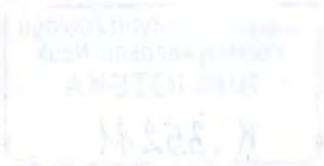


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DISSERTATION

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**Taxonomical, zoogeographical and phylogenetical relations
among Indo-Pacific *Psiloptera* DEJ., *Dicercomorpha* DEYR.,
and related genera
(Coleoptera: Buprestidae)**

**Polish Academy of Sciences
Museum and Institute of Zoology**

Warszawa

1999

6.35211

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Muzeum i Instytut Zoologii
Polskiej Akademii Nauk
BIBLIOTEKA
K. 35211

D. 82/99-10

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INTRODUCTION

South-east Asia harbours the world-richest fauna of the **Buprestidae LEACH**: in the number of species it possibly yields precedence to South America, being however second to none as regards diversification on the generic or subtribal level. But this extremely interesting faunal complex is still very poorly known, and the hitherto accumulated knowledge remains in the form of a multitude of individual descriptions, accidental distributional data, not always reliable host-plant records, &c., having - at least since CASTELNAU & GORY (1835-1841) - never been the object of comprehensive taxonomic review. Of course, there exists a world catalogue (OBENBERGER 1926-1937), first seven volumes of a planned world revision (KERREMANS 1904-1914), revisions of some genera (e.g. *Paratrachys* SND. - HOLYŃSKI 1992; *Philanthaxia* DEYR. - BÍLÝ 1993; *Endelus* DEYR. - THÉRY 1932, &c.) and faunistic reviews for some smaller areas (e.g. Laos - BAUDON 1966, 1968), while for the Malay Archipelago (DEYROLLE 1864), Philippines (FISHER 1921, OBENBERGER 1924) and the former French Indochina (DESCARPENTRIES & VILLIERS 1963-1967) even more ambitious - though old and/or still badly incomplete - studies have been published, but the bulk of available taxonomic and faunistic information remains hopelessly dispersed among thousands of separate original publications.

Psilopterina LAC., one of the largest and most widely distributed subtribes of the **Buprestidae LEACH** (several hundred - above 700 according to OBENBERGER 1926b, 1930 - species in some 15 genera inhabiting almost all tropical and subtropical areas of the world), are represented in the Indo-Pacific Region by 10 genera and more than 100 species. The taxon comprises big or at least medium-sized, frequently colourful species, many of which are rather common, but nevertheless even their taxonomic relations and geographical distribution (to say nothing about bionomy) remain relatively poorly known: the last comprehensive review of the "Groupe **Psilopterites Lac.**" (KERREMANS 1910) is almost nine decades old and includes only a part of the subtribe as presently understood, the last full catalogue (OBENBERGER 1926b) also appeared more than seventy years ago, and except for the recent revision of Indochinese *Psiloptera* SOL. by AKIYAMA & OHMOMO (1994) no other more than exiguous contribution to the knowledge of the Indo-Pacific representatives of the **Psilopterina LAC.** has been published in the present century; as the easily understandable consequence the status and affinities of most forms are often falsely interpreted, names wrongly applied, and specimens in collections notoriously misidentified.

The aim of this paper is to recapitulate the present state of knowledge, clarify some hitherto unresolved taxonomic questions, describe several new taxa, and propose a hypothetical reconstruction of phylogeny. Undoubtedly, the best solution would be a comprehensive taxonomic revision of the group, and of course I will aim at approaching this ideal as closely as possible, yet I am fully aware that, as a whole, my work is not likely to attain so high a level of completeness: being a "private person" (not a worker of any scientific institution) I have limited possibilities to borrow literature or material for study from public libraries and collections, thence too many types and too significant proportion of other relevant material and publications

will remain forever beyond my reach. This is especially true of the (in the Indo-Pacific) widest distributed genus *Ovalisia* KERR., whose numerous forms have been known only from the type-series, dispersed among many - European or oversea - museums, most of which refuse loan of material to "private entomologists" (moreover, this genus is currently under study by Russian entomologist Igor ZYKOV, what - by introducing the element of "competition" - makes the access to important material still more difficult). This situation forced me to restrict the taxonomic scope of the present work by exclusion of *Ovalisia* KERR. [s.l.] from revision at the specific/subspecific level (fortunately, this is not likely to disturb the structure of the paper or influence the conclusions). So I hope that even in this imperfect form, systematically presented results of the study of the material available to me, supplemented with the data accumulated in the available literature, will provide a useful basis for further, more profound analysis of this fascinating fauna.

ZOOGEOGRAPHICAL FRAMEWORK

In traditional zoogeographical regionalizations, South-East Asia is almost invariably considered a separate entity, the Oriental Region. Its southern (Indian Ocean), eastern (Pacific Ocean) and northwestern (Indus Valley, Himalaya) limits are rather sharply defined, but there are differences in opinions as to their northeastern (most frequently taken as Yang-tse Valley and Tokara Strait) and southeastern (WALLACE's, WEBER's, or LYDEKKER's Line) parts. So defined Orientalis has been proposed by pioneers of scientific zoogeography (SCLATER 1858, WALLACE 1876) within the frame of the scheme of geographical classification of land faunas, based almost exclusively on "higher" **Vertebrata** and undisputably well reflecting many avian or mammalian patterns. However, with increasing knowledge of insects, spiders, snails, *etc.*, it became evident that the scheme cannot be considered universal: the distribution of all too many taxa does decidedly not agree with that of vertebrates. In particular, various groups of **Arthropoda** fit rather the system proposed by phytogeographers: for them, the marine barrier between the Sunda and Sahul Shelves has apparently been of but secondary importance, New Guinea shows biogeographical affinity with South Asia rather than with Australia, and islands of Oceania are populated mostly by a depauperate version of the same fauna. Thus, from the perspective of such groups, all the vast area between India and Marquesas forms a single zoogeographical unit (separated from the Australian Region by Torres Strait and Coral Sea). There exists no generally accepted name for this unit, and various terminological solutions adopted by students of respective (represented behind the LYDEKKER's Line by subgroups of Asian rather than Australian affinity) taxa invariably obscure the real faunal patterns, leading to confusion and misinterpretations.

Thus, some workers follow the "modern" tendency to refuse any zoogeographical regionalization just on grounds of different groups showing different patterns and interregional borders being frequently unclear. In my opinion, such an attitude is a splendid example of throwing out the baby with the bath-water: certainly

we should be aware of the weaknesses of regional zoogeography, but must not overestimate these weaknesses, either; the borders of Atlantic Ocean or Sahel are no less unclear than those of Palaearctis or Neotropis, Devonian or Miocene are well defined periods in temporal distribution of some groups of organisms but do not correlate with any significant event in the history of others, and nevertheless nobody denies the need for such terms! As far as many animal taxa do show congruent patterns of distribution, faunal regionalizations make sense and provide a useful tool in zoogeographical studies.

Other zoologists discuss the relations in the studied taxa in terms of the classical (as defined by WALLACE 1876), *Orientalis* and *Australis*, apparently not bothering with the evident irrelevance of these vertebrate-based regions to the distributions observed in groups under their study. Still others properly define the zoogeographical unit at issue as extending from India to Oceania, but misleadingly refer to it as *Oriental Region*!

As the remarkably coherent pattern of Asian (instead of Australian) affinities of the New Guinean and Oceanian faunas is characteristic of a considerable variety (perhaps the majority) of invertebrate taxa, it seems desirable to have an unequivocal term for so delimited region (very exactly congruent with the Indo-Polynesian Province of marine biogeographers - *cf. e.g.* fig. 1 in BRIGGS 1999); as the **Buprestidae LEACH** are among the taxa concerned, it seems warranted to introduce such a term here. Apparently the most appropriate is "Indo-Pacific": the first (Indo-) component of the name alludes to the western portion of the Region, geographically a part of the Indian Ocean drainage area, almost identical with what was referred to as "India" in the historical past, and having derived the present names of its main subdivisions (India, Indochina, Indonesia) from the same root; the second (-Pacific) points to the eastern portion, composed of the majority of islands of the Pacific and extensive south-Asian continental areas adjacent to that Ocean. The term has not been coined by me: it appears from time to time in zoogeographical literature, usually as a quasi-synonym of *Oriental*; what I am proposing here, is to discriminate between these two names: to call "Oriental" the Region not extending beyond Wallacea, and "Indo-Pacific" that including [parts of] Oceania (nb. similar distinction seems warranted in the case of *Ethiopian vs. Afrotropical*: one of them should be retained for the Region considered as restricted to continental Africa only, and the other for the concept including Madagascar and surrounding islands - zoogeographically it makes a very important difference!) - we should know, what are we speaking about! In other words, the classical term has been proposed - and remains perfectly appropriate - for groups (like birds) showing the major faunal dichotomy at the WALLACE'S (WEBER'S, LYDEKKER'S) Line, and just therefore its application to those taxa (*e.g.* to the **Buprestidae LEACH**), for which the line of main contrast is marked with Torres Strait and Coral Sea, is disturbingly misleading. It would certainly not make much sense to coin a special name for any slight variant, but so drastically disparate concepts should find a terminological expression!

GEOGRAPHICAL SCOPE

One of the main aims of my work is to provide a summary of presently available factual knowledge, which eventually might serve as base for systematical, zoogeographical, evolutionary syntheses - among others, concerning the borders of the Region and the extent of penetration of its faunal elements into adjacent territories. To meet this purpose, the geographical scope of the review must be marked out rather broadly: it should assuredly comprise not only all the areas where Indo-Pacific taxa actually dominate, but also all those where they are likely to make a significant component of predominantly Palaeartic or Australian faunae.

As far as the family **Buprestidae** LEACH is concerned, Oceania harbours nothing more than a strongly depauperate representation of the south-east Asian fauna - the only exceptions being New Zealand with its ancient, astonishingly poor in terms of number of taxa but very peculiar jewel beetles of undoubtedly Australian affinities; New Caledonia with a mixture of Australian and Indo-Pacific elements; and Hawaii with but three recorded species, all evidently introduced. The buprestid fauna of south China and Riu-Kiu Islands apparently consists almost exclusively of Indo-Pacific elements; these become progressively less numerous towards the north, but many of them reach as far as Manchouria, Korea, and northern parts of Honshu - the transition seems smoothly gradual, without anything like clear-cut zoogeographic boundary. On the west, the Desert of Thar provides a much better defined limit, but even that barrier has been crossed by many buprestids in both directions. Several taxa of unmistakably Indo-Pacific origin occur also in northernmost Australia (York Peninsula, Arnhem Land), while several Australian forms found their way to relatively dry parts of southern New Guinea. All this makes the delimitation of the territorial scope of the review a very difficult task: any decision will be arbitrary.

For practical reasons (many labels, especially in older collections, read simply "India", "China", &c.) it has been convenient to draw the limits of the study area along the political boundaries - this is why I include into my review all the species reported from Pakistan, Korea, and Japan. As to China, it is obviously impossible to leave its south-eastern provinces out of consideration but, on the other hand, eventual inclusion of vast north-western areas like Sinkiang, harbouring practically no Indo-Pacific elements, would also make not much sense. Thus, I will take into account all the species recorded from the Asian continent east and south of the following line (map 1): western and northern boundary of Pakistan - northern boundaries of India, Nepal, Bhutan and Burma to the Sinotibetan Range (Hengtuanshan) - western borders of Yunnan, Szechuan and south Kansu - Huang-ho river across Kansu - northern boundaries of Ninghsia-huei, Shensi, Shansi, Hopei and Liaoning - northern border of Korea; I include also all the Japanese Islands as well as all islands of the Indian Ocean east of 70°E and north of 12°S, those of the Malay Archipelago north of the Timor Sea, Arafura Sea and Torres Strait, and of the Pacific north of the Coral Sea and 30°S, west of 130°W, and south of 40°N.

TAXONOMIC TREATMENT

Exact phylogenetic relations between species, genera, or higher groups within the **Buprestidae** LEACH have hardly ever been seriously analysed (among the few exceptions are *e.g.* the attempts of BELLAMY 1989, 1990, 1991a, 1991b, &c., and HOLYŃSKI 1992a, 1992b, 1992c, 1994b, 1997) and remain virtually unknown; my remarks on that matter should of course be looked upon as mere tentative working hypotheses. One could argue that it would be better to abstain from expressing so subjective views, because they are likely to prove eventually erroneous, but - as Rabindranath TAGORE warns - "*if you close the door to all mistakes, the truth will remain outside*"! Even if "a false hypothesis" is literally not - as the well-known saying has it - "of greater worth to the scientific progress than the valid one", it is anyway of greater worth than none, at least as a target for criticism and discussion paving a way for closer approximations of the reality!

The understanding of the taxonomic relations within the family also remains still "*in statu nascendi*": several authors (BELLAMY 1986, 1988, 1989; BELLAMY & al 1987; COBOS 1955, 1975, 1976, 1979; HOLYŃSKI 1984, 1988; KUROSAWA 1988, 1990; LEVEY 1978; NELSON 1982; NELSON, BELLAMY 1991; RICHTER 1952; TÔYAMA 1986, 1987 - see BELLAMY 1985 for the then up-to-date summary) have recently proposed more or less drastic - usually weakly substantiated - modifications of particular aspects of the traditional system of LACORDAIRE (1857) and KERREMANS (1893a), but neither most of these nor the new general classification advocated by COBOS (1980, 1986) can claim to have gained general acceptance. The most recent comprehensive, critical reassessment of the suprageneric subdivisions of the family is that proposed by me (HOLYŃSKI 1993b), and this has been followed here.

One general point of disagreement between many of my colleagues and me - responsible for a significant part of the discrepancies in the preferred classifications - is my dislike for the current fashion of apparently endless splitting of basic (genus, tribe, family) supraspecific taxa on grounds of minor details of morphology (especially genitalia and wing-venation), and consequent exaggeration of taxonomical ranks: proposed subfamilies usually deserve - in my opinion - at most the rank of tribes, most tribes should be considered subtribes, the bulk of newly erected genera function much better as subgenera or circles (*sensu* HOLYŃSKI 1992c). I do not see any advantage of such "crumbling" practice, which only generates superfluous complication of the system (*e.g.* the number of genera within the family like **Buprestidae** LEACH [and generally within the usual scope of interest of one taxonomist] should - in my opinion - remain within the limits of easy memorizability) provokes unnecessary nomenclatural changes, and unduly obscures affinities among the analysed groups, not improving - contrary to what is frequently claimed - the expression of relations within them (this goal is served much better with consistent application of intermediate - subfamily, subtribe, subgenus, circle, superspecies, &c. - categories). The "need" for splitting and up-grading is often apparently (though not always explicitly) derived from the "literal" (and, indeed, the most consistent) interpretation of basic principles of cladistic classification, leading however to an evidently endless process: if we, for example (as NELSON & BELLAMY 1991 do), set

the **Schizopodinae LEC.** apart into a separate family on the grounds of its being the sister-group of all the remaining buprestids, then another taxon (in this case perhaps the **Julodinae LAC.**) becomes the sister-group of "all the rest" and, consequently, "must" be removed and its rank elevated (causing, in turn, the "necessity" of further advance of the "**Schizopodidae LEC.**"); after eventual promotion of the **Julodinae LAC.** still another subfamily or tribe will find itself in similar position, &c., &c., &c. - this process can (and, if we wish to be consistent, must!) be continued until each species becomes a separate Kingdom (or, to make this slight exaggeration exact, until each taxon contains at most two subtaxa of immediately lower category, in which case we would either need a hierarchy of about 15 categories for the presently known *ca.* 20 000 buprestid species and at least 20 for 1 000 000 animals, or we should consider *e.g.* the present genus *Agrilus* *CURT.* no less than a subclass - and all these are only "mathematical" estimates, based on absolutely unrealistic assumption that each circle contains two species, each subgenus two circles, each genus two subgenera, &c.; if we wish to have a biologically useful classification, we must accept many monotypic taxa of various ranks, what means further enormous multiplication of the necessary hierarchical steps)...

