Arquivos de Zoologia

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ABSTRACT

The suborder Myxophaga Crowson, 1955, at present including the families Torridincolidae, Hydroscaphidae, Sphaeridae and Lepiceridae, is critically analyzed in relation to the other three suborders of Coleoptera. The study is heavily based on new forms of Torridincolidae and Hydroscaphidae discovered in recent years in southeastern Brazil by the author, and which are described in the taxonomic part. Torridincolidae are studied in more depth than the other families, and new data on internal and external anatomy of adults and immature stages are supplied.

The author concludes that Myxophaga is a valid suborder of Coleoptera, its components representing primitive beetles, which are to be considered as somewhat intermediate between the two main suborders, Adephaga and Polyphaga. As already pointed out by some earlier authors, but substantiated with more examples, Myxophaga share important characters with both suborders.

Ecological and geographic data available are analyzed.

In the taxonomic part the following taxa are described:

- 1. Torridincolidae. Hintonia, nom. nov., for Ptyopteryx Reichardt & Costa, 1967 (nec Ptyopteryx Kolenati, 1848). A second species is added to this formerly monotypic genus: castalia (type-locality, Brazil, Rio de Janeiro, Nova Friburgo). Ytu, gen. n.. type-species, Ytu zeus, sp. n. (type-locality, Brazil, São Paulo, Itu), including the following new species (their type-localities in parentheses): artemis (Brazil, Espírito Santo, Venda Nova), athena (Brazil, Paraná, Morretes), cupidus (Brazil, Rio de Janeiro, Teresópolis), demeter (Brazil, Rio de Janeiro, Teresópolis), hephaestus (Brazil, São Paulo, São Sebastião), morpheus (Brazil, Rio de Janeiro, Areal), and phebo (Brazil, São Paulo, Salesópolis). A larva from South Africa, described by Bertrand (1962) as belonging to Hydraenidae, is transferred to this family, and considered an undescribed genus, only referred to as genus B, because the original material was inaccessible, and only the larva is known.
- 2. Hydroscaphidae. Scaphydra, gen. n., type-species Hydroscapha hintoni Reichardt, 1971, is described for three Brazilian species of Hydroscaphidae recently described by the author.

INTRODUCTION

The present paper is a direct result of a casual discovery made in 1966, when I received a small beetle for identification from my col-

Museu de Zoologia, Universidade de São Paulo. Adapted version of a "livredocência" thesis presented to the Departamento de Zoologia, Instituto de Biociências, Universidade de São Paulo, in 1973.

league Naercio A. Menezes. He was interested in its identification because it had been found in the stomach of a fish he studied. This was the first Brazilian species of the suborder Myxophaga to be described.

The identification of this undescribed species revealed that it belonged to an undescribed genus of a family discovered and described only a few years earlier (1964). This led to a series of events which end with the presentation of this paper. I have delayed publication of the data several times, especially because of discoveries of materials which continuously changed the concepts within the group.

Having decided to publish the results now, however, does not mean that I consider the study complete. On the contrary, I am sure that the material here described is but a small part of the Neotropical fauna of Myxophaga; it is restricted to a small area in southeastern Brazil, a convenient and not geographic limitation, since I only had in mind to cover thoroughly a certain area. The lack of new discoveries in this area, in spite of continuous collecting efforts, suggests that a good sampling has been achieved, especially in relation to Torridincolidae. The same is not, however, true for Hydroscaphidae, a family I also had the opportunity to discover in Brazil.

Even though I am not presenting a complete study, it seems to me that the data included are very important, and that publication should not be delayed any more. The interest in the supra-generic classification of beetles has been very great in recent years, and it seems important to publish my data immediately, in spite of several data being speculative and possibly provisory, as will be mentioned in the text.

The prime object of this paper is to give a more consistent fundament to the suborder Myxophaga, study its relationships with the other suborders of Coleoptera, as well as study relationships between the four families included. It was thus necessary to study the structure of each family; Torridincolidae and Hydroscaphidae, the two only families as yet represented in Brazil, were more thoroughly and carefully analysed.

The critical consideration of Myxophaga presented, is almost exclusively based on unplublished data on Torridincolidae and Hydroscaphidae. In presenting the conclusions in the first part, I am antecipating myself to the taxonomic descriptions presented in the second part.

In spite of a rather large number of new data added to the definition of Myxophaga, I reached the conclusion that this suborder is characterized by a larger number of intermediate than exclusive characters. Parenthetically I should mention that the same appears to be true of Archostemata, even though my knowledge of this suborder is not as deep, and mostly based on the literature.

In spite of this conclusion I accept the suborder Myxophaga, especially because it united four families formerly scattered within the

suborders Adephaga and Polyphaga. The problem, however, could also be solved by adopting the treatment of a superfamily Sphaerioidea, as was done by Crowson himself posteriorly (1956) to the description of Myxophaga.

Besides the study of structure and relationships of the suborder, the families Torridincolidae and Hydroscaphidae are redefined by the irclusion of several undescribed forms.

It will soon become apparent that the larger part of the material at hand was that of Torridincolidae, and because of this the study of this family is more complete than that of Hydroscaphidae; data on Sphaeridae and Lepiceridae have been extracted from the current literature, and are included in the paper with the only purpose of giving a complete view of the suborder. For the same reason I give a catalog of the known forms of each family.

It will also be seen that a considerable number of problems remains unsolved. The volume of data needed for some interpretations is immense. There is no doubt that the understanding of the structure of Myxophaga is only in its beginnings. There is urgent need of a careful analysis of the known forms of *Sphaerius* and *Hydroscapha* on the basis of present knowledge. Their habitat being known, it is almost certain that within a few years there will be good materials of the Old World species, which up to now have only been known from typescries (frequently also only unique types). It is also necessary to study some aspects of these families, such as their internal anatomy. Still unknown are ecological preferences of the species and genera; nothing certain is known on their feeding habits (supposedly they feed on algae).

MATERIAL AND METHODS

Most of the material perused for this study was collected by myself, and is kept in the Museu de Zoologia, Universidade de São Paulo (MZSP). Of the other Museums I contacted, only the Field Museum of Natural History, Chicago, United States (FMNH) has one of the Brazilian species of Torridincolidae, collected by Fritz Plaumann.

Paratypes of the new species will eventually be deposited in the United States National Museum, Washington, D.C. (USNM); the Museum of Comparative Zoology, Cambridge, Mass. (MCZC); the American Museum of Natural History, New York, N.Y. (AMNH); the British Museum (Natural History), London, England (BMNH); the H. E. Hinton collection, Bristol, England (HEHC); and the Musée National d'Histoire Naturelle, Paris, France (MNHN).

Unfortunately I was unable to study material of *Torridincola rhodesica*, most specimens of wich are still in hands of its author, Dr. W. A. Steffan (Johannes Gutenberg-Universität, Mainz, Germany), who did not return them to their original institutions after finishing the description.

Little is to be said about techniques and methods. For the taxonomic part I have followed classic models of entomology, adapting them, where necessary, to modern techniques. For the study of certain details several specimens were mounted on slides in Canada Balsam, after clearing them for one or two minutes in boiling H_2O_2 .

Some specimens were prepared by the usual coating method for study in the "scanning electron microscope" of the Laboratory of Professor Howard E. Hinton, Department of Zoology, University of Bristol, England. These specimens were kept in H. E. Hinton's collection.

ACKNOWLEDGMENTS

During the elaboration of this paper I became indebted to several persons and institutions, to which I am very grateful.

I owe very much to Paulo Emílio Vanzolini, who has always supported my work, directly or indirectly, in all phases, without measuring efforts, and always finding time to discuss it.

This work was very much influenced by Howard E. Hinton, University of Bristol, England. A fellowship received from the Conselho Nacional de Pesquisas (Rio de Janeiro, Brazil) and the Royal Society (London, England), supplemented by the Fundação de Amparo à Pesquisa do Estado de São Paulo (São Paulo, Brazil), enabled me to work in Professor Hinton's laboratory. I am very much indebted to Professor Hinton for having found time to spend working with the "scanning electron microscope", as well as for lengthy discussions on the subject of this paper. The dedication of one of the genera of Torridincolidae is but a token acknowledgment for the support received from this great zoologist.

Bartyra, my wife, has been extremely helpful in many ways, including collection of specimens.

My friends Lícia Maria Neme, Ubirajara R. Martins, R. L. Araujo, John F. Lawrence and T. L. Hlavac were helpful in revision and criticism of the manuscript in its several phases of development. It gives me pleasure to acknowledge their help.

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Last but not least, I would like to single out greek mithology, where I frequently found peace to meditate on the progress of the work. The

new species of Torridincolidae are named after some of the more impressing personages of greek mithology as acknowledgment.

THE SUBORDERS OF COLEOPTERA

Four suborders of Coleoptera are generally recognized as valid (Crowson, 1955; Arnett, 1968). The more recently defined and delimited suborders Archostemata and Myxophaga have been added to the classic suborders Adephaga and Polyphaga, established for a long time (see *e.g.* Kolbe, 1908; 1911).

An attempt by Jeannel (1949) and Paulian (1949b) of further subdividing the Polyphaga in two suborders, Heterogastra and Haplogastra, has not found wide acceptance (see *e.g.* Bradley, 1947:77); the suborder Aplicalae, erected by King (1955) for the genus *Atractocerus*, has not been accepted either.

Although this paper is primarily concerned with Myxophaga, it seems convenient and necessary to review the history of Archostemata, since the two suborders have in common not being as easily characterized as Adephaga and Polyphaga.

Archostemata

On the basis of morphology and folding pattern of metathoracic wings, Forbes (1926: 62-63, 113) placed the families Cupedidae and Micromalthidae in a new suborder Archostemata, a group already defined as a category of lower status by Kolbe (1908), but restricted to Cupedidae. In Kolbe's system Archostemata formed an "Unterabteilung" of the suborder Heterophaga (= Polyphaga).

At present the suborder Archostemata is well established (see *e.g.* Peyerimhoff, 1933: 82; Atkins, 1958; 1963: 141; Hennig, 1969: 352; Crowson, 1971: 273) and almost universally accepted. Machatschke (1962) goes as far as proposing ordinal rank for Archostemata, which he considers a "Schwestergruppe" of Coleoptera, uniting both in the superorder Elytraria.

Bradley (1947: 76) rejects a distinct suborder for Cupedidae, including this family in Adephaga.

The inclusion of Micromalthidae in Archostemata, however, is still in discussion. Closer relationships between Micromalthidae and Cupedidae were first suggested by Peyerimhoff (1913). Van Emden (1932) accepted *Micromalthus* as related to Adephaga, considering the similarities with Malacodermata (a group of Polyphaga which includes the Cantharoidea) as of *habitus* only. Arnett (1968: 141) excluded Micromalthidae from Archostemata, placing the family in its original position, in Cantharoidea. The same treatment is suggested by Machatschke (1962: 121, footnote).

Several fossil families, especially of Permian age, are also included in Archostemata, but as will be seen below, the identity of some of these as true Coleoptera is currently being challenged.

Myxophaga

In the same paper in which the Archostemata were defined, Forbes (1926: 60-61) showed the extant relationships between four families of uncertain position, which Crowson later (1955) grouped in a fourth suborder, with the name of Myxophaga. Forbes grouped Cyathoceridae (= Lepiceridae), Sphaeriidae (= Sphaeridae*), Hydroscaphidae and Clambidae in the suborder Adephaga, in the vicinity of the superfamily Hydradephaga, the Adephaga with aquatic habits. This new position of the families was thus justified: "... The following four families have universally been scattered among the Polyphaga, but the first of them [Lepiceridae] shows unmistakable characters of the Hydradephaga, both in wing and other body characters, and the remainder [Sphaeridae, Hydroscaphidae and Clambidae] show at least some traces of Adephagous characters and are linked to them. With Clambus these Adephagous traces become negligibly small, and the genus was viewed by me as of hopelessly uncertain affinity until I examined the linking types...".

In a much later paper on the folding of wings, Forbes (1947: 72) considered Clambidae as having a system all of their own, and again stressed the fact that *Sphaerius* ("superficially an unchallenged clavicorn") and *Hydroscapha* ("always placed near the Staphylinidae"), have identical wings (*l.c.*: 73). The latter is a rather strange statement because of the absence of the oblong cell in *Hydroscapha* (fig. 38).

Crowson (1955: 3, 4, 10-11) formally defined the fourth suborder of Coleoptera, almost exclusively based on Forbes' studies (1926). The suborder included the first three families mentioned by Forbes, Lepiceridae, Sphaeridae and Hydroscaphidae, and a fourth family, Calyptomeridae, the latter with some doubts.

The family Calyptomeridae was erected by Crowson (1955: 11) solely for the clambid genus *Calyptomerus* Redtenbacher, 1848 (Clambidae were already considered as related to the other Myxophaga by Forbes in the 1926 paper). The position of Calyptomeridae within the Myxophaga was provisory (Crowson, 1955). A few years later Crowson (1960: 111) excluded the family from his suborder, without any discussion. Still later the same author (1967: 211) mentioned that *Calyptomerus* was again included in Clambidae (*apud* Endrödy-Yunga, 1959). Arnett (1968: 48, 440) also excluded the Clambidae (with *Calyptomerus*) from the Myxophaga.

I should mention that in the treatment of the beetles of the British Isles, Crowson (1956) only noted the existence of the suborder Myxophaga, referring the families included in it to the superfamily Sphaerioidea of Polyphaga.

^(*) In antecipation to a decision by the Commission on Zoological Nomenclature, I acept Clarke's (1970) proposal of emmending the coleopterous family name to Sphaeridae, because of homonymy with Sphaeridae in Mollusca, which have priority.

Machatschke (1962: 125) considered it wrong to segregate Calyptomeridae, Lepiceridae, Sphaeridae and Hydroscaphidae from the remaining Adephaga.

Hennig (1969: 354-355), on the other hand, apparently does not agree with the separation of Myxophaga from Polyphaga, and does not discuss the group in detail, only considering a "Schwestergruppenverhältnis" between Myxophaga and Polyphaga.

I also have to state that Böving & Craighead (1931) and Peyerimhoff (1933), who based their systems of Coleoptera primarily on larval characters, even though referring to Forbes' paper (1926), did not accept the inclusion of Lepiceridae, Sphaeridae, Hydroscaphidae and Clambidae in Adephaga. In both papers these families are part of Polyphaga. I should also mention that at the time of their studies the immature stages of Myxophaga were only very poorly known.

After 1960 the concept of Myxophaga was very much widened by the discovery of the family Torridincolidae, described by Steffan in 1964.

The structure of Myxophaga

Table 1 summarizes some important characteristics of the four suborders of Coleoptera (including data of the present paper). It clearly shows that Archostemata and Myxophaga, but especially the latter,

	<i>ADEPHAGA</i>	ARCHOSTEMATA	MYXOPHAGA	POLYPHAGA
LARVAE				
nº leg segments	5	5 *	4	4
tarsal claws	2	2	1	1
urogomphi	+ , ,	_	±	-
PUPAE	exarate	? exarate	obtect	exarate + obtect
ADULTS				
notopleural suture	+	+	+	_
oblong cell	+	+	<u>+</u>	_
galea	+	+	_	+
pre-apical mand. tooth	-	-	+	_
wings	folded	rolled	folded + rolled	folded
metasternum-coxae	fused	free	free	free
Malpighian tubes	4	4	6	4-6
testes	tubular	tubular	tubular	follicular
ovaries	polytrophic	polytrophic	? polytrophic	acrotrophic
abdominal ganglia	independent	?	fused	fused

Table 1. The suborders of Coleoptera.

^(*) The literature is not consistent in relation to larvae of Micromalthidae. Van Emden (1932: 256) clearly states that larvae of Cupedidae and Micromalthidae "... sind auch ohne Zweifel eng verwandt, insbesondere weisen die einen wie die anderen die Beingliederung der Adephagen-larven auf". Böving & Craighead (1931), however, more than once state "... except in the instars of Micromalthus, which are legless or have three-jointed legs" (pp. 9, note 3; 10, note 6), and illustrate the I instar larva (pl. J, fig. 2) with 5 segments and 2 claws.

have a series of characters intermediate between Adephaga and Polyphaga, their characterization being somewhat difficult.

According to Crowson (1955: 10) Myxophaga is a heterogeneous group of Coleoptera with a certain number of characters in common. In the adult these characters are:

- a. prothorax with distinct notopleural sutures (not unique character);
- b. membranous wings with closed and well developed oblong cell (fig. 36; not unique character, and absent in Hydroscaphidae, fig. 38);
- c. maxillae without galea (fig. 10; apparently unique character);
- d. mandibles with distinct mola (fig. 9; not unique character), and with pre-apical, articulated tooth on left mandible (apparently exclusive character; the Hydraenidae, a family with hydrophiloid relationships, of the suborder Polyphaga, however, has a similar structure in both mandibles, considered by Beier & Pomeisl, 1959: 82-84, fig. 11b, as a "prostheca mobilis");
- e. tarsi with reduced number of segments (not unique character).

Characters of immature stages were not taken in account, since only the larva of Hydroscaphidae was known at the time.

There are thus no doubts that the families of Myxophaga represent four very heterogeneous and independent lineages, possibly very old ones. The homogeneity of each family, on the other hand, is very strong, even though the extant data may not be sufficiently representative.

At the time of the description of Myxophaga as a suborder, larvae of only one of its families were known: Hydroscaphidae (Böving, 1914). The immature stages of the Torridincolidae (Steffan, 1964; Bertrand, 1965: 1371-1373) and Sphaeridae (Britton, 1966) have become known more recently. Those of Lepiceridae are still undiscovered.

Larvae have taken a very important role in the suprageneric classification of Coleoptera since the publication of Böving & Craighead's classic work (1931; see also Peyerimhoff, 1933). In some instances the study of larvae only reinforces concepts based on the imago; in others it provokes very deep modifications.

Unfortunately the data from immature stages of Myxophaga add very little to a better definition of the group. As occurs with the adults of the families of Myxophaga, their larvae differ very much from each other. Hinton (1967: 956-957), however, stresses as very important two larval characters Myxophaga have in common: a. they are the only known aquatic larvae with spiracular gills; b. they are the only insect larvae with plastron.

Very little is known on the pupae of Myxophaga (which is also true for Coleoptera in general). Böving (1914: 170, fig. II) knew a single pupa of *Hydroscapha natans*, but did not describe it because of its poor state of preservation. Bertrand (1965: 1371-1373, fig. 30) and Hinton (1968: 120-122, figs. 33-34) described the pupa of *Torridincola* in detail; the pupae of *Hintonia* and *Ytu* are described below. It seems

to me that the only character these pupae have in common is both being obtect pupae.

After the finding of Torridincolidae (Steffan, 1964), there have been very important discoveries in the suborder, but it seems to me that there has been no important addition to its definition by exclusive characters.

Britton (1966) for the first time described a larva of a species of Sphaeridae. Reichardt & Costa (1967) described a second genus of Torridincolidae, the first non-African genus of the family. Hinton (1967, 1968, 1969a) published a series of papers on respiratory mechanisms in Myxophaga (exclusive Lepiceridae). I have described the first three Neotropical Hydroscaphidae (Reichardt, 1971b).

In this paper I bring together a series of new informations on Myxophaga, almost exclusively Neotropical. I describe one new genus and nine new species of Torridincolidae from southeastern Brazil; the larvae and pupae of the two Brazilian genera are described. For the first time are presented new (the first to be published) data on the internal anatomy of adult Torridincolidae. Based on my field experience I discuss the ecology of the Brazilian Torridincolidae and Hydroscaphidae. The Brazilian species of Hydroscapha (Reichardt, 1971b) are referred to a new genus.

I also consider the South African hydraenid larva described by Bertrand (1962) as belonging into Torridincolidae.

With these new data the family Torridincolidae, unknown less than ten years ago, becomes the most diversified family of Myxophaga. Hydroscaphidae, described almost 100 years ago, with no changes in its concepts during this time, has its definition very much changed by the discovery of a quite different. Brazilian genus.

The geographic distribution of the two families is changed. The Torridincolidae were only known from Africa (Rhodesia, Zaire and Madagascar) and Brazil (State of Rio de Janeiro); they are now recorded from South Africa and southeastern Brazil (fig. 1). Hydroscaphidae, a family until recently thought to be of boreal distribution (d'Orchymont, 1945) was recently recorded for the first time in the Neotropical Region (Reichardt, 1971b). Hinton (1969: 153) also refers to a Mexican species of Hydroscapha, without describing it.

There is a certain conflict between the new and some of the older data. Britton (1966: 1198), for example, commented on the absence of urogomphi in larvae of Myxophaga as a Polyphagan character. It is true that Hydroscapha, Sphaerius and Torridincola lack urogomphi (even though there are two short processes on the IX abdominal segment in Steffan's illustration of the larva; my fig. 119), but the Torridincolid genera Hintonia, Ytu, and B have them well developed (figs. 52, 54, 120).

In view of the considerable expansion of data on Myxophaga in recent years, it is hoped that with the intensification and refinement of collecting methods, there will be an increase of material of Myxophaga in collections. I should stress here that after having discovered the habitat of *Hintonia* and *Ytu*, I have collected over 1,000 specimens of Torridincolidae in southeastern Brazil, and at the same time collected the first South American specimens of Hydroscaphidae. Based on my collecting experience I assert that Torridincolidae are very common beetles, only not having been colected earlier because of their very small size, and due to lack of collecting in their habitat in the Neotropical Region. A further proof of this is the recent discovery by myself, in the same habitat, of over 100 specimens of four different species of Hydraenidae, a family of Hydrophiloidea of which only two species have thus far been described from Brazil (Blackwelder, 1944a: 85). Besides the possibility of discovering more Torridincolidae and Hydroscaphidae in Brazil (the material on which this paper is based has only been collected in a very restricted area in southeastern Brazil; see fig. 1), I am almost certain that the other two families of Myxophaga, Sphaeridae (up to now known from the Old World. United States and Guatemala), and Lepiceridae (exclusively known from Mexico, Central America and Venezuela), will also be discovered here. A better knowledge of these families, their ecology, their immature stages, etc., will be fundamental for a better understanding of the suborder.

With reference to all stages, it can be concluded that Myxophaga is a very heterogeneous group, only characterized by a few poorly defined and not exclusive characters, mostly of adults. The confirmation of certain characters, at present registered for Torridincolidae, in the other families of Myxophaga, may eventually give a more solid foundation to the suborder.

There is, thus, no doubt that any discussion on the Myxophaga must be very provisory, and may well have to be subjected to profound modifications in the near future.

In opposition to the heterogeneity of the suborder there is a very evident homogeneity of the members of each family, especially Torridincolidae and Hydroscaphidae, which are treated in more detail in this study. In the Torridincolidae this homogeneity is not restricted to the adults, but is also true for the immature stages. Allied to the peculiar, perhaps relict, geographic distribution, this homogeneity could indicate a great antiquity of the group, as well as very little evolutive plasticity.

Relationships of Myxophaga

According to Crowson (1955: 10; 1960: 112) the Myxophaga had a common origin with Polyphaga, having diversed from these at a very early stage; in 1971 (p. 237) this author says that "it seems possible that Myxophaga descend from the oldest aquatic adaptation of the Coleoptera as the Cupendidae come from the earliest wood-borers". Analysing the existing data, including the larva of Sphaerius, Britton

(1966: 1198) accepted Myxophaga as a valid group, with characters both of Adephaga and Archostemata (prothorax with notopleural suture, membranous wings with oblongum), as well as of Polyphaga (adults: with clavate antennae, aedeagus with basal piece, metacoxae not fused to metasternum, reduced number of tarsal segments; larvae: with five-segmented legs, single tarsal claw, absence of urogomphi), and considered them as representing a distinct evolutionary line which diverged from the remaining Coleoptera near the origin of the Archostemata.

The present study of Myxophaga, but especially of Torridincolidae, adds a series of new characters important to the classification of the suborder, especially some of the internal anatomy.

The six free Malpighian tubes of *Hintonia britskii* and *Ytu zeus* (fig. 51) represent the primitive number and type of Malpighian tubes in Coleoptera; furthermore six is the number most frequently found in Polyphaga. Apparently this is the first record of number of Malpighian tubes in Myxophaga. Peyerimhoff (1933: 101) placed Sphaeridae and Hydroscaphidae in the Staphylinoidea + Hydrophiloidea, mentioning that both have only four Malpighian tubes, without reference to the source of this important information. Only for one of the families, Hydroscaphidae, did this author mention the need of confirmation of the data. I think that both families have to be more critically examined in this regard before any conclusion can be drawn from the data.

