata series, show a striking similarity to many Southeast Asian species of Section A, Pseudoficalbia, and it is this fact more than any other that has influenced the present arrangement. It would appear that the immature stages are more often better indicators of affinities than are the adults, notwithstanding the occasional obvious convergence demonstrated in some species. At any rate, the limited use of immature stages as apparent indicators of affinities cannot be overlooked.

Perhaps one could look upon Edwards' group D and related species as representing a separate subgenus or, at most, a separate section equal to the above. However, for the present, I view the six described species as representing the shillitonis series of Section A. The very unique, broad Sabathine-like scales covering the entire scutum in this series are unusual but not totally unexpected in a genus that exhibits a varying degree of broad scutal scales in a majority of species. The reduced or absent acrostichal setae are also unique for this series. There seems to be a peculiar correlation between the very broad, dense, overlapping scutal scales and the reduction of acrostichals and occasionally of dorsocentrals in some species of other genera, but I am not prepared to speculate on the significance of such a phenomenon. Acrostichals are not completely absent in all species belonging to this series, and for this reason I place little weight on this one character in the genus Uranotaenia. This leaves the dense covering of broad scutal scales as the only unique adult character possessed by all species (if there are, in fact, this many valid species), and, except for this one character, the series is typical of species in Section A. Probably the dense covering of broad scutal scales is no more unusual than the complete absence of broad thoracic scales found in the metatarsata. The presence of setae on the ninth tergum of males, as pointed out by Edwards (1941), is present in a considerable number of species of Section A. The distimere appears to be more robust, basally, than others, but otherwise the terminalia

appears very much as others in Section A. I cannot take a strong stand on this point because, with the exception of shillitonis, the evaluation is based primarily upon descriptions and illustrations. The known larvae and pupae recall the Sabathines in general appearance. The absence of a comb plate on segment VIII of the larva and the greatly developed pupal setae 9-VII-VIII in shillitonis are also found in other species that utilize natural containers for development, especially those that utilize Nepenthes pitchers in Southeast Asia. The peculiar chitinous boss of larval segment X could be significant, but too few larvae of this series are presently known. The question must remain open until all stages of this interesting and obviously primitive group are more thoroughly examined. With more intensive study, it may be found that this group deserves separation from Section A. In my opinion, separation at this time on the basis of a single adult character would only confuse matters.

CONCLUSIONS AND DISCUSSION. It can be seen that the foregoing conclusions were arrived at, almost entirely, without considering the presence or absence of lines of broad, colored scales on the adult thorax. While the various arrangements of these scales are very useful in specific determinations, they are apparently of limited value in determining affinities. Most of the characters used for defining groups recognized in this paper appear to be less subject to individual, specific variations than those previously used (especially the primary entry character for each couplet used here), and, in my opinion, the groups recognized here are natural. Even though this may prove true with time, it must not be supposed that anything like finality is claimed for the conclusions presented here. Many stages remain either unknown or very incompletely known. Many questions require much closer examination, while others will apparently always be the subject of personal opinion. Examination of new and additional material will surely necessitate the partial modification of some views expressed here. We have at least demonstrated that groups within the genus can be categorized in all stages, and from this we gain an insight into the many and varied habits of species and, ultimately, a much better understanding of the position occupied by this unique and interesting genus. In this respect, it is interesting to note the intriguing proposition made by Mattingly (1971) on the two modes of egg laying habits noted in the genus. Mattingly suggested, in his paper, that the two modes of egg laying might be representative of the Uranotaenia s. str. and Pseudoficalbia. If we accept the present concept of two subgenera, several sections and series, we find that both types are found in Section A of Pseudoficalbia. The three known species of colocasiae Edwards (eggs in rafts), ascidiicola Meijere and bimaculata Leicester (eggs laid singly) belong to two distinct series within Section A. In the series to which colocasiae apparently belongs, a few species utilize ground water collections for egg laying. The other two species known to lay eggs singly on the water surface belong to the same series, and all of the 15 or so species of this series, with known immature stages, utilize exclusively, restricted, natural container habitats such as pitcher plants, bamboo, tree holes, etc. Although evidence based on three species is by no means conclusive, it does illustrate the potential value of recognizing natural categories on both morphological and biological grounds.