In this review - as in my other works - I follow the synthetic ("evolutionary") "taxonomical philosophy". The main purpose of biological systematics (like any other branch of science) is to provide hypotheses of maximal predictive power; consequently, the ultimate "test of goodness" of a classification (as scientific hypothesis) is the extent to which the (morphological, ecological, physiological, genetical, or any other) characteristics of an organism may be deduced from its placement in the system. Species - by definition - evolve independently, and immediately after speciation each genetical change in any of the daughter species can only increase the difference between them; later on, changing direction of selective forces (or, in some cases, "genetic drift") may eventually cause some degree of convergence, but that involves only a fraction of characters, while others continue to diverge. Arguably, even in the most striking cases of convergent evolution, the accumulation of differences overwhelmingly surpasses the development of similarities (even if occasionally few superficial resemblances can make the appearance of the opposite). That is to say, the disparity between any two lineages always increases in time (the respective species are more different now, than their ancestors were at any time in the past) - "overall" convergence does not exist! The obvious consequence of this statement is, that the best classification (that of maximal predictive power) must not contain polyphyletic groupings, and this - not any kind of "evolutionary dogma" - makes systems agreeing with phylogeny the only acceptable. The continuous, irreversible increase of difference means, that the groupings based on "overall similarity" would always agree with phylogeny; this, however, is not necessarily true of small - and rarely approaching "statistical randomness" - samples of potentially relevant characters available to taxonomists: prevalence of convergent features among those actually examined is, unfortunately, by no means rare, what disqualifies purely phenetic approach as in principle wrong (though in practice phenetic methods can - and frequently do - produce correct classifications). On the other hand, the tempo of

divergence - the rate of accumulation of new characters ("apomorphies" in cladistic terminology) - varies enormously between lineages, rendering many paraphyletic taxa more informative (of greater predictive power) than the respective holophyletic ones; the disregard of this fact is the "original sin" of cladistic classifications.

The Indo-Pacific Region contains much higher proportion of insular areas than any other large zoogeographical division of the world. One of the obvious consequences of this situation is a very common occurrence of closely related but strictly allopatric forms. The most widely accepted definition of biological species ("*species are groups of actually or potentially interbreeding natural populations, which are reproductively isolated from other such groups*" - MAYR 1940) is not directly applicable to such cases: the "potential interbreeding" is a hopelessly abstract theoretical concept, virtually useless in the interpretation of particular taxonomic relations - it is practically impossible to prove the lack of intrinsic reproductive isolation between allopatric populations (experiments in captivity, under unnatural conditions, being obviously inconclusive), and their existence can also be convincingly demonstrated only in rare (at least among closely related forms) cases of crude genetical, embryological, or morphological incompatibility. In my opinion, the best way to escape from this "*cul-de-sac*" is the abandonment of the word "potentially" in MAYR's definition, *i.e.* acceptance of geographical - or, more exactly, spatial - isolation (on an equal footing with other kinds of reproductive barriers) as important criterion of specific level of divergence. As I have shown (HOLYŃSKI 1977, 1992d), there is no serious theoretical reason for the discrimination of territorial isolation in this respect: species is a unit of evolution, and thus "*evolving separately from others and with its own unitary evolutionary role and tendencies*" (SIMPSON 1961); the kind of the isolating mechanism that assures the independence of evolutionary development in particular case is obviously irrelevant - it is only its efficiency that counts, and geographical barriers are at least as efficient as others!

However, it would be obviously impracticable to treat any isolated population as a separate species - this would inevitably lead to nomenclatural and taxonomic chaos - so it seems most advisable to ascribe the species rank only to those, which have already run along their divergent evolutionary paths so far away, that the reversal seems evolutionarily impossible. As far as sympatric and synchronic bisexual forms are concerned, this in fact amounts to no more than a different formulation of MAYR's "principle of reproductive isolation", but in the case of allopatric (allochronic, parthenogenetic) populations evolutionary irreversibility can be judged only on the grounds of phenotypic (in practice, almost always morphological) criteria [to be sure, reproductive isolation between sympatric forms is also in but rarest instances actually observed, being almost invariably deduced from the existence of morphological hiatus (to avoid misinterpretation please note, that I use the word "morphology" in its traditional, broad sense: while for some authors "morphological difference" means only the difference in shape or structure, I include here all those features - form, size, sculpture, colour, &c. - detectable on a motionless specimen by the sense of vision)]. Theoretically, the differentiation of genotypes can be considered irreversible, if at least one of the alleles, or combination of alleles ("supergene") fixed (present in all

individuals) in one population does never occur in the other; in practice, such a disparity in gene pools remains undetectable: we can only observe and assess its phenotypic manifestations. Consequently, I propose to accept explicitly (it is generally accepted tacitly) a very simple, workable, and at the same time remarkably precise and theoretically sound criterion of "full species status": constant morphological differences; according to this criterion, allopatric species is a group of populations showing constant morphological characteristics, *i.e.* consisting of unequivocally determinable (on the basis of morphology) individuals. Such approach, proposed by me more than twenty years ago (HOLYŃSKI 1977), had been later independently formulated by CRACRAFT (1983) and is recently achieving increasing acceptance (NIXON & WHEELER 1990, ZINK & MCKITTRICK 1995, &c.) as "phylogenetic species concept" [species is "*the smallest aggregation of populations (sexual) or lineages (asexual) diagnosable by a unique combination of character states in comparable individuals (semaphoronts)*" - NIXON & WHEELER 1990].

Surely this is not a perfect solution: it does not fully exclude the reversibility of speciation, it makes allopatric sibling species undetectable, some purely phenotypic differences may be mistaken for genetical ones, &c. This is evidently a very serious shortcoming as compared to some ideal procedure allowing to establish the evolutionary status of any population beyond doubt. Unfortunately, such a possibility does not exist, the currently accepted practice of evaluating the diversification of allopatric populations against the "scale" of differences observed between sympatric taxa, has all the above-mentioned flaws and several - more important! - additional ones: it is highly subjective, equivocal criterion based, at that, on totally false series of assumptions (that phenotypic disparities in sympatry develop comparably to those occurring between geographically isolated forms, that the degree of morphological differentiation is a reliable indicator of intrinsic reproductive isolation, that the evolutionary - and, consequently, taxonomic - meaning of the latter is the same for sympatric forms as for those never meeting in nature, &c.); in this comparison, the "determinability rule" seems almost faultless...

To recapitulate, I advocate (and follow in my works - for more detailed discussion see HOLYŃSKI 1992d) three complementary definitions of species (whenever possible, we should apply that of the highest rank):

(1) **theoretical definition** (a modification of SIMPSON's evolutionary criterion): "*species are reproductively isolated groups of genetically (through common ancestry) interrelated populations, whose gene pools have differentiated beyond limits of reversibility*"; this is the most general formulation, closest to the basic tenets ("species concept") and applicable in principle to all groups of organisms, but transgression of the limits of reversibility is very seldom directly demonstrable in actual cases, so we usually must try the second-choice

(2) **semi-theoretical definition** (an adaptation of MAYR's "biological" criterion): "*species are groups of interbreeding populations, reproductively isolated by intrinsic mechanisms from other such groups*"; among allopatric, allochronic, parthenogenetic, &c. populations interbreeding obviously does not occur, and the

proof or disproof of intrinsic reproductive isolation is either [almost] never possible or irrelevant, so this definition can be actually applied to co-existing bisexual forms only; however, even in overwhelming majority of such instances we have no data on the reproductive isolation as such - this can only be inferred from the observed phenotypical (usually morphological) hiatus, what in fact means recurrence to the only universally serviceable

(3) **working definition** (a re-formulation of HOLYŃSKI's [1977] morphological criterion): "*species are groups of populations, showing - at least in one class of individuals (sex, caste, developmental stage) - consistent unique combinations of morphological characters*".

For less differentiated populations AMADON's (1949) rule should be applied: if more than 75% of specimens are determinable, we have to do with a subspecies; if less, the form at issue does not warrant taxonomical recognition.

METHOD OF PHYLOGENETIC ANALYSIS

Any method of phylogenetic analysis must be based on the assumption that evolution is generally a process of diversification: organisms become more and more dissimilar, while convergence - however frequent - concerns always only a minority of evolving characters. An important implication of this statement is, that taxa sharing recent common ancestor show usually closer resemblance to one another than to any taxon of more remote genealogical affinity, what in principle would make it possible to interpret phenetic distances between taxa as reflecting their phylogenetic relationships. Unfortunately, the correlation between the degree of phenotypic divergence and recency of common ancestry is disturbed by unequal "tempo of evolution": in some lineages more characters change than in others, making the resulting taxa "excessively" different from all the others - also from their closest relatives.

Generally accepted way to eliminate this confusing effect is to take into consideration only synapomorphies, *i.e.* only those character-states inherited by the respective taxa from their last common ancestor - this, however, immediately creates a new problem of distinguishing synapomorphies from symplesiomorphies and convergences (in the broad sense: for the purposes of the present discussion parallelisms, reversals, &c. are considered as special cases of convergence). Several possible methods have been proposed to recognize synapomorphies, but most of them - palaeontological, ontogenetical, functional, &c. - do not work in groups like most insects, where fossils are unknown or extremely rare, larvae develop in quite different directions than adults, and function of most characters is not even guessed on. So, outgroup comparison would remain as the only valid method of establishing polarity of characters and - thence - synapomorphies. But is outgroup comparison truly reliable? It would certainly be, if two conditions are met: if (*before the analysis!*) we know for sure what is the closest outgroup ("sister-group") of the group under investigation, and if there is no convergence. In most cases none of these conditions is

fulfilled: we can of course suppose that the taxa involved in the analysis are monophyletic [but even in this we cannot be absolutely sure] while as to their *holophyly*, or especially as to the relations between them, only intuitive "beliefs" are available at the start; it is just the aim of the analysis to elucidate these points! One could say, that synapomorphies may serve to define holophyletic groups, but so our reasoning becomes clearly circular: we use synapomorphies to determine holophyletic groups, in order to find potential outgroups, which then will be used to recognize synapomorphies! So, what is the solution? In the absence of convergences ("homoplasies") it would be easy: those character-states common to several taxa could be only either (if restricted to the ingroup) synapomorphies or (if present also in outgroups) symplesiomorphies, and all characters would be distributed congruently. But in the overwhelming majority of actual cases the distribution is not congruent, different characters point to different patterns: evidently not all the states shown by outgroups are true symplesiomorphies, and not all those present only in the ingroup are true synapomorphies - several convergences are included. I do not see any *general* (*i.e.* not restricted to rare special cases) possibility to distinguish between synapomorphies (or symplesiomorphies) and convergences individually, *before* the analysis: it can be done only on the basis of congruence with other characters, *i.e.* as a *result* of analysis!

Such analysis can be performed in different ways according to different basic assumptions; currently the most popular seems to be the "overall parsimony": that the phylogenetic tree most likely to reflect the true relations will be the "shortest" one. I am not persuaded that this assumption is just, thence I have devised a procedure not dependent upon it, based instead on what could be defined as "iterative" or "stepwise" parsimony [from the most important "diagnostic characters" of this procedure - recognition of sister-groups on the grounds of *Minimal Iteratively Corrected* distances, and *SEQ*uential reconstruction of ancestors - I call it *MICSEQ*]. My reasoning may be best explained with the analogy to a "real" tree (an oak, a beech, a maple). Such a tree sprouts as a single shoot and grows by adding more and more tissue at the tip; after attaining some length it forks: two (or sometimes more) twigs start to grow in different directions, at different rate; then again one or both of them ramify further, and this process is repeated many times (fig. 17A). Now suppose that we have such a tree before us, but for some reason or another we see only the tips of its terminal twigs - the "body" itself remains invisible (fig. 17B). In such situation it would be very difficult to "reconstruct" the true topology of the tree: probably the only feasible procedures would be either successive joining of closest neighbours (which could produce the topology strikingly different from the true one - fig. 17C), or "overall parsimony", *i.e.* search for the "shortest possible" (in terms of the sum of lengths of all branches) tree on the assumption that this is most likely to represent the true relations (however, the result - similar to that shown on fig. 17D [I am not perfectly sure, that this is actually *the* most "parsimonious" tree, but it is anyway much "shorter" than the original!] - would not be much better). However, the situation changes if we can remove all those portions of tissue, which have been added to each twig after its having branched off from its "sister twig", *i.e.* if we can cut the twigs off at their bases, which thus become the visible "tips" (fig. 17E). Now we would see that

the bases of some pairs of twigs - even if originally their tips were not neighbours - are immediately close to one another: they are "sister branches". If we now treat the just found common base of each pair of "sister twigs" as the tip of a "terminal" twig of earlier generation, and repeat the procedure of "cutting off" (figs. 17F,G,H), we disclose the deeper layers of common bases, *i.e.* further "sister relations". After several rounds we have our tree fully reconstructed.

Of course, the three-dimensional "botanical" tree - or, the less so, two-dimensional diagram - cannot adequately illustrate multidimensional phylogenetic relations, but if our knowledge about the evolution is true, the "genealogical tree" of any group of taxa is - at least in most important respects - analogous to the tree described above: each group arises as single ancestral lineage, which repeatedly branches giving rise to many twigs, each of them "growing" (by accumulating new "portions of tissue" - apomorphies) in different direction and at different rate, so that the distances between the ends of "terminal twigs" (actually examined taxa) very imperfectly reflect the genealogical relations between them. We can, however, make the real "sister-relations" immediately recognizable by a procedure equivalent to "cutting off" the terminal twigs of a "real" tree: exclusion of autapomorphies "reduces" each taxon to its last ancestor shared with sister taxon. This is, of course, the "theory"; in practice convergences ("homoplasies") disguise some autapomorphies as "symmorphies" (character-states occurring in more than one taxon), so that the "twigs" are "cut" not at the very base, but somewhere above it, thus making the picture less clear; however - unless the convergences are overwhelmingly numerous, in which case *no* method of phylogenetic reconstruction based on character analysis could give reliable results - even so the genealogical relationships (except if the successive nodes are very close to one another, *i.e.* in cases of "near-polytomy") remain recognizable.