The testes of Torridincolidae (examined in *Hintonia britskii* and *Ytu zeus*) are tubular and coiled; all other Coleoptera with this type of testes, *e.g.*, Adephaga and Archostemata, have polytrophic ovaries, and it is almost certain that Torridincolidae also have polytrophic ovaries.

Thus, while the Malpighian tubes link Torridincolidae to Polyphaga, the reproductive system is more similar to that of Adephaga and Archostemata. Even though these data on the internal anatomy of Torridincolidae should not be extended to the other families of Myxophaga (see comments above on Peyerimhoff, 1933), they increase the number of non-exclusive characters already mentioned by Britton (1966), but on the other hand seem to stress the primitivity of Myxophaga.

In a general way the known Myxophaga fit well Crowson's characterization of the "primitive coleopteron" (1955: 1-3), but they lack the elytral structure of Cupedidae and other extinct families of Archostemata (a well developed system of longitudinal ribs). It seems, however, that too much weight has been put on these fossils. Crowson (1971: 237), for example, says that "recent paleontological studies have confirmed the antiquity and separateness of the group (Archostemata)". Kukalova (1969), however, based on ample material, including a hind wing, transferred some of these fossil Archostemata (the families Tshekardocoleidae Rohdendorf, 1944 and Oborocoleidae Kukalova, 1969) from Coleoptera to the Order Protelytroptera.

In the absence of fossil Myxophaga any more precise conclusion on the relationships between this and the other suborders of Coleoptera, is premature. There is no doubt, however, that they are primitive beetles, which possibly represent an evolutionary lineage separated from the original stock of Coleoptera before the diversification of Polyphaga, but which was unable to become established, and whose present representatives are only relict testimonies of a group which had a much larger diversification, as has been the case of Archostemata, a suborder with several extinct families.

Torridincolidae

Taxa included and catalog

To date Torridincolidae only included two monotypic genera, the African Torridincola Steffan, 1964 and the Brazilian Hintonia. In the literature there are records of two additional, still undescribed species of Torridincola, from Zaire and Madagascar (Bertrand, 1965: 1365; 1966: 1737). I also consider an African larva described by Bertrand as belonging to the Hydraenidae, as representing an undescribed genus of Torridincolidae. Unfortunately I was unable to study the original specimen(s) of this larva, and since the adults are still unknown, I prefer not to name the genus, as not to get involved with nomenclatorial problems at this stage. As the genus is important for some inferences in this paper, I refer to it simply as genus B. I also describe a second Brazilian species of Hintonia, as well as the new Brazilian genus Ytu, with eight new species.

Torridincola Steffan, 1964: 193 (type-species, original designation, Torridincola rhodesica Steffan, 1964).

rhodesica Steffan, 1964: 194-199, figs. 1-9 (type-locality, Rhodesia, near Salisbury).

Hintonia, nom. n. (type-species, original designation, Ptypteryx britskii Reichardt & Costa, 1967).

Ptyopteryx Reichardt & Costa, 1967: 13-14 (nec Ptyopteryx Kolenati, 1848).

britskii Reichardt & Costa, 1967: 14-19, 12 figs. (Ptyopteryx; type-locality, Brazil, Rio de Janeiro, São Fidelis).

castalia, sp. n. (type-locality, Brazil, Rio de Janeiro, Nova Friburgo).

Ytu, gen. n. (type-species, present designation, Ytu zeus, sp. n.).

artemis, sp. n. (type-locality, Brazil, Espírito Santo, Venda Nova).

athena, sp. n. (type-locality, Brazil, Paraná, Morretes).

cupidus, sp. n. (type-locality, Brazil, Rio de Janeiro, Teresópolis).

demeter, sp. n. (type-locality, Brazil, Rio de Janeiro, Teresópolis).

hephaestus, sp. n. (type-locality, Brazil, São Paulo, São Sebastião).

morpheus, sp. n. (type-locality, Brazil, Rio de Janeiro, Areal).

phebo, sp. n. (type-locality, Brazil, São Paulo, Salesópolis).

zeus, sp. n. (type-locality, Brazil, São Paulo, Itu).

Genus B ("Hydraenidae genus, propre Prosthetops", of Bertrand, 1962: 1068-1072; larvae from South Africa, near Assaigabos River).

THE IMMATURE STAGES

Larvae

In all genera of Torridincolidae (including genus *B*) each of the eight first abdominal segments carries a pair of lateral spiracular gills (figs. 52-56, 60, 61, 119-120), which are covered with a thin plastron mesh, a character unique in coleopterous larvae (Hinton, 1967: 957--958).

In the two known instars of *Torridincola rhodesica* (the II and III according to Hinton, 1967), these gills are three-segmented (Hinton, 1967: 957, figs. 1A, 1B), and are directly articulated to the abdominal segment.

In the known instars of Hintonia and Ytu the gills are only two-segmented (figs. 60, 61), and are inserted on lateral projections of the abdominal segments. In Hintonia these sockets are less developed than in Ytu, and the first two pairs are directly articulated on the segment, as in Torridincola.

The two Brazilian genera differ slightly from each other in the structure of the gills, especially in proportions of segments, but both differ very much from *Torridincola* in this regard. In the African genus the external opening of the spiracular atrium is placed at the apex of the III (last) segment (Hinton, 1967: 957, figs. 1A, 1B), while in *Hintonia* and *Ytu* the opening is placed more or less in the middle of the II (last) segment, which is abruptly narrowed behind the opening, being thinner from here to the apex (figs. 60, 61). This strangulation suggests a division of the segment, but even microscopic preparations did not show any real segmentation.

In genus B, morphologically similar to the Brazilian genera, the gills are described as three-segmented, and are articulated on lateral sockets, as in Ytu. Unfortunately the description does not mention the position of the opening of the spiracular atrium.

Ytu and B are characterized by a fringe of "friction setae" along the lateral margins of the thoracic segments. It is interesting that in the early instars of Ytu this fringe is reduced to a very few individual setae (figs. 55. 56). The function of the fringe is not known, but a similar structure is also found in larvae of other aquatic Coleoptera, as e.g. Psephenidae. It could function to enlarge the dorsal surface of the larva, to offer a larger surface to the water which flows over the larva, thus giving it a better fixation on the substrate.

Pupae

The pupae of *Hintonia* (fig. 7a), *Ytu* (figs. 57, 58) and *Torridincola* (Bertrand, 1965: 1371-1373, fig. 30; Hinton, 1968: 120-122, figs. 31-34) are characterized by a pair of spiracular gills, covered with a fine plastron mesh, on each of the two first abdominal tergites [and not on the metathoracic and first abdominal tergites, as described by

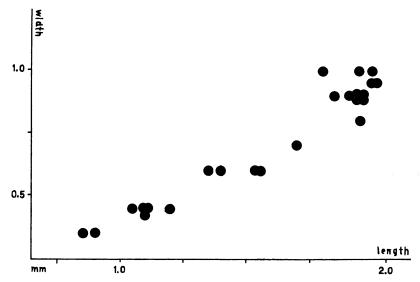
Bertrand (1965: 1372, fig. 30)]. It is interesting to note that the pupa of *Hintonia* and *Ytu* is obtect, a type of pupa which only occurs in certain families of Coleoptera, all of the suborder Polyphaga (Staphylininae, Ptiliidae, Corylophidae, Coccinellidae and Chrysomelidae). According to Hinton (1946) all Coleoptera have adecticous pupae, and most are exarate.

The known pupae of Torridincolidae are unique among beetles, by remaining within the cuticle of the last larval instar, which serves as a cocoon, and splits open along the medial ecdysial line to expose the spiracular gills (fig. 57). In my opinion this is not evidence of primitivity, but adaptation to the habitat. The pupa does not have any own means to fix itself on the rock to resist the water flowing over it, and, therefore, it is the last larval instar which fixes itself on the substrate.

The number of larval instars

Myxophaga are said to go through three larval instars. I suspect this is mainly based on the fact that Adephaga and other primitive beetles only have three larval instars. Böving (1914: 170) says that "... three larval stages are in the material of Hydroscapha natans and evidently no more occur". Britton (1966: 1196) seems to have confirmed this number for the Australian Sphaerius ovensensis: although he does not mention three instars, he refers to the I instar and two later ones. Hinton (1967: 956, table 1) mentions three larval instars for Myxophaga.

Even though the Brazilian material of larvae I have at hand is extensive, it is not absolutely conclusive in this regard. One of the



Graph 1. Linear regression for maximum width of specimen against total length of a sample of 24 larvae of *Hintonia britskii* from Mangaratiba.

TABLE 2. Measurements (in mm) of larvae of *Hintonia britskii* from Mangaratiba, Rio de Janeiro (1-2.IV.1972). Width at mesonotum; length including urogomphi.

	width	length		width	length
Instar I	0.35	0.85		0.80	1.95
	0.35	0.90	0		1.85
				0.90	1.90
Instar II	0.43	1.10		0.90	1.95
	0.45	1.05		0.90	1.95
	0.45	1.10	Instar IV	0.90	1.95
	0.45	1.10	Instal IV	0.90	1.95
	0.45	1.20		0.95	2.00
				0.95	2.00
	0.60	1.35		1.00	1.80
	0.60	1.40		1.00	1.95
Instar III	0.60	1.55		1.00	2.00
	0.60	1.55			
	0.70	1.70			

main problems I had with larvae of Ytu was the impossibility of identifying them with certainty because of lack of specific characters, as well as because of the sympatry of several species.

Nevertheless several distinct instars can be recognized in the samples of the different species. Three different instars are recognizable in the sample of Ytu athena, and two different ones in samples of Ytu zeus. One large sample of Hintonia britskii (24 larvae from Rio de Janeiro, Mangaratiba), has four different larval instars, which are easily distinguished from each other by body proportions, as well as other characters, as discussed elsewhere.

As this sample of *Hintonia britskii* shows a relatively continuous growth curve (graph 1), without larger gaps between the different instars, it seems that at least for this species four larval instars are the rule. The large gap in size between the II and the next larval instar in *Ytu athena* (0.9 and 1.68 mm respectively) also suggests that at least one more larval instar must occur in that species.

ADULTS

Internal anatomy

Because of the general orientation of this work, relatively little was done on the internal anatomy of Torridincolidae. In part this was also due to the lack of properly fixed material at certain stages. Nevertheless I discovered at least two interesting facts in the internal anatomy of the family (data refer to only two species, *Hintonia britskii* and *Ytu zeus*): a. there are six Malpighian tubes, which end freely in the body cavity (fig. 51); b. testes are tubular and coiled.

Alimentary duct: mid-gut destitute of anterior caeca; hind-gut forming a short but sharp curve in the abdominal region, before ope-

ning into rectum. Six Malpighian tubes, which apparently are turned towards rectum, and end freely in the body cavity.

Six is the primitive number of Malpighian tubes in Coleoptera (Kolbe, 1908: 159; Bradley, 1947: 75); it is also the number typical of Polyphaga, even though some families have only four. Adephaga and Archostemata (at least *Priacma serrata*, apud Atkins, 1958: 534) have only four.

Male reproductive organs: testes tubular and coiled; one pair of accessory glands.

Tubular and coiled testes are typical of Adephaga (Kolbe, 1908: 159; Peyerimhoff, 1933: 100; Jeannel, 1949: 882) and Cupedidae (Atkins, 1963: 140), and have never been found in Polyphaga. They apparently represent the primitive type of testes (Bradley, 1947: 75). As the groups of Coleoptera with this type of testes always have polytrophic ovaries, it is most probable that Torridincolidae also have polytrophic ovaries.

Nervous system (only examined in Hintonia britskii; fig. 7b): ventral nerve cord reduced to three ganglia, all placed in the thorax.

There is a great variation in the nervous system in Coleoptera. According to Kolbe (1911: 54-57) concentration of the ventral nerve cord, such a found in *Hintonia*, should not be interpreted as of primary systematic importance, but should be considered as a byproduct of a reduction of the abdomen in size. A more or less intense concentration of the ventral ganglia apparently occurs even in closely related groups.

Unfortunately nothing is known on the internal anatomy of the remaining genera, neither of any of the other families of Myxophaga.

External anatomy

The respiratory system (and respiration)

Torridincolidae have plastron respiration (see Thorpe & Crisp, 1949; Thorpe, 1950). For Torridincolidae this type of respiration was discovered and carefully described by Hinton (1967, 1968, 1969a). Usually plastron respiration is restricted to a single stage in the natural history of any species (Hinton, 1969a: 132), being especially common in eggs and pupae of Diptera.

To date Torridincolidae are the only known insects in which plastron respiration evolved in the three vital stages, at least in some species. Larvae of Torridincolidae are the only known larvae with spiracular gills covered with a plastron mesh. The only known pupae of Coleoptera with spiracular gills are those of Psephenidae and Torridincolidae (Hinton, 1966: 212; 1968: 114-122).

It should be mentioned again that in regard to respiration larvae of Myxophaga have in common being the only aquatic larvae with spiracular gills, and the only larvae of insects bearing a plastron (Hinton, 1967: 956-957).

Larvae, pupae and adults of *Torridincola rhodesica* have a plastron. In the Brazilian genera there is a plastron in all larvae and pupae, as well as in adults of *Hintonia*. Adults of *Ytu* lack a plastron.

All segments of all spiracular gills of larvae are covered with a fine plastron mesh. The two pairs of spiracular gills of the pupa of *Hintonia* and *Ytu* have a longitudinally striated plastron mesh (fig. 7a) very similar to the structure of the plastron of the pupa of *Torridincola* (Hinton, 1968, figs. 31-34), although the former have not been examined in the "scanning electron microscope".

The plastron of the adult of *Hintonia britskii* was described by Hinton (1969a: 132, pl. I); the other species of the genus, *Hintonia castalia*, has the same type of plastron (figs. 97-98). It is a very peculiar, periodic structure, which produces strong iridescence. *Hintonia* is the only known insect in which a plastron also functions as a diffraction surface (Hinton, 1970: 46, 47). The selective advantage, if any, of a ventral surface of diffraction is unknown (see also Hinton, 1969a: 133), and difficult to be understood. The beetle would have to be turned over for the iridescence to be noted. In such a position the beetle would immediately be washed away by the water flowing over the waterfall in which it lives, and the iridescence would not have had any utility for the beetle. The development of such a periodic structure could simply be coincidental to the development of a plastron with parallel ridges.

The lack of a plastron in the eight species of Ytu is of great interest, since it suggests an independent origin of the plastron of Torridincola and Hintonia, or simply the loss of the plastron in Ytu. The quite different structure of the plastron of Torridincola (fig. 100) and Hintonia (fig. 99) seems to support an independent origin, already suggested for the plastron of other families (Hinton, 1969a: 139).

Membranous wings and flight capacity

All genera of Torridincolidae have the typical hind wings of the suborder Myxophaga (Forbes, 1926; Crowson, 1955): normally developed wings with very reduced vein system, oblong cell ("oblongum"; absent in Hydroscaphidae), and a marginal fringe of long setae (Britton, 1966: 1198, figs. 2-3; Crowson, 1955: 4, fig. 1b; Forbes, 1926, figs. 19-22; Reichardt & Costa, 1967: 17, fig. 1; Steffan, 1964: 197, fig. 1).

The four families of Myxophaga have very similar wings, including the folding method, as already mentioned by Forbes (1926: 60-61, 113, figs. 19-22). The segregation of the families in a distinct group, as discussed above, was based almost exclusively on this character. The wings of at least two of the families, Sphaeridae and Torridincolidae, also have another character in common: they are folded in the basal half, and rolled in a double spiral apically (Britton, 1966: 1198, fig. 2; figs. 34, 35). This folding pattern, not yet verified for Hydroscaphidae, may well prove to be typical for the suborder; it may, however, be the type of wing folding of Haliplidae and the Old World genus Hygrobia (Hygrobiidae) mentioned by Forbes (1947: 72), as "... folded as if such a spiral had been ironed flat".

It is well possible that important characters will be found in the internal surface of elytra, where auxilliary mechanisms for the folding of the wings are placed. In *Ytu zeus* and *Scaphydra hintoni* the internal surface of the elytra has a network of striae, as well as small setae and structures which may be sensory organs (figs. 103-106). See also comments on setae on abdominal tergites VI and VII of *Sphaerius*, which, according to Lesne (1936), also have an auxiliary function in the folding of the wings.

As mentioned elsewhere (Reichardt & Costa, 1967: 17), the wings of *Hintonia britskii* are extremely similar to those of *Torridincola rhodesica*. The same is true for the wings of *Ytu*.

Only Hintonia castalia has atrophied wings (fig. 37), which in resting position are unfolded under the elytra. The wings of species of Ytu measure about 1.5 mm when unfolded; those of Hintonia castalia only measure 0.7 mm. The vein system is extremely reduced, and the "oblongum" lacking. As other structures normally related to the reduction of wings [according to Darlington (1936: 152) in Carabidae there is a physical connection between the atrophy of wings, atrophy of the flight muscles, degeneration of the metathorax, and finally rounding of the humeri] seem to be normally developed in Hintonia castalia, this suggests a relatively recent loss of the wings. Hintonia castalia is the second known Myxophagan with reduced wings: Scaphydra angra (Reichardt, 1971b) was the first one to be described. Of this Hydroscaphidae, however, I have only seen the holotype, and nothing else can be said about its wings besides their reduction; of Hintonia castalia I have enough material of both sexes, and all specimens have reduced wings.

The presence of normally developed hind wings, however, is not sufficient for a species to be able to fly. Jackson (1952) discussed cases of aquatic beetles with normal wings, but incapable of flying because of the atrophy of the flight muscles.

I only know a single reference in the literature on flight of Myxophaga: Paulian (1949a: 371) says in the description of *Hydrosca-pha saboureaui*, from Madagascar, that "... adultes rampaient dans les algues et nous avons pu noter la facilité de leur envol en plein soleil".

I have seen *Ytu demeter* flying when completely dry (Teresópolis, 31.VIII.1971). Other Neotropical Torridincolidae most probably also use their wings for flight.

At one occasion, at Areal (13.XII.1969) I collected a few adults of *Hintonia britskii* together with adults of *Ytu hephaestus* and *Ytu phebo*. No larvae were collected. If my observations of different habitats for the two genera, as discussed below, are correct, *Hintonia britskii* should not have been found in the same habitat as *Ytu*. In my opinion *Hintonia britskii* can only have reached this place by flying from nearby Rio Piabanha, where I did not collect, but where I noted some typical spots for *Hintonia*. This supposition is strenghtened by the fact that I have collected other times at the same locality, in different times of the year, without having found *Hintonia britskii* again, while *Ytu*

hephaestus and Ytu phebo were present, together with other species of Ytu and larvae of this genus.

I believe that the species of Torridincolidae disperse mainly by flight. Several times I have found completely dry certain localities in which I had collected at other times, and it is very probable that during the drought adults fly away.

The abdomen

Adults of Torridincolidae are characterized by five visible abdominal sternites. In *Torridincola* and *Ytu* the sternites are normally developed, with complete and visible sutures.

In *Hintonia* the abdomen is different, and its structure was incorrectly described in the original report (Reichardt & Costa, 1967: 14), as T. H. Hlavac was kind enough to point out. The genus was described as only having four sternites, and it was suggested that the semi-lunar depression between sternites III and IV (the penultimate and the last), could represent a vestigial V sternite. Microscopic preparations, however, disclosed a segment hidden under the I (fig. 32). Thus *Hintonia* has five sternites as the other genera, although only four are externally visible.

The half-moon shaped structure of *Hintonia*, originally interpreted as the vestigial V segment, is still a puzzle. It is found in both species of the genus, and in both it is dimorphic: in males it is simple, while in females it is continued towards the apex of the segment, along the median line. This depression seems to be somehow related to an almost spherical tubercle placed in it (fig. 96), which seems to be connected to a keel which runs along the three proximal sternites. A second bulbous structure is found in the middle of the hidden abdominal sternite, as can be seen in microscopic preparations (fig. 32), and which most probably is related to the system. One hypothesis for this complex structure could be a glandular system which produces a substance for the fixation of the animal on the substrate.

Genitalia

Only the male genital apparatus was studied in detail. This is mainly due to the experience with other groups of Coleoptera, in which only the male genitalia shows variation at specific level. The study of the female genitalia of a few species confirmed the lack of important characters. As the primary goal of the study of the genitalia was the discovery of additional specific characters and not the morphology of the genitalia, I have restricted myself to the male. The female genitalia of *Hintonia britskii* is shown in Reichardt & Costa, 1967, fig. 7.

I have studied the male genitalia of all species described below, and in a few cases it is a very important character, if not for the recognition of the species, at least for the confirmation of its identification by external characters.

Some difficulties inherent to the small size of the aedeagus (about 0.5 mm in length), as well as the few specimens available for dissection in some cases, prevented examination of certain details in some species. I think, however, that they are present in all.

Fundamentally the male genitalia of the Brazilian species is identical to that of *Torridincola rhodesica* (Steffan, 1964: 197-198, figs. 4-5), with globose basal piece (pars basalis or phallobasis), elongate and curved aedeagus (aedeagus or penis), with two lateral lobes (parameres) of variable development, long, each with two relatively short apical setae. The aedeagus is split longitudinally to a variable extent (about half its length in *Hintonia*, about one third in *Torridincola*). In the species of *Ytu* the aedeagus is also split longitudinally, but not as conspicuously as in the other genera, and in some species there may even be a secondary fusion of the lobes. In *Torridincola* the lateral lobes are long, only slightly shorter than the aedeagus; in *Hintonia* and *Ytu* they are relatively short, with the apical setae longer than the parameres. There seems to be no difference in the lateral lobes of *Hintonia* and *Ytu*, but there is some inter-specific variation.

Although the genitalia of Torridincolidae agrees in a general way with that of Coleoptera (Lindroth & Pálmen, 1956: 69; 1970: 80), it is of a very peculiar type, especially in regard to the longitudinal splitting of the aedeagus, and the lateral lobes with apical setae. A well developed basal piece seems to be a derivative character, but an interpretation of the genitalia as a whole is very difficult. It seems certain that the genitalia of Torridincolidae does not fit into any of the four fundamental types of Lindroth & Pálmen (1956: 72-73; 1970: 84-86). It certainly shows some similarities, even if superficial, with that of some species of Hydraenidae (Balfour-Browne, 1971, fig. 2).

Unfortunately the genitalia of the other Myxophaga are very poorly known, if at all. Sharp & Muir (1912: 530-531, pl. LXII, figs. 123, 123a) described the genitalia of Lepicerus horni (Lepiceridae), without mentioning Sphaeridae and Hydroscaphidae. The genitalia of Lepicerus is very strange, and not at all similar to that of Torridincolidae. It seems, however, possible that the part called "tegmen" by Sharp & Muir (l.c., fig. 123; a term applied to the basal piece and the lateral lobes together), is really the aedeagus. Sharp & Muir show a "tegmen" split longitudinally in the anterior half. If my interpretation is correct, this could be a very interesting link between the families.

The only known reference to the genitalia of Sphaeridae is found in Lesne (1936: 246): "Édéage petit, très évolué, comportant primitivement un paramère en forme de manchon ouvert dorsalement et contenant un pénis plus ou moins réduit. A l'extrémité basilaire du manchon paramérique, du côté droit, est appendu un sclérite sacciforme asymétrique qu'il faut homologuer avec la pièce basale".

The male genitalia of Hydroscaphidae differs very much from that of Torridincolidae (and Coleoptera in general) by the lack of parameres. Sexual dimorphism and reproduction

The sexual dimorphism of *Hintonia britskii* was discussed in the original description (Reichardt & Costa, 1967: 17). Males have a simple semi-lunar depression between the last and the penultimate abdominal sternites; in the females the same depression is prolonged along the median line to the apex of the sternite. *Hintonia castalia* has the same sexual dimorphism. The importance and function of this depression were discussed above.

Hintonia britskii also shows sexual variation in size: males are slightly smaller than females. In Hintonia castalia the difference in size between sexes is only very small, practically inexistant.