The accompanying list assigns all presently known species of the genus to one or the other of the two proposed subgenera. I have made an exhaustive effort to correctly assign species according to the definition presented here. Since several assignments are made on the basis of descriptions only, there remains the possibility that one or two may later prove to be wrongly assigned, though I do not anticipate such an occurrence. Of the subgenus Uranotaenia, 96 valid specific taxa, one subspecies and five varieties are listed. Of the Pseudoficalbia, 69 valid specific taxa, two varieties and two subspecies are listed. There are presently 23 known, undescribed species from Southeast Asia which will be treated at a later date. The later inclusion of these species to the list will bring the number and distribution of species to 105 Uranotaenia, 83 Pseudoficalbia. Valid specific names are listed without underlining, recognized varieties and subspecies are indented without underlining, and recognized synonyms are indented and underlined so that each category may be easier to identify.

WORLD LIST OF SPECIES IN THE SUBGENERA URANOTAENIA AND PSEUDOFICALBIA WITH NEW SYNONYMY FOR SOUTHEAST ASIAN SPECIES *

SUBGENUS URANOTAENIA

1. aequatorianna Levi-Castillo
2. alba Theobald *
3. albescens Taylor *
4. alboabdominalis Theobald *
5. alboannulata (Theobald) *
6. albosternopleura Peters
7. amiensis Peters
8. andavakae Doucet
9. annandalei Barraud *
   - nanseica Bohart and Ingram *
10. antennalis Taylor
11. apicalis Theobald *
12. arguellesi Baisas *
13. argyrotarsis Leicester *
    - parangensis Ludlow *
14. balfouri Theobald *
15. barnesi Belkin *
16. benoiti Wolfs
17. bertii Cova Garcia and Rausseo
18. bilineata Theobald *
    - var. fraseri Edwards *
    - var. connali Edwards *
    - var. obsoleta Edwards
19. bimaculiala Leicester *

An * following a name indicates that specimens of one or more stages under that name have been examined by me and, in the case of listed synonyms, it includes the type. The category "variety" as applied here is that of Stone, Knight and Starke (1959).