In the absence of convergences, the "overall parsimony" algorithms, my "branch-cutting" procedure, and any other theoretically sound method of phylogenetic analysis would give exactly the same results, and these results would exactly reflect the true evolutionary relations; in practical situations (with convergences) the results may be different, but how big these differences may be, and which procedure gives the results closest to the truth, is of course not clear for the moment. Anyway, that proposed here has the advantage of being more "straightforward", easier to compute, and more perspicuous step-by-step, than other algorithmic procedures known to me. It seems also more "robust" to the "noise" produced by convergences, *i.e.* in the case of discrepancy between my results and those obtained by other method, my reconstruction will probably be closer to the truth - but this, of course, could be proven or disproven only after more analyses and comparisons have been done.

The "algorithm" of the analysis is simple in principle, though explanation of some details may seem rather cumbersome. My study has been based on morphological characters: molecular, genetical, physiological, ethological, &c. evidence is neither available from the literature, nor have I possibilities (skill, equipment, funds) to perform the respective studies and/or evaluate their results. Morphological differences are evidently not equivalent - individually variable characters, appearing frequently in various combinations in other groups, functionally

correlated to others, of simple genetical basis, &c. are less informative than those stable within species, unique to the group under study, functionally independent, genetically complicated - so the initial step of the analysis must be "weighing", *i.e.* determination of the value of difference ("cost of transformation") between each pair of character-states. Weighing may be equal ("unweighed" characters) or differentiated (between characters and/or between particular steps in transformation-series, which itself may be linear, branched, circular, or a combination of these); of course, there is usually no exact measure of the transformation-cost, so weighing is always a more or less subjective procedure - but we cannot avoid it: so-called "unweighed" characters are in fact those weighed equally (all have been ascribed the same value), what is at least as subjective decision as any other!... Weighed values are then used to construct the first "distance-matrix", where the "corrected distance" between each pair of taxa is the sum of differences between the respective *non-automorphous* states of all characters; an automorphous character-state is "downgraded" to its closest neighbour in the transformation-series (only "terminal" states - those at ends of a linear [portion of] transformation-series at the actual stage of analysis - can be considered automorphous; circular transformation-series may be regarded as a combination of two or more linear ones, thence some or all of its character-states may be considered "terminal", while others are assumed to be "transitional"), what in case of a binary character is equivalent to its elimination from further analysis.

The lowest value in the resulting matrix is selected as representing the distance between the pair of closest relatives. Of course, in ideal cases (*i.e.* in absolute absence of convergences) corrected phenotypic distance between sister taxa should be zero: a taxon can differ from its "sister" only in character-states newly developed in - and, so, unique for - one of them, and these automorphies are not taken into consideration. Convergences (appearance of "the same" features in not directly related taxa) may make such characters "countable", increasing the corrected distance above zero, but anyway the assumption that the lowest value in the distance-matrix relates to a pair of sister taxa seems reasonable. We link them together in our incipient cladogram, and reconstruct - on the basis of the character-states common to both (those differing are left as unresolved) - their immediate common ancestor, which then replaces them in the distance-matrix (where the unresolved characters are represented by the states of one of the "daughter" taxa).

If the corrected distances between other ("non-sister") taxa were directly correlated to the degree of genealogic affinity between them, the distance-matrix could be directly transformed into phylogenetic tree - the relation is, however, not that simple! The complication derives from the fact, that "uniqueness" is a *relative* property: each character-state first appeared as an "automorphy" of a newly evolved taxon, and became "symmorphous" only in its descendants - or after its convergent development in another lineage. In other words, a feature not automorphous for any of the terminal taxa, appears as automorphous at some deeper level of the evolutionary tree, changing the "corrected distances" (this fact complicates the phylogenetic reconstruction - which must be performed step by step, from the terminal taxa to the "root" - but, on the other hand, it accounts for the considerable reduction of the

confusing effects of convergences: in the course of analysis, many convergent features either disappear or become "transformed into automorphies" just where they would otherwise be most dangerous: towards the base of the cladogram)! So, the new (resulting from the replacement of the original sister-taxa with their reconstructed ancestor) distance-matrix must be recalculated according to the - possibly changed - automorphies. Choosing again the lowest value from the distance-matrix, pairing the respective taxa as sister-groups, reconstructing their ancestor, recalculating the new distance-matrix, and repeating this procedure until only three taxa have been left, we arrive at almost fully resolved cladogram.

The three-taxon stage sets the unsurmountable limit to the analysis: any feature distinguishing one taxon from the remaining two is "automatically" its automorphy, so all the corrected distances equal zero and there is no way to discriminate among the three theoretically possible arrangements [a(bc), b(ac) and c(ab)]! Worse still, this is only one aspect of more general limitation: the procedure does not distinguish between plesio- and apomorphies, thence any branch of the genealogical tree - including its "bottom branch", *i.e.* in fact the "trunk" - ending with two taxa will be "recognized" as terminal "twig" with a pair of sister-groups (the resulting cladogram is unrooted); in other words, if the two basalmost branches of the true phylogenetic tree are represented by single taxa, they will behave as sister-groups (the corrected difference between them - unless some convergences are involved - will become zero), and the same situation will arise as soon as the originally more complex basal branches will be "reduced" in the course of analysis to single (ancestral) taxa. There is no way to overcome this limitation, so we must evade it: since basal (and, fortunately, *only* basal) branches may pose the problem, we should "push them up"; this can be done simply by adding "still more basal" branch[es], *i.e.* by including outgroup[s] in the analysis.

In this "abstract" form the procedure is perhaps hardly comprehensible even in general outlines, so it will certainly be useful to illustrate it with - and explain the details on - a concrete example (see Appendix).

The genealogies presented here (figs. 1-16), the first attempt to reconstruct the phylogenetic relationships within the **Psilopterina LAC.**, are also the first results obtained by MICSEQ: the program evolved together with the reconstructions and - especially its computerized version and "know-how" - still remains *in statu nascendi*. This situation unavoidably led to some shortcomings and inconsistencies (the procedure applied to the first analyzed *Cyphonota DEL.* or *Capnodis ESCH.* differed in some details from that employed for *e.g. Spinthoptera CSY.*, and the latter was also not quite identical to the version developed until the intergeneric relationships within all the subtribe were reconstructed). The results obtained under such circumstances must, naturally, be treated with caution greater than usual and - especially where they seem to be in conflict with current taxonomic or zoogeographic knowledge - far-reaching conclusions should not be drawn too hastily.

CONVENTIONS OF PRESENTATION

Only new taxa are described in detail, otherwise the description has been restricted to most distinctive characteristics. Particular statements concerning the respective form have not always been checked against all the "material examined": *e.g.* identification keys were primarily constructed on the basis of all the accessible representatives of the taxon, but if the process of verification eventually revealed the necessity of making some improvements, the final version may be partly or totally based on only those specimens available to me thereafter; measurements are almost invariably taken from only a part of the determined individuals, and this is especially true of descriptions, made typically with but my own collection before me. The measurements given are as a rule based exclusively on specimens measured by me (with their number in square brackets); if exceptionally they are taken from other sources, then the relevant literature is quoted. Length of the body is measured from the anteriormost point of head to the tips of elytra; width measurements were taken always just behind humeral protuberances, even if this was not the widest part of the body. Geographical distribution is wordily presented according to both literature and collections, but maps include exclusively the data from the specimens examined by me (and from holotypes, which "by definition" surely belong to the taxon in question).

When reviewing a particular fauna, one can never assume to have included all the taxa really occurring there - to the contrary, future discoveries of species, genera &c. hitherto unknown from the study area are always to be expected. The resulting incompleteness, as potential source of confusion, is obviously a serious shortcoming of any taxonomic monograph (especially keys). Complete elimination of this deficiency as regards animals yet unknown to science is evidently impossible, but the danger of misidentification of taxa wrongly considered extralimital can be reduced to minimum. To this end, the "ideal" key to Indo-Pacific **Psilopterina** LAC. should include all (*i.e.* also those *not* known to occur in the Region) genera, all subgenera of Indo-Pacific genera, all species of Indo-Pacific subgenera, and all subspecies of Indo-Pacific species; this would enable any representative of an unexpected taxon to be recognized as such and put aside for special treatment. I tried to follow this principle whenever extralimital subunits of an Indo-Pacific taxon are not too numerous [their names are put in square brackets]; otherwise - for obvious practical reasons - only those known or likely to occur in the study area can be included. For the same purpose of minimizing the probability of misinterpretations, I try to avoid characters applying only to the keyed taxa; that is to say, if *e.g.* the colouration is indicated as "green or blue", it is intended to mean (unless the contrary is explicitly stated) that all - Indo-Pacific and extralimital, included in the key or not - known species of the respective group of taxa are either green or blue.

In the "material examined" - unless specifically stated otherwise - only specimens from the area under study are included, what in case of common but predominantly extralimital species may lead to seemingly contradictory statements (like "material examined: none", followed by discussion of variability).

In phylogenetic reconstructions I have included all the available taxa occurring or likely to occur in the study area, but the number of considered extralimital species (and those of *Ovalisia* KERR. s.l.) is restricted to few (selected from among the representatives of possibly all main morphological tendencies).

Like in my other recent works, in the enumeration of the type-material the individual labels (except those added by myself) are cited in quotation mark; my own labels are not cited - according to my current custom they are two or three: white determination-label (e.g. "Psiloptera jasienskii HOL. det. R. Hołyński 1997" - the year of determination written vertically on the left); red holotype- or green paratype-label (e.g. "Psiloptera jasienskii HOŁYŃSKI HOLOTYPE"), and - if belonging to my collection - small white collection-label with specimen-identifying signature (e.g. "coll. RBHOŁYŃSKI BPbnr"); specimens in my collection not belonging to type-series bear two (determination- and collection-) of these labels.

Collection names are abbreviated as follows:

- CLB = Charles L. BELLAMY, Pretoria, SOUTH AFRICA;
- ISUA = Instituut voor Systematiek en Populatiebiologie, Universiteit van Amsterdam, Amsterdam, HOLLAND
- KA = Kôyô AKIYAMA, Yokohama, JAPAN;
- KBIN = Koninklijk Belgisch Instituut voor Natuurwetenschappen, Bruxelles, BELGIUM;
- MCGD = Museo Civico di Storia Naturale "Giacomo Doria", Genoa, ITALY
- NHM = Natural History Museum, London, ENGLAND;
- NNHM = Nationaal Natuurhistorisch Museum, Leiden, HOLLAND;
- RBH = Roman B. HOŁYŃSKI, Milanówek, POLAND;
- SB = Svatopluk BÍLÝ, Praha, BOHEMIA
- UN = Ulf NYLANDER, Valbo, SWEDEN;
- ZIRAN = Zoologičeskij Institut, Rossijska Academia Nauk, Petersburg, RUSSIA

Besides, the following abbreviations are used in morphological descriptions:

- dfp = "dense-and-fine punctulation" or "densely-and-finely punctulate"; refers to the type of sculpture, especially characteristic of representatives of some subtribes (including **Psilopterina** LAC.) of the **Buprestini** LEACH, occurring mainly in depressed areas (foveae, sulci), and consisting of fine, dense, regular punctulation on usually distinctly microsculptured background, covered with dense pubescence and frequently pulverulent.
- L = length
- W = width
- BW = basal width
- AW = apical width
- MW = maximum width
- V = width of vertex between eyes
- H = width of head with eyes

SYSTEMATIC REVIEW OF INDO-PACIFIC TAXA

Psilopterina LAC.

- Psilopterites LACORDAIRE 1857
- = Dicercites KERREMANS 1893
- = Capnodini JAKOBSON 1913
- = Poecilonotini ALEXEEV et BEBKA 1970

General characteristics:

Large, nearly (except Oceania) cosmopolitan (maps 2-27) subtribe, variously interpreted by previous authors. In the traditional scheme, proposed by LACORDAIRE 1857 and accepted with little modifications by virtually all subsequent students, it was divided (on sole grounds of different distribution of antennal sensory pores) as two separate tribes between two subfamilies: the **Chalcophorinae LAC.** ("**Psilopterini LAC.**") and **Buprestinae LEACH** ("**Dicercini KERR.**"); it was RICHTER (1949, 1952) who pointed out to the untenability of such classification and merged the "**Dicercini KERR.**" with **Psilopterini LAC.** (and, by the way, **Chalcophorinae LAC.** with **Buprestinae LEACH**), but his arguments were totally neglected - the adherence of buprestidologists to the traditional arrangement and to the single-feature VIC[Very Important Character]-taxonomy was overly strong... Almost half a century later TÔYAMA (1987) removed *Pseudoperotis* OBB. to newly erected **Pseudoperotini TMA.**, and I (HOLYŃSKI 1993b) - in the framework of general rearrangement of buprestid classification - ranked the above-mentioned "tribes" and "subfamilies" as subtribes of the large tribe **Buprestini LEACH**, confirmed the merger of the "**Dicercini KERR.**" into, and removal of the **Pseudoperotina TMA.** (to which I added also *Chalcopoecila* THS.) from, the **Psilopterina LAC.**, and separated some other groups (**Phrxiina** COB., **Haplotrinchina** HOL.) traditionally included (at least in part) in the "**Dicercini KERR.**". At last BÍLÝ (1997) has shown, that *Pagdeniella* THY., considered hitherto as a close relative of *Philanthaxia* DEYR. (**Anthaxiini C.G.: Bubastina** OBB.), is in fact inseparable from *Ovalisia* KERR. So understood, the **Psilopterina LAC.** include some 600 or 700 species in ca. 15 genera, of which 10 (*Cyphonota* DEJ., *Capnodis* ESCH., *Dicercomorpha* DEYR., *Tristria* g.n., *Touzalinia* THY., *Psiloptera* DEJ., *Archepsila* g.n., *Dicerca* ESCH., *Poecilonota* ESCH. and *Ovalisia* KERR.), with ca. 100 species, occur in the Indo-Pacific Region or its vicinities.

Phylogenetic relations:

To my knowledge, reconstruction of phylogenetical relationships within the **Psilopterina LAC.** has never been attempted. The intergeneric affinities resulting from my analysis (fig. 1) are in some cases strikingly different from those expected intuitively and/or incompatible with published classifications; moreover, relations suggested by this "general" tree (for the subtribe as a whole) are not always congruent with those emerging from the analyses of particular [groups of] genera. This is a common - although, of course, unpleasant - phenomenon, occurring with most phylogenetic reconstructions, thence it is always prudent to take any "unorthodox"

result with caution until it is supported by other data and/or other analyses; this warning holds especially true for situations like this, when phylogenetically never studied group is analysed with a new, insufficiently tested procedure. However, in particular cases the problems seem to have resulted from more specific circumstances; those concerning the Indo-Pacific groups will be discussed with the respective taxa, here I will mention - and, as far as possible, explain - only the uncertainties as to the phylogenetic affinities of some extralimital [groups of] genera.

Rather than being a close relative of *Psiloptera* DEJ., *Sororcula* HOL. appears as the basalmost [except for *Ovalisia* KERR. s.l., the position of which is, however, highly doubtful and will be discussed under that taxon] branch within the subtribe.