One of the species groups of *Ytu* is characterized by opaque and only faintly iridescent males, and brightly, intensely iridescent females. In this group striae and interstices are better developed in females. This sexual dimorphism is typical of the *Zeus* species group, which includes *Ytu zeus*, *Ytu hephaestus*, *Ytu athena* and *Ytu phebo*. Although the sexual dimorphism is usually clearly developed, it is frequently impossible to sex specimens by external characters.

Males of Ytu zeus show an additional sexually variable structure: a tuft of white setae on the metasternum, and a smaller one on the prosternum (figs. 83-86). These setae, completely absent in females, are most probably placed near the opening of scent glands, also known in other groups of aquatic beetles (Hinton, in litt.).

Representatives of the *Cupidus* species group apparently lack sexual dimorphism, except *Ytu demeter* and *Ytu morpheus*, whose males have a pair of small, conic tubercles on the metasternum

Sexual variation in size also occurs, but is very slight. Only in Ytu demeter are males conspicuosly larger than females; in this species size is practically the only reliable character to distinguish it from females of Ytu artemis (Graph 2).

Very little is known on reproduction in Myxophaga. There are several references in the literature to the maturation of a single egg in Myxophaga. Böving (1914: 170) and Paulian (1949a: 373) record it for Hydroscapha natans (from the United States) and Hydroscapha saboureaui (from Madagascar). Lesne (1936: 247) mentions it for species of Sphaerius. Britton (1966: 1196) has found the same phenomenon in Sphaerius ovensensis, an Australian species. In Scaphydra pygmaea and Scaphydra hintoni, both from Brazil, I have found one and two to three eggs respectively (Reichardt, 1971b).

Females of Ytu zeus apparently also mature only a maximum of three to five eggs at a time, but obviously more than once during life. The eggs are relatively large $(0.2 \times 0.4 \text{ mm})$, and their surface is covered with small tubercles, very difficult to be resolved by the light microscope (fig. 102).

It seems, therefore, that the maturation of a small number of eggs (one to five) at a time, is a trend common to Myxophaga, even though it has also been recorded for other, unrelated groups, such as the Staphylinidae.

Copulation occurs in the water, and has been observed in several species of *Ytu* at various times of the year. Collections of *Ytu* zeus made at regular intervals of about four weeks in a single locality (Valinhos and Itu, state of São Paulo), indicate that this species completes development from egg to adult in slightly less than four weeks.

Habits and ecology

All known Torridincolidae are aquatic in all phases of their life history.

The types of *Torridincola rhodesica* (larvae and imagos) were collected in temporary mountain streams ("temporare Bergbäche") of dry areas in southern Africa. These streams can dry out completely for three to four months during the year (Steffan, 1964: 198). According to the same source of information, other animals of this biocenose are Diptera (Chironomidae and Simulidae) and mites.

Bertrand (1965: 1365; 1966: 1737; 1969: 729, 731) recorded all stages of two undescribed species of *Torridincola* in Madagascar and Zaire. They were always collected in the hygropetric habitat, e.g., the film of water which flows over rocks ("rochers suintants ou ruisselants").

The larva of Hydraenidae (genus *B*) was also collected in this habitat ("sur un rocher ruisselant, voisin d'un affluent de la branche de Berg river désignée par Harrison comme Assaigabos River..."; Bertrand, 1962: 1068).

Except for the reference for *Torridincola rhodesica*, all other African species of Torridincolidae were collected in the hygropetric habitat (see Bertrand, 1966: 1731), e.g., in the film of water which flows over rocks in mountainous regions. The study of this habitat, although not new (according to Bertrand, 1966, the term was coined by Thienemann in 1905), seems still to be in its beginnings. The African hygropetric fauna is relatively well collected and studied, especially through the efforts of Bertrand. Very little has been done in Brazil, or in the Neotropical Region in general (see also Spangler, 1972: 139).

The Brazilian genera of Torridincolidae are also aquatic, but apparently only *Ytu* occurs in the hygropetric habitat. Up to now *Hintonia* has only been collected in waterfalls.

Hintonia

The original specimens of *Hintonia britskii* were found in the stomach of a fish, *Oligosarcus jenynsii* (Günther, 1863) collected by my colleague Heraldo A. Britski. The relatively large number of specimens, about 20, suggested a common species.

When I first collected at the type-locality, córrego Pedra d'Água, near São Fidelis, I found abundant material of the species, both larvae and adults. I have since collected *Hintonia britskii* in several localities over a large area in southeastern Brazil (fig. 3), always on rocks in waterfalls and cascades or fast running streams in the coastal mountains of Brazil (only once, in Areal, was *Hintonia britskii* collected in the hygropetric habitat, together with *Ytu hephaestus* and *Ytu phebo*, but this case must be considered as accidental and was studied and discussed above.

Adults and larvae of *Hintonia britskii*, and in one instance a single pupa, were found in the same biotope in all localities, but larvae seem to prefer faster running water (perhaps because it is more oxigenated). Adults are found closer to the margin, always completely submersed in the running water, on the surface of the rocks covered with algae and other detritus. There was always less than one or two cm of water in the place of collection, usually a few millimeters. Adults move around very slowly, always in contact with the rock. Several couples were found in copulation. Individuals were collected one by one, with the help of tweezers, a very difficult, tiresome and non-productive process in running water.

The first specimens of *Hintonia castalia* were collected together with *Hintonia britskii*, having only been identified as a distinct species after study in the laboratory. In the second locality I collected only *Hintonia castalia*. This locality (mountains in Nova Friburgo) is a slightly different habitat, an abandoned stone-quarry, but the species was only collected in places of very fast runing water, a kind of artificial cascade, where I never found a single species of *Ytu*.

Larvae of *Hintonia britskii* were collected together with the adults, but apparently in faster running waters. They also live on the surface of rocks, fixed to algae, in a maximum depth of one or two cm, always completely covered by the film of water. Two different larval instars were collected at the same locality, at the same time; four in another one

The only pupa of *Hintonia* I have colected was found in the same habitat, together with adults and larvae of *Hintonia britskii*.

Ytu

All species of Ytu described below were collected in the hygropetric habitat, especially along roads in southeastern Brazil. In this rather specialized and little explored habitat, larvae, pupae and adults live in conditions similar to waterfalls, e.g., submersed, on the surface of algae-covered rocks. They supposedly live on a diet of algae (Crowson, 1955:3).

The habitat of Ytu is much less constant than waterfalls. The film of water suffers more directly the consequences of drought. It can even disappear completely, as I have observed in some localities where I collected more than once. The film of water is also much

thinner than in a waterfall, and being directly exposed to the sun, its temperature can rise much more easily. In regard to the complete drying out, the hygropetric habitat is more similar to the habitat in which *Torridincola rhodesica* was first collected (temporary streams).

Some details of the ecology of species of Ytu are worth being mentioned, but their study is made difficult by the impossibility of recognition of the different species in the field. As will be seen below usually several species occur in the same locality.

Species of *Ytu* apparently prefer light colored rocks, as I discovered in several localities (Domingos Martins, Angra dos Reis, etc.); they are always found on small spots of lighter colored rocks. In localities exclusively with dark rocks, they are usually more scarce, if not absent. In certain localities, as Itu and Valinhos, they were always found on the pink granite, typical of the region.

Most of the localities of Ytu are well above sea level (usually above 400 m, when in the mountains), or in the inland plateau (where the mean altitude is about 500 m, but which may be as low as 250 m, as in Andrade Pinto). Some localities are at sea level. In some mountains the same species was collected from the bottom to the top (Serra de Nova Friburgo, from Cachoeiras do Macacu, at about sea level, to Alto da Serra, at about 920 m).

Species of Ytu apparently occur in their habitat throughout the year, as long as there is water. Ytu zeus was collected in the Serra da Esperança. Paraná, in winter (june), in water with temperature below 10°C. In another locality, Valinhos, São Paulo, I collected the same species during most part of the year. In this latter locality I noted intense variation in the percentage of immature and adult individuals throughout the year, showing that at least Ytu zeus must have several generations a year.

In most localities, especially in those north of the Tropic of Capricorn (see discussion at p. 99), there are several species of Ytu, with a maximum of five in Areal (besides Hintonia britskii), Nova Friburgo and Teresópolis. I should mention that several species can be found in a very limited and homogeneous area, of less than one square meter. Even when two species can be distinguished in the field because of size difference, as in Ytu demeter and Ytu cupidus, I failed to find any habitat difference for the species. Ytu zeus and Ytu athena are allopatric in a large part of their area, but are sympatric and syntopic in Santa Catarina and Rio Grande do Sul.

Sympatry of congeneric species of Myxophaga has already been recorded for Lepiceridae (Lepicerus horni and Lepicerus bufo, collected "in damp trash piles near the margins of streams at Tejupilco, District of Temescaltepec", Mexico; Hinton, 1934: 160) and Sphaeridae (six species of Sphaerius in Hoa Binh, North Vietnam; Lesne, 1936). The two species of Lepicerus are sympatric and syntopic; the data for the six species of Sphaerius are not exact, and it is possible that they are only sympatric.

The present study shows that some Myxophaga are common beetles, and, more important, demonstrates the coexistence of more than one

species in a same locality. This problem should be more carefully studied, since it appears to colide with "Gause's theorem", also known as the "principle of competitive exclusion", according to which "Two species cannot coexist indefinitely in the same locality if they have identical ecological needs" (Mayr, 1970: 43). It is true that I know very little about the species of Ytu that coexist in the same locality. It is not known if the species have different ecological needs or not, nor is it known if the species coexist for a long time, or if they are in the process of competitive exclusion. The probabilities of distinct ecological needs for very closely related species are very small judging from the restricted habitat they live in.

The fauna of the biotope

Waterfalls (habitat of *Hintonia*)

The biotope of Hintonia has a relatively smaller and less well diversified fauna than that of Ytu. Only few arthropods were observed and collected; they all belong to the Class Insecta.

Order Ephemeroptera: larvae (several localities).

Order Trichoptera:

Rhyacophilidae: Rhyacophila (?), larvae (Rio de Janeiro: Nova Friburgo).

Helicopsychidae: larvae (Rio de Janeiro: São Fidelis).

Order Hemiptera:

Saldidae: one adult (*Rio de Janeiro*: Nova Friburgo).

Order Diptera:

Psychodidae: larvae and pupae of Maruina sp. (Espírito Santo: Santa Teresa; Rio de Janeiro: Mangaratiba).

Order Coleoptera:

Hydrophilidae (P. J. Spangler det.): adults of Oocyclus schubarti d'Orchymont (Rio de Janeiro: São Fidelis); Tropisternus nitidulus Brullé (Rio de Janeiro: São Fidelis).

Hygropetric habitat (biotope of Ytu)

The fauna of this habitat seems to be much more diversified than that of waterfalls.

Insecta

Order Ephemeroptera: larvae (several localities).

Order Trichoptera: larvae of Helicopsychidae and (?) Leptoceridae (*Rio de Janeiro*: São Fidelis, Cachoeiras do Macacu and Nova Friburgo; *São Paulo*: Valinhos).

Order Hemiptera:

Veliidae: Velia sp. (nymphs and adults; Espírito Santo: Santa Isabel; Rio de Janeiro: Teresópolis; São Paulo: São Sebastião):

Gelastocoridae: Gelastocoris sp. (one adult, Rio de Janeiro: Serra das Araras).

Order Diptera:

Simuliidae: larvae (São Paulo: Valinhos);

Stratiomyidae: larvae and pupae; one adult (*Rio de Janeiro*: Andrade Pinto, Serra das Araras; *São Paulo*: Itu);

Dolichopodidae: adults (São Paulo: Itu);

Ephydridae: adults (Paraná: Guarapuava, Matelândia);

Psychodidae: pupae of Maruina sp. (São Paulo: São Sebastião).

Order Coleoptera:

Hydrophilidae (P. J. Spangler det.): adults of Oocyclus schubarti d'Orchymont (Rio de Janeiro: Andrade Pinto, Cachoeiras do Macacu, Itatiaia, São Fildelis and Serra das Araras; São Paulo: São Sebastião and Valinhos); Oocyclus decorus (Kuwert) (Rio de Janeiro: Serra das Araras); Oocyclus fryanus Balfour-Browne (Rio de Janeiro: Andrade Pinto, Nova Friburgo and Serra das Araras; São Paulo: Cubatão and São Sebastião); two undescribed species of Oocyclus (Rio de Janeiro: Teresópolis); Tropisternus nitidulus Brullé (Rio de Janeiro: Nova Friburgo); new genus and species (Rio de Janeiro: Itatiaia and Teresópolis; São Paulo: São Sebastião);

Hydraenidae: adults of four new species, probably of new genus (Balfour-Browne, in litt.) (Rio de Janeiro: Itatiaia; Guanabara: Rio de Janeiro; São Paulo: Salesópolis and São Sebastião; Paraná: Morretes; Santa Catarina: Santa Cecília; Rio Grande do Sul: Rio Pelotas and Nova Petrópolis);

Dytiscidae, Hydroporinae, (?) Desmopachria sp., adults (São Paulo: São Sebastião; Guanabara: Rio de Janeiro). Dytiscinae (?), larvae (Rio de Janeiro: Andrade Pinto);

Elmidae: one adult (São Paulo: Salesópolis);

Hydroscaphidae: adults of three species of Scaphydra (Rio de Janeiro: Angra dos Reis, Teresópolis, Andrade Pinto; Espírito Santo: Rio Jucu).

Mollusca, Gastropoda:

Physidae: *Physa* sp. (*São Paulo*: Cubatão); Succineidae (*São Paulo*: São Sebastião).

Amphibia: tadpoles of *Thoropa* sp. (*Rio de Janeiro*: Teresópolis, and other localities).

Discussion of the fauna

Coleoptera are the more abundant insects in the hygropetric habitat, and among these undoubtedly the Hydrophilidae, with several species of *Oocyclus* (some undescribed, and at present being studied by P. J. Spangler, United States National Museum).

Among Coleoptera the discovery of Hydroscaphidae (unknown from the Neotropics until then) and Hydraenidae, a small family of Hydrophiloidea, of which only two species are known from Brazil, is of great interest. The four species of Hydraenidae (at present being studied by J. Balfour-Browne, England), collected with Ytu seem to have a preference for more hidden places, being usually found under a layer of moss which covers the rocks ("habitat bryomadicole", according to Bertrand, 1966: 1732).

Both Hydroscaphidae and Hydraenidae seem to be much less common than Torridincolidae: I have only collected 13 specimens of *Scaphydra*, about 100 of Hydraenidae, but over 1,500 specimens of *Ytu*.

Geographic distribution

Any conclusion on the geographic distribution of the family is premature. Data are accumulating quite fast, suggesting that what is presently known, including the geographic distribution, may change.

The family is at present only known from southeastern Brazil and Africa (Rhodesia, Zaire, South Africa and Madagascar). The uniformity of the known members of the family strongly suggests that this distribution could possibly be the result of continental drift.

In the Neotropical Region the family has a very restricted distribution (probably because of the lack of collections in other areas), having been recorded only in a narrow strip along the Atlantic coast, from Espírito Santo (a little south of Rio Doce, at about 20°S) to northeastern Rio Grande do Sul (about 29°S) (Figs. 1, 2). In Espírito Santo, Rio de Janeiro and eastern São Paulo this strip is very narrow, less than 100 km wide; in southern São Paulo, Paraná and Santa Catarina the distribution extends more to the interior, reaching as much as 400 km inland in Paraná. In Rio Grande do Sul the distribution is limited to a small area in the northeast of the state. Primarily this distribution coincides with the distribution of the Atlantic Forest, including that of the Araucaria Forest in the south.

Up to now there is a coincidence of this distribution with that of the coastal mountain chain in Brazil. Waterfalls and rocks covered with a film of water, the habitat of the known forms, have a certain relation with the mountain system.

I have no doubt that the presently known distribution of Torridincolidae in Brazil is an artifact of collections, especially judging by the distribution of mountains in Brazil and the Neotropical Region in general. It should not be forgotten that the Brazilian species were first collected in their natural habitat less than three years ago, and I have since concentrated my collecting activities in southeastern Brazil, having done a quite complete sampling of the area, especially in the states of Espírito Santo and Rio de Janeiro.

Certain details of the distribution of *Hintonia* and *Ytu* are very interesting. The two species of *Hintonia* and six of *Ytu* (*Ytu hephaestus, Ytu demeter, Ytu artemis, Ytu phebo, Ytu cupidus* and *Ytu morpheus*) are distributed from Espírito Santo, through Rio de Janeiro, Guanabara to São Paulo, here a little south of the Island of São Sebastião, at about 23°50'S (Figs. 5, 6). About here are the northern limits of the two other species, *Ytu zeus* and *Ytu athena*. These species have a peculiar distribution (fig. 4): *Ytu zeus* is abundant in southeastern São Paulo, Paraná and Santa Catarina and northeastern Rio Grande do Sul. In São Paulo and Paraná, *Ytu zeus* has not been collected in the coastal region, but always a little to the interior. In the coastal region of São Paulo and Paraná it is apparently replaced by *Ytu athena*, apparently without superposition. In Santa Catarina and Rio Grande do Sul the two species occur together in the coastal, mountainous region.

The transition area between faunistic elements, which roughly coincides with the Tropic of Capricorn (23°27'S) has already been recorded as important for the distribution of a group of Cerambycidae, the tribe Ibidionini (Martins, 1971: 1363, fig. 690). In Camarotine weevils (Reichardt, 1971a) there also seems to be a certain relation.

Cerambycidae have their distribution directly related to plant formations (their larvae develop in timber), but Martins did not locate any reference on possible changes in the composition of forests, except that more or less at this latitude begins the sub-tropical forest of Araucaria. It is probable that the change of fauna is caused by a change in climate, since there is stronger influence of frost during winter south of this line. It is most interesting that Martins records a certain number of species which occur along the whole Atlantic Forest, some which occur north of the Tropic of Capricorn only, and a smaller number of species whose distribution begins at the Tropic and extends south

A critical study of the distribution of the species of *Camarotus* (Reichardt, 1971a) shows that about half of the species of *Camarotus* occurs in the Atlantic Forest; of these six are distributed throughout the Atlantic Forest, eight only north and five only south of the Tropic of Capricorn. I should, however, note that only few specimens of *Camarotus* are known, and not sufficient for a careful analysis, several species being only known from single specimens.

Torridincolidae and Hydroscaphidae do not cross the Tropic of Capricorn, but are apparently limited by it.

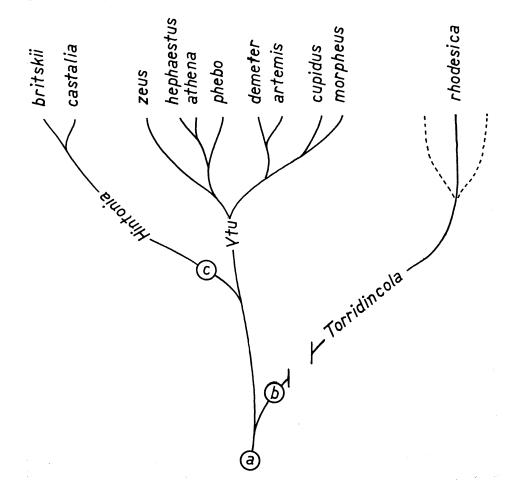
Phylogeny

Due to the poorly known Old World fauna any theory on the phylogeny of the genera of Torridincolidae must be considered provisory.

In the adult phase, the common ancestor of the Torridincolidae must have had the fundamental characters of the family, and the abdomen with five visible sternites, without plastron. In Africa Torridincola maintained the ancestral abdomen with five externally visible sternites, and must have evolved the plastron. In Brazil Ytu, with the ancestral type of abdomen without plastron, represents the most primitive lineage of the family. Hintonia on the contrary evolved a special type of abdomen, with only four sternites visible externally, and, independently must have evolved the peculiar, iridescent plastron. As discussed above, the abdominal structure of Hintonia could be interpreted as a specialization in adaptation to the habitat.

The two species of *Hintonia* are morphologically very close, suggesting a very recent origin.

In the genus Ytu the phylogeny is more complex. There are two species groups, the Zeus species group, characterized by the presence



of strong sexual dimorphism, and the *Cupidus* species group, without sexual dimorphism. Within the *Zeus* species group there is the interesting case of *Ytu zeus*, which has pro- and metasternal setae in males. Within the *Cupidus* species group two species, *Ytu cupidus* and *Ytu morpheus* have small scales on the dorsal surface. A proposed phylogeny is illustrated in the figure on page 101.

Hydroscaphidae

History, forms included and catalog

Hydroscapha, described for the North American species natans. was placed in a family of its own in the original description (Leconte, 1874). Its affinities were not clear, but Leconte suggested relations with Hydrophilidae, Scaphidiidae and perhaps Ptiliidae. In the same year Sharp described the first European species of Hydroscapha, and emphasized the relationships with the Ptiliidae. Mattews (1876: 8) also suggested relations between the two families. Reitter (1909: 264) included Hydroscaphidae, Sphaeridae and Ptiliidae in the Ptiliida of Polyphaga. Based on the larva of Hydroscapha natans, Böving (1914: 172) placed the genus in the Hydrophilidae, in a subfamily of its own, the Hydroscaphinae. Later on, still based on larval characters, Böving & Craighead (1931: 25), considered Hydroscapha as belonging to a distinct family, included in the superfamily Staphylinoidea, next to Limnebiidae. This position was also maintained in Peyerimhoff's system (1933: 101). Based on certain adult characters, d'Orchymont (1945, 1946) linked Hydroscaphidae to Staphylinidae and Ptiliidae, in the group of the Staphyliniformia of Polyphaga. In more recent papers the family is placed in the vicinity of the Ptiliidae, among Polyphaga (e.g. Paulian, 1949b: 996).

The most recent, but very much outdated catalog of the family (Csiki, 1911), lists only five species of *Hydroscapha*, four from Europe and Asia Minor, and one from the United States (California). Many more species have been described since, but their validity is doubtful. This becomes very evident in d'Orchymont (1945, 1946), who analysed materials from Europe, Asia Minor and southeastern Asia, and reached the conclusion that the four Old World species considered valid in Csiki (1911), actually represent a single species, which apparently has a continuous distribution from southern Europe to southeastern Asia. Other authors, e.g. Hinton (1969b), accept this interpretation. It is very unfortunate that d'Orchymont's papers were not up to date, not including some species already described at the time, which, judging solely from their distribution, may well be more synonyms of *Hydrosca-pha granulum* (Motschulsky, 1855), the species discussed above.

One of the great needs in this family is thus a revision of the Old World forms.

Accepting d'Orchymont's concept for Hydroscapha granulum, Hydroscapha, the only genus of the family to date, includes five species

in Europe and Asia, a single species in Northern Africa, one in Madagascar and one in the United States (California and Arizona). The first Neotropical species of the genus is from Mexico, but has not yet been described (Hinton, 1969b: 153).

The three species I discovered in southeastern Brazil and which were described in the genus Hydroscapha (Reichardt, 1971b), are here removed to a new genus, Scaphydra.

- Hydroscapha Leconte, 1874: 45 (type-species, original designation, Hydroscapha natans Leconte, 1874).
 - granulum Motschulsky, 1855: 84 (Lymnobius; type-locality, Turkey, Izmir); d'Orchymont, 1845: 14 (synonymy).
 - crotchi Sharp, 1874: 103 (type-locality, Spain, Madrid).
 - gyrinoides Aubé, 1863: 127 (*Limnebius*; types from France, Frejus and Asia Minor).
 - sharpi Reitter, 1887: 508 (type-locality, Russia, Lenkoran). longicauda Rey (type-locality, Spain, Madrid. See Peyerimoff, 1922: 74, note 1, on the description and date of this species).

Distribution: southern Europe (Spain, France, Italy, Greece, Creta, Bulgaria and Russia), Asia Minor and southeastern Asia (North Vietnam).