20. briseis Dyar *

21. caeruleocephala Theobald *

22. caliginosa Philip *

23. calosomata Dyar and Knab *

albitarsis Gordon and Evans

24. campestris Leicester *

25. chorleyi Edwards *

var. hamoni Grjebine

26. christophersi Barraud *

27. civinskii Belkin *

28. clara Dyar and Shannon *

delae Baisas

29. coatzacoalcos Dyar and Knab *

basalis Howard, Dyar and Knab

30. cooki Root

31. davisi Lane

32. diraphati Peyton and Klein *

33. ditaenionota Prado *

burkii Lane

34. dumonti Doucet

35. edwardsi Barraud *

36. falcipes Banks * REVALIDATED HERE

37. fimbriata King and Hoogstraal *

38. geometrica Theobald *

39. gerdae Slooff *

40. hebes Barraud *

nii Lien * NEW SYNONYMY

41. heiseri Baisas

42. hopkinsi Edwards *

43. hystera Dyar and Knab *

bicolor Martini

martinii Lane

44. incognita Galindo, Blanton and Peyton *

45. lanei Martínez and Prosen

46. lateralis Ludlow *

cancer Leicester *

ceylonica Theobald *

propria Taylor

cairnsensis Taylor

47. leucoptera (Theobald) *

48. longirostris Leicester *

49. lowii Theobald *

continentalis Dyar and Knab

minuta Theobald

monilis Shannon and Del Ponte

50. ludlowae Dyar and Shannon *

51. macfarlanei Edwards *

campestris var. zelena Barraud * NEW SYNONYMY

52. mathesoni Lane

53. mayeri Edwards *

54. mendiolai Baisas *

55. metatarsata Edwards *

innotata Dyar and Shannon * NEW SYNONYMY

56. micans Leicester *

57. moresbyensis Peters

58. nataliae Lynch Arribalzaga *

    rowlandii Theobald

    noctivaga Neiva and Pinto

    argenteopennis Peryassú

    capitis Shannon and Del Ponte

59. neireti Edwards *

60. neotibialis King and Hoogstraal *

61. nivea Leicester *

    triangulata Ludlow *

62. nivipes (Theobald) *

    albofasciata Taylor

63. novaguinensis Peters

    ssp. alticola Peters

64. orientalis Barraud *

65. orthodoxa Dyar *

66. otiezai Perez Vigueras

67. pallidocephala Theobald *

    similis Theobald

    caerulea Theobald

    abnormalis Theobald *

68. pallidoventer Theobald *

69. palmierimi de Meillon and Rebelo *

70. paludosa Galindo, Blanton and Peyton *

71. paralateralis Peters

72. paranovaguinensis Peters

73. philonuxia Philip *

74. prajimi Peyton and Rattanarithikul *

75. pulcherrima Lynch Arribalzaga *

    urania Shannon and Del Ponte

    modesta Martini

    var. elnora Paterson and Shannon

76. pygmea Theobald *

77. rampae Peyton and Klein *

78. reyi Baisas * REVALIDATED HERE

79. rutherfordi Edwards *

80. sapphirina (Osten Sacken) *

    coquilletti Dyar and Knab

81. setosa King and Hoogstraal *

82. sexaueri Belkin *

83. socialis Theobald *

84. solomonis Belkin *

85. sombooni Peyton and Klein *

86. subnormalis Martini *

    roperi Edwards *

87. subtibioclada King and Hoogstraal *

88. telmatophila Galindo, Blanton and Peyton *

89. testacea Theobald *

    unilineata Leicester *

90. tibialis Taylor

91. tibioclada King and Hoogstraal *

92. trapidoi Galindo, Blanton and Peyton *

93. trilineata Leicester *

94. typhlosomata Dyar and Knab *

95. unimaculiala Leicester *

96. wysockii Belkin *

SUBGENUS PSEUDOFICALBIA

1. andreae Doucet

2. anhydor Dyar *

ssp. syntheta Dyar and Shannon *

3. annulata Theobald *

var. apicotaeniata Theobald *

4. ascidiicola Meijere *

5. atra Theobald *

nigerrima Taylor

6. bicolor Leicester *

fusca Leicester *

leicesteri Edwards

7. bimaculata Leicester *

8. browni Mattingly *

9. brumpti Doucet

10. cachani (Doucet)

11. cavernicola Mattingly *

12. colocasiae Edwards *

13. combesi Doucet

14. demeilloni Peyton and Rattanarithikul *

15. devemyi Hamon

16. diagonalis Brug *

17. douceti Grjebine

18. fusca Theobald *

inornata Theobald *

19. garnhami Someren

20. gigantea Brug *

21. gouldi Peyton and Klein *

22. grenieri Doucet *

23. henrardi Edwards *

24. hirsutifemora Peters *

25. hongayi Galliard and Ngu

26. husaini Qutubuddin

27. jacksoni Edwards *

stonei Bohart and Ingram * NEW SYNONYMY

28. kalabahensis Haga *

29. koli Peyton and Klein *

30. kraussi Grjebine

31. lagunensis Baisas *

32. lavieri Doucet

33. lucyae Someren *

34. lui Lien *

35. luteola Edwards *

36. lutescens Leicester *

37. maculipleura Leicester *

38. mashonaensis Theobald *

39. mattinglyi Qutubuddin *

40. maxima Leicester *

41. micromelas Edwards *

42. modesta Leicester *

    tubanguii Baisas * NEW SYNONYMY

43. montana Ingram and de Meillon *

44. moultoni Edwards *

    brevirostris Edwards * NEW SYNONYMY

45. nepenthes (Theobald) *

46. nigripes (Theobald) *

47. nigromaculata Edwards *

    bimaculata Theobald

48. nivipleura Leicester *

49. nivipous Theobald *

    candidipes Edwards

50. novobscura Barraud *

51. obscura Edwards *

    papua Brug * NEW SYNONYMY

    philippinensis Delfinado * NEW SYNONYMY

52. ornata Theobald *

    var. musarum Edwards *

53. painei Edwards *

54. pandani (Theobald) *

    pauliani Doucet

55. pseudohenrardi Peters *

56. pseudomaculipleura Peyton and Rattanarithikul *

57. pylei Baisas *

58. quadrimaculata Edwards *

59. quinquemaculata Bonne-Wepster *

60. recondita Edwards *

61. rossi Delfinado *

62. shillitonis Edwards *

63. spiculosa Peyton and Rattanarithikul *

64. stricklandi Barraud *

65. sumethi Peyton and Rattanarithikul *

66. tsaratananae Doucet

67. unguiculata Edwards *

    ssp. pefflyi Stone *

68. xanthomelaena Edwards *

69. yovani Someren *

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