Contrary to my earlier (HOLYŃSKI 1993b) proposal to include *Chalcopocila* THS. into the **Pseudoperotina** TMA., phylogenetic reconstructions (figs. 2, 3) place it invariably as the sister-group of *Achardella* OBB., and this seems indeed to be its true position; together with *Oedisterna* LAC. they appear as the second (after *Sororcula* HOL.) basalmost lineage on the "general" cladogram (fig. 1) what is compatible with one (fig. 2) of the more specific reconstructions, but rather contradicted by another (fig. 3). The relations between the **Pseudoperotina** TMA., *Chalcopocila* THS./*Achardella* OBB., *Oedisterna* LAC., *Ectinogonia* SPIN., and the *Psiloptera* DEJ.-group certainly demand further study.

The feature of potentially most important consequences is the position of the clade **Pseudoperotina** TMA.-*Hypoprasis* F.G.-*Chalcophorella* KERR.: these taxa were initially included in the analysis as preferred *successive outgroups* (only when, in the course of reconstruction, their unexpected placement became obvious, I was forced to use the undoubtedly not immediately related *Euchroma* DEJ. and *Epistomentis* SOL.), but have consistently (cf. figs. 1, 2, 3) appeared as a *single ingroup* well "within" the **Psilopterina** LAC.! If this reconstruction is correct (what seems highly probable), the **Psilopterina** LAC. are paraphyletic in relation to this clade, and the suggested (TÔYAMA 1987, HOLYŃSKI 1993b) affinities between *Hypoprasis* F.G. and **Pseudoperotina** TMA. are confirmed.

The exact position of *Icarina* ALL. remains uncertain: while according to the cladogram for *Polybothris* DEJ. (fig. 9) this group seems to make a clade with "*Polybothris*" *coquereli* (FRM.) and *Psiloptera* DEJ. (s.str.), in the "general" reconstruction (fig. 1) it appears as an outgroup to all the *Psiloptera* DEJ. s.l. and related genera (*Ectinogonia* SPIN., *Capnodis* ESCH., *Cyphonota* DEJ., &c.).

Generally, the degree of congruence among the cladograms related to *Psiloptera* DEJ. s.l. - by far the largest, widest distributed and most variable genus in the subtribe - is very poor, the main source of confusion being probably the polyphyletic nature of its subgroups (making, in various combinations, the "Operational Taxonomic Units"): it seems almost sure that e.g. several circles traditionally included into *Spinthoptera* CSY. are much closer to some groups of *Psiloptera* DEJ. s.str., and others to some *Lampetis* DEJ., than to one another. I tried to minimize this effects by separate treatment of some "suspected" species (*P. comorica* MNNH., *P. alluaudi* KERR., *P. coquereli* FRM., *P. bicarinata* (THB.) or groups like "*Psiloptera* [D]", or "*Psiloptera*

[H]" - referring to the specific cladogram for *Psiloptera* DEJ. s.str. (fig. 8), where "D" means the ancestor of the clade including the species from *P. pertyi* (C.G.) to *P. attenuata* (F.), and "H" the ancestor of those from *P. rubromarginata* (CHVR.) to *P. weddelli* LUC. - this, however, proved evidently insufficient.

Perotis DEJ. rather consistently appears very close to, or even within, *Spinthoptera* CSY. (fig. 1, 10) or *Lampetis* DEJ. (fig. 7) (the uncertainty being probably the result of the above-mentioned taxonomic confusion concerning these subgenera). On the other hand, phylogenetic affinities of *Latipalpis* SOL. remain nebulous: one reconstruction (fig. 1) shows it as the sister-group of *Perotis* DEJ., on the other (fig. 2) it appears as closest to the **Pseudoperotina** LAC., while according to still another (fig. 12) it branched off somewhere between the lineage including *Touzalinia* THY. and that leading to *Dicerca* ESCH. and *Poecilonota* ESCH.!

In my earlier paper (HOLYŃSKI 1988) I proposed to include *Notobubastes* CART. (previously considered a member of the "**Bubastini** OBB.") as a subgenus into *Psiloptera* "SOL."; this suggestion is more (fig. 7) or less (fig. 3) clearly supported by some reconstructions, being however evidently contradicted by the "general", intergeneric cladogram (fig. 1), where it appears as the sister-group to *Hilarotes* THS.; on the other hand, the position of the latter (traditionally included in the "**Chalcophorini** LAC.") near the *Touzalinia* THY.-*Dicercomorpha* DEYR.-*Tristria* HOL.-complex, supports my other hypothesis (HOLYŃSKI 1993b).

With so many doubts and incongruencies, and especially in view of the relatively early stage of development of both the applied procedure and phylogenetic studies of the group, it would be obviously premature to put too much confidence in the "general" cladogram and to base e.g. a reclassification of the **Psilopterina** LAC. or the reconstruction of their zoogeographic history on it. On the other hand, trees obtained for particular [groups of] genera seem usually much more trustworthy, making the taxonomic and zoogeographic conclusions sufficiently reliable - I will present my interpretations under the respective taxa.

Key to the Indo-Pacific genera of the subtribe Psilopterina LAC.:

- 1 (2) Body very short: L:W<2.25 *Cyphonota* DEJ.
- 2 (1) Body more elongated: L:W>2.35
- 3 (4) Body totally glabrous, even ventral side without pubescence
..... *Capnodis* ESCH.
- 4 (3) At least some parts of underside pubescent
- 5 (6) Inner surface of femora deeply longitudinally furrowed (to receive tibiae in repose) between pair of smooth carinae extending from tip to near base (figs. 85, 86) *Dicercomorpha* DEYR.
- 6 (5) Femora without distinct furrows, at most with slight poorly delimited depression on apical half (figs. 87, 88)
- 7(14) Medial parts of prosternal process separated from lateral rims by deep striae; scutellum small, not wider than interstria, or elytra with 13 striae

- 8 (9) Elytra with 13 striae; 1., 3., 6., 9., and 12 interstria elevated as costae
 *Tristria g.n.*
- 9 (8) Elytra with 10 striae (scutellar not counted); all interstriae equally elevated
- 10(11) 11. interstria interrupted - like others - by coarse foveolate punctures and not
 clearly delimited from epipleura, so elytral margin (especially in apical part)
 distinctly crenulate *Touzalinia THY.*
- 11(10) 11. interstria smooth, clearly delimited from epipleura, so elytral margin not
 crenulate
- 12(13) If lateral margins of pronotum sinuated and crenulated, then disc with distinct
 smooth reliefs and/or not depressed mediobasally
 *Psiloptera DEJ.*
- 13(12) Pronotal sides deeply sinuated and coarsely crenulated
 before posterior angles; disc without distinct smooth reliefs, broadly and
 deeply depressed at middle of basal part *Archepsila g.n.*
- 14 (7) Prosternal process without lateral striae and/or scutellum rather large, much
 (usually two times or more) wider than long; elytra with 10 striae
- 15(16) Scutellum small, about as long as wide, not wider than 2. interstria (fig. 57) .
 *Dicerca ESCH.*
- 16(15) Scutellum large and/or much wider than long, much wider than 2. interstria
 (fig. 56)
- 17(18) Elytra distinctly caudate; scutellum more than twice wider than long;
 pronotum with very conspicuous smooth median carina
 *Poecilnota ESCH.*
- 18(17) Elytra not caudate, or scutellum but slightly wider than long and pronotum
 without smooth median carina *Ovalisia KERR.*

Cyphonota DEJ.

Cyphonota DEJEAN 1833

General characteristics:

Small genus, containing 2 subgenera: *Phelix MARS.* including only a single very poorly known N-African species [*C. tetrum (C.G.)*], and *Cyphonota DEJ. s. str.* with 6 known species distributed from Morocco, through Mediterranean countries to Near and Middle East (map 2); 1 species touches the borders of the area under study in Belouchistan. Very short, ovate, convex, rather small (7.5-20 mm. - RICHTER 1952), dark (bronzed- or blackish-brown) body, apically broadly rounded elytra, and characteristic oblique elytral band in most species, make representatives of this genus easily recognizable.

Phylogenetic relations:

The closest relative of *Cyphonota DEJ.* is apparently *Capnodis ESCH.* (figs. [1, 4, 5). I have never seen *C. tetrum (C.G.)*, and have no substantiated opinion as to the affinities of *sg. Phelix MARS.*, thence I restrict my remarks to the nominotypical subgenus.

The phylogenetical relations within *Cyphonota* *DEJ. s.str.* as reconstructed by MICSEQ [fig. 4 - the character-states of *C. escalerae* (*OBB.*) and *C. luristanicum* (*RICHT.*), known to me only from descriptions, are based mainly on RICHTER 1952] agree very well with intuitive assessment. Both main lineages have representatives as well in Middle Asia as in western Mediterranean; however, the diversity in the former area seems greater, what might suggest eastern origin of the subgenus - the conclusion supported also by the fact that *C. escalerae* (*OBB.*) and *C. lawsoniae* (*CHVR.*) are apparently further differentiated from their immediate ancestors (more "automorphous") than their closest relatives, respectively *C. euphraticum* (*C.G.*) and *C. turcomanicum* (*KR.*).

Key to the subgenera of *Cyphonota* *DEJ.*:

- 1 (2) Body blackish-blue. Elytra lustrous, impunctate [*Phelix* *MARS.*]
- 2 (1) Body brown or brownish-black. Elytra distinctly striatopunctate
*Cyphonota* *DEJ. s. str.*

Sg. *Cyphonota* *DEJ.*

Cyphonota *DEJEAN* 1833
 = *Cyphosoma* *MANNERHEIM* 1837
 = *Coeculus* *CASTELNAU et GORY* 1839

Type-species: *Buprestis sibirica* *FABRICIUS* 1781
 = *Buprestis tatarica* *PALLAS* 1773]

General characteristics:

The distribution area of the nominotypical subgenus, including all but one species of *Cyphonota* *DEJ.*, is practically identical to that of the genus.

***Tataricum*-circle**

***Cyphonota turcomanicum* (*KR.*)**

Coeculus turcomanicus *KRAATZ* [in *HEYDEN et KRAATZ*] 1883
 = *Coeculus fulvovittis* *REITTER* 1887

Material examined:

1 ex.

Characters (fig. 25):

7.7×3.7 mm. [length 7.5-16.5 mm. according to RICHTER 1952]. Bronzed-brown with bright cupreous bottoms of punctures and dfp areas. Obliquely longitudinal, depressed, sharply but somewhat irregularly delimited, wide (except in anterior third) dfp stripe runs from humeral protuberance to apex of each elytron; another, short and indistinct dfp band extends along elytral margin from humeri to basal third. Whitish, recumbent pubescence is long and dense on sides of front, at anterior angles of pronotum, in dfp areas of elytra, and on sides of underside; otherwise short, sparse and indistinct. Front trapezoidal, wider than long, with rather regular, coarse and

extremely dense puncturation at middle of upper part, where it becomes as sparse as on vertex; fine stria extends from midlength of front to occiput. Antennae short (not reaching midlength of pronotal sides); 1. joint ovoid, somewhat longer than thick; 2. and 3. subequal, thinner and shorter than 1., globularly subconical; 4. *ca.* as long and wide as 1., subtriangular, 5. somewhat shorter, triangular; 6.-10. *ca.* as short as 2. or 3., wider than long, rhomboidal; 11. as long as 10. but narrower. Pronotum widest at middle, very broadly cordate; anterior margin distinctly, base strongly bisinuate, sides strongly roundedly convergent to apex, somewhat less strongly, sinuately so to slightly obtuse basal angles; surface regularly convex, puncturation rather uniform, coarse, laterally very dense and confluent, medially somewhat sparser; prescutellar pits transverse, narrowly and indistinctly separated, make appearance of single striola; lateral carina traceable on basal half, completely obliterated anteriorly. Elytra very short; humeral angles almost perfectly rounded, sides very slightly divergent to midlength, then broadly arcuately tapering to roundedly truncated apices; no posterolateral denticulation or apical denticles, sutural angle right. Elytral striae coarse and irregular, more or less disrupted into separate punctures anteromedially, very fine but more continuous posterolaterally; discal interstriae slightly convex, lateral flat. Each elytron with two depressed dfp bands: one prominent, oblique, beginning as narrow and not quite continuous sulcus above humeral protuberance, then widened (wider than two intervals) and running almost to suturoapical angle (but not reaching either suture or apex); other shallow, short and indistinct along basal third of elytral margin. Epipleura rather wide, subparallel to metacoxae, practically disappear behind them. Prosternum shallowly emarginate apically, prosternal process bordered with deep and coarse marginal stria, median part rather sparsely but coarsely punctured, more than 3× wider than smooth lateral rim. Sides of sternum and abdomen dfp, median parts more or less coarsely but sparsely punctured. of rather coarsely but sparsely punctured; hind margin of metacoxae shallowly trisinate, without denticle; anal sternite rounded at apex in female, truncated in male (RICHTER 1952).

Remarks:

This species is closely related to North-African *C. lawsoniae* (CHEVR.), from which it differs in somewhat less developed elytral dfp bands, more widely separated prescutellar pits, and some other details (in fact, according to the phylogenetic reconstruction (fig. 4), *C. lawsoniae* (CHEVR.) seems to be rather a "daughter-taxon" of *C. turcomanicum* (KR.): their reconstructed last common ancestor does not show any difference from the latter).

C. turcomanicum (KR.) is widely distributed (map 2) in Middle Asia (Tadjikistan, Usbekistan, Turkmenia) and Persia; the specimen in my collection labelled "PASNI, BALUCHISTAN, 11-4-35", on which this description has been based, is - to my knowledge - the first reported from the peripheries of the Indo-Pacific Region.

***Capnodis* ESCH.**
Capnodis ESCHSCHOLTZ 1829

General characteristics:

Small genus, containing 15 known species distributed in Mediterranean countries and in Middle Asia (map 3), with 5 species reported to occur at the peripheries of the Indo-Pacific Region: in Pakistan and subhimalayan areas of NW-India. Representatives of this genus are medium-sized to big (11-41 mm. - RICHTER 1952), dark (brown to black, with usually characteristic pattern of cupreous-bronzed - covered on fresh specimens with white waxy coating - dfp depressions), almost totally glabrous beetles of cordate pronotum, small (sometimes almost imperceptible) scutellum, and more or less caudate and finely punctatostriate elytra.

Phylogenetic relations:

Interesting feature of the genealogic tree shown on fig. 5 (the characters of three species not known to me in nature - *C. semisuturalis* MARS., *C. jacobsoni* RICHT. and *C. marquardtii* RTT. - have been taken mainly from RICHTER 1952) is the position of *C. porosa* (KL.) as not only the sister-group, but in fact the "mother-taxon" of all the remaining representatives of the genus: the common ancestor seems to have differed so slightly from *C. porosa* (KL.) that, if found today, it would be classified as at most a subspecies of the latter! The five species approaching or entering the studied area represent three separate clades, *C. miliaris* (KL.) being the (relatively plesiomorphic) sister-taxon of *C. indica* THS., and *C. parumstriata* BALL. showing the closest affinity to *C. excisa* MÉN. (and *C. alfierii* THY.).