- hunanensis Chih, 1948: 75-77, fig. 1 (type-locality, China, Hunan, Hungshan).
- mauretanica Peyerimhoff, 1922: 73, fig. 1 (type-locality, Algeria, Mouzaia).
- natans Leconte, 1874: 46 (type-locality, United States, California, Los Angeles).
 - Distribution: United States (California and Arizona).
- saboureaui Paulian, 1949a: 371-373, fig. 17 (type-locality, Madagascar, 60 km S of Ankavandra).
- substrigosa Champion, 1920: 170 (type-locality, India, Kumaon, Ranikhet).
- takahashii Miwa, 1935: 352-353, fig. (type-locality, Taiwan, Taihoku, Shinten).
- turbinata Champion, 1925: 173 (type-locality, India, Kumaon, Bodiar).
- Scaphydra, gen. n. (type-species, present designation, Hydroscapha hintoni Reichardt, 1971).
 - angra Reichardt, 1971b: 291 (Hydroscapha; type-locality, Brazil, Rio de Janeiro, Angra dos Reis).
 - hintoni Reichardt, 1971b: 290-291, figs. 1-6 (Hydroscapha; typelocality, Brazil, Rio de Janeiro, Andrade Pinto).

pygmaea Reichardt, 1971b: 291 (Hydroscapha; type-locality, Brazil, Espírito Santo, Rio Jucu).

External anatomy

Membranous wings

Hydroscapha lacks an important hind wing character of Myxophaga: the "oblongum" (Forbes, 1926: 61, fig. 22), Scaphydra hintoni also lacks the cell (fig. 38).

The reduction of the wings of *Scaphydra angra* has already been discussed above. The very scarce material of this species, did not allow a better study of the wings. I can only add that the reduced wing is kept unfolded under the elytra, and that in this position it does not reach the apex of the elytra.

Abdominal structure

There still persist some doubts about the abdominal structure of Hydroscaphidae. The main problem is the displacement of sternites in relation to tergites (as also happens in Staphylinidae). D'Orchymont (1945: 7-11) discussed the abdomen of *Hydroscapha* in detail. There are eight tergites and seven sternites (there are also eight tergites in *Scaphydra hintoni*, fig. 113).

Most descriptions of species of *Hydroscapha* refer to the dense and recumbent pilosity on abdominal tergites II and III. Normally this pilosity is covered, at least partially, by the elytra. Paulian (1949a: 371-372), for example, says that: "... tergite abdominal II avec une dense pubescence épineuse de chaque côté du milieu en deux plages transversales où les soies s'orientent de dehors en dedans; tergite III avec une dense pubescence dont les soies sont dirigées d'avant en arrière".

The correct number of abdominal tergites being eight, this recumbent pilosity is placed on tergites III and IV, on the III directed from the middle of the tergite to the sides, and on the IV from the anterior to the posterior part (fig. 114).

The function of these setae is unknown. They may be related to the retention of an air bubble under the elytra, as suggested by Schwarz (1914: 168) and Böving (1914, fig. I). Hinton (1969b: 156), however, says that "it is possible that Hydroscapha carries a bubble of air under the elytra, but this was not confirmed"; this author puts some doubts on this suggestion because Hydroscapha is unable to renew the air bubble, since it lives in a certain depth of water.

Lesne (1936: 243, fig. 14) described combs of recumbent setae on the posterior margin of tergites VI and VII of *Sphaerius*, suggesting that they have an auxilliary function in the folding of wings. A strong tooth in the middle of the elytral margin, in its internal part, and turned to the suture, which according to Lesne would only be a locking mechanism, could well be related to the folding of the wings.

The structure of the last visible abdominal segment (tergite VIII and sternite VII; Reichardt, 1971b, fig. 4) is very complex, with a series of apparently retractile (or at least mobile) spines. The sexual dimorphism of this segment is discussed below.

Genitalia

D'Orchymont illustrated the aedeagus of *Hydroscapha granulum* and *Hydroscapha natans* (d'Orchymont, 1945: 12, figs. 7, 8). Chih (1948, fig. 1) described and figured the aedeagus of *Hydroscapha hungnensis*.

Basically the aedeagus of Hydroscaphidae is similar to that of Torridincolidae, but seems to lack lateral lobes (d'Orchymont, 1945, mentions "... semble dépourvu de paramères"), and the aedeagus is not split longitudinally. Due to the size of Hydroscaphidae (smaller than Torridincolidae), however, it is possible that the mentioned structures exist, but that they have not been evidenced in the micro-preparations.

I describe below (fig. 62) the aedeagus of *Scaphydra hintoni*. It is a thin, long and coiled structure. Unfortunately the preparation of the single male mounted on slide does not show details of the apex; lateral lobes are not visible either.

It is difficult to compare this genitalia with that of the species of Hydroscapha and Myxophaga in general. It is interesting to note that in Hydroscapha hunanensis (Chih, 1948: 76, fig. 1) the aedeagus has the "...proximal end coiled inward", a character which shows some similarities, even though not as clearly developed as in $Scaphydra\ hintoni$.

Sexual dimorphism

Hydroscapha has sexual dimorphism of the dorsal tegument (males are smooth and shiny, females opaque and microrugose), and of the last abdominal sternite, which in females is complete, but in males shows a deep median incision in the posterior margin (Peyerimhoff, 1922; d'Orchymont, 1945: 7).

In *Scaphydra hintoni*, the only species of which I know both sexes, the last abdominal sternite shows the same sexual dimorphism (fig. 62). The scarcity of the material, however, did not allow a conclusion on the dorsal sculpture.

Habits and ecology

The ecology of *Hydroscapha natans*, a species which lives in hot springs in Arizona, was first described by Schwarz (1914). According to Schwarz (*l.e.*), Paulian (1949a: 371) and Hinton (1969b: 153), *Hydroscapha* lives in swift streams, swimming freely or fixed on algae (Hinton, *l.c.*: 156, mentions that "... they live several inches to as

much as two to three feet beneath the surface of swift streams..."). Miwa (1935: 353), however, found *Hydroscapha takahashii* in a "muddy place at the entrance of a tunnel near Shinten, whereinto a clear water is flowing from above along the wall".

The three species of Scaphydra were collected in the hygropetric habitat, together with the species of Ytu. Hinton (in litt.) collected the Mexican species of Hydroscapha in the same habitat. This also coincides with the description of the habitat of the Taiwanese species (Miwa, 1935).

Geographic distribution

There is no doubt that the geographic distribution of Hydroscaphidae, as known today, only reflets the poor collecting in certain areas and habitats.

The two known genera occur in the Neotropical Region: *Hydroscapha*, possibly a Nearctic element, whose distribution extends from Mexico to Panama and Peru (Hinton, 1969b; *in litt.*), and *Scaphydra*, most probably en endemic element, with its distribution restricted to southeastern Brazil.

Here the species of *Scaphydra* have a distribution similar to that of *Hintonia* and the group of six species of *Ytu* (Torridincolidae), as was discussed in more detail above. It is interesting to note the absence of *Scaphydra* south of the Tropic of Capricorn. This is most probably not due to lack of collecting, since I have looked for them in every locality I have collected Torridincolidae.

Phylogeny

Because of the scarcity of elements I do not venture to propose a phylogeny of the family. As becomes clear from what has been said, very much less is known on the Hydroscaphidae than on Torridincolidae, and it seems to me that very little is known of their real distribution.

One of the difficulties with a phylogeny resides in the almost impossibility of the correct interpretation of the characters of the two genera. Accepting what is usually said for Coleoptera in general, the reduction of antennal segments (eight in Hydroscapha and five in Scaphydra) could be taken as a derivative character (according to Crowson, 1955: 1-3, the ancestral beetle had 11-segmented antennae). Even more difficult is the interpretation of the serration of the abdominal segments. I have no idea about its function, and could not suggest any hypothesis.

Scaphydra could perhaps be considered as a specialized element, which was isolated from the ancestral Hydroscapha, and remained isolated in southeastern Brazil, where it evolved independently. The presence of at least one species of Hydroscapha in northwestern South America, suggests a second invasion of the genus, perhaps of very recent date, if one admits colonization of South America via North America.

Sphaeridae

(= Sphaeriidae, see note on p. 78)

The oldest known species of Myxophaga is *Sphaerius acaroides* Waltl, 1838, from Europe. Genus and species were described as new (Waltl, 1838: 272), but apart from the reference "*Ephistemus*? Westwood" [Cryptophagidae] after the name *Sphaerius*, and a comparison in form of the new genus to *Agathidium* Panzer [Anisotomidae], there was no family assignment for *Sphaerius*.

Erichson (1845) placed *Sphaerius* among the Trichopterygidae (= Ptiliidae), in a distinct tribe, Sphaerina, having apparently been the first author to segregate the genus in a group of its own.

Ever since the systematic position of Sphaeridae has been discussed, but usually the family has been related to the Ptiliidae, a family at present included in Polyphaga. Lacordaire (1854: 224) was the first author to consider Sphaerius at family level, having described the family of the "Sphériens", next to the "Trichoptérygiens". Matthews (1876: 8) placed Sphaeridae, Sphaeridiidae (*), Helophoridae and Hydrophilidae in a group he called "Philhydra", emphasizing the hydrophiloid relationships of Sphaeridae. A few years later, however, the same author (1899: 209) mentioned that the "... Sphaeriidae form a small and somewhat isolated family exhibiting no special affinity to any group except the Sphaeridiidae, and to them only in outward appearance and in the subsolid capitulum of their antennae". Reitter (1909: 264) placed Sphaeridae, Ptiliidae and Hydroscaphidae in Ptilliida, within the superfamily Staphylinoidea of Polyphaga. It is still in the vicinity of the Ptiliidae that the family is found in most papers (Kolbe, 1911: 61; Peyerimhoff, 1933: 101; Lesne, 1936; Blackwelder, 1944a: 85; Paulian, 1949b: 977; Costa Lima, 1952: 343).

A single genus of Sphaeridae, *Sphaerius* Waltl, 1838, is known at present (following Britton, 1966, *Neosphaerius* Oke, 1954, is here considered a synonym). The most recent World Catalog (Csiki, 1910) lists only six species. Eighteen are known at present. Their geographic distribution is very peculiar, perhaps again due to the lack of proper sampling in certain areas. A large number is only known from the type-material. The species have been recorded from Madagascar, southern Europe, Asia Minor, southeastern Asia, Australia, United States, and a single species from Guatemala (also collected in Mexico, Hinton, *in litt.*), the latter obviously a nearctic element which invaded the Neotropical Region.

^(*) A group of aquatic Coleoptera related to Hydrophilidade. Some authors consider it as a distinct family; most include it in the Hydrophilidae as a subfamily (Crowson, 1955: 21, 23).

Catalog

- Sphaerius Waltl, 1838: 272 (type-species, Sphaerius acaroides Waltl, 1838, by monotypy); Matthews, 1899: 209-215 (Revision); Lesne, 1936: 241-248 (Revision of the Old World species).

 Microsporus Kolenati, 1846: 64 (type-species, Microsporus obsidianus Kolenati, 1846).
 - Neosphaerius Oke, 1954: 57-59 (type-species, original designation, Neosphaerius ovensensis Oke, 1954); Britton, 1966: 1194 (Synonymy).
 - acaroides Waltl, 1838: 272 (type-specimens from Germany, Passau and München); Lesne, 1936: 248, figs. 2-5, 7-8, 11, 13, 15). obsidianus Kolenati, 1846: 64.
- Distribution: Europe (France, Italy, Rumania, Austria, Germany, Belgium, Holland and Scandinavia).
 - coenensis Oke, 1954: 59 (Neosphaerius; type-locality, Australia, Queensland, Coen).
 - coomani Lesne, 1936: 248, figs. 1, 6, 9, 12, 17-18 (type-locality, North Vietnam, Hoa Binh).
 - cribratus Lesne, 1936: 248 (type-locality, North Vietnam, Hoa Binh).
 - favosus Lesne, 1936: 248 (type-locality, North Vietnam, Hoa Binh). hispanicus Matthews, 1899: 212, 214 (type-locality, "Spain"); Lesne, 1936: 248, fig. 14.
- Distribution: Europe (Spain and France) and northern Africa (Algeria and Tunisia).
 - laeviventris Champion, 1923: 47, fig. a (types from India, Kumaon, Tanakpur and Ranikhet); Lesne, 1936: 248.
 - madecassus Paulian, 1949a: 373-374, fig. 18 (type-locality, Madagascar, Manambolo).
 - obsoletus Lesne, 1936: 248 (type-locality, North Vietnam, Hoa Binh).
 - ovensensis Oke, 1954: 59, figs. 1-11 (Neosphaerius; type-locality, Australia, Victoria, Harrietville); Britton, 1966: 1194, figs. 1-8.
 - Distribution: Anstralia (Victoria and New South Wales). papulosus Lesne, 1940: 1-3, figs. 1-3 (type-locality, Burma, Washaung).
 - perlaevis Lesne, 1936: 248 (type-locality, North Vietnam, Hoa Binh).
 - politus Horn, 1868: 132 (type-locality, United States, "California"); Matthews, 1899: 212, 214 (described as new species).

scutellaris Leconte, 1878: 599 (Orthoperus; types: Canada, Ontario, Michipicoten River; British Columbia, Lake Labache; United States, "Illinois"); Matthews, 1899: 212.

lucidus Casey, 1900: 67 (Orthoperus scutellaris var.; type-locality, United States, Washington, Spokane).

piceus Casey, 1900: 67 (Orthoperus scutellaris var.; types from United States, "New York" and "Ohio").

Distribution: Canada (British Columbia and Ontario) and United States (Washington, California, Illinois, Ohio and New York).

spississimus Lesne, 1935: 216-217 (type-locality, Corsega, Pisciatella); 1936: 248.

Distribution: Corsega, Sardegna and Israel.

tesselatus Lesne, 1936: 248, fig. 10 (type-locality, North Vietnam, Hoa Binh).

texanus Matthews, 1899: 212, 213 (type-locality, United States, "Texas").

tropicus Matthews, 1888: 157-158 (type-locality, Guatemala, Guatemala); 1899: 212, 215.

Discussion

The Sphaeridae are also aquatic beetles, but their habits differ from those of Torridincolidae and Hydroscaphidae. Most species have been found in the wet sand of river beaches (Lesne, 1936: 241; Britton, 1966: 1194; Arnett, 1968: 212). Only the larva of one of the two Australian species has thus far been made known (Britton, 1966).

I have no doubt that the absence of the family in certain areas of the World, especially in South America, is due to lack of collecting in the proper places, allied to the very minute size of the beetles (0.5 — 0.9 mm).

Sphaeridae are easily characterized among Myxophaga by the almost spherical, very smooth and shiny body with ventral depressions for the reception of the legs, trimerous tarsi, posterior coxae large and contiguous, abdomen with only three visible sternites, and 11-segmented antennae. With reference to the number of abdominal sternites, Lesne (1936: 242-243) considers four and not three sternites, the posterior limits of the podothecae representing the suture between sternites I and II.

Lepiceridae

(= Cyathoceridae)

Lepicerus, the type-genus of the family was described by Motschulsky (1855) as a member of the Georyssidae (apud Hinton, 1936: 472). Sharp (1882: 141) was the first author to consider the genus

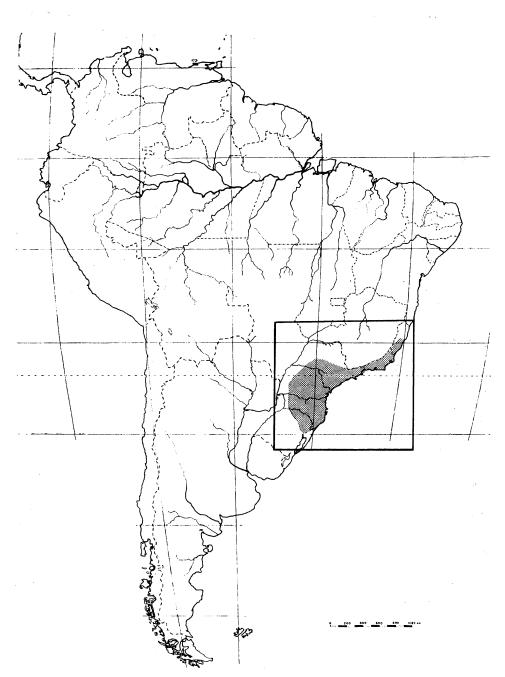


Fig. 1, collecting area of Torridincolidae and Hydroscaphidae in southeastern Brazil.

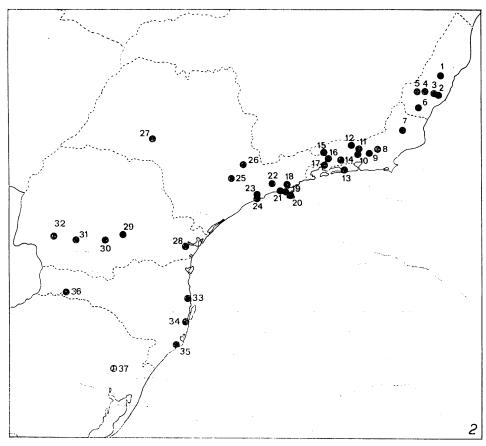


Fig. 2, localities. Espírito Santo: 1, Santa Teresa; 2, Santa Isabel; 3, Domingos Martins; 4, Venda Nova; 5, São João de Viçosa; 6, Atílio Vivacqua. Rio de Janeiro: 7, São Fidelis; 8, Nova Friburgo; 9, Teresópolis; 10, Petrópolis; 11, Areal; 12, Andrade Pinto; 14, Serra das Araras; 15, Itatiaia; 16, Rio Claro; 17, Angra dos Reis. Guanabara: 13, Rio de Janeiro. São Paulo: 18, Caraguatatuba; 19, São Sebastião; 20, Ilha de São Sebastião; 21, 15 km S of São Sebastião; 22, Salesópolis; 23, Cubatão; 24, São Vicente; 25, Itu; 26, Valinhos; 27, Marília. Paraná: 28, Morretes; 29, Serra da Esperança; 30, Guarapuava; 31, Nova Laranjeiras; 32, Matelândia. Santa Catarina: 33, Balneário de Camboriu; 34, 20 km S of Florianópolis; 35, Tubarão; 36, São Carlos. Rio Grande do Sul: 37, Nova Petrópolis

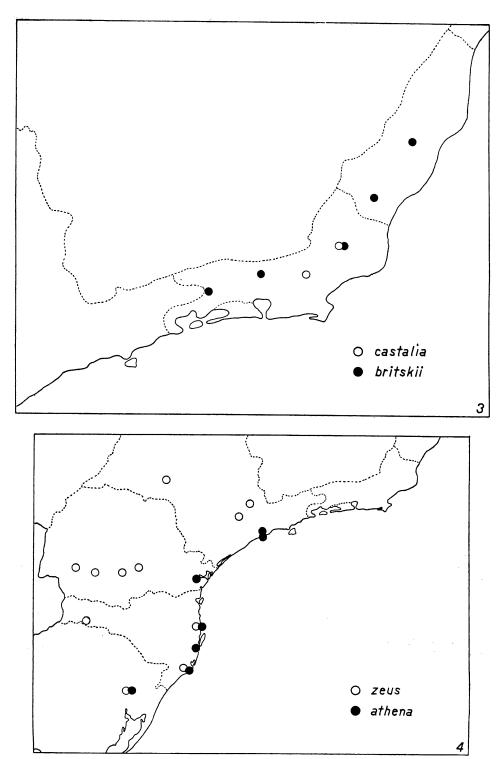
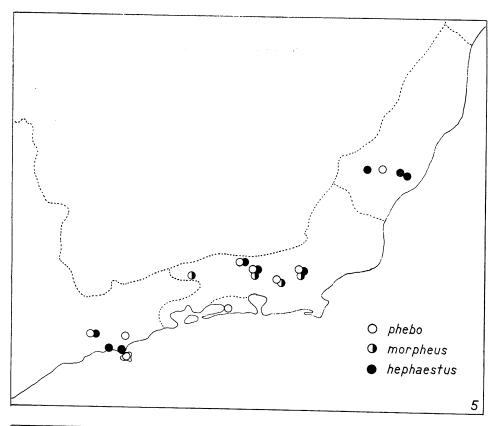
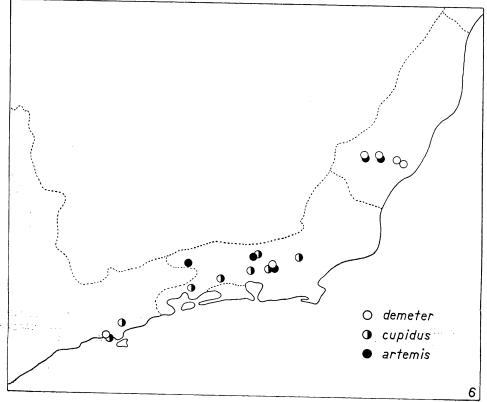
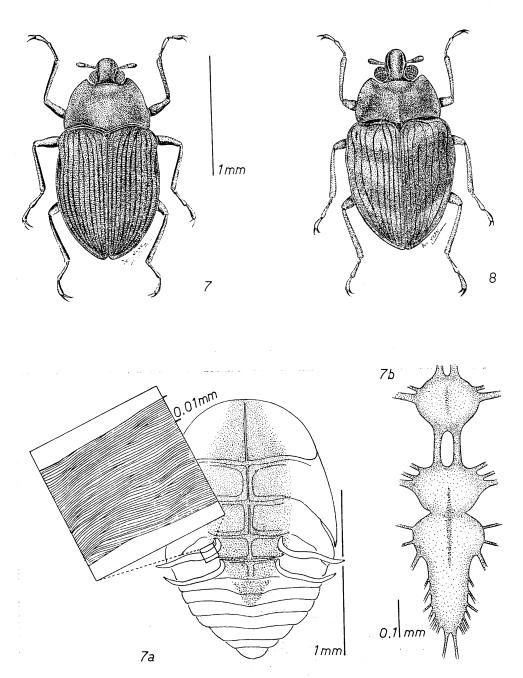


Fig. 3, distribution of species of Hintonia. Fig. 4, distribution of some species of Ytu.

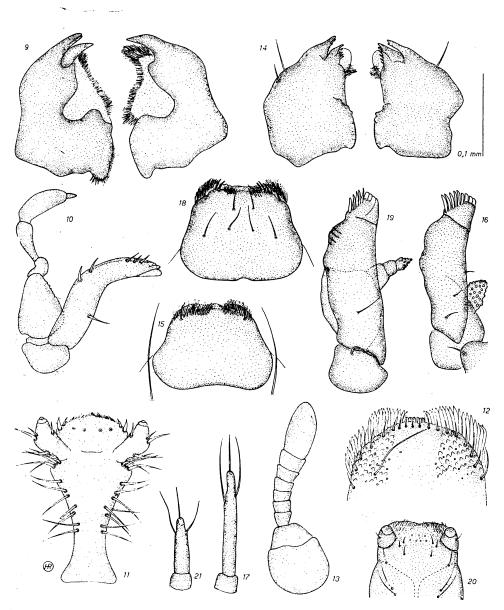




Figs. 5 and 6, distribution of some species of Ytu.

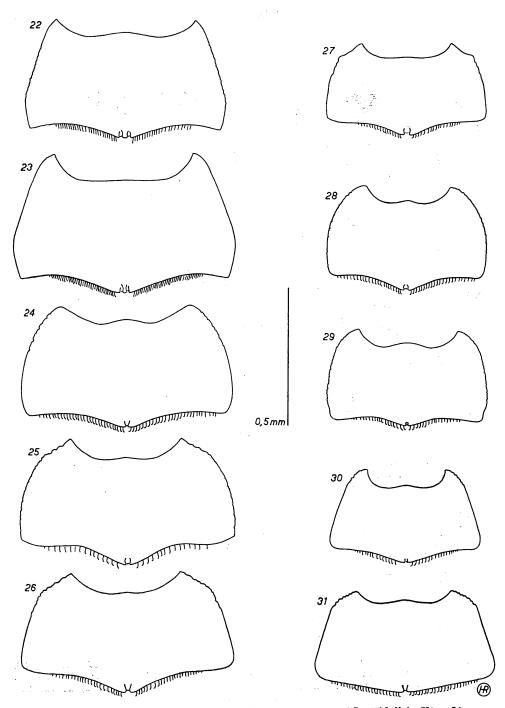


Hintonia britskii. 7, male from Atílio Vivacqua; 7a, pupa from Mangaratiba, with magnification of surface of spiracular gill; 7b, pro-, meso- and metathoracic ganglia of male from Mangaratiba. 8, Ytu zeus, male from Matelândia.

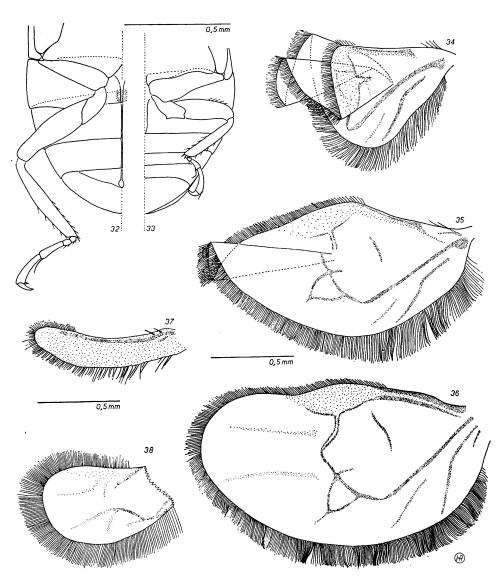


Ytu zeus: adult (from Itu), 9, mandibles; 10, maxilla; 11, labium; 12, labrum; 13, antenna; larva (from Itu), 14, mandibles; 15, labrum; 16, maxilla; 17, antenna.

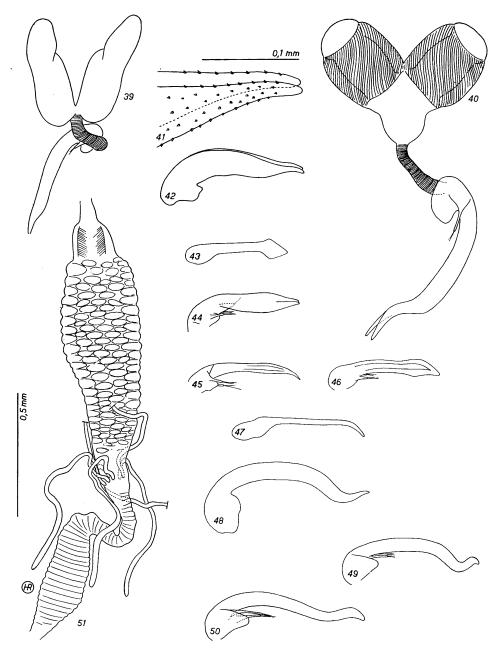
Hintonia britskii: larva (from Santa Teresa), 18, labrum; 19, maxilla; 20 labium; 21, antenna.



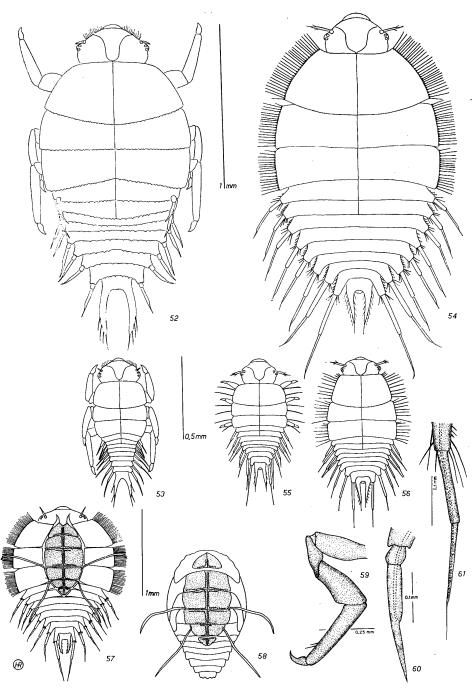
Pronota. Hintonia: 22, britskii (São Fidelis); 23, castalia (São Fidelis). Ytu: 24, zeus (Itu); 25, hephaestus (Areal); 26, athena (Morretes); 27, phebo (Areal); 28, demeter (Venda Nova); 29, artemis (Teresópolis); 30, morpheus (Teresópolis), 31, cupidus (Angra dos Reis).



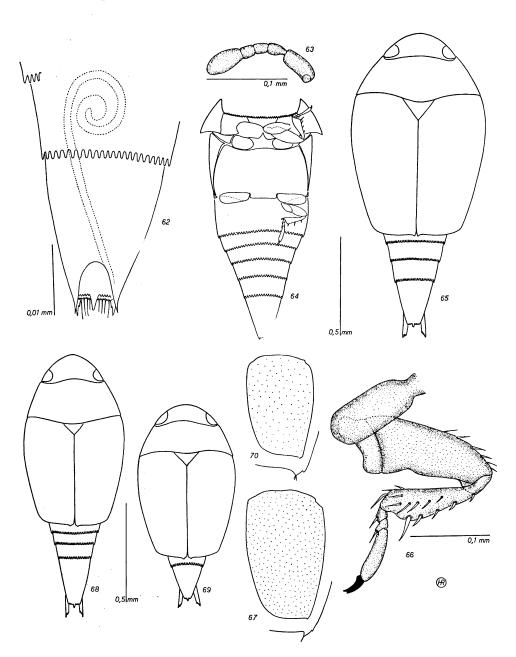
Metathorax and abdomen of males: 32, Hintonia britskii (São Fidelis); 33, Ytu hephaestus (Areal). Wings: 34, 35, Ytu zeus (Itu); 36, Ytu hephaestus (Areal); 37, Hintonia castalia (São Fidelis); 38, Scaphydra hintoni (Andrade Pinto).



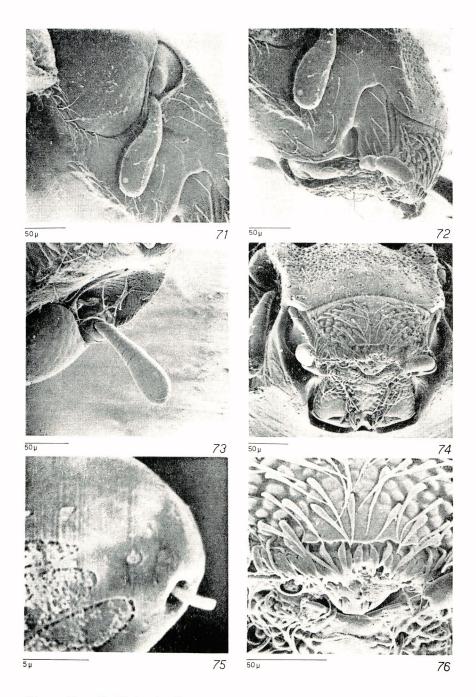
Male genital apparatus: 39, Hintonia britskii (São Fidelis); 40, Ytu zeus (Valinhos). Aedeagi: 41, 42, Hintonia castalia (São Fidelis); Ytu: 43, cupidus (Angra dos Reis); 44, artemis (Teresópolis); 45, 46, demeter (Venda Nova); 47, phebo (Areal); 48, zeus (Itu); 49, athena (Morretes); 50, hephaestus (Areal). 51, Digestive duct of Ytu zeus (Valinhos).



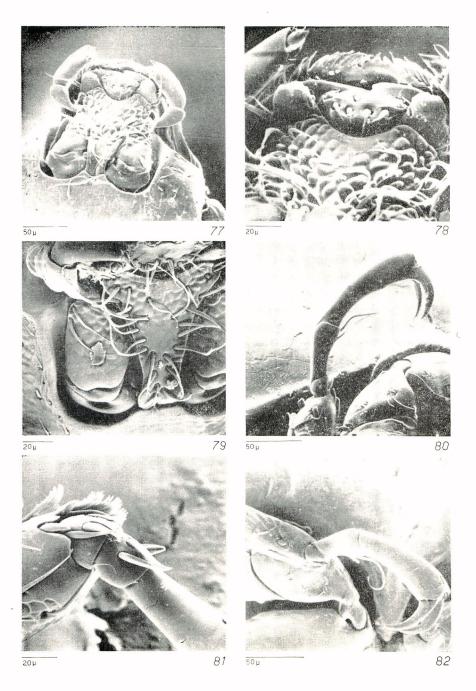
Larvae: Hintonia britskii, 52, last instar (Santa Teresa); 53, (?) I instar (idem); Ytu athena (Morretes), 54, last instar; 55, (?) I instar; 56, (?) II instar. Pupa of Ytu, 57, inside last larval cuticle (Serra da Esperança); 58, exposed (São João de Viçosa). 59 front leg of larva or Hintonia britskii; 60, spiracular gill of same species; 61, same of Ytu sp.



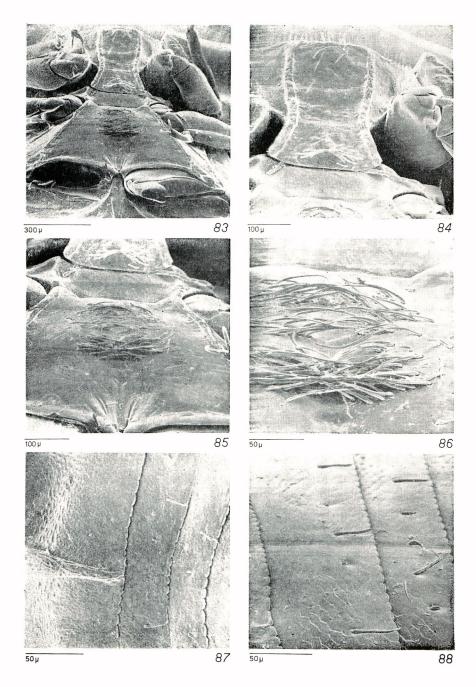
Scaphydra hintoni: 62, abdomen (with aedeagus); 64, ventral view of thorax and abdomen; 65, Q paratype from Andrade Pinto; 66, front leg; 67, elytron. Scaphydra angra: 68, holotype Q; 70, elytron. Scaphydra pygmaea: 63 antenna; 69 holotype Q.



Ytu cupidus: 71, 72, head. Ytu zeus: 73, ventral view of head. Ytu artemis: 74, frontal view of head: 76, mouthparts. Hintonia britskii: 75, apex of antenna.

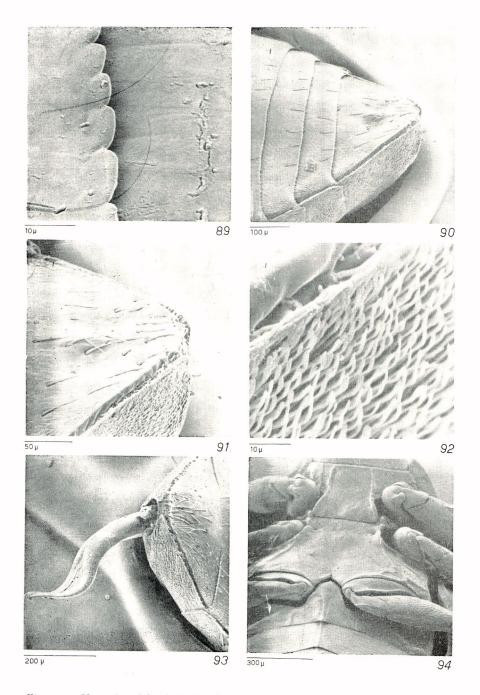


 $\label{eq:cupidus: 77, 78, mouthparts; 80, middle tarsus. $Ytu\ zeus: 81, front tarsus. $Ytu\ phebo: 82, hind tarsus. $Hintonia\ britskii: 79, mouthparts.$}$



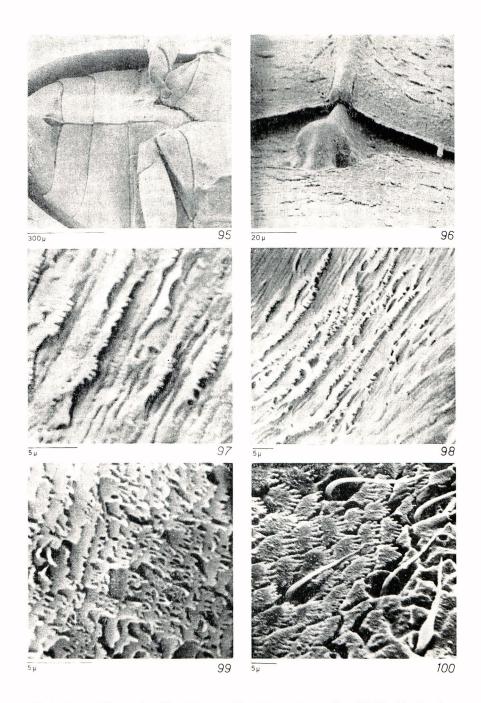
 $Ytu\ zeus,$ male: 83, ventral view; 84, prosternum; 85, metasternum; 86, metasternal setae; 88, abdominal sternites I-IV. $Ytu\ phebo,$ male: 87, idem.





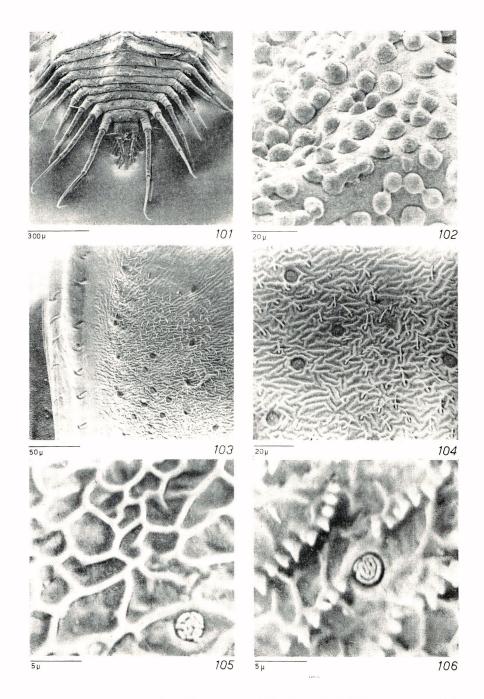
 $Ytu\ zeus:$ 89, male, abdominal sternites I-II; 90-92, abdomen; 93, male, abdomen and aedeagus. $Hintonia\ castalia:$ 94, ventral view of thorax and abdomen.





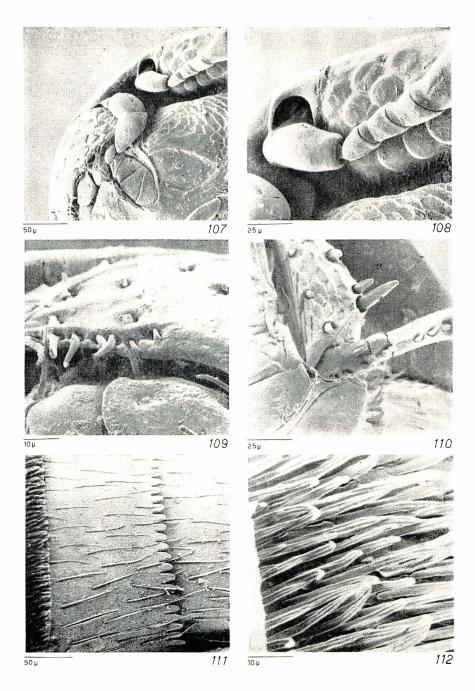
 $Hintonia\ castalia$, male: 95, abdomen: 96, abdominal sternites III-IV; 97, 98, plastron of II sternite. $Hintonia\ britskii$: 99, plastron of IV sternite. $Torridincola\ rhodesica$: 100, plastron of last sternite.



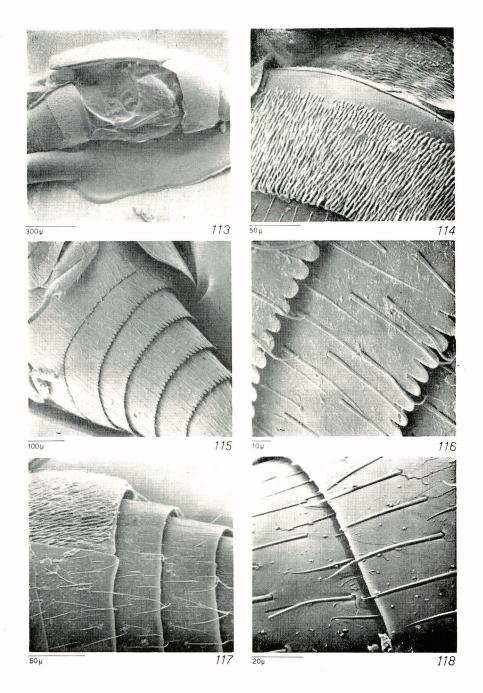


 $Ytu\ zeus:\ 101,\ larva;\ 102,\ surface\ of\ egg;\ 103,\ internal\ surface\ of\ elytron;\ 104,\ idem.$ Scaphydra hintoni: 105, 106, idem.

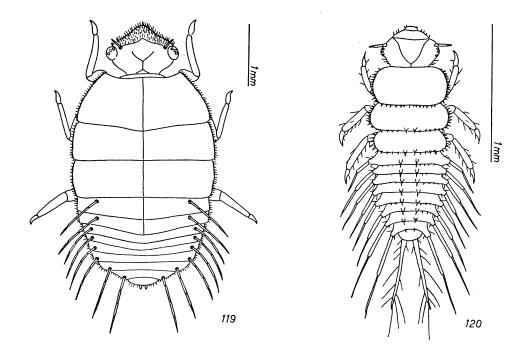




Scaphydra hintoni: 107, ventral view of head; 108, antenna; 109, labrum; 110, front tibia and tarsus; 111, sides of abdomen; 112, setae of IV tergite.



 $Scaphydra\ hintoni:\ 113,\ lateral\ view;\ 114,\ tergites\ III\ and\ IV;\ 115,\ abdomen;\ 116,\ sternites\ II-IV.\ Hydroscapha\ sp.\ (México):\ 117,\ abdomen.\ Hydroscapha\ granulum\ (Bulgaria):\ 118,\ tergites\ IV-V.$



Larvae: 119, Torridincola rhodesica (from Steffan, 1964). 120. Genus B (adapted from Bertrand, 1962).

as forming a distinct family, but described it as a new genus, *Cyathocerus*, because of ignorance of Motschulsky's paper. Sharp discussed the new genus as being a beetle "... which shows no relationship of an evident character to any of the hitherto described Coleopterous families... The position of the family may for convenience be near *Georissus*, to which it bears a certain similarity in size and sculpture, though on investigation it does not appear to be specially allied to the family".

The similarities of *Georyssus* and *Lepicerus* seem not to be more than external, very similar also in form to *Epimetopus*, a genus of Hydrophilidae.

More recent authors (Blackwelder, 1944b: 274; Costa Lima, 1953: 89-91) have included the Lepiceridae and Georyssidae in the superfamily Dryopoidea, Polyphaga. In his study of larval Coleoptera, Peyerimhoff (1933) does not mention the family (its larva is still unknown), but cites Georyssidae, whose larva was also undescribed at the time. The Georyssidae were included in a group of Polyphaga composed of the superfamilies Dascilloidea, Byrrhoidea, Dryopoidea and Sternoxia (Peyerimhoff, 1933: 102). Van Emden (1956) described the larva of Georyssus, concluding that this beetle only forms a subfamily of Hydrophilidae (see also Reichardt, 1973).

Based on the study of the male genitalia, Sharp & Muir (1912: 530-531, 616-619), although placing the Lepiceridae next to Georyssidae, found some affinities with the Cucujoidea (suborder Polyphaga), especially with the family Trogositidae (I have discussed above, at p. 92, that there is the possibility that the genitalia of *Lepicerus horni* was misinterpreted by these authors).

Forbes (1926: 60) found characters of undoubtedly Hydradephagan relations in Lepiceridae.

The relatively scarce material known to date has prevented better study of the relationships of the family. The only known specimens are those of *Lepicerus horni* described by Sharp (1882, 1887), and those collected by Hinton (1934, 1936) together with *Lepicerus bufo*. The material of *Lepicerus horni* collected by E. Simon in Venezuela, and listed by Grouvelle (1889: 165), was not located by myself in Grouvelle's collection (Paris Museum, 1971).

Lepicerus inaequalis Motschulsky, described from Panama, could well be a synonym of Lepicerus horni, a species distributed from Mexico to Venezuela (accepting Grouvelle's identification as correct). The type of Motschulsky's species, however, has not been examined critically by recent authors, and the original description is too short for any conclusion.

Catalog

Lepicerus Motschulsky, 1855: 4 (type-species, Lepicerus inaequalis Motschulsky, 1855, by monotypy).

Cyathocerus Sharp, 1882: 142-144 (type-species, by monotypy, Cyathocerus horni Sharp, 1882); Hinton, 1936: 472 (Synonymy).

bufo Hinton, 1934: 162 (Cyathocerus; type-locality, Mexico, Temescaltepec, Tejupilco).

horni Sharp, 1882: 144, pl. IV, fig. 18 (Cyathocerus; type-locality, Guatemala, Guatemala); Hinton, 1934: 161-162 (Cyathocerus; Mexico).

Distribution: Mexico, Guatemala, Costa Rica, Panama and Venezuela.

inaequalis Motschulsky, 1855: 4 (type-locality, "Panama").

Discussion

Very little is known on the habits of Lepiceridae. Hinton (1934: 161) collected two species "in damp trash piles left in certain protected corners of a canyon by the alternate rising and receding of the river"; Grouvelle (1889: 165), who cites *Lepicerus horni* from Venezuela, says "... cette espèce vit sous les pierres, dans les endroits secs et légèrement sabloneux". It is possible that *Lepicerus* has habits similar to *Sphaerius*.

Immature stages are still unknown.

The geographic distribution of Lepiceridae is much more restricted than that of the other Myxophaga: it is the only family restricted to the Neotropical Region. It is, however, possible that the known distribution only reflects the lack of collections in other areas, as in the other families of Myxophaga.

The Lepiceridae are characterized by the uni-segmented tarsi, antennae with only four segments and abdomen with five visible sternites.

TAXONOMY

KEY TO FAMILIES OF MYXOPHAGA

TORRIDINCOLIDAE

Torridincolidae Steffan, 1964: 199; Reichardt & Costa, 1967: 13; Hinton, 1967: 957-958; 1968: 120-122, 156-158; 1969a: 131.

Adults. Very small sized beetles (1 to about 2.5 mm total length), dark colored, almost black, frequently with metallic sheen. Head slightly produced anteriorly. Antennae nine-segmented, scape and pedicel forming a single, globose piece; other segments slightly transverse, increasing in diameter towards apex; last segment longer than wide, clubbed. Mouthparts: mandibles with distinct mola, and the left mandible with articulated pre-apical tooth. Maxillae with single maxillary lobe. Abdomen with four or five visible sternites. Tarsi tetramerous. Membranous wings well developed, with marginal fringe of long hairs; venation reduced, with well developed oblong cell (= oblongum).

^(*) Crowson (1955: 11) says "Tarsi 2- or 3-segmented...", an incorrect reference, since both Sphaeridae and Hydroscaphidae have trimerous tarsi.

Male genitalia: aedeagus elongate and more or less deeply split longitudinally along the median line; lateral lobes short or long, each with a pair of long, terminal setae.

Larvae. Well characterized by eight pairs of spiracular gills on abdominal segments I to VIII. Antennae with two-segments (three in genus B), with short scape and long apical segment. Thorax and abdominal tergites I and II with median longitudinal (ecdysial) suture well visible. Abdominal segment IX with or without urogomphi; segment X small, hidden under IX. Legs of the Polyphagan type, with five segments and simple claw. Number of larval instars probably four.

Pupae. Adecticous and obtect (see Hinton, 1946), The pupa remains inside the cuticle of the last instar, which is split open dorso-longitudinally to expose the dorsal parts of the pupa. Characterized by a pair of tubular or laminar, unsegmented and relatively long spiracular gills on the first two andominal tergites.

Type-genus, by original designation, Torridincola Steffan, 1964.

Taxonomic discussion

Relationships of Torridincolidae with the other families of Coleoptera, but especially with the other families of Myxophaga, have been discussed in detail above.

KEY TO GENERA (ADULTS)

- - All elytral striae very distinct. Pronotum only very little narrower than elytra at base, its sides always strongly divergent towards base. III tarsal segment about as long as IV. Abdomen with four or five visible sternites, either with plastron on three distal segments, or without plastron. Southeastern Brazil . . 2

KEY TO GENERA (LAST INSTAR LARVAE)

- 3. Lateral margin of thoracic segments with short setae. Thorax longer than wide. Meso-, metathorax and eight first abdominal tergites with a pair of piliferous tubercles along median line. Legs visible from above. 1.5 mm. South Africa Genus B
 - Lateral margin of thoracic segments with fringe of long setae. Thorax wider than long. Piliferous tubercles absent along median line of thorax and abdomen. Legs completely hidden under the body. 1.7 mm. Southeastern Brazil . . . Ytu, gen. n.