Sg. *Capnodis* ESCH.
Capnodis ESCHSCHOLTZ 1829

Type-species: *Buprestis cariosa* PALLAS 1773

Key to the Indo-Pacific species of *Capnodis* ESCH.:

- 1 (2) Front sparsely, almost regularly punctured. Pronotum with five sharply delimited reliefs on very densely and regularly punctured background *C. carbonaria* (KL.)
- 2 (1) Front with irregular, at least partly very dense and confluent punctation, from which some smooth elevated spaces emerge. Pronotal surface between large reliefs very unevenly punctured, with many small irregular callosities
- 3 (6) Metacoxal denticle obtuse, rounded at tip (fig. 78)
- 4 (5) Posterior angles of pronotum right. Elytra with prominent striae, consisting of coarse and at least partly confluent punctures. Prosternal process not bordered [*C. miliaris* (KL.)]

- 5 (4) Posterior angles of pronotum decidedly acute. Elytra with indistinct (especially on anterior half) rows of fine and widely spaced punctures. Prosternal process bordered with row of deep punctures, usually confluent into stria *C. indica* THS.
- 6 (3) Metacoxal denticle acute, sharp (fig. 80)
- 7 (8) Pronotal sides simply sinuate before posterior angles; midline of pronotum not sulcate. 4., 6., 8. and 10. elytral interstria much narrower than others (fig. 33) *C. parumstriata* BALL.
- 8 (7) Proepisterna broadly and deeply excavated to receive profemora, thence lateral margin of pronotum with broad and deep angular incision at base (fig. 53); midline (at least on basal half) deeply sulcate. Elytral interstriae of equal width *C. excisa* MÉN.

Carbonaria-circle

Capnodis carbonaria (KL.)

Buprestis carbonaria KLUG 1829

This widely - from Greece to Kashmir (map 4) - distributed species, well characterized by the combination of very regular puncturation of the pronotal "background", distinct dfp spots on elytra, and prosternal process bordered with row of deep confluent punctures, shows marked geographical variability. Three subspecies [KERREMANS (1911) and THÉRY (1936) consider them as simple synonyms or varieties, OBENBERGER (1926) and RICHTER (1952) as separate species] have been distinguished, one of which reaches the westernmost periphery of the Indo-Pacific Region:

Key to subspecies of *C. carbonaria* (KL.)

- a (d) Median pronotal relief large, not divided longitudinally
- b (c) Median relief on pronotum long, extending beyond midlength, usually touching small prescutellar spot [*C. carbonaria* (KL.) s.str.]
- c (b) Median relief on pronotum short, not reaching midlength [*C. c. henningi* FALD.]
- d (a) Median relief of pronotum reduced to pair of small smooth spots at anterior margin *C. c. sexmaculata* BALL.

[*Capnodis carbonaria* (KL.) s.str.]

Buprestis carbonaria KLUG 1829

= *Capnodis Lefebvrei* CASTELNAU et GORY 1836

East-mediterranean race, occurring from Greece to Israel and Caucasus; reported also from Crimea.

[*Capnodis carbonaria henningi* FALD.]

Capnodis henningi FALDERMANN 1835

Inhabits the area around southern coasts of the Caspian Sea.

Capnodis carbonaria sexmaculata BALL.
Capnodis sexmaculata BALLION 1870
= *Capnodis kashmirensis* FAIRMAIRE 1891

Material examined:

14 ex. [1♂, 1♀, 12♂]

Characters (fig. 31):

Male [1] 24×9.5; female [1] 26.5×11 mm. [length 16-28 mm. - RICHTER (1952)]. Black with white waxy coating within punctures. Epistome very broadly and rather shallowly emarginated; front trapezoidal, somewhat wider than long, broadly and shallowly depressed at middle of anterior half, sparsely and somewhat irregularly covered with moderately coarse punctures. Pronotum (fig. 52) widest at anterior $\frac{2}{5}$, broadly cordate: apical margin shallowly but distinctly bisinuate, with median lobe reaching to level of inconspicuous obtuse anterior angles; base with very broad prescutellar lobe reaching far beyond level of sharply acute posterior angles; sides sinuately convergent in basal sixth, then broadly roundedly expanded; pronotal puncturation very regular, moderately coarse and very dense (interspaces forming but narrow ridges between punctures) but not confluent, very slightly sparser at middle of disk, leaving three pairs of smooth shining reliefs: large rounded on sides of base, small rounded on sides of anterior third, and small roundedly triangular at middle of anterior margin; lateral carina distinct from base to apex, interrupted by not dense but rather coarse (similar to those on disk) punctures and thence looking somewhat crenulate in dorsal aspect. Elytra obliquely truncate at humeri, sides then subparallel to midlength, arcuate to near apices and distinctly sinuate ("caudate") just before them; striae inconspicuous, consist of sparse rows of moderately coarse, shallow punctures; even (2., 4., 6., 8., 10.) interstriae sparsely uniserially punctured, odd (1., 3., &c.) ones with widely spaced, small, inconspicuous dfp foveae. Anterior margin of prosternum deeply triangularly emarginate between broadly rounded lobes; prosternal process rather sparsely covered with coarse punctures, which laterally (but not apically) fuse into bordering stria; proepisterna and rest of undersurface with very sparse, irregularly distributed, coarse punctures. Metacoxal denticle (fig. 79) right or obtuse; anal sternite narrowly rounded at apex in female, roundedly truncated in male.

Remarks:

Besides reduced and divided median relief of pronotum, *C. c. sexmaculata* (BALL.) differs from the remaining subspecies in less conspicuous elytral dfp spots and minor details of elytral and ventral sculpture. *Capnodis kashmirensis* FRM., treated as distinct species by KERREMANS (1911) and OBENBERGER (1926b), is - as THÉRY (1936) and RICHTER (1952) justly observed - not distinguishable from this race.

C. c. sexmaculata (BALL.) inhabits (map 4) Middle Asia (Turkmenia, Uzbekistan, Tadjikistan) and Pakistan (Chitral, Kashmir, Baluchistan).

Miliaris-circle

[*Capnodis miliaris* (KL.)]

- Buprestis miliaris* KLUG 1829
- = *Buprestis daedalea* STEVEN 1830
- = *Buprestis albisparsa* FALDERMANN 1830
- = *Capnodis metallica* [*melattica* err.] BALLION 1870
- = *Capnodis aurata* ABEILLE DE PERRIN 1904
- ? = *Capnodis mysteriosa* OBENBERGER 1917
- = *Capnodis Magdelainei* THÉRY 1929

Occurs from Turkey, Cyprus and Syria to Caucasus and Tadjikistan; specimens from Afghanistan (described as *m. afghanica* OBB.) are said to be smaller, slenderer, and have deeper elytral rows of punctures; according to RICHTER (1952) they "may represent distinct subspecies" which "perhaps ... occurs also in Pakistan".

***Capnodis indica* THS.**

- Capnodis indica* THOMSON 1881
- = *Capnodis vermiculata* FAIRMAIRE 1891

Material examined:

52 ex. [3♂, 4♀, 45♂]

Characters (fig. 32):

Males [3] 22-24×8.5-9.5; females [4] 23-26×8.5-10.5 mm. Cupreous-bronzed, elevated spaces usually somewhat darker, or sometimes (*v. vermiculata* FRM.) black; bottoms of punctures covered with white waxy coating. Front very coarsely and densely sculptured, with but few small elevated reliefs left among irregularly, longitudinally confluent punctures. Pronotum widest just before midlength, sides arcuately narrowed to apex and similarly so to posterior fourth, deeply sinuate at sharply acute posterior angles; apical and basal margins bisinuate, with anterior angles more, posterior less produced than the respective median lobes. Besides three pairs (basal, anterodiscal, and - usually indistinct - medioapical) of smooth reliefs similar to those in *C. carbonaria sexmaculata* (BALL.) (though anterodiscal not wider separated from one another than basal), one - also frequently obsolete - irregularly broadly lanceolate anteromedian "mirror"; surface between them with coarse, sparse on disc, dense laterally, very dense around (especially anterodiscal) reliefs; lateral carina entire, strongly upturned and sinuate (to receive profemur) in basal fourth and nearly straight (in lateral aspect) before. Elytral striae very fine, obsolete (except sometimes near apex), numerous broad (occupying together *ca.* half of elytral surface) irregular depressed areas coarsely and very densely but regularly (like typical dfp but much coarser) punctured. Anterior margin of prosternum broadly arcuately emarginate; prosternal process striatomarginate; undersurface coarsely but rather sparsely punctured; metacoxal denticle (fig. 78) obtuse; anal sternite narrowly rounded at apex in female, truncated or shallowly emarginated in male.

Remarks:

Closely related to *C. miliaris* (KL.), differs in lesser size, acute posterior angles of pronotum, finer elytral striae, striatomarginate prosternal process, usually bronzed [in *C. miliaris* (KL.) usually black] colouration, &c. Extensive, irregular, densely punctured surfaces on elytra make *C. indica* THS. easily distinguishable from all the remaining easternmost (occurring in or near the former British India) species of *Capnodis* ESCH. *C. vermiculata* FRM., treated by KERREMANS (1911) as separate species and supposed by RICHTER (1952) ("as it has its area - Kashmir") to be distinguishable at subspecific level, seems to be a simple colour variety: in Kashmir *forma typica* (and intermediates) also occurs, and no stable difference other than colouration and somewhat sparser punctures in elytral striae (which, however, is highly variable) has ever been suggested.

Subhimalayan species, distributed (map 5) from Afghanistan (RICHTER 1952), through Punjab and Kashmir, to Kumaon and Nepal.

Excisa-circle

Capnodis parumstriata BALL.

Capnodis parumstriata BALLION 1871
= *Capnodis costulata* FAIRMAIRE 1902a

Material examined:

5 ex. [1♂, 4♀]

Characters (fig. 33):

Male [1] 25.5×10 mm. (Length 26-35 mm. according to RICHTER 1952). All-black, with white waxy coating at bottoms of punctures. Frontal reliefs emerging from very coarsely and densely punctured depressions few, small, irregular, but highly elevated. Pronotum cordate, widest at midlength; sides subparallel in basal sixth, roundedly expanded before; apical margin very slightly bisinuate, basal more strongly so. Main reliefs similarly distributed to those in *C. carbonaria* (KL.) s. str., but broader and less regular in shape; only anterodiscal reliefs separated: laterobasal and medioapical pair confluent with unpaired anteromedian and prescutellar ones; besides, numerous irregular, small, sharply delimited callosities emerge from very dense, uniform puncturation of depressed surface; lateral carina entire, upturned and deeply sinuate just before base, broadly arcuate and coarsely crenulate otherwise. Elytral striae very deep, continuous, inconspicuously punctured; interstriae smooth, 2. slightly, 4., 6., 8. ca. 3× narrower than others. Anterior margin of prosternum narrowly, rather deeply, arcuately emarginate; prosternal process laterally (not apically) bordered with deep, coarsely punctured stria; ventral puncturation coarse but sparse; metacoxal denticle (fig. 80) sharply acute; anal sternite narrowly rounded at apex in female, broadly truncated in male.

Remarks:

RICHTER (1952) - without argumentation - places this species "close to *C. cariosa* PALL. and *C. jacobsoni*" RICHT., but in my opinion it is related rather to *C. excisa* MÉN. and - especially - *C. alfierii* THY., the latter showing the same peculiarity of narrowed 4., 6., and 8. interstriae which distinguishes *C. parumstriata* BALL. from all the remaining species.

The area of distribution of this species (map 6) extends from Turkmenia to Pakistan (Chitral, Punjab, Baluchistan).

***Capnodis excisa* MÉN.**

Capnodis excisa MÉNÉTRIÉS 1848

Material examined:

None

Characters (fig. 34):

Length, according to RICHTER (1952), 22-31 mm. Black with white waxy coating within punctures. Frontal reliefs large, puncturation of depressed parts coarse and very dense at middle, much sparser on peripheries. Pronotum (fig. 53) widest at midlength; sides broadly rounded with deep, nearly rectangular incision in basal fifth, bordering very conspicuous, smooth, deep excavation of proepisterna to receive femora in repose; both apical and basal margins rather deeply bisinuate; anterior angles prominent, posterior sharply acute. Laterobasal and laterodiscal pairs of reliefs large, irregular, free; medioapical pair coalescent with prescutellar and anteromedian reliefs into broad, widened anterad, smooth elevation occupying median third of pronotal surface; depressed surface coarsely, regularly, very densely punctured with numerous small to medium-sized, smooth, elevated reliefs throughout; median line sulcate, sulcus deep in basal half, shallow apically; lateral carina entire but very blunt and coarsely punctured. Elytral striae continuous or consisting of rows of coarse punctures; interstriae smooth or with very sparse but rather coarse punctures, odd ones with densely punctured foveae [in some specimens foveae extend - especially on sides - to even intervals, forming irregular depressed areas similar to, though much smaller and less conspicuous than, those in *e.g. C. miliaris* (KL.)]. Anterior margin of prosternum deeply but narrowly emarginate; prosternal process deeply striatomarginate laterally (not apically); proepisterna crossed with two longitudinal, coarsely and very densely punctured depressions; ventral puncturation coarse but very sparse; metacoxal denticle sharply acute; anal sternite laterally bordered with densely punctured depressions, apex rounded in female, truncated in male.

Remarks:

The closest relative of this species is apparently Arabian *C. alfierii* THY. [described as its variety, then (RICHTER 1952) treated as subspecies]: they share the characteristic structure of femoral excavations on proepisterna, distinguishing them

from all other species, but differ in elytral interstriae (equal in *C. excisa* MÉN., conspicuously unequal in *C. alfierii* THY.).

Occurs (map 3) in Transcaucasia, Turkmenia, Usbekistan, Tadjikistan, Persia, and - according to OBENBERGER (1926) and RICHTER (1952) - also in Baluchistan.

***Dicercomorpha* DEYR.**

Dicercomorpha DEYROLLE 1864

General characteristics:

Small genus of 11 species in two subgenera, distributed (maps 15-17) from Siam and Andamans to Java, New Guinea and Philippines (apparently absent from Borneo and - except probably [but see remarks under *D. dammarana* sp.n.] for Dammar Is. at the eastern end - Lesser Sundas). Diagnostic character of *Dicercomorpha* DEYR. is a deep sulcus extending on inner surface of each femur from apex to far behind middle and bordered with a pair of smooth carinae (figs. 85, 86). Besides, it differs from the related genera in characteristic combination of: slender 3. antennomere; more or less carinate elytra with dfp spots (sometimes confluent onto transverse fasciae or longitudinal intercostal bands); bituberculate apical margin of prosternum; prosternal process regularly convex, without bordering stria (except *D. damarana* sp. n.); deeply sulcate metasternum and 1. sternite; metacoxae without distinct denticle; &c. *D. javanica* C.G. shows slight sexual dimorphism in apex of anal sternite (rounded in female, truncated in male), not appreciable in the remaining species.