Hintonia, nom. n.

Ptyopteryx (nec Kolenati, 1848: 73, for Trichoptera) Reichardt & Costa, 1967: 13-14; Hinton, 1969a: 132.

Adult. Head slightly produced anteriorly; eyes reniform, not prominent, without incision, with posterior part hidden under front margin of prothorax. Frons and vertex regularly convex, finely micro--rugose and deeply punctate; from separated from antennae by a sharp, longitudinal keel which runs from anterior margin of eye to clypeus; fronto-clypeal suture not visible. Two gular sutures. Antennae short, about as long as the largest diameter of eye; with nine segments; scape large and pedicel relatively small, together forming a spheroid piece; six following segments short and regularly increasing in diameter towards apex; apical segment as long as the four preceding segments together, clubbed. Labrum large, almost completely covering the mandibles, with long and dense pilosity anteriorly, and very long, recumbent setae in the middle. Mandibles relatively large, the left one with articulated pre-apical tooth, and both with distinct mola. Maxillae with single maxillary lobe; maxillary palpi with elongate, apical segment. Labium with fused glossae and paraglossae; labial palpi short, apparently with elongate basal segment and two very small, hidden, apical segments. Pronotum anteriorly as wide as head, regularly widened towards basal third, where it forms a slight angle, and from here on narrows abruptly; anterior and posterior angles sharp; basal margin with median emmargination, with two small and parallel incisions in the middle (figs. 22, 23), the incisions only visible in microscope preparations; with a pre-basal carina underneath, which runs almost parallel to basal margin, and is densely pilose. Surface more or less regular, very convex, glabrous, punctate or micro-rugose.

Scutellum very small, triangular, sides slightly curved, base straight. Elytra wider than base of pronotum, regularly widened from humeri to middle, where they are widest; abruptly narrowed in a regular and smooth curve from middle to sutural angle; the latter sharp. Elytra very convex, finely micro-rugose and punctate-striate. Each elytron with 13 striae, some partially erased and irregular, especially near lateral margin in the transverse depression just behind humeri. Interstices convex, except the pre-marginal, which is continuous and keeled; pre-marginal stria deeper, more densely and more irregularly punctate than others. Prosternum with large prosternal process, almost as wide anteriorly as the whole length of prosternum; coxal cavities open behind, separated from each other almost as much as length of prosternum. Mesosternum very short, shorter than wide, and slightly wider than prosternal process; middle coxal cavities slightly more separated than anterior ones. Metasternum much longer, depressed in the middle; transverse suture well visible; posterior coxae closer than median ones. Legs long, tarsi tetramerous (fig. 32), claws simple; posterior trochanters without denticle on posterior margin. Membranous wings well developed in the type-species, with fringe of long, marginal setae; venation reduced, oblong cell closed (Reichardt & Costa, 1967, fig. 11); folded as in the species of Ytu. Hintonia castalia with reduced hind wings, with a single, reduced vein (costa) and unfolded (fig. 37). Abdomen with four visible sternites, I, II and III about equally long; short segment hidden under I (fig. 32), only visible in microscope preparations; last sternite about twice as long as III, with a semi-lunar depression basally. In females the depression is prolonged towards apex (figs. 95, 96). Visible sternites I, II and III with median keel, which ends in a bulbar structure in the depression of last sternite (fig. 96). Three distal sternites with iridescent plastron (figs. 97-99). Male genitalia with elongate aedeagus, which is split longitudinally in a variable extension; lateral lobes short and small, each with two terminal setae.

Immature stages. Larvae of Hintonia, most probably of the type-species, were collected in most localities where I collected adults. In most samples are represented more than a single instar. In one from Santa Teresa, Espírito Santo, I have two instars, several of the last and a single one possibly of the first instar. These are described below. As the last instar is more diagnostic, it is described first; only distinctive characters are given for the other instars.

More recently I collected a larger sample (24 larvae in Mangaratiba, Rio de Janeiro, 1-2.IV.1972), in which it is possible to distinguish four different instars. They are best separated by body proportions: as the larvae grow, they increase in width relatively to length, as shown in graph 1 and table 2.

A single pupa, probably of the same species, was collected more recently too (14.II.1972) in Mangaratiba, Rio de Janeiro, and is described below.

Last instar larva (fig. 52). Total length, 1.93 mm; width at mesonotum, 0.90 mm. Head small, transverse, partially covered by the pronotum. Mouthparts completely hidden under the labrum (fig. 18); mandibles with well developed mola and prostheca (fig. 14); maxillae with distinct cardo and stipes, galea and lacinia apparently fused; with short, three-segmentd palpi (fig. 19), last segment of palpi with pointed tubercles; labium densely pilose anteriorly, with short, two--segmented palpi (fig. 20). Antennae (fig. 21) inserted in front of the ocellar protuberance, two-segmented, with small, spheroid, basal segment, and longer apical segment, the latter with three setae, two pre-apical and one apical. Each ocellar protuberance apparently with three ocelli. Frontal and epicranial sutures clearly impressed. Surface impunctate, glabrous on frons and vertex, with a series of long and erect setae (about as long as antennae) around front margin, between antennae and labrum. Thorax about twice as long as head, widest in mesothorax; slightly wider than long; medio-longitudinal suture clearly impressed; surface finely granulate, also granulate along lateral margins; glabrous and impunctate. Prothorax slightly longer than meso- and metathorax, these about equally long; posterior margin of the three thoracic segments finely dentate. Lateral margins of prothorax in continuous curve with anterior margin, without angle. Abdomen with ten visible segments, about as long as thorax, each segment about as long as the preceding, decreasing regularly in width towards apex. Segment I narrower than metathorax; medio-longitudinal suture present in tergites I and II; surface of tergites granulate, their posterior margin finely and irregularly dentate. Segments I to VIII with a spiracular gill on each side; gills directly articulated to tergite, two--segmented, with short and globose basal segment (about as long as wide), and a long apical segment; the latter covered with fine plastron mesh (fig. 60). Each gill with tracheal branch which opens more or less in the middle of the apical segment. Segment IX slightly wider than long, without gills, but with a pair of unsegmented urogomphi, which are longer than the spiracular gills, about four times as long as segment IX. Segment X short, bilobed, partially hidden under IX. Legs with five segments (fig. 59), front and median coxae globose, the posterior ones transversely elongate; trochanters triangular; femora long, widest in the middle; tibiae slightly longer than femora, wider at base than at apex; tarsi uni-segmented, with a single, curved claw. Front legs only slightly separated; middle and hind coxae separated from each other about as much as their own width; femora reaching margin of thorax; tibiae and tarsi visible from above.

First (?) instar larva (fig. 53). Total length, 0.9 mm; width at mesonotum, 0,35 mm. This instar differs very much from the larva described above, by the head, which is about as wide as the prothorax, as well as by the almost completely smooth, non-granulate cuticle, the posterior non-dentate margin of the thoracic and abdominal tergites, and by the spiracular gills. These are only slightly shorter than those of the last instar, but the basal segment is about as long as the

apical segment; in this instar the plastron mesh is also restricted to the apical segment.

Pupa (fig. 7a). Adecticous, obtect. Protected by the cuticle of the last larval instar, which opens along the median, ecdysial line, from the head to the II abdominal tergite, exposing the dorsal parts of the pupa. The exposed part is heavily sclerotized from the prothorax to the IV abdominal tergite, the sclerotized part diminishing towards the abdomen, being very small and triangular in the IV tergite. Remaining parts weakly sclerotized, white. Head hidden under pronotum; wings well developed, almost touching each other ventrally; abdomen with nine visible segments; each of the two first segments with a pair of laminar, flattened spiracular gills arising from the antero-lateral angle of the sclerotized part. Gills shorter than abdomen (each gill about as long as the width of the sclerotized part of the corresponding abdominal tergite). Surface of gill very finely and longitudinally striate (fig. 7a, inset.).

Type-species, by original designation, *Ptyopteryx britskii* Reichardt & Costa, 1967.

Taxonomic discussion

After the publication of *Ptyopteryx* (1967), I collected numerous specimens of *Hintonia britskii* (larvae, pupa and adults), as well as a new species of the genus. In consequence it was possible to study the genus more carefully, and it is necessary to make some corrections and additions.

First of all I discovered that *Ptyopteryx* Reichardt & Costa, 1967 is preoccupied by *Ptyopteryx* Kolenati, 1848, a genus proposed for an European Trichopteran. The new name *Hintonia* is proposed as a replacement for *Ptyopteryx* Reichardt & Costa, 1967. The name is given in honor of Professor Howard E. Hinton, F. R. S., University of Bristol, whom I owe very much.

Hintonia is easily distinguished from Torridincola and Ytu by the number of visible abdominal sternites (four in Hintonia, five in the other genera). With Torridincola Hintonia shares the presence of abdominal plastron, but while in the former the plastron has a scaly structure and covers all five sternites, in Hintonia the plastron is iridescent and covers only the three distal segments. Other characters which distinguish Hintonia from Ytu are: two basal incisions of pronotum (a single one in Ytu); hind trochanters unarmed (toothed in Ytu); legs long and visible from above (short and in part hidden under the body in Ytu); and elytra with larger number of elytral striae. Mouthparts of Hintonia, Ytu and Torridincola are very similar, differing only in minor details.

Larvae of *Hintonia* differ very much from those of the other genera, especially by the completely glabrous lateral margins of thoracic segments. From *Ytu* larvae of *Hintonia* are also distinguished by the

relatively short spiracular gills (shorter than urogomphi in Hintonia, longer in Ytu), and by the exposed legs (completely hidden under the body in Ytu). Very interesting to note are the completely different maxillary palpi (figs. 16 and 19) of the two genera.

In the pupal stage *Hintonia* differs from *Ytu* (and *Torridincola*) by proportionally shorter and laminar spiracular gills (in *Ytu* they are long and cylindrical).

Hintonia seems to be the more evolved genus of Torridincolidae, especially because of the peculiar abdominal structure, with only four externally visible sternites, and the also very peculiar iridescent plastron. Only two species are known, both very closely related. The almost complete reduction of wings in Hintonia castalia, without an atrophy of other structures normally related to winglessness, perhaps indicate a quite recent origin of this species. The two species of Hintonia occur more or less sympatrically with six species of Ytu (figs. 3-5), north of the Tropic of Capricorn. As discussed in detail elsewhere, Hintonia lives in waterfalls, while Ytu occurs in the hygropetric habitat.

KEY TO SPECIES

1. Pronotum densely and coarsely punctate. Wings normally developed and folded under elytra. Aedeagus as in fig. 39. Slightly larger species (1.50-1.85 mm), females visibly larger than males britskii (Reichardt & Costa, 1967)

Hintonia britskii (Reichardt & Costa, 1967), comb. n.

(Figs. 7, 7a, 7b, 18-22, 32, 39, 52-53, 60, 75, 79, 99)

Ptyopteryx britskii Reichardt & Costa, 1967: 14-17, figs. 1-12 (Type-locality, Brazil, Rio de Janeiro, São Fidelis; Holotype &, MZSP); Hinton, 1969a: 132, figs. 1a-f.

Male. Black and shiny, frequently with brownish elytra; legs brown, with black knees. Sides of pronotum regularly curved, with a slight angle near base (fig. 22). Surface of pronotum convex and regular, densely and coarsely punctate. Elytra punctate-striate, the striae very clearly punctate; interstices convex, with fine and irregular, transverse striae; pre-marginal interstices keeled, continuous from humeri to sutural angle. Depression between abdominal sternites III and IV semi-lunar. Wings normal. Aedeagus short and robust, abruptly narrowed near apex (fig. 39).

Female. Colored as male, but frequently punctures of head, pronctum and elytral striae with intense metallic sheen. Semi-lunar depression on abdominal sternites III and IV prolonged in the middle towards apex. Larger in size than males.

	8	φ
Total length	1.50-1.85 (1.70)	1.67-1.92 (1.77)
Elytral length	0.95-1.25 (1.15)	1.15-1.32 (1.23)
Pronotal width (base)	0.62 - 0.80 (0.72)	0.70-0.77 (0.73)
Maximum elytral width	0.77 - 1.05 (0.94)	0.92-1.12 (1.00)

Internal anatomy (specimens from São Fidelis and Mangaratiba, Rio de Janeiro). Alimentary duct as in Ytu zeus (p. 138, fig. 51), anterior part of mid-gut destitute of caeca; hind-gut with a short curve in the abdominal region. Six Malpighian tubes, which apparently are turned backwards towards rectum, and ending freely in the body cavity. Male reproductive organs: testes longer than wide, tubular and coiled; one pair of elongate accessory glands (fig. 39) which are fused basally, and are connected to a single, short ejaculatory duct, which opens in the aedeagus. It was impossible to see where the testes are connected to the system. Nervous system: ventral nerve cord (fig. 7b) reduced to three ganglia, the prothoracic ganglion, which is closely connected to the mesothoracic ganglion, and this connected to the more or less elongate metathoracic ganglion. Brain and suboesophageai ganglion about equally well developed, about the same size as the prothoracic ganglion.

Material examined (see fig. 3)

Brazil. Espírito Santo: Atílio Vivacqua (Rio Muqui), 3.IV.1969 (H. Reichardt & P. E. Vanzolini) (7 &, MZSP); Santa Teresa (Rio Saltinho, 675 m), 1-2.IV.1969 (H. Reichardt) (11 &, 7 &, MZSP); idem (Cachoeira Santa Lúcia), 1-2.IV.1969 (H. Reichardt) (16 &, 27 &, MZSP). Rio de Janeiro: Areal (10 km SE, 500 m), 13.XII.1969 (H. Reichardt) (4 &, 7 &, MZSP); Mangaratiba (Cachoeira do Saí), 14.II.1972 (H. & B. Reichardt) (8 &, 12 &, MZSP); idem, ibidem, 7.III.1973 (H. Reichardt) (5 &, 10 &, MZSP); São Fidelis (Córrego Pedra d'Água), 25.I.1965 (H. Britski) (Holotype &, MZSP; 9 &, 7 & paratypes); idem, 18.XII.1968 (H. Reichardt) (35 &, 64 &, MZSP); ibidem, 30.VIII.1971 (H. & B. Reichardt) (1 &, 8 &, MZSP).

Taxonomic discussion

Hintonia britskii is extremely similar to Hintonia castalia. The first four specimens of the latter, collected together with over 100 specimens of Hintonia britskii, were only discovered when the large sample was prepared and measured.

Hintonia britskii is slightly larger in size; its females are slightly larger than males; the pronotum is much more coarsely punctate

(usually only micro-rugose, but frequently finely punctate in *Hintonia* castalia); and its aedeagus is quite distinct.

Hintonia castalia, sp. n. (Figs. 23, 37, 41, 42, 94-98)

Types

Holotype &. Brazil. Rio de Janeiro: Nova Friburgo (Serra, 920 m), 28.VIII.1971. H. & B. Reichardt) (MZSP).

Paratypes. Brazil. Rio de Janeiro: idem (13 à, 14 a, MZSP); São Fidelis (Córrego Pedra d'Água), 18.XII.1968 (H. Reichardt) (4 à, MZSP).

Male. Bluish-black, with brownish legs and black knees. Sides of pronotum regularly curved, widening from apex to base, and widest slightly before base, and from here on narrowed abruptly (fig. 23); lateral margins smooth (even in microscope preparations). Surface convex and regular, finely micro-rugose, and in several specimens with fine and weakly developed punctures. Elytra striate-punctate, striae not as clear as in Hintonia britskii; interstices very slightly convex; pre-marginal interstice keeled, well visible from above. Abdomen as in Hintonia britskii. Wings reduced, not folded, only with vestiges of costal vein (fig. 37). Aedeagus short, relatively robust, not abruptly narrowed at apex as in Hintonia britskii; apex (fig. 41) with fine spines.

Female. Semi-lunar depression between abdominal sternites III and IV prolonged in the middle towards apex.

	8	Q
Total length	1.37-1.75 (1.56)	1.45-1.75 (1.58)
Elytral length	0.92 - 1.17 (1.06)	1.00-1.12 (1.08)
Pronotal width (base)	0.65 - 0.70 (0.67)	0.62 - 0.70 (0.67)
Maximum elytral width	0.85 - 0.97 (0.91)	0.80 - 1.05 (0.91)

Taxonomic discussion

As seen above *Hintonia castalia* is extremely similar to *Hintonia britskii*. One of the most striking characters of *Hintonia castalia*, however, is the reduction of the hind wings in all known specimens, of both sexes.

Hintonia castalia has a more restricted distribution (fig. 3), but this is most probably due to lack of collecting in certain areas.

Ytu (*), gen. n.

Adult. Head as in Hintonia, also slightly produced anteriorly (figs. 71, 72); eyes large, reniform, not incised, and not very prominent.

^(*) Ytu, Guarani for cascade, waterfall. To be used as masculinum name.

Surface very finely micro-rugose, impunctate. Frons separated from antennal area by a sharp keel which runs from anterior margin of eye eye to clypeus. Fronto-clypeal suture indicated by a shiny line. Two gular sutures. Antennae (fig. 13) with nine segments, proportions of segments as in *Hintonia*; insertion of antennae not visible from above, next to eyes; in resting position the antennae are directed forwards (fig. 74). Mouthparts as in Hintonia. Labrum (fig. 12) with thick and apparently flattened setae in front; the very conspicuous, recumbent pilosity in the middle of labrum of Hintonia, apparently absent. Mandibles (fig. 9) large, with distinct mola; internal margin densely pilose; with sharp apical tooth; left mandible with movable pre-apical tooth. Maxillae (fig. 10) as in Hintonia, with apical segment of palpi slightly more developed than in that genus. Labium (fig. 11) as in Hintonia. Pronotum anteriorly about as wide as head, regularly curved towards base; lateral margins regularly curved or with more or less well developed angle in front of the middle; lateral margin, in microscope preparation, finely serrate, mainly in front of the middle; anterior margin concave; posterior margin emarginate in the middle, here with a small incision (fig. 24, only visible in microscope preparation); with pre-basal carina almost parallel to base, and densely pilose underneath. Surface convex, frequently very irregular, with the indication of relief designs of a certain regularity and constancy, especially on disc and sides; whole surface micro-rugose and impunctate (granulate in Ytu hephaestus); glabrous. Scutellum as in Hintonia. Elytra wider than pronotum at base, with very rounded humeri; regularly widened towards the middle, where they are widest, and from here abruptly narrowed in a regular curve towards the sutural angle; the latter sharp. Strongly convex, finely micro-rugose and deeply punctate-striate or sulcate. Each with nine striae; striae incomplete, in part fused with others in the transverse depression behind humeri. Structure of striae and interstices variable. Thoracic sternites as in *Hintonia*. Legs shorter than in *Hintonia* (posterior femora only reaching the lateral margin of abdomen; in Hintonia about half of posterior femora exposed); posterior trochanters with a small tooth on free margin (fig. 33). Tarsal formula and relative size of tarsomeres as in Hintonia; middle and hind legs with tarsomere I frequently hidden in tibia and invisible from certain angles (figs. 80-82). Wings normally developed and folded in all species. Venation as in *Hintonia* (figs. 34-36). Abdomen with five visible sternites, I slightly longer than each of the three following, which are about equally long; last sternite twice as long as I (fig. 93). In some species sternite I with longitudinal keel, sharp or flat, more or less cuneiform (fig. 87). Posterior margin of sternites I to IV finely dentate (fig. 89); dentation not visible under light microscope. The two distal pleurites covered with dense and short pilosity (fig. 92). Male genitalia as in Hintonia.

Immature stages. As was discussed in more detail elsewhere, I found great difficulties in the specific identification of larvae of Ytu, in part because of the sympatry of the species. Only two species are in

part allopatric, having their larvae been collected in the area where there is no overlap. Even so I was unable to distinguish them. For this reason the collected larvae are not included in the type-series.

A second difficulty is the number of larval instars, a question which was discussed above (p. 86). Three different larval instars are described below, base on materials collected in Morretes, a locality where I only collected Ytu athena (the first two instars), and Valinhos, where only Ytu zeus occurs (last instar). As with Hintonia 1 first describe the last instar larva, and after that only give some distinguishing characters for the earlier instars. It should be noted that there should be at least one more instar, between the second and the last one, as happens with Hintonia.

The pupa described below was also collected in Morretes, and most probably belongs to *Ytu athena*; other pupae were collected at other localities, but here again I could not find characters to identify them to species.

Last instar larva (fig. 54). Total length (including urogomphi), 1.86 mm; width at mesonotum, 0.95 mm. Head small, partially covered by prothorax; mouthparts very weakly sclerotized, completely covered by the large labrum (fig. 15); mandibles (fig. 14) with well developed mola and prostheca; maxillae (fig. 16) with distinct cardo and stipes, galea and lacinia apparently fused, with a small, short and uni-segmented palp, which is covered with small, spheroid tubercles. Laterally the head bears a hemispheric protuberance with three ocelli. Antennae (fig. 17) inserted in front of this protuberance, with two segments, the basal segment globose and small, the apical segment long, with three setae, two pre-apical and one apical. Frontal and epicranial sutures clearly visible. Head glabrous, except for a few setae near antennae and anterior margin of head. Pronotum more than twice as wide as head; meso- and metanotum much wider; each segment wider than long; median longitudinal (ecdysial) suture well impressed; surface glabrous, except for a few, short setae. Lateral margin of thoracic segments finely dentate, each denticle with a long and thin seta (setae slightly longer than antennae); prothorax with about 25 setae on each side, meso- and metathorax with 15 to 20 setae each. Prothorax longer than the other segments, its anterior margin straight and angulate anteriorly. Meso- and metathorax about equally developed, each about half as long as prothorax. Posterior margin of thoracic segments straight. Abdomen more or less as long as thorax, with ten visible segments, each about as long as the next, and regularly narrowed towards apex. Segment I slightly narrower than thorax. Median longitudinal (ecdysial) suture present on first two tergites. Posterior margin of tergites straight; segments I to VIII with a lateral, cylindrical and relatively long, tubercular projection (slightly longer than antennae), on each of which is inserted a bi-segmented spiracular gill (fig. 61). First segment of gill long and cylindrical, the apical segment filiform and covered with fine plastron mesh; each gill with a tracheal branch which opens in the apical segment, in about the middle, where the gill is strangulated. Segment IX without gills and with a pair of long urogomphi (shorter than the spiracular gills, or about four times as long as segment IX); segment X small, globose, placed ventrally to the IX and almost completely covered by it. Legs with five segments. Coxae globose, except the posterior ones which are slightly transverse; trochanters triangular; femora and tibiae more or less of same length; tarsi with single claw. All legs separated from each other by a distance about equal to the diameter of the corresponding coxa; completely hidden under the thorax (invisible from above; fig. 54).

First (?) instar larva (fig. 55). Total length (including urogomphi), 0.8 mm; width at mesonotum, 0.34 mm. Head relatively large (thorax only slightly wider than head). Thorax little expanded laterally, with smooth lateral margins, and only two marginal setae on each segment. Spiracular gills bi-segmented, basal segment long and thick, and apical segment filiform; apical segment of gills VII and VIII very long, much longer than basal segment. Urogomphi longer than the basal segment of VIII pair of gills. Dorsal surface smooth, non-granulate. Apical half of tarsi and claws visible from above.

Second (?) instar larva (fig. 56). Total length (including urogomphi), 0.9 mm; width at mesonotum, 0.4 mm. Only very little larger than first instar larva. Head relatively large. Lateral margins of thoracic segments very weakly dentate, meso- and metathorax with six to seven marginal setae each, the prothorax with ten. Spiracular gills as in the first instar; apical segment always shorter than basal one. Urogomphi slightly shorter than basal segment of VIII pair of gills. Legs completely hidden under body. Dorsal surface smooth, as in the first instar.

Pupa (figs. 57, 58). As in Hintonia. The sclerotized (exposed) part of the pupa consisting of the three thoracic and the first three abdominal tergites, the last of the abdominal tergites with very small, triangular, sclerotized area. Each of the first two abdominal tergites with a pair of relatively long, tubular spiracular gills (only slightly shorter than abdomen), which are covered by a longitudinally striated plastron mesh (striae apparently more widely spaced than in Hintonia). The spiracular gills emerge from the antero-lateral angle of the sclerotized part of the segments.

Type-species, Ytu zeus, sp. n.

Taxonomic discussion

The absence of abdominal plastron easily distinguishes adults of Ytu from Hintonia and Torridincola. From Hintonia, Ytu is also distinguished by the number of visible abdominal sternites (four in Hintonia, five in Ytu), the small denticle on free margin of metatrochanters (absent in Hintonia) and the single basal incision of pronotum (two in Hintonia).

Larvae of Ytu are distinguished from Hintonia by the presence of a fringe of long setae along lateral margins of thoracic segments. Torridincola and genus B also have a fringe of setae, but in these genera the setae are very short and inconspicuous. Larvae of Torridincola differ from those of Hintonia, Ytu and genus B by the lack of urogomphi. Genus B, which also has a thoracic fringe of setae, though short, is easily distinguished from Ytu by the presence of a pair of piliferous tubercles along median line of meso-, metathorax and eight first abdominal tergites. Ytu is also unique among the known larvae by having legs completely hidden under the body.

Pupae of Ytu seem to be most similar to those of Torridincola (apud Bertrand, 1965: 1371-1373, fig. 30). Only from description it is impossible to distinguish them. The pupa of Ytu differs much from Hintonia by having proportionally longer, and tubular spiracular gills.

The lack of abdominal plastron allied to the simple abdominal structure of adults of Ytu seem to indicate that it is the more primitive of the known genera. Nevertheless it seems to be the more successful genus, with a total of eight species. These new species are all very similar, but easily distinguished by a few characters. They can be segregated in two species groups, one of which is characterized by intense sexual dimorphism (especially of iridescence) and keeled abdominal sternite I, and the second by the absence of both. The species group with sexual dimorphism includes Ytu zeus, Ytu hephaestus. Ytu athena and Ytu phebo; the second includes Ytu cupidus, Ytu morpheus, Ytu artemis and Ytu demeter. Besides the characters mentioned above, the species of the two groups show a certain similarity in the form of aedeagus: in the Zeus species group, three species (Ytu zeus. Ytu athena and Ytu hephaestus) have a very similar aedeagus (figs. 48, 49 and 50), while Ytu phebo has a completely different aedeagus (fig. 47). Of the four species of the Cupidus species group, Ytu morpheus, Ytu artemis and Ytu demeter have a very similar aedeagus (figs. 44, 45), while Ytu cupidus has a different aedeagus (fig. 43).

The species of Ytu have a very interesting distributional pattern, which was discussed at length above. Most species (six) occur north of the Tropic of Capricorn, and in a great part of the area the species are sympatric. Only Ytu zeus and Ytu athena occur south of the Tropic, being apparently allopatric in the states of São Paulo and Paraná, but sympatric in Santa Catarina and Rio Grande do Sul (fig. 4).

KEY TO SPECIES

1.	Abdominal	sternite	Ι	with	longitu	ıdinal	keel	in	the	midd	lle	(f)	ig.
	87)												2
	Abdominal	sternite	T	witho	ut keel								Ę

2.	Elytral interstices keeled, keels clearly but sparsely granulate. Females intensily iridescent. Aedeagus as in fig. 50. 1.6 - 1.85 mm
	Elytral interstices at maximum very convex, never keeled 3
3.	Lateral margins of pronotum in regular curve (fig. 24). Females usually slightly iridescent and shiny, with IX elytral interstice swollen behind the middle; males opaque, non-iridescent, with IX interstice only very little swollen, and with white setae on pro- and metasternum (figs. 84-86). Aedeagus as in fig. 48. 1.45 - 1.62 mm zeus, sp. n.
	Lateral margins of pronotum angulate in front of the middle 4
4.	Lateral margins of pronotum with a sharp angle in front of the middle (fig. 27). Two to three discal elytral striae sulcate, lateral ones punctate. Aedeagus as in fig. 47. 1.2 - 1.3 mm
	Lateral margins of pronotum only slightly angulate anteriorly (fig. 26). Elytral striae equally punctate, punctures not very clear. Aedeagus as in fig. 49. 1.62 - 1.87 mm athena, sp. n.
5.	Lateral margins of pronotum forming a slight angle in front of the middle (fig. 31). Dorsal surface with small, white scales; on elytra scales are placed in a single row along interstices. Aedeagus as in fig. 43. 1.37 - 1.62 mm cupidus, sp. n.
	Lateral margins of pronotum not angulate 6
6.	Pronotum trapezoidal, with almost straight lateral margins; base much wider than apex (fig. 30); surface without relief designs, but with two thin sulci parallel to lateral margins. Dorsal surface with small, white scales, which on elytra are placed in a double row along interstices. Aedeagus short and robust, similar to that of Ytu artemis and Ytu demeter. 1.40 - 1.57 mm morpheus, sp. n.
	Pronotum with regularly curved lateral margins 7
7.	Smaller species (1.42 - 1.57 mm). Metasternum of males without conic tubercles

ZEUS SPECIES GROUP

tubercles on metasternum demeter, sp. n.

Species characterized by intense sexual dimorphism of iridescence and sculpture of dorsal surface. Males opaque and finely micro-rugose, rarely iridescent; females shiny and smooth, frequently with intense metallic sheen. Abdominal sternite I with longitudinal keel. Aedeagus long and large, hooked at apex (except in *Ytu phebo*).

Species included: Ytu zeus, sp. n.
Ytu hephaestus, sp. n.
Ytu athena, sp. n.
Ytu phebo, sp. n.

Ytu zeus, sp. n.

(Figs. 8-17, 24, 34-35, 40, 48, 51, 73, 81 83-86, 88-93, 101-104)

Types

Holotype &. Brazil. São Paulo: Itu (Km 72 of Rodovia Castelo Branco, 700 m), 3.IV.1970 (H. Reichardt) (MZSP).

Paratypes. Brazil. São Paulo: idem (19 \$, 14 \$, MZSP); ibidem, 17.IV.1970 (H. Reichardt) (8 \$, 6 \$, MZSP); ibidem, 5.VI.1970 (H. Reichardt) (3 \$, 5 \$, MZSP); ibidem, 12.VII.1970 (A. Scivittaro & M. Menezes) (16 \$, 4 \$, MZSP); Marília, V. 1947 (F. Plaumann) (23 \$, 14 \$, FMNH); Valinhos (700 m), 13.IX.1969 (H. Reichardt) (16 \$, 4 \$, MZSP); idem, 20.III.1970 (H. Reichardt) (3 \$, MZSP); ibidem, 24.IV.1970 (H. Reichardt) (8 \$, 6 \$, MZSP); ibidem, 22.V.1970 (H. Reichardt) (6 \$, 4 \$, MZSP); ibidem, 19.IV.1970 (H. Reichardt) (4 \$, 3 \$, MZSP); ibidem, 27.VII.1970 (H. Reichardt) (2 \$, 6 \$, MZSP). Paraná: Guarapuava (66 km W) 27.VI.1969 (H. Reichardt) (1 \$, MZSP); Matelândia, 27.VI.1969 (H. Reichardt) (2 \$, 2 \$, MZSP); Nova Laranjeiras (15 km W), 27.VI.1969 (H. Reichardt) (7 \$, 12 \$, MZSP); Serra da Esperança (29 km E of Guarapuava), 18.VI.1969 (H. Reichardt) (10 \$, 14 \$, MZSP). Santa Catarina: Balneário de Camboriu, 4.XII.1971 (H. & B. Reichardt) (17 \$, 13 \$, MZSP); São Carlos (300 m), V.1957 (F. Plaumann) (19 \$, 11 \$, FMNH); Tubarão, 4.XII.1971 (H. & B. Reichardt) (17 \$, 13 \$, MZSP). Rio Grande do Sul: Nova Petrópolis (600 m), XI.1959 (F. Plaumann) (2 \$, FMNH); idem, 6.XII.1971 (H. & B. Reichardt) (2 \$, MZSP).

Male. Opaque, surface finely micro-rugose, weakly iridescent (except for recently moulted specimens, which are intensely iridescent). Lateral margins of pronotum regularly curved, not angulate (fig. 24), finely serrate in front of the middle. Surface of pronotum, especially disc, regularly convex, without sulci or relief designs. Elytral interstice IX swollen (when seen from above, interstice IX partially hides the elytral margin, especially behind the middle); striae well impressed, clearly punctate; elytral interstices, especially discal ones, flat or only slightly convex. Prosternum with a few long, decumbent, medially directed, white setae on each side of the prosternal process (fig. 84); the same kind of setae, more numerous, on metasternum (fig. 85). Abdominal sternite I with clearly visible, cuneiform keel. Aedeagus large and long, hooked at apex (figs. 40, 48).

Female. Shiny and frequently iridescent, especially on head and pronotum. Elytral interstices very swollen, convex and distinct, especially the discal ones and the IX. Pro- and metasternum glabrous.

Total length	1.45 - 1.62	(1.54)
Elytral length	1.00 - 1.12	(1.06)
Pronotal width at base	0.57 - 0.65	(0.60)
Maximum elytral width	0.75 - 0.95	(0.84)

Internal anatomy (specimens from Valinhos, São Paulo). Alimentary duct (fig. 51) destitute of caeca anteriorly; hind-gut forming a sharp curve in the abdominal region, just before opening into rectum. Six Malpighian tubes which end freely in the abdominal cavity, and are turned towards rectum. Male reproductive organs (fig. 40): testes elongate, tubular and coiled; one pair of capsule-shaped accessory glands which basally are fused and open into the short ejaculatory duct.

Taxonomic discussion

The white pro- and metasternal setae (figs. 83-86) of males, and the swollen IX elytral interstice (especially behind the middle), easily distinguish this species from all other know forms. The aedeagus of Ytu zeus (figs. 40, 48) is similar to that of Ytu hephaestus and Ytu athena.

The geographic distribution of Ytu zeus is very peculiar: the species occurs only south of the Tropic of Capricorn (fig. 4), from the state of São Paulo south to Rio Grande do Sul. In the northern part of the range (states of São Paulo and Paraná) the species has only been collected to the interior, but in the southern part (states of Santa Catarina and Rio Grande do Sul) it occurs from the coast to the interior. Here, in the southern part of the range, Ytu zeus occurs sympatrically with Ytu athena, but in the states of São Paulo and Paraná the two species occur parapatrically, Ytu zeus in the interior, and Ytu athena along the coast.

Ytu hephaestus, sp. n.

(Figs. 25, 33, 36, 50)

Types

Holotype & Brazil. São Paulo: São Sebastião, 2.X.1971 (H. & B. Reichardt) (MZSP).

Paratypes. Brazil. Espírito Santo: Domingos Martins, 26.XII.1969 (H. Reichardt) (1 ex., MZSP); São João de Viçosa (34 km W), 21.XII.1969 (H. Reichardt) (2 exs., MZSP); Santa İsabel, 26.XII.1969 (H. Reichardt) (4 exs., MZSP). Rio de Janeiro: Andrade Pinto, 8.IV.1970 (H. Reichardt) (2 exs., MZSP); Areal (10 km SE), 13.XII.1969 (H. Reichardt) (3 exs., MZSP); Mangaratiba, 7-8.III.1973 (H. & B. Reichardt) (4 exs., MZSP); Nova Friburgo (Serra, 920 m), 31.VII.1971 (H. & B. Reichardt) (2 exs., MZSP); Resende, 1.II.1972 (H. Reichardt) (1 ex., MZSP). São Paulo: Salesópolis (Estação Biológica de Boracéia, 850 m), 24.IX.1971 (H. Reichardt) (2 exs., MZSP); São Sebastião, 2.X.1971 (H. & B. Reichardt) (21 exs., MZSP); idem, 15.XI.1971 (H. Reichardt) (14 exs., MZSP); ibidem (15 km S), 3.X.1971 (H. & B. Reichardt) (1 ex., MZSP); ibidem, 15.XI.1971 (H. Reichardt) (1 ex., MZSP); ibidem, 15.XI.1971 (H. Reichardt) (1

Male. Finely micro-rugose, opaque, but frequently iridescent, especially on pronotum and elytral carinae. Sides of pronotum not angu-

late, in regular curve (fig. 25), with strong and irregular serration in front of the middle. Surface of pronotum convex and irregular, with very clear granulation, especially on disc, and with very clear, longitudinal keel. On each side of keel a more or less well indicated, circular elevation. Elytra striate, striae very clearly and sparsely punctate, the lateral ones with large and more or less foveolate punctures; interstices keeled, the keels finely granulate, with sharp edges. Lateral keels less sharp; granules on edges of keels iridescent. Keel of abdominal sternite I well developed. Aedeagus long and thin, hooked at apex (fig. 50).

Female. Finely micro-rugose and intensely iridescent; interstices more sharply keeled than in males.

Total length	1.60 - 1.85 (1.75)
Elytral length	1.07 - 1.35 (1.24)
Pronotal width at base	0.65 - 0.77 (0.72)
Maximum elytral width	0.80-1.15 (0.98)

Taxonomic discussion

Ytu hephaestus is best characterized by the keeled interstices, the pronotal granulations and the longitudinal keel on pronotum, all unique characters. A very closely related species is Ytu athena, with very similar aedeagus, and in which the elytral interstices are frequently very convex, but never truly keeled. Ytu hephaestus is also closely related to Ytu zeus, but as seen under that species, they cannot be confused.

The sexual dimorphism of *Ytu hephaestus* is usually very pronounced, but it is frequently very difficult to sex certain specimens, and there seems to be a certain amount of variation.

The geographic distribution of Ytu hephaestus (fig. 5) is ample, extending from the state of Espírito Santo to the state of São Paulo.

Ytu athena, sp. n. (Figs. 26, 49, 54-56)

Types

Holotype & . Brazil. Paraná: Morretes, 17.VI.1969 (H. Reichardt) (MZSP).

Paratypes. Brazil. São Paulo: Cubatão, 14.X.1971 (H. Reichardt) (3 exs., MZSP); São Vicente, 10.X.1971 (H. Reichardt) (2 exs., MZSP); Paraná: Morretes, 17.VI.1969 (H. Reichardt) (9 exs., MZSP). Santa Catarina: Balneário de Camboriu, 4.XII.1971 (H. & B. Reichardt) (9 exs., MZSP); Florianópolis (20 km S), 4.XII.1971 (H. & B. Reichardt) (32 exs., MZSP); Tubarão, 4.XII.1971 (H. &

B. Reichardt) (5 exs., MZSP). Rio Grande do Sul: Nova Petrópolis, 6.XII.1971 (H. & B. Reichardt) (5 exs., MZSP).

Male. Finely micro-rugose and opaque, slightly iridescent, especially on sides of pronotum; these forming a slight angle at about middle (fig. 26); in microscope preparations very irregularly serrate, especially in anterior half. Surface of pronotum convex and regular, with two weakly developed, circular elevations on disc. Elytral striae very weakly indicated, with unclear punctures; interstices very convex. not keeled. Abdominal sternite I with well developed keel. Aedeagus long, hooked at apex (fig. 49).

Female. Shiny and strongly iridescent. Surface of pronotum very convex and irregular, with two well developed, circular elevations on disc. Elytral striae well developed, with clear punctures; interstices more convex than in males.

Total length	1.62-1.87 (1.73)
Elytral length	1.12-1.30 (1.21)
Pronotal width at base	0.65 - 0.75 (0.71)
Maximum elytral width	0.90 - 1.05 (0.98)

Taxonomic discussion

As seen above Ytu athena is most closely allied to Ytu hephaestus, but while the latter has clearly keeled elytral interstices, Ytu athena only has very convex interstices. In other regards the two are very similar, are about the same size, but are completely allopatric. Its geographic distribution (fig. 4) is very peculiar, and was already discussed in detail under Ytu zeus. The somewhat angulate lateral margins of pronotum easily separate Ytu athena from Ytu zeus and Ytu hephaestus; Ytu phebo, also included in this species group, has very clearly angulate lateral margins of pronotum, but is distinguished from Ytu athena by a series of characters, but especially by its much smaller size.

Ytu phebo, sp. n. (Figs. 27, 47, 82, 87)

Types

Holotype & Brazil. São Paulo: Salesópolis (Estação Biológica de Boracéia, 850 m), 24.IX.1971 (H. Reichardt) (MZSP).

Paratypes. Brasil. Espírito Santo: Venda Nova, 21.XII.1969 (H. Reichardt) (4 exs., MZSP). Rio de Janeiro: Andrade Pinto, 13.XII. 1969 (H. Reichardt) (3 exs., MZSP); idem, 8.IV.1970 (H. Reichardt) (9 exs., MZSP); Areal (10 km SE), 13.XII.1969 (H. Reichardt) (6 exs., MZSP); idem, 8.IV.1970 (H. Reichardt) (8 exs., MZSP); Cachoeiras do Macacu, 31.VIII.1971 (H. & B. Reichardt) (1 ex., MZSP);

Mangaratiba, 7-8.III.1973 (H. & B. Reichardt) (105 exs., MZSP); Nova Friburgo (Serra, 200 m), 31.VIII.1971 (H. & B. Reichardt) (2 exs., MZSP); Teresópolis (6 km W, 1,000 m), 8.IV.1970 (H. Reichardt) (2 exs., MZSP). Guanabara: Rio de Janeiro (Barra da Tijuca), 1.IX.1971 (H. & B. Reichardt) (1 ex., MZSP). São Paulo: Caraguatatuba (400 m), 19.VII.1970 (H. Reichardt) (8 exs., MZSP); Ilha de São Sebastião (Toca), 14.XI.1971 (H. Reichardt) (10 exs., MZSP); Salesópolis (Estação Biológica de Boracéia, 850 m), 24.IX. 1971 (H. Reichardt) (25 exs., MZSP).

Male. Finely micro-rugose and strongly opaque, without iridescence. Sides of pronotum clearly angulate in front of middle (fig. 27); margins irregularly but strongly serrate. Surface of pronotum very irregular, with two almost erased circular elevations on disc. Elytra deeply striate, the two or three discal striae sulcate, with almost imperceptible punctures; remainder clearly punctate, punctures of more lateral striae foveolate. Abdominal sternite I keeled. Aedeagus long and thin, slightly bent downwards apically (fig. 47).

Female. Shiny and strongly iridescent, especially on pronotum. Surface of the latter very irregular, the circular elevations well developed. Punctures of elytral striae clearly visible.

Total length	1.20 - 1.30 (1.26)
Elytral length	0.85 - 0.95 (0.88)
Pronotal width at base	0.45 - 0.50 (0.48)
Maximum elytral width	0.60 - 0.67 (0.65)

Taxonomic discussion

Ytu phebo is well characterized by its very small size, as well as by the elytral sculpture: it is the only species in which the elytral striae are sulcate on disc and punctate on sides. As seen above, the angulate lateral margins of pronotum are also present in Ytu athena, but here they are only slightly angulate.

Ytu phebo is not very closely related to the other species of the Zeus species group. The sexual dimorphism of iridescence and keeled abdominal sternite I are present in Ytu phebo, but its aedeagus (fig. 47) is quite distinct from that of the other species of the group.

Ytu phebo has a very wide geographic distribution (fig. 5), extending from the state of Espírito Santo south to the state of São Paulo. In the latter it was also collected in the island of São Sebastião, of the coast, being the only species represented there.

CUPIDUS SPECIES GROUP

A species group characterized by the almost complete absence of sexual dimorphism of dorsal sculpture and iridescence, as well as absence of keel on abdominal sternite I. Aedeagus short and robust, the longitudinal splitting frequently very apparent. Ytu cupidus with different, spear-shaped aedeagus.

Ytu morpheus and Ytu cupidus dorsally covered with very small, white scales. Ytu demeter and Ytu morpheus with peculiar sexual dimorphism: males with two small, conic tubercles on metasternum.

All species of this group occur north of the Tropic of Capricorn (figs. 5, 6).

Species included: Ytu demeter, sp. n.

Ytu artemis, sp. n. Ytu morpheus, sp. n. Ytu cupidus, sp. n.

Ytu demeter, sp. n.

(Figs. 28, 45, 46; graph 2)

Types

Holotype & Brazil. Rio de Janeiro: Teresópolis (1,250 m), 31.VIII.1971 (H. & B. Reichardt) (MZSP).

Paratypes. Brazil. *Rio de Janeiro*: Nova Friburgo (Serra, 920 m), 28.VIII.1971 (H. & B. Reichardt) (19, MZSP); Teresópolis (Serra, 400 m), 29.VIII.1971 (H. & B. Reichardt) (10\$, 11\$, MZSP); *idem* (900 m), 28.VIII.1971 (H. & B. Reichardt) (5\$, 7\$, MZSP); *ibidem* (1,000 m), 31.VIII.1971 (H. & B. Reichardt) (10\$, 1\$, MZSP); *ibidem* (1,250 m), 31.VIII.1971 (H. & B. Reichardt) (7\$, 3\$, MZSP). *São Paulo*: São Sebastião (15 km S), 3.X.1971 (H. & B. Reichardt) (4\$, 4\$, MZSP).

Specimens not included in type-series (see discussion below): *Espírito Santo*: Domingos Martins, 26.XII.1969 (H. Reichardt) (8 exs., MZSP); Santa Isabel, 26.XII.1969 (H. Reichardt) (2 \(\rho\), MZSP); São João de Viçosa (34 km W), 21.XII.1969 (H. Reichardt) (1 \(\frac{\pi}{\pi}\), 2 \(\rho\), MZSP); Venda Nova, 21.XII.1969 (H. Reichardt) (2 \(\rho\), MZSP).

Male. Opaque, finely micro-rugose, sometimes with very faint iridescence; elytral margin, especially behind middle, testaceous; more rarely margin of pronotum also testaceous; a small testaceous, more or less circular spot behind the middle of elytra, limited by the marginal and the IV stria (from margin); ventrally also testaceous on epipleurae and lateral parts of thoracic segments. Pronotum with lateral margins regularly curved and finely serrate (fig. 28). Surface convex and very irregular, with two more or less ovoid elevations on disc; median line not impressed. Elytra striate-punctate, punctures visible, especially in lateral striae; interstices convex. Metasternum with two small, more or less conic tubercles placed near median line, and closer to posterior than median coxae (absent in specimens from Espírito Santo). Abdominal sternite I not keeled. Aedeagus short and robust (figs. 45, 46).

Female. Slightly more shiny than male, but also micro-rugose; with very faint iridescence. Pronotal surface more irregular, with ovoid elevations better defined. Striae with more clear and confluent punctures. Metasternum without tubercles.

	<i>\$</i>	φ.
Total length	1.70-1.92 (1.80)	1.70-1.85 (1.78)
Elytral length	1.12 - 1.35 (1.23)	1.15-1.27 (1.22)
Pronotal width at base	0.67 - 0.75 (0.70)	0.62-0.72 (0.67)
Maximum elytral width	0.92 - 1.02 (0.96)	0.90 - 1.00 (0.95)

Taxonomic discussion

Ytu demeter is extremely similar to the sympatric and syntopic Ytu artemis. Males of the type-series of Ytu demeter (states of Rio de Janeiro and São Paulo) have two small conic tubercles on metasternum, a character which immediatly distinguishes males of this species from Ytu artemis. Males from various localities in the state of Espírito Santo, however, in spite of agreeing in all characters (including size and proportions) with the remainder specimens, do not have the metasternal tubercles. Even so, the two species are distinguished by size: while Ytu demeter measures 1.70 to 1.92, Ytu artemis only measures 1.42 to 1.57 mm (graph 2).

Besides the sexual dimorphism of metasternal tubercles (a character Ytu demeter only shares with Ytu morpheus), there is also sexual variation in size: in average males are slightly larger than females (see measurements).