Phylogenetic relations:

The phylogenetic analysis of the genus *Dicercomorpha* DEYR. is presented in detail in the Appendix, and its results are shown on fig. 11. The distributional history of the genus (map 28) may be envisaged as follows:

The "general" cladogram for the **Psilopterina** LAC. shows *Tristria* g.n. and *Touzalina* THY. - both inhabiting the continental part of South-East Asia - as the closest relatives of *Dicercomorpha* DEYR., what allows to suggest Indochinese Peninsula as the area of origin of the latter genus; such hypothesis is further supported by the fact that one species of *Dicercomorpha* DEYR. still occurs there, and that it is just *D. vitalisi* BRG., apparently the basalmost subbranch of the basalmost branch of the genealogical tree. To be sure, fossils assigned to "*Touzalina* Thery, 1922 / *Psiloptera* Solier, 1833", "*Psiloptera* Solier, 1833 / *Dicercomorpha* Deyrolle, 1864", or "*Touzalina* Thery, 1992 / *Dicercomorpha* Deyrolle, 1864" were described from Middle Eocene of the famous Messel locality in Germany (HÖRNSCHEMEYER & WEDMANN 1994, WEDMANN & HÖRNSCHEMEYER 1994), and the presence of the respective genera there is by no means *a priori* unconceivable: the occurrence of now [sub-]tropical animals in Europe in Tertiary is a common phenomenon and the **Psilopterina** LAC. are frequently encountered among them; however, the identification of particular genera (except, perhaps, *Psiloptera* DEJ.) - based mainly on

the "exclusion" of other recent taxa on grounds of one or two (usually themselves poorly documented) characters - does not seem convincing, and anyway even if *Dicercomorpha DEYR.* had indeed existed and was widely distributed in remote geological past, the last common ancestor of the *extant* species has most probably lived relatively recently (perhaps in Pliocene) in continental South-East Asia.

This ancestor (M in the character- and distance-matrices shown in the Appendix) - reconstructed as a slender, golden-green beetle similar to modern *D. vitalisi BRG.* (although with longer, better developed lateral carina on pronotum, and rather weakly elevated elytral costae) - gave rise to two lineages: one (let us refer to it - after its ancestor - as *H*) remained initially on the continent, the other (*L*) seems to have dispersed over the - slowly approaching their present arrangement - islands of the Malay Archipelago. Eustatic oscillations of the sea-level in Pleistocene enabled one group of populations (*I*) to enter (probably along the northern route: through Palawan) Philippines, and the other (*K*) to invade the Sunda Islands. The Philippinean lineage had colonized the west-central part of the archipelago (Palawan, Mindoro, Masbate, southern Luzon are inhabited until now by *D. argenteoguttata THS.*) and then spread in both directions: to the North (northern Luzon - *D. mutabilis SND.*) and South (Panay-Negros-Mindanao - *E*, ?*D. fasciata WATH.*: exact distribution of the latter remains unknown, but on grounds of this zoogeographical reconstruction I dare to hypothesize that it inhabits the southernmost Philippine island[-s]), as far as Southern Moluccas: Ceram and Amboina (*D. interrupta DEYR.*) and Bouru (*D. subcineta DEYR.*). The Sundan population extended all along the Lesser Sunda arc to reach Damar I. (*D. dammarana sp.n.*), then dispersed in the opposite direction to the Andamans (*D. farinosa THS.*), and at last - through Celebes, Bangkei and Sula Is. - to Northern Moluccas (from where they apparently outcompeted and displaced the representatives of the *Subcineta-circle*: this seems to be the most plausible explanation for the disjunction between Philippines from where *D. fasciata WATH.* has been described and Southern Moluccas inhabited by *D. subcineta DEYR.* and *D. interrupta DEYR.*). This lineage persisted (as *D. multiguttata DEYR. s.str.*) until now between Celebes and Gebeh, having then dispersed to Philippines (*D. m. saundersi KERR.*) and New Guinea (*D. m. grosseguttata THS.*); on Halmahera and surrounding islands has evolved also *D. albosparsa (C.G.)*, now apparently sympatric with *D. multiguttata DEYR. s.str.*, but their taxonomic and distributional relations demand more detailed study on larger (and more exactly labelled) material.

Representatives of the "insular" lineage (descendants of *L*), now showing strongly disjunctive (Andamans on the West, Celebes, Philippines, Moluccas, New Guinea and Damar on the East) area, must have previously occurred also on Greater Sundas; they might have been displaced from there by later southward expansion of the "continental" branch from the Indochinese Peninsula (now inhabited by *D. vitalisi BRG.*), through Sumatra (*D. viridisparva THY.*) to Java [*D. javanica (C.G.)*], though total absence of *Dicercomorpha DEYR.* on Borneo and Lesser Sundas (except Damar) remains unexplained.

Key to the Indo-Pacific subgenera of *Dicercomorpha* DEYR.

- 1 (2) Elytral costae obliterated in anterior half, only apically conspicuous; dfp areas in form of isolated spots or transverse fasciae .. *Dicercomorpha s.str.*
- 2 (1) Elytral costae highly elevated and prominent throughout; dfp areas in form of longitudinal intercostal bands *Mirolampetis sg.n.*

S g. *Dicercomorpha* DEYR. s. str.

Dicercomorpha DEYROLLE 1864

Type-species: *Buprestis albosparsa* CASTELNAU & GORY 1836

The nominotypical subgenus, including all but one species, inhabits all the distribution area of the genus except Andaman Is.

Key to species of the subgenus *Dicercomorpha* DEYR. s. str.

- 1 (6) Elytral dfp spots arranged transversally and at least partly confluent into fasciae
- 2 (5) Pronotum without dfp areas. All elytral spots included into fasciae, covered with long and very dense pubescence
- 3 (4) Elytra with 1 dfp fascia *D. (s.str.) subcincta* DEYR.
- 4 (3) Elytra with 3 dfp fasciae *D. (s.str.) interrupta* DEYR.
- 5 (2) Pronotum with large transverse dfp depression at anterior angles. Elytra, besides fasciae, with some separate spots; pubescence in dfp areas short and moderately dense *D. (s.str.) fasciata* WATH.
- 6 (1) All elytral spots isolated, rounded
- 7(16) Elytra with 9 - ca. 25 (at least 4 discal) prominent, pubescent and (in fresh specimens) pulverulent dfp spots, otherwise glabrous or with but few small and indistinct dfp foveolae. Pronotum definitely wider at midlength than at base
- 8(11) Lateral row consists of 4 large spots
- 9(10) Pronotum green *D. (s.str.) mutabilis* SND.
- 10 (9) Pronotum black *D. (s.str.) argenteoguttata* THS.
- 11 (8) Lateral row consists of at least 6 small spots
- 12(13) Prosternal process bordered with deep stria *D. (s.str.) damarana* sp. n.
- 13(12) Prosternal process without bordering stria
- 14(15) Ventral surface (including epipleura) with no or predominantly green (without any purplish) metallic shine. Largest elytral spots more than twice as wide as interstriae *D. (s.str.) multiguttata* DEYR.
- 15(14) Ventral surface predominantly purplish, or at least subhumeral part of epipleura with purplish stripe. Largest elytral spots at most by a half wider than elytral interstriae *D. (s.str.) albosparsa* (C.G.)
- 16(13) Elytra without or with but few (2 on disc and some along lateral border) regular dfp spots, but instead with dense rows of small pubescent foveolae. Pronotum not or but indistinctly widened from base to midlength

- 17(18) Median sulcus of pronotum deep, basally widened into broad prescutellar depression *D. (s.str.) javanica* (C.G.)
- 18(17) Median pronotal sulcus very shallow, indistinct, prescutellar depression reduced to small shallow fovea *D. (s.str.) vitalisi* BRG.

Subcincta-circle

Dicercomorpha (s. str.) subcincta DEYR.

Dicercomorpha subcincta DEYROLLE 1864

Material examined:

20 ex.

Characters (fig. 35):

19.5-23×7.5-9 mm. [16]. Black with very slight metallic (purplish on pronotum and anterior half of elytra, greenish posteriorly) shine; somewhat obliquely transverse dfp fascia (reaching from lateral margin to about 3. stria) at anterior $\frac{2}{5}$ of elytra, and outer half of metacoxae, covered with very dense (completely concealing surface), long, recumbent golden-orange pubescence. Front with rather coarse and dense, highly elevated smooth reliefs. Pronotum widest at midlength; surface with coarse but sparse punctures at middle, very densely irregularly sculptured on sides; median line with narrow and irregular, coarsely and densely punctured sulcus in anterior half, and small prescutellar fovea at base - undifferentiated in between; narrow sulciform depression along apical margin broadly interrupted at middle; prehumeral foveae deep and long; no dfp areas. Elytral costae prominent on apical half, very indistinct anteriorly; striae more or less continuous, coarsely and densely punctured. Anterior margin of prosternum shallowly triangularly (with deeper incision at middle) emarginate between two prominent tubercles; prosternal process without border, smooth at middle, rather densely punctured on sides; proepisterna coarsely irregularly reticulate; ventral puncturation rather sparse, somewhat denser - but not distinctly dfp - at anterior angles of first 2 or 3 sternites.

Remarks:

D. subcincta DEYR. is the closest relative of *D. interrupta* DEYR., with which it shares the unique feature of well developed transverse, covered with dense and long pubescence, elytral fasciae (otherwise only in *D. fasciata* WATH. elytral dfp spots are partly included into fasciae - in other species they are fully isolated - and in all of them pubescence in the spots is short and rather sparse).

This species seems to be endemic of Bouru Is. (map 17): the single specimen allegedly from Ceram in KBIN has been certainly mislabelled.

***Dicercomorpha (s. str.) interrupta* DEYR.**

Dicercomorpha interrupta DEYROLLE 1864

Material examined:

37 ex.

Characters (fig. 36):

18.5-24×7.5-9.5 mm. [27]. Black with metallic (slight purplish or blue dorsally, stronger greenish ventrally) shine; three transverse fasciae - one immediately behind base, reaching to first (scutellar not counted) stria; one slightly oblique at anterior $\frac{2}{5}$ of elytra, extending to 3. stria; and one (usually disrupted into 2 or 3 spots) at apical fourth, also touching 1. (sutural) stria; laterally all extend to the marginal stria - on each elytron, and outer half of metacoxae, covered with very dense, long, recumbent orange pubescence. Front with coarse and dense smooth reliefs. Pronotum widest at midlength; surface coarsely but sparsely punctured at middle, very densely, irregularly, confluent punctate-reticulate on sides; median line with narrowly, irregularly sulcate in anterior half, foveolate before scutellum, and flat in between; transverse postapical sulcus only laterally distinct; prehumeral foveae deep and long; otherwise pronotum regularly convex. Elytral costae prominent on apical half, almost completely obliterated anteriorly; striae usually not depressed, consist of dense rows of separate punctures. Anterior margin of prosternum shallowly emarginate (in "bracket" - { - shape) between two prominent tubercles; prosternal process without bordering stria, but with irregular row of deep - though usually not very dense - punctures on its place; median portion smooth or with but few scattered punctures; proepisterna coarsely irregularly ocellate-reticulate; ventral puncturation rather coarse and sparse, somewhat denser - with some small and indistinct dfp spaces - at anterior angles of basal sternites.

Remarks:

D. interrupta DEYR. is closely related to *D. subcincta* DEYR., but can be distinguished at glance by having three (rather than one) transverse elytral fasciae; otherwise it differs in usually not distinctly depressed elytral striae, more coarsely punctured interstriae, uniserial (though somewhat irregular) row of punctures bordering the prosternal process, distinctly greenish colouration of ventral side, &c.

The species inhabits (map 17) southern Moluccas: Ceram and Amboyna; the locality "Boeroe" (3 ex. in NNHM) - if not representing an accidental introduction - must be a result of mislabelling.

Dicercomorpha (s. str.) fasciata WATH.

Dicercomorpha fasciata WATERHOUSE 1913

Material examined:

Holotype: "Type" "Philippine islands" "Sharp Coll., 1905-313." "*Dicercomorpha fasciata*, (Type) Waterh." [NHM]

Characters:

Ca. 18.5×7.5 mm. (damaged specimen). Violet-black above, bluish-black below; broad transverse (interrupted at middle) postapical depression and small spaces at inner margins of prehumeral foveae on pronotum, five transverse (disrupted into separate spots) fasciae on elytra, posterolateral portion of metacoxae, and large area at anterior angles of 1. sternite, dfp; these dfp spaces brassy, covered with short and rather sparse yellowish (on dorsal side) or denser, longer and darker orange (beneath) pubescence. Front with network of coarse and dense smooth reliefs. Pronotum widest at midlength; puncturation coarse and sparse at middle, very dense, irregularly reticulate on sides; narrow sulcus in anterior half of median line separated from prescutellar fovea by flat, undifferentiated space; prehumeral foveae deep, sulciform. Elytral costae well developed on apical $\frac{2}{3}$, indistinct anteriorly; striae consist of dense and coarse punctures. Emargination of anterior margin of prosternum semicircular; prosternal process without bordering stria, almost uniformly covered with moderately dense and coarse punctures; proepisterna coarsely, irregularly, confluent ocellate; sides of metasternum rather densely, median parts and abdomen sparsely punctured.

Remarks:

D. fasciata WATH. is morphologically intermediate between *D. interrupta* DEYR. and *D. subcineta* DEYR on the one hand, and *D. argenteoguttata* THS. on the other; its characteristic pattern of separate, but arranged into five fasciae, elytral dfp spots makes it easily distinguishable from all its congeners.

As far as I am aware, only the holotype has been known heretofore, so details of geographical distribution cannot be clarified.

Multiguttata-circle

Dicercomorpha (s. str.) mutabilis SND.

Dicercomorpha mutabilis SAUNDERS 1874

Material examined:

Holotype: "Type" "Philippin. 161" "D. mutabilis E.S. Type" "Saunders 74.18" [NHM]

Additional material: 20 ex.

Characters (fig. 37):

14.5-22.5×5.5-9 mm. [11]. Head, pronotum, scutellum, part of elytral suture and dfp spots, ventral side and legs vivid green; rest of elytra purplish-black; elytral spots (typically 11 on each elytron) large, rounded, covered with not very dense paleyellowish pubescence and - in fresh specimens - white pulverulence. Front

coarsely, irregularly punctured among smooth reliefs. Pronotum widest at midlength; puncturation on disc rather fine and sparse, sides covered with very dense, irregular jumble of punctures and elevated callosities; sulcus on anterior part of midline not reaching prescutellar fovea; prehumeral foveae narrow, deep, long. Elytral costae only apically distinct; striae represented by rows of relatively fine punctures. Emargination of anterior margin of prosternum brace-shaped; prosternal process without bordering stria, sparsely and rather finely punctured all-over; proepisterna coarsely and densely ocellate; ventral surface rather coarsely, sparsely punctured and glabrous; lateral third of metacoxae and anterolateral portions of sternites dfp, covered with not very dense recumbent pubescence.

Remarks:

This species is easily recognizable by its contrasting colouration and combination of large elytral pubescent dfp spots with totally glabrous pronotum.

The labels of most specimens examined by me indicate only the general locality "Philippine Is.", only two - "Luzon" and "Mt. Province" (also on Luzon) - are more detailed, so little can be said about the range of distribution of this species (map 17).

Diceromorpha (s. str.) argenteoguttata THS.

Diceromorpha argenteo-guttata THOMSON 1879b

? = *Diceromorpha viridicollis* THOMSON 1879b

= *Diceromorpha Strandi* OBENBERGER 1926a

Material examined:

26 ex.

Characters (figs. 22, 38):

15-22×6-9 mm. [19]. Black with slight bluish, violet or purplish shine; sometimes metallic lustre is stronger, cupreous or green (?v. *viridicollis* THS.?); transverse lateroapical depression, prescutellar and prehumeral foveae on pronotum, 11 large elytral spots, lateral half of metacoxae, and anterolateral spaces on sternites dfp, pubescent and pulverulent. Front with irregular elevated reliefs emerging from narrow, finely and densely punctulated depressions. Pronotum widest at midlength; puncturation on disc coarse but sparse, on sides very dense and irregularly confluent; prescutellar fovea rather broad, anterior sulcus separated from it by undifferentiated space; prehumeral foveae narrow, elongated. Elytral costae obliterated anteriorly; perisutural and lateral striae continuously depressed, others represented by very dense, almost confluent rows of coarse punctures. Anterior margin of prosternum shallowly semicircularly emarginate between pair of tubercles; puncturation of prosternal process variable in coarseness and density, sometimes distinctly concentrated in irregular lateral bands approaching formation of bordering stria; proepisterna with network of narrow smooth reliefs encircling dense ocellate punctures; sides of metasternum rather densely, median parts and abdomen (except extensive anterolateral dfp spaces) sparsely punctured.

Remarks:

D. argenteoguttata THS. is apparently related to *D. mutabilis* SND., but dark colouration and dfp spots on pronotum make it easily distinguishable. Superficially it resembles *D. multiguttata* DEYR. (especially ssp. *grosseoguttata* THS.) which, however, has elytral spots smaller and more numerous, median sulcus on pronotum continuous with somewhat elongated prescutellar fovea, and distinct dfp spot on the inner side of prehumeral carina (separating it from the sulciform prehumeral fovea). I do not see anything in the description of *D. strandi* OBB. which would distinguish it from this species, while "ob *viridicollis* Thoms. eine Varietät dieser Art oder eine selbständige Art oder doch nur ein Synonym der *mutabilis* E. Saund. ist, läßt sich leider nach der lakonischen Thomson'schen Beschreibung nicht feststellen" (OBENBERGER 1926a).

Most of the specifically labelled (*i.e.* not only "Philippine Is.") specimens (map 17) have been collected on Masbate; the exceptions are Palawan: Brookes Point, Mindoro, Luzon: Manilla and Mt. Maquiling, and Colombia: Manitousloue (I have been unable to find the latter locality on available maps, but the occurrence of *D. argenteoguttata* THS. in Colombia seems anyway unconceivable).

Dicercomorpha (s. str.) dammarana sp.n.

Dicercomorpha cupreomaculata damarae HOSCHECK in coll.

Material examined:

Holotype: "Dammer Insel" "2598" "Typus" "*Dicercomorpha cupreomaculata* Saund. ssp. *Damarae*. m. n. ssp., Det. Hoscheck 1942" [KBIN]

Paratype: "Dammer Insel" "2599" "Typus" [RBH: BPhvo]

Holotype:

21.5×7.5 mm. Bronzed-brown, with cupreous (covered with short yellowish pubescence and also yellowish pulverulence) spots distributed as follows: four along anterior margin of pronotum, one on each side at basal third, five along baser (one in each prehumeral fovea, one at some distance anteromedially to it, and one inconspicuous in prescutellar fovea), 14 larger and numerous smaller on elytra; ventral surface without distinct dfp spaces.

Epistome rather deeply arcuately emarginate, separated from front by distinct (though irregular) transverse carina. Front trapezoidal, broadly and deeply excavated in lower half, flat above; supraantennal and perioocular carinae distinct; anterior depression finely and very densely granulate, upper part covered with dense irregular network of elevated reliefs contouring punctiform depressions; pubescence longbut sparse, yellowish. Eyes rather prominent, *ca.* 1.5× longer than wide. V:H=0.45. Antennae reaching to *ca.* anterior fourth of pronotal sides; 1. joint egg-shaped, twice longer than wide; 2. spherical, distinctly narrower than 1.; 3. subconical, as wide as and *ca.* 1.5× longer than 2.; 4. club-shaped, as long as 1 but only as wide as 3.; 5. similar to 4.; 6. as long as but distinctly wider than 4., triangular; 7.-10. progressively shorter, 11. roundedly rhomboidal, as long as 6.

Pronotum wide (L:BW:AW=1:1.8:1.3); sides sinuately divergent to midlength, then rounded and almost straightly tapering to just behind apex, where they suddenly become subparallel (forming very distinct "collar"; apical margin rather deeply bisinuate with broadly truncate median lobe, base almost straight. Disk convex, with deep sulciform transverse depression laterally along base, deep sulcus on anterior half of median line (joining - through shallow depression - elongate prescutellar fovea), and depressed dfp spots enumerated above; puncturation coarse, very sparse on disc but very dense and irregularly confluent on sides; surface between punctures distinctly micropunctulate and very finely shagreened; lateral carina smooth, almost entire, broadly produced downwards between basal tenth and apical fourth. Scutellum roundedly trapezoidal (with very small triangular process at middle of posterior margin), concave, finely punctulate and distinctly microsculptured.

Elytra 1.8× longer than wide; base slightly wider than that of pronotum; sides subparallel to midlength, then roundedly convergent to apical sixth and sinuately so to obliquely truncate and sharply bidenticulate apices. Costae distinct apically, obliterated towards base; striae continuous and depressed between costae, but anteriorly represented by rows of separate coarse punctures; large dfp foveae rounded.

Anterior margin of prosternum very shallowly emarginated (almost straight) between two tubercles. Prosternal process (fig. 68) subparallelsided to behind procoxae, then cuneately narrowed to broadly rounded apex; deep lateral striae - running close to margins and parallel to them - not joining at tip; lateral rims smooth, median portion very coarsely but sparsely punctured. Proepisterna with irregular (in both shape and distribution) foveolate punctures among network of broad smooth reliefs. Metasternum and 1. sternite broadly and deeply longitudinally depressed along midline (traces of depression discernible also on 2. sternite); median parts of sternum and basal sternite with sparse simple punctures, which on sides are ocellate, very dense, and on abdomen more or less longitudinally confluent. Metacoxal denticle (fig. 77) almost totally obliterated. Anterior angles of 1.-4. abdominal segments with smooth reliefs; anal sternite with shallow arcuate preapical transverse depression, apex rounded..

Paratype (fig. 39):

Somewhat bigger (18.5×7.5 mm.), with indistinctly carinate median line of anal sternite, but otherwise virtually identical to the holotype.

Remarks:

I cannot imagine why HOSCHECK considered this taxon as a subspecies of "*Dicercomorpha*" *cupreomaculata* SND.: in fact, the latter represents a separate genus (*Tristria* g.n.) and has virtually nothing in common with *D. dammarana* sp. n.! The new species is evidently a member of the *mutabilis-argenteoguttata-multiguttata-albosparsa*-group, differing from the former in the presence of dfp spots on pronotum, from the latter three in their absence on abdomen, and from all in colouration, excavated anterior part of front, striatomarginate prosternal process, &c.

Known only from the type-series. The type-locality (map 17) is uncertain: there exist at least two islands of this name (variously spelled as Dammer, Dammar, Damar, or Damma) in Indonesia - one near the southern tip of Halmahera, and another at the eastern end of the Lesser Sunda chain, East of Wetar and Roma - and it is impossible to decide with certainty which of them the type-specimens have been collected on. Morphological distinctiveness and phylogenetic relations suggest long time of its separation, what seems much less conceivable on small islet in the midst of the distribution areas of such expansive species as *D. multiguttata* DEYR. and *D. albosparsa* (C.G.), than on a bigger and isolated island - thence the Lesser Sundan provenience of *D. dammarana* sp.n. seems more probable than its North Moluccan origin.

***Dicercomorpha* (s. str.) *multiguttata* DEYR.**

Dicercomorpha multiguttata DEYROLLE 1864

This species shows considerable geographical variability in colouration: specimens from Philippines (*saundersi* KERR.) are usually green, those from New Guinea (*grosseguttata* THS.) black, the representatives of Moluccan populations being morphologically intermediate (greenish-black). These forms have been usually treated as separate species, but - the differences being slight and not always consistent - they evidently represent but poorly differentiated geographical races. The nomenclatural questions have also not yet been satisfactorily clarified, thence some confusion (to which I have also contributed, having until recently attributed the name *multiguttata* DEYR. to Philippinean population, and joining the Moluccan and New Guinean as *grosseguttata* THS...) is seen in collections. *D. multiguttata* DEYR. was described from "I. Mysole, Key, N. Guinea (Dorey)", so the name can only be applied to either Moluccan or New Guinean form; it is certainly somewhat inconvenient to have just the morphologically instable, intermediate, perhaps taxonomically invalid race as nominotypical, but though I have never seen specimens from Mysol or Key, DEYROLLE (1864) describes the type-specimens as "bronzé verdâtre foncé", what fits the typical colouration of Moluccan rather than New Guinean population; on the other hand, the latter is rather widely known as *grosseguttata* THS., so designation of the former as the nominotypical subspecies avoids further nomenclatural confusion. Though some specimens from Mindanao show morphological characteristics of the nominotypical form, and some Moluccan beetles are virtually identical to New Guinean ones, generally the three races can be distinguished as follows:

Key to subspecies of *D. multiguttata* (DEYR.)

- a (b) Dorsal side green or blue *D. (s.str.) m. saundersi* KERR.
- b (a) Dorsal side black with or without metallic shine
- c (d) Ventral side with distinct greenish shine *D. (s.str.) multiguttata* (DEYR.) s.str.
- d (c) Ventral side with very faint purplish shine or without any
..... *D. (s.str.) m. grosseguttata* THS.

Dicercomorpha (*s. str.*) *multiguttata saundersi* KERR.
Dicercomorpha saundersi KERREMANS 1919
= *Dicercomorpha albosparsa* var. *nigroviridis* FISHER 1926

Material examined:

21 ex.

Characters:

16-23×6-9 mm. [13]. Uniformly dull green, some specimens darker greenish-blue or even violet-black; five dfp spots along anterior margin, and seven at base, of pronotum, as well as some 20 on elytra, 1 or 2 on each metacoxa, and one transverse anterolateral on each sternite, finely pubescent and covered with white pulverulence. Front with irregular network of elevated reliefs. Pronotum widest at midlength; puncturation on disc coarse but very sparse, on sides very dense and irregularly confluent; prescutellar fovea broad and elongate, almost always confluent with median sulcus; prehumeral foveae narrow, elongated, separated by smooth carina from round additional dfp fovea posited anteromedially; transverse anterolateral depression on each side disrupted into two dfp foveae, also anterior end of median sulcus, prescutellar and prehumeral foveae dfp. Elytral costae prominent posteriorly, obliterated towards base; striae represented by rows of very coarse, almost confluent punctures. Anterior emargination of prosternum semicircular with more or less distinct incision at middle; puncturation of prosternal process uniform, moderately coarse and sparse; proepisterna with ocellate punctures of variable density; sides of metasternum with rather dense, median parts and abdomen with sparse and rather fine puncturation.

Remarks:

Both the description and original localities of *D. "albosparsa" v. nigroviridis* FISHER leave little doubt as to its identity with *D. m. saundersi* KERR. Exactly labelled material (map 16) has been too scarce for reliable delimitation of the distribution area of this subspecies and the extent of the zone of intergradation with *D. multiguttata* DEYR. *s. str.*: the examined specimens from Samar [2] and Leyte [2] are typical, green; of the remaining 17, collected on Mindanao or labelled only "Philippines", three are dorsally greenish- or bluish-black and one black with no appreciable metallic shine (all have dull greenish underside), so being morphologically undistinguishable from the nominotypical race; the racial identity of a specimen from Palawan remains also unclear.

Dicercomorpha (s. str.) *multiguttata* DEYR. s. str.
Dicercomorpha multiguttata DEYROLLE 1864

Material examined:
33 ex.

Characters (fig. 40):

16-22×6-9 mm. [13]. Dorsally black with greenish or purplish shine, ventrally blackish-green; otherwise as *D. m. saundersi* KERR.

Remarks:

The Moluccan populations show some variability in colouration: some specimens are decidedly greenish dorsally, approaching the Philippinean race, some others are difficult to distinguish from *D. m. grosseguttata* THS.; besides, until recently I confused the latter with the nominotypical race, what makes my earlier identifications unreliable. So, it is not yet possible to demarcate exactly the distribution area (map 16) of this subspecies: it certainly occurs on Celebes, Peleng, Obi, Batjan, Halmahera and Gebeh islands, but it is not clear which race inhabits Palawan on the one hand, and Salawatti, Mysol and Kei on the other.

Dicercomorpha (s. str.) *multiguttata grosseguttata* THS.
Dicercomorpha grosseguttata THOMSON 1878a

Material examined:
108 ex.

Characters:

10.5-23.5×4-9.5 mm. [85]. Dorsally and ventrally black with or without faint purplish shine; otherwise as *D. m. saundersi* KERR.

Remarks:

This race is most stable in colouration; it certainly inhabits New Guinea and Waigeo (map 16), the populations of Salwatti, Mysol, and perhaps Kei may also belong here.

Dicercomorpha (s. str.) *albosparsa* (C.G.)
Dicercomorpha albosparsa CASTELNAU et GORY 1836

Material examined:
131 ex.

Characters (fig.41):

17.5-24×6.5-9.5 mm. [107]. Dorsal side black with more or less distinct greenish, bluish, or purplish shine; ventrally the shine is usually stronger and almost always totally or partly (at least in basal portion of epipleura) cupreous-red or purplish; 9-12 dfp spots on pronotum, ca. 20 on elytra, 2 on each metacoxa, and

transverse space on each side of anterior margin of sternites, pubescent and pulverulent (dorsal spots relatively small). Front with irregular network of highly elevated smooth reliefs elevated reliefs emerging from densely punctulated depressions. Pronotum widest at midlength; puncturation on disc coarse but sparse, on sides very dense and irregularly confluent; prescutellar fovea prolonged into deep median sulcus; prehumeral foveae narrow, elongated, separated by smooth carina from dfp spots medial to their anterior ends. Elytral costae obliterated anteriorly; first two (from suture) composed of rather fine, others of very coarse punctures. Anterior margin of prosternum shallowly semicircularly emarginate, sometimes with indistinct median incision; puncturation of prosternal process uniform, coarse and rather dense; proepisterna with moderately dense ocellate punctures; sides of metasternum rather densely, ventral surface rather finely and sparsely (somewhat less so on metasternal sides) punctured.

Remarks:

D. albosparsa (C.G.) is very closely related to - and after clarification of distributional details may prove to be but subspecifically (or not at all) distinct from - *D. multiguttata* DEYR.; it differs from the latter in smaller dorsal spots and cupreous or purplish basal sulcus of epipleura, but none of these characters is fully consistent (variability in spotting in both species makes this feature practically useless in extremal cases, and some - even if very rare - specimens of *D. albosparsa* (C.G.). have all the ventral surface, including epipleura, greenish).

D. albosparsa (C.G.) was described from Java, but does certainly not occur there (I have also seen a specimen labelled "Sumatra", what is equally erroneous). Unfortunately, old labels (especially those quoting "India", "Java", "Manila", "Singapore" and some other customary localities) are frequently unreliable, and increasing proportion of recently collected specimens are obtained from "dealers" and very often also mislabelled, what makes the clarification of geographical distribution very difficult. Most specimens of *D. albosparsa* (C.G.) bear the labels "Morotai", "Halmahera", "Ternate", "Kaioa", "Kasiruta", or "Batchian", suggesting Northern Moluccas as the species' homeland (map 15); occasionally encountered localities like Ceram, Salawati or New Guinea (Sorong) must be treated with caution.

Javanica-circle

***Dicercomorpha* (s. str.) *javanica* (C.G.)**

Dicercomorpha javanica CASTELNAU et GORY 1836

Material examined:

139 ex.

Characters (fig. 42):

Males [12] 14.5-18.5×5.5-7; females [44] 16.5-22.5×5.5-8.5 mm. Brassy to cupreous, with four (two on each elytron) major and very numerous small (somewhat larger on lateral margins) elytral pulverulent dfp spots; also pulverulent and dfp are

two spots on each metacoxa and one transverse at each anterior angle of sternite, and the same white pulverulence covers (at least in fresh specimens) bottom of each puncture, what gives the beetle characteristic farinose appearance. Front with network of irregular smooth reliefs elevated reliefs. Pronotum widest at midlength but only slightly narrowed to base; puncturation on disc coarse and dense, on sides very dense and irregularly confluent; median sulcus deep, entire; prescutellar fovea poorly differentiated; postapical depression and prehumeral foveae shallow and inconspicuous. Elytral costae obliterated anteriorly; striae deep, continuous; interstriae narrow, convex. Anterior margin of prosternum semicircularly emarginate; prosternal process coarsely and rather densely punctured throughout; ocellate punctures of proepisterna moderately dense; ventral surface (except at middle of metasternum and 1. sternite) coarsely and rather densely punctured.

Remarks:

D. javanica (C.G.) makes a well defined group with *D. viridisparsa* THY. and *D. vitalisi* BRG.: besides morphological affinities, the three species are also geographically closest, occupying - unlike the remaining members of the subgenus *Dicercomorpha* DEYR. s. str. - the "continental" (West of the Wallace's Line) part of its area. *D. javanica* (C.G.) is the endemic of Java (map 15; the locality "Ceram" for one specimen in the NNHM is certainly erroneous).

***Dicercomorpha* (s. str.) *viridisparsa* THY.**

Dicercomorpha viridisparsa THÉRY 1935b

Material examined:

Holotype: "A. I. v. H., Solok" "*Dicercomorpha viridisparsa* Thery TYPE" [NNHM]

Characters:

Female [? - sex determined under the assumption of the dimorphism in anal sternite as in *D. javanica* (C.G.)] 20.5×7.5 mm. Dull green with cupreous-bronzed shine on reliefs (especially on head, pronotum and sternum; no dfp spots on pronotum, very numerous small foveae (no major spots) on elytra, transverse spaces on metacoxae and at anterior angles of sternites. Front with coarse, highly elevated smooth reliefs and narrow dfp depressions between them. Pronotum widest at midlength, almost imperceptibly narrowed to base, much more strongly to apex; puncturation coarse, dense, confluent throughout, especially so on sides; median sulcus indistinct, prescutellar fovea broad; postapical depression shallow and inconspicuous, prehumeral foveae punctiform. Elytral costae anteriorly obliterated; striae consist of small dfp foveae separated by narrow smooth "bridges"; laterally striae confused; interstriae narrow, convex. Anterior margin of prosternum semicircularly emarginate; prosternal process coarsely and rather densely punctured; proepisterna with broad, irregular, ocellate punctures within network of smooth reliefs; sides of metasternum rather densely, rest of ventral surface (except at middle of metasternum and 1. sternite) coarsely and but somewhat sparser punctured.

Remarks:

D. viridisparva THY. is obviously very closely related to *D. javanica* (C.G.): green colouration, indistinct median sulcus of pronotum, lack of major elytral spots, and punctures of striae replaced with dfp foveae, makes it easily distinguishable, but had the single known specimen been found on Java, I would rather consider it an individual variety of the latter. However, Solok is a locality on Sumatra (map 15), and this geographical separation suggests that the above-mentioned morphological differences are of real taxonomic value.

As an inhabitant of Sumatra, this is the westernmost representative of the subgenus *Dicercomorpha* DEYR. s. str.

Dicercomorpha (s. str.) *vitalisi* BRG.

Dicercomorpha vitalisi BOURGOIN 1922

Material examined:

1 ex.

Characters:

Female [? - sex determined under the assumption of the dimorphism in anal sternite as in *D. javanica* (C.G.)] 20×7 mm. Pronotum cupreous, otherwise bright green with slight (head, elytra, prosternum) to strong (metasternum, abdomen) golden shine; no dfp spots on pronotum, very numerous small, inconspicuous pubescent foveae (no major spots) on elytra, lateral portions and transverse spaces along posterior margins of metacoxae, and indistinct anterolateral areas on sternites, similarly sculptured. Supraantennal and periocular carinae highly elevated, continuous, smooth; otherwise frontal reliefs rather indistinct among relatively broad dfp depressions. Pronotal sides very shallowly sinuate in posterior half, ca. as wide at base as at midlength, strongly roundedly tapering to apex; disc with moderately coarse and dense puncturation, sides with deep foveolate depressions within very irregular, dense network of smooth reliefs; median sulcus indistinct, prescutellar fovea small; postapical depression irregular and inconspicuous, narrowly sulciform; prehumeral foveae elongated, somewhat indefinite among coarse irregular reliefs. Elytral costae distinct almost to base; striae consist of rows of fine (suturally) to very coarse (laterally) punctures; intercostal interstriae flat, with numerous small, shallow dfp foveae. Anterior margin of prosternum semicircularly emarginate; prosternal process (fig. 69) coarsely and rather densely punctured; proepisterna with rather dense ocellate punctures; median parts of metasternum and abdomen sparsely punctured, otherwise ventral side with coarse and dense reticulate-punctate sculpture. Metacoxal denticle (fig. 76) totally obliterated. Metafemur (figs. 85, 86) with well developed sulcus.

Remarks:

BOURGOIN (1922) considered his new species closely related to "*D.*" *cupreomaculata* SND., to which, indeed, it shows superficial similarity. Closer examination, however, reveals some important differences in structure of pronotum

(median sulcus, prehumeral foveae), elytra (number of striae, distribution of dfp spaces), ventral side (almost regularly convex metasternum and 1. sternite, deeply striatomarginate prosternal process), and femoral sulci (weak on posterior, almost absent on anterior legs) strongly suggesting the removal of "*Dicercomorpha*" *cupreomaculata* *SND.* to a separate genus (*Tristria* *g.n.*). In fact, the closest relatives of *D. vitalisi* *BRG.* are *D. javanica* (*C.G.*) and, especially, *D. viridisparva* *THY.*, from which it differs in bright colouration, small prescutellar fovea and barely indicated median sulcus on pronotum, flat interstriae and some other details.

D. vitalisi *BRG.* is the only known continental (map 15) representative of *Dicercomorpha* *DEYR.*: BAUDON (1966) reported it from Laos, while the specimen before me (UN: 2633) comes from northern Siam.

Sg. *Mirolampetis* s.g. n.

Type-species: *Dicercomorpha farinosa* THOMSON 1879a

Very regular elytral costae, prominent all-over their length; virtually lacking striae, and totally dfp intercostal stripes make this monospecific subgenus highly distinctive. It is also separated geographically, solely representing the genus on the Andaman Islands.

***Farinosa*-circle**

***Dicercomorpha (Mirolampetis) farinosa* THS.**

Dicercomorpha farinosa THOMSON 1879a

Material examined:

15 ex.

Characters (fig. 43):

18-23.5×7-9.5 mm. Black with brassy shine; prehumeral foveae, median line, and pair of rather broad spots between them, as well as transverse lateroapical depression and several irregular spaces, on pronotum dfp; intercostal dfp spaces make 5 regular longitudinal stripes on each elytron; on ventral side only indistinct dfp spaces on sides of metacoxae and at anterior angles of sternites. Supraantennal and periocular carinae highly elevated, continuous, smooth; otherwise frontal surface dfp with but few, mostly longitudinal, narrow reliefs. Pronotal sides parallel or very slightly convergent in basal half (not wider at midlength than at base), then abruptly, straightly or somewhat sinuately tapering to apex; disc very sparsely, sides very densely punctured; median sulcus very deep throughout, prescutellar fovea represented with triangular widening of it; postapical depression rather distinct; prehumeral foveae broad and long, somewhat oblique, accompanied by similar more medial space. Elytral costae high throughout, totally smooth; striae hardly discernible; intercostal interstriae concave, dfp, pubescent and pulverulent. Anterior margin of prosternum deeply semicircularly emarginate; prosternal process covered with moderately coarse and dense puncturation; proepisterna with rather dense ocellate

punctures; median parts of metasternum finely and sparsely, rest of ventral side coarsely and rather densely punctured.

Remarks:

This species is probably a relative of the *D. albosparsa* (C.G.) - group, but stands isolated in both morphological and geographical sense: it is endemic to the Andamans (map 15).

Tristria g. n.

General characteristics:

The type-species of this subgenus used to be placed in *Dicercomorpha* DEYR.; however, structure and ornamentation of elytra, striatomarginate prosternal process, sulcate median line of pronotum, additional striae on elytra, and some other peculiarities make its separation at generic level warranted.

Phylogenetic relations:

Tristria g.n. consistently (fig. 1, 3, 11) appears as the closest relative of *Dicercomorpha* DEYR. and *Touzalinia* THY.; further affinities to *Hilarotes* THS. and - especially - *Notobubastes* CART., though not unconceivable, demand confirmation.

Sg. *Tristria s. str.*

Type-species: *Dicercomorpha cupreomaculata* SAUNDERS 1867

***Cupreomaculata*-circle**

***Tristria cupreomaculata* (SND.)**

Dicercomorpha cupreomaculata SAUNDERS 1867

Material examined:

Syntypes: "T" "Type" "Laos, Mouhot" "Saunders 74.18" [1 ex. (NHM)]; "TYPE?" "TYPE" "Mouhot" "Camboja" "Fry Coll. 1905.100" "*Dicercomorpha cupreomaculata* ES." [1 ex. (NHM)]

Additional material: 1♂

Characters:

Male [1] 17×5.5 mm. Dull golden-green with numerous small spots on elytra (each spot centered on a costa and extending on each side to neighbour interstria), as well as reliefs of pronotum and abdomen, violet-black; elytral dfp foveae and some other depressed areas golden-cupreous; legs green.

Epistome rather shallowly, arcuately emarginate. Front flat; trapezoidal, not separated from epistome; sculpture consists of network of very prominent, sharply elevated, predominantly longitudinal smooth ridges and very densely but rather coarsely punctured depressions between them; periocular stripes not distinctly

developed; no perceptible pubescence; vertex rather wide; eyes prominent, *ca.* 2× longer than wide.

Pronotum wide; sides slightly, almost straightly convergent in basal half and much more strongly, roundedly so before midlength; anterior margin almost straightly truncated, base bisinuate with median lobe protruding to the level of slightly acute posterior angles. Disk convex, prebasal depression inappreciable, lateral carina very irregular but traceable almost to apex; base with deep punctiform fovea near each posterior angle; median line deeply, narrowly furrowed and densely, finely punctulate; broad space on each side of median furrow smooth, elevated, coarsely and very sparsely punctured; lateral parts with rather irregular, large elevated reliefs and dense fine punctulation in between. Scutellum relatively large, trapezoidal, much wider than long, convex.

Elytral sides obliquely truncated at humeri, then subparallel to midlength, strongly arcuately convergent to $\frac{6}{7}$ and deeply sinuate before apices; lateral margin smooth; external apical denticle sharp, sutural not prominent. Each elytron with six (sutural, 4 discal, and marginal) elevated costae, separated by 1, 2, 2, 2, and 2 interstriae; striae not continuously depressed, consist of dense rows of coarse puncture; interstriae (including costae) interrupted here and there with small dfp foveae.

Anterior margin of prosternum deeply arcuately emarginated between two prominent denticles; prosternal process (fig. 67) parallelsided to behind procoxae, then sinuately narrowed to broadly rounded apex; deep lateral striae extend to apex but remain separate, both narrow lateral rims and 4× wider median space absolutely smooth; proepisterna rather densely, very coarsely, regularly foveolate. Metasternum shallowly sulcate along median line, sparsely and finely punctured on median parts, coarsely and rather densely, irregularly on sides; hind margin of metacoxae with but broadly rounded obtuse tooth at medial third. 1. sternite convex, median depression represented only by row of punctures on (otherwise smooth) intercoxal process, rest of surface - like that of 2., 3., and 4. segments - very densely and regularly, finely punctulate with some smooth elevated reliefs at sides; anal sternite coarsely and less densely punctured, truncate apically. Aedoeagus chestnut-brown.

Remarks:

SAUNDERS (1867) mentioned only Laos as the type-locality, so the second "type" (that from "Camboja") rather does not belong to the type-series. This seemingly very rare species is known only from Cambodia, Laos and Siam (map 18).

***Touzalinia* THY.**
Touzalinia THÉRY 1922

General characteristics:

Small (one species with three subspecies) group, occupying the area at the junction of the Indian, Indochinese, and Chinese Provinces of the Indo-Pacific Region (map 18).

Phylogenetic relations:

Close affinity of *Touzalinia* THY. to *Tristria* g.n. and *Dicercomorpha* DEYR. (fig. 1, 3) seems well corroborated. The sister-group relationship between this triade and *Hilarotes* THS. [Australian *Notobubastes* CART. seems rather misplaced here), if confirmed, would add yet another example to the interesting group of East Asian - Middle American connections.

Sg. *Touzalinia* THY.
Touzalinia THÉRY 1922

Type-species: *Touzalinia psilopteroides* THÉRY 1922

***Psilopteroides*-circle**

***Touzalinia psilopteroides* THY.**
Touzalinia psilopteroides THÉRY 1922

The variability of this rather poorly known species seems to show geographical pattern, warranting recognition of three subspecies:

Key to subspecies of *T. psilopteroides* THY.

- a (d) Colouration (golden- to bluish-) green
- b (c) Pronotal sides subparallel before base *T. p.siamensis* D.V.
- c (b) Pronotal sides divergent before base *T. psilopteroides* s.str.
- d (a) Colouration purplish-red *T. p. belladonna* HOŁ.

***Touzalinia psilopteroides siamensis* D.V.**
Touzalinia psilopteroides siamensis DESCARPENTRIES et VILLIERS 1963

Material examined:
None

Remarks:

This form is unknown to me in nature. According to DESCARPENTRIES & VILLIERS (1963) it differs from nominotypical form in having sides of pronotum subparallel in basal part; puncturation of pronotal disc, elytra and ventral side finer; oblique pronotal depression closer to lateral margin; elytral apices more deeply emarginated; their external denticle longer and sharper; tubercles of the anterior margin of prosternum more prominent. The validity of these differences seems,

however, doubtful: all show considerable variability also within the Yunnanese population.

Type-locality is "Thailand"