Ytu artemis, sp. n. (Figs. 29, 44, 74, 76; graph 2)

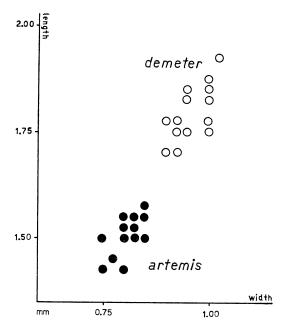
Types

Holotype &. Brazil. Espírito Santo: Venda Nova, 21.XII.1969

(H. Reichardt) (MZSP). Paratypes. Brazil. *Espírito Santo:* São João de Viçosa (34 km W), 21.XII.1969 (H. Reichardt) (1 ex., MZSP); Venda Nova, 21. XII. 1969 (H. Reichardt) (4 exs., MZSP). Rio de Janeiro: Areal (10 km S), 8.IV.1970 (H. Reichardt) (1 ex., MZSP); Itatiaia (1,000 m), 2.IX.1971 (H. & B. Reichardt) (20 exs., MZSP); Teresópolis (Serra, 400 m), 29.VIII.1971 (H. & B. Reichardt) (13 exs., MZSP); idem (Serra, 900 m), 4.IV.1969 (H. Reichardt & P. E. Vanzolini) (17 exs., MZSP); *ibidem*, 14.XII.1969 (H. Reichardt) (1 ex., MZSP); ibidem, 28. VIII. 1971 (H. & B. Reichardt) (19 exs., MZSP); ibidem 1,000 m), 31.VIII.1971 (H. & B. Reichardt) (15 exs., MZSP); *ibidem* (1,250 m), 31.VIII.1971 (H. & B. Reichardt) (1 ex., MZSP).

Dark and shiny, most specimens with slight iridescence; elytral margin and a small, more or less circular spot near margin and just behind middle of elytra, testaceous; ventrally epipleurae and sides of thoracic segments also testaceous. Sides of pronotum regularly curved (fig. 29), with finely serrate margins in anterior half. Surface of pronotum very convex and irregular, with two transverse, more or less ovoid elevations on disc. Elytra striate-punctate, punctures not very clear, somewhat confluent. Abdominal sternite I not keeled. Aedeagus short and robust (fig. 44).

Total length	1.42 - 1.57 (1.50)
Elytral length	0.95-1.10 (1.02)
Pronotal width at base	0.52 - 0.62 (0.57)
Maximum elvtral width	0.75 - 0.85 (0.81)



Graph 2. Linear regresion for total length of specimen against maximum width of specimen of Ytu demeter and Ytu artemis.

Taxonomic discussion

As seen above, Ytu artemis is very closely related to Ytu demeter; both are best distinguished by size (graph 2) and by the somewhat different aedeagus (fig. 44).

It is possible that *Ytu artemis* is covered dorsally with small, deciduous, white scales, as *Ytu morpheus* and *Ytu cupidus*. It seems that such scales are easily rubbed off, and because of their smallness I am not sure about their existence in the material at hand.

Ytu artemis is in great part sympatric with Ytu demeter (fig. 6).

Ytu morpheus, sp. n.

(Fig. 30)

Types

Holotype & Brazil. Rio de Janeiro: Areal (10 km SE), 27.VIII. 1971 (H. & B. Reichardt) (MZSP).

Paratypes. Brazil. *Rio de Janeiro: idem*, 8.IV.1970 (H. Reichardt) (1\$\delta\$, 1\$\gamma\$, MZSP); *ibidem*, 27.VIII.1971 (H. & B. Reichardt) (12\$\delta\$, 17\$\gamma\$, 1 ex., MZSP); Cachoeiras do Macacu, 31.VIII.1971 (H. & B. Reichardt) (1\$\gamma\$, MZSP); Itatiaia (Véu de Noiva, 1,100 m), 20.IV.1969 (H. Reichardt) (1\$\delta\$, MZSP); Nova Friburgo (Serra, 640 m), 28.VIII.1971 (H. & B. Reichardt) (1\$\delta\$, MZSP); Teresópolis (Serra, 900 m), 4.IV.1969 (H. Reichardt & P. E. Vanzolini) (2\$\delta\$, 2 exs., MZSP); *idem*, 28.VIII.1971 (H. & B. Reichardt) (1\$\gamma\$, MZSP); *ibidem* (1,100 m), 31.VIII.1971 (H. & B. Reichardt) (2\$\gamma\$, MZSP).

Male. Shiny, slightly iridescent on head and pronotum; dorsally with small, white scales (scales are probably easily rubbed off, since they are frequently absent from certain areas), on elytra forming a double row in each interstice. Pronotum with almost straight sides, trapezoidal in form, much wider at base than in front (fig. 30), with finely serrate margins in front of the middle. Elytra very finely striate, punctures not well visible; interstices convex. Metasternum with two small, conic tubercles near the median line, placed closer to posterior than median coxae. Abdominal sternite I unkeeled. Aedeagus short and robust, similar to that of Ytu demeter and Ytu artemis.

Female. Shiny, with more intense iridescence on head, pronotum and base of elytra. Metasternum without tubercles.

Total length	1.40 - 1.57	(1.50)
Elytral length	0.97 - 1.12	(1.10)
Pronotal width at base	0.60 - 0.70	(0.66)
Maximum elytral width	0.82 - 0.95	(0.91)

Taxonomic discussion

Ytu morpheus is well characterized by its general form: it is the only species with trapezoidal pronotum. Males of Ytu morpheus are characterized by the two small, conic tubercles on metasternum, a character shared with Ytu demeter. The dorsal scales of Ytu morpheus are not easily seen, and are often rubbed off (they are best observed in recently moulted specimens). The only other species of the genus with scales on dorsal surface is Ytu cupidus, where the scales form a single row on each elytral interstice (double row in Ytu morpheus).

As seen above, apparently Ytu artemis also has scales, but the material at hand is not enough for certainty.

Ytu morpheus is only known from a few localities in the state of Rio de Janeiro (fig. 5).

Ytu cupidus, sp. n. (Figs. 31, 43, 71-72, 77-78, 80)

Types

Holotype & Brazil. Rio de Janeiros Teresópolis (Serra, 900 m), 14.XII.1969 (H. Reichardt) (MZSP).

Paratypes. Brazil. Rio de Janeiro: Angra dos Reis (Alto da Serra, 500 m), 3.V.1970 (H. Reichardt) (27 exs., MZSP); idem, 10.III.1973 (H. & B. Reichardt) (22 exs., MZSP); Areal (10 km SE), 8.IV.1970 (H. Reichardt) (2 exs., MZSP); Cachoeiras do Macacu, 31. VIII.1971 (H. & B. Reichardt) (50 exs., MZSP); Nova Friburgo (Serra, 640, m), 28. VIII. 1971 (H. & B. Reichardt) (15 exs., MZSP); Petrópolis (Serra, 600 m), 29. VIII. 1971 (H. & B. Reichardt) (47 exs., MZSP); Serra das Araras (350 m), 1.IX.1971 (H. & B. Reichardt) (36 exs., MZSP); Teresópolis (Serra, 400 m), 29.VIII. 1971 (H. & B. Reichardt) (1 ex., MZSP); idem (Serra, 900 m), 4.IV.1969 (H. Reichardt & P. E. Vanzolini) (5 exs., MZSP); ibidem. 14.XII.1969 (H. Reichardt) (19 exs., MZSP); ibidem, 8.IV.1970 (H. Reichardt) (17 exs., MZSP); ibidem (Comary, 830 m), 28.VIII. 1971 (H. & B. Reichardt) (52 exs., MZSP); ibidem (Pecegueiros), 28. VIII. 1971 (H. & B. Reichardt) (66 exs., MZSP). São Paulo: Caraguatatuba (400 m), 19. VII. 1970 (H. Reichardt) (25 exs., MZSP); São Sebastião (15 km S), 3.X.1971 (H. & B. Reichardt) (1 ex., MZSP).

Dark and shiny, frequently with very weak iridescence on whole body; head, pronotum and elytra with small, white, deciduous scales, which on elytra form a single row in each interstice (as in Ytu morpheus scales are also frequently rubbed off). Pronotum with an obtuse angle in front of the middle (fig. 31), and margins finely serrate. Surface convex and more or less regular, with two discal, ovoid elevations, which frequently are somewhat erased. Elytra striate-punctate, punctures well visible, especially on lateral striae, where they are larger and better developed. Abdominal sternite I without keel. Aedeagus short and thin, spear-shaped at apex (fig. 43).

Total length	1.37 - 1.62	(1.49)
Elytral length	0.90 - 1.17	(1.01)
Pronotal width at base	0.55 - 0.67	(0.62)
Maximum elytral width	0.75 - 0.95	(0.85)

Taxonomic discussion

Ytu cupidus is well characterized by the shape of the apex of the aedeagus (fig. 43), as well as by the scales of dorsal surface. The only other species with scales on dorsal surface (see also notes on Ytu artemis) is Ytu morpheus, but while Ytu morpheus has a double row on each interstice, Ytu cupidus has a single row.

Ytu cupidus occurs north of the Tropic of Capricorn (fig. 6), in the states of Rio de Janeiro and São Paulo.

Genus B

(Fig. 120)

"Hidraenidae genus, groupe *Prosthetops*" Bertrand, 1962: 1068-1072, figs. 2-3 (larvae from Assaigabos River, South Africa).

Last (?) instar larva (fig. 120). Total length (including urogomphi), 2.0 mm; width at mesonotum, 0.55 mm. Head relatively large; mouthparts covered by the large labrum (Bertrand, 1962, fig. 3A); mandibles (Bertrand, l.c., figs. 3B, 3C) similar to those of Ytu (fig. 14), but with more distinct prostheca; maxillae (Bertrand, l.c., figs. 3D, 3E) with very short and small galea and lacinia (apparently only indicated by the bifid apex), and three-segmented palpi; labium (Bertrand, l.c., fig. 3F) small, with palpi better developed than in Hintonia. Ocellar protuberances lateral, each with three dorsal and two ventral ocelli. Antennae inserted in front of ocellar protuberance, with three segments, the basal segment small, globose, the second longest. Frontal and epicranial sutures clearly indicated, the latter very short. Pilosity restricted to a few setae behind ocelli; and others along front margin. Thorax longer than wide, about as long as abdomen (urogomphi excluded). Prothorax only slightly shorter than mesoand metathorax together; wider than head; mesonotum widest of all, but only slightly wider than pro- and metanotum; lateral and posterior margins of thoracic segments with small tubercles, on which are inserted small setae (Bertrand, l.c., fig. 3G); a pair of strong, setigerous tubercles next to median line, near posterior margin of meso- and metanotum. Abdomen with ten visible segments; segments about equally long; I widest (about as wide as metanotum), other segments regularly decreasing in width towards apex; segments I to VIII with lateral, cylindrical and relatively long, tubercular proiection, on each of which is inserted a tri-segmented spiracular gill. First segment of gill very long, second about as long, but thinner, and third very short and sharp. Gills of VII and VIII segments longer. Segments I to VIII with setigerous tubercles along median line. Segment IX without gills, but with very long, three-segmented urogomphi (about as long as gill of VIII segment). Segment X small, only sclerotized anteriorly, with a pair of setae and spines posteriorly. Legs with strong claws; visible from above.

Taxonomic discussion

The above description is based on Bertrand's original description. The larva(e) was collected by Mr. Henry Bertrand himself, together with adults. The latter were determined by Mr. J. Balfour-Browne as belonging to an undescribed genus of Hydraenidae, close to *Prosthetops* (Bertrand, 1962: 1069; *in litt.*; J. Balfour-Browne, *in litt.*).

I do not challenge the identification of the adults, but I do not think that the larvae can be associated with adults of Hydraenidae. In the description Bertrand mentions a superficial similarity to larvae of Tenebrionaria collected in the same (hygropetric) habitat in Zaire and Madagascar, which were posteriorly described as Torridincola. I am inclined to consider this resemblance not only as superficial. Bertrand places excessive importance on the mouthparts to classify the larvae as Hydraenidae, leaving aside important structures as spiracular gills, typical of Torridincolidae and unknown in Hydraenidae (in the key to larval Hydraenidae from Africa, Bertrand, 1962: 1073, separates the present larva from the other Hydraenidae by the presence of spiracular gills). In spite of the importance given to the mouthparts, in the discussion Bertrand (1962: 1072) says that Hydraenidae have mouthparts different from those of Hydrophiloidea, due to their alimentary habits, thus stripping the mouthparts of any importance they could have in morphological relationships.

Unfortunately I was unable to locate specimens of this larva. Nevertheless I propose to transfer it to Torridincolidae.

The mouthparts are very similar to those of Hintonia, differing only in very slight characters. A few other characters of this larva are quite distinct from those of the other larvae. There is no reference to the longitudinal ecdysial suture on thorax and the two first abdominal tergites (neither is it represented in the figure); it could, however, be obliterated by the very coarsely rugose dorsal surface. The antennae are described as three-segmented, while Hintonia and Ytu have only two segments; the spiracular gills are also tri-segmented. Torridincola apparently has three segments, but both Hintonia and Ytu have only two. I should, however, note that the correct interpretation of the number of segments is quite difficult. The most strange character of genus B are the three-segmented urogomphi. As seen elsewhere, there is variation in the presence or absence of these structures, but when present they are always unsegmented (it is also strange that no clear segmentation is visible in Bertrand's illustration).

The systematic position of genus B is very difficult to be discussed in the absence of adults. Some characters seem to indicate relationships to Hintonia and Ytu (the presence of urogomphi), while others relate it to Torridincola (three-segmented gills). The setigerous tubercles of meso-, metanotum and eight first abdominal tergites, are a quite unique character of the genus.

HYDROSCAPHIDAE

Hydroscaphidae Leconte, 1874: 45; Matthews, 1876: 1; Csiki, 1911: 3-4; d'Orchymont, 1945: 1; Crowson, 1955: 11, 28; Steffan,

1964: 199; Arnett, 1968: 213-214.

Hydroscaphinae; Böving, 1914: 172.

Adults. Minute beetles (less than 1 mm to about 2 mm total length), usually brownish-dark colored, smooth and shiny [according to d'Orchymont (1945: 9) males of Hydroscapha are smooth and shiny, while females are opaque and more rugose]. Body fusiform, with part of abdomen exposed by truncate elytra.

Head small, visible from above, with relatively large eyes, placed near front margin, in part dorsally, in part ventrally; facetation relatively coarse. Mouthparts and antennae on ventral face of head. Antennae with five or eight segments, scape always the largest segment, and the last elongate, claviform. Mouthparts not examined (see Arnett, 1968: 213, for a description). Elytra short, exposing part of abdomen. Abdomen with six visible sternites and eight tergites, of the latter only the three or four posterior ones exposed. Tergites III and IV densely pilose (fig. 114). Anterior coxae contiguous, median and posterior ones separated. Anterior coxal cavities open behind. Tarsi trimerous. Posterior coxae with well developed femoral plates. Membranous wings well developed, with fringe of long, marginal setae; venation reduced, and oblong cell absent. Male genitalia described for some species, aedeagus apparently well developed, not longitudinally split, and without lateral lobes.

Larvae. Known only for Hydroscapha natans (Böving, 1914; Böving & Craighead, 1931: 25, 26, pl. 9, figs. A-F; Hinton, 1967: 958, fig. 1C). They are mainly characterized by a pair of peculiar spiracular gills on prothorax and abdominal segments I and VIII.

Pupae. Very poorly known. Böving (1914) is the only author to mention the pupa of Hydroscapha natans, without describing it.

Type-genus, by original designation, Hydroscapha Leconte, 1874.

Taxonomic discussion

Relationships of Hydroscaphidae with the other families of Myxophaga were discussed above.

The family is well characterized by the fusiform body (which at least superficially is similar to the form of certain Staphylinidae, as for example, *Vatesus*), with truncate elytra, the structure of antennae and tarsi.

As to the number of antennal segments, Hydroscapha has eight, while Scaphydra only five. There has always been very much discussion on the number of antennal segments of Hydroscapha. D'Orchymont (1945: 4-7, fig. 4) established that the correct number is

eight, but in spite of this there still are wrong references in the literature, such as nine segments in Arnett (1968: 213) and eight or nine in Crowson (1955: 11, 28).

KEY TO GENERA (ADULTS)

1. Antennae with eight segments. Sutural angle of elytra rounded.

Posterior margin of abdominal tergites and sternites straight
(fig. 118). Old World, Nearctic and Neotropical Regions

Hydroscapha Leconte, 1874

Scaphydra (*), gen. n.

Body elongate-ovoid, with lateral margins continuous from head to apical external angle of elytra; these truncate and exposing part of abdomen, which is narrower than elytra at apex, and narrows gradually towards apex.

Head relatively small, forming a regular curve from one eye to the other. Eyes reniform, with one half dorsal and the other half ventral; facetation relatively coarse (fig. 107). Antennae and mouthparts ventral. Antennae with five segments (figs. 63, 108), with elongate scape (about as long as the the following together), apical segment enlarged, claviform, of about the size of scape. Mouthparts not dissected (see fig. 107). *Pronotum* anteriorly about as wide as head, regularly widened towards base; anterior margin concave; posterior margin slightly emargined in the middle; posterior and anterior angles sharp. Surface shiny, sparsely punctate, each puncture with fine seta. Scutellum relatively large, triangular, surface sculptured as pronotum. Elytra at base as wide as pronotum, regularly widened towards first third, where they are widest; from here on regularly narrowed towards the rounded apical external angle. Posterior margin more or less straight. Sutural angles with a small denticle with apical seta(e). Surface shiny and smooth, also sparsely punctate, each puncture with fine seta. Internal surface of elytra (figs. 105, 106) with mesh of carinae, small spines and peculiar sensory (?) organs. Prosternum narrow, with small prosternal process, which does not reach the middle of anterior coxae (fig. 64); anterior coxal cavities open behind; coxae contiguous. Posterior margin finely serrate. Mesosternum narrower than prosternum, reduced to mesosternal process, which is wider than long, and clearly separates middle coxae. Metasternum only slightly shorter than wide, depressed in the middle, with large metasternal process which separates posterior coxae; these slightly

^(*) The generic name is an anagram of *Hydroscapha*; to be used in the feminine, as *Hydroscapha*.

more separated than middle coxae. Legs (figs. 66, 110) short, practically hidden under body. Coxae large and transverse, the posterior ones with femoral plates. Tibiae widened towards apex, spiny externally. Tarsi trimerous (fig. 66), with simple claws. Membranous wings (fig. 38) normally developed, as in Hydroscapha with marginal fringe of long setae, reduced venation and absent oblong cell. Folded and completely hidden under elytra; Scaphydra angra with reduced wings. Abdomen with six visible sternites and eight tergites (figs. 113, 115); lateral sutures between sternites and tergites only present in the last segment. Segments wider than long, descreasing in width towards apex. Last visible segment longer than wide, ending in apical spines and setae, which apparently are retractile; last sternite complete in females, with a deep incision in males (fig. 62). Posterior margin of some abdominal segments finely serrate. Tergites and sternites shiny and smooth, with sparse punctures, each puncture with a relatively long seta, except tergites III and IV which bear a cover of dense and long pilosity, on the III directed from the middle to sides, and on IV backwads (figs. 112, 114). Male genitalia (fig. 62).

Type-species, Hydroscapha hintoni Reichardt, 1971.

Taxonomic discussion

The three species I am now transferring to a new genus were originally described in Hydroscapha (Reichardt, 1971b), but in that paper I already mentioned that they formed a very distinct evolutionary lineage within the family. It seems to me that the reduced number of antennal segments and the peculiary serrate posterior margin of abdominal tergites and sternites of these species, as opposed to the homogeneity of Hydroscapha throughout the Old World, United States and even Neotropical Region (Hinton, 1969b), preclude their inclusion in Hydroscapha. It is true that some of the species of Hydroscapha are only known from types, and have not been critically studied in recent years, and may, therefore, not actually belong in the genus, but this does not interfere with the above reasoning.

In general form the two genera are hardly distinct, but besides the differences already mentioned, they probably differ in many more, if minor characters. Unfortunately immature stages of *Scaphydra* are unknown. They may, eventually, bring to light interesting characters, as happened with Torridincolidae.

The three species of *Scaphydra* are extremely similar, only being distinguished by very few and subtle characters. It is interesting to note, however, that one of the species, *Scaphydra angra*, has reduced wings.

Up to the present the genus in restricted to southeastern Brazil, where it has a distribution similar to that of *Hintonia* (fig. 3), north of the Tropic of Capricorn.

KEY TO SPECIES

Scaphydra hintoni (Reichardt, 1971), comb. n.

(Figs. 38, 62, 64-67, 105-116)

Hydroscapha hintoni Reichardt, 1971b: 290-291, figs. 1-6 (Type-locality, Brazil, Rio de Janeiro, Andrade Pinto; holotype 9, on slide, MZSP).

Dark brown and very shiny. Pronotum widest at base, where it measures about three times its length (1.0:0.35); surface punctate, each puncture with a recumbent seta. Scutellum triangular, its surface with sculpture and pilosity as pronotum. Elytra widest in basal third, and here slightly wider than pronotum at base; each elytron twice as long as wide (1.0:0.5), truncate et apex; apical external angle rounded, sutural angle with a small denticle and short seta (fig. 67). Surface punctate, each puncture with recumbent seta; punctures and pilosity disposed as on pronotum. Abdomen with four anterior tergites and basal half of fifth covered by elytra; tergites III and IV densely pilose (fig. 114), remaining tergites with long and sparse, recumbent setae. Tergites V to VII and sternites I to V with finely serrate posterior margins. Females with complete last abdominal sternite, males with deeply incised last sternite. Aedeagus (fig. 62) fine and long, without lateral lobes, spirally coiled.

Total length 1.47
Length from apex of head to apex of elytra 1.05
Maximum elytral width 0.90

Material examined

Brazil. Rio de Janeiro: Andrade Pinto (250 m), 13.XII.1969 (H. Reichardt) (Holotype 9, 13 paratype on slide, 13 paratype on pin and 4 paratypes in alcohol, MZSP; 2 paratypes, HEHC); idem, 8.IV.1970 (H. Reichardt (1 paratype in alcohol, MZSP); Teresópolis (6 km W, 1.000 m), 8.IV.1970 (H. Reichardt) (19 paratype on slide, MZSP).

Taxonomic discussion

Scaphydra hintoni is the only species of which several specimens, of both sexes, are available. It is very similar to Scaphydra pygmaea, being best distinguished by size (*). It is also similar to Scaphydra angra, but this species has reduced hind wings, and the posterior margin of abdominal tergite IV is serrate (not serrate in the other two species).

Scaphydra angra (Reichardt, 1971), comb. n. (Figs. 68, 70)

Hydroscapha angra Reichardt, 1971b: 291 (Type-locality, Brazil, Rio de Janeiro, Angra dos Reis; holotype 9, on slide, MZSP).

Dark brown and very shiny; antennae darker than other parts. Pronotum widest at base, where it is about twice as wide as long (1.0:0.5). Elytra more sparsely punctate than in *Scaphydra hintoni* (figs. 67, 70); each elytron twice as long as wide (1.0:0.5); denticle of sutural angle sharper, apparently with three apical setae (fig. 70). Abdomen with three first tergites and three-fourths of IV covered by elytra; tergites IV to VII with posterior margin serrate. Membranous wings reduced, about 0.25 mm long, not reaching apex of elytra, and unfolded.

Total length	1.27
Length from apex of head	
to apex of elytra	0.86
Maximum elytral width	0.50

Material examined

Brazil. Rio de Janeiro: Angra dos Reis (Alto da Serra, 500 m), 3.V.1970 (H. Reichardt) (Holotype Q, on slide, MZSP).

Taxonomic discussion

Even though very close to the other two species, *Scaphydra angra* is well characterized by the reduced hind wings, and the posterior margin of abdominal tergite IV which is serrate (not serrate in the other species).

The holotype of $Scaphydra\ angra$ is a female (last abdominal sternite complete), without eggs in the abdomen.

^(*) Specimens of Hydroscaphidade frequently retract the abdomen, and it seems to me, therefore, that the best measurement is the length from front margin of head to apex of elytra.

Scaphydra pygmaea (Reichardt, 1971), comb. n.

(Figs. 63, 69)

Hydroscapha pygmaea Reichardt, 1971b: 291 (Type-locality, Brazil, Espírito Santo, Rio Jucu; holotype 2, on slide, MZSP).

Dark brown, very shiny. Pronotum widest at base, almost three times as wide as long (1.0:0.35). Elytra sparsely punctate and pilose, as in *Scaphydra angra*; each elytron slightly more than twice as long as wide (1.0:0.45); sutural denticle of elytra as in *Scaphydra hintoni*. Abdomen retracted, only with last and half of penultimate tergites exposed; tergites V to VII serrate posteriorly.

Total length 1.03
Length from apex of head
to apex of elytra 0.80
Maximum elytral width 0.50

Taxonomic discussion

Scaphydra pygmaea is very similar to Scaphydra hintoni, and as seen above, best distinguished by size. The holotype is a female (last abdominal sternite complete), without eggs in the abdomen.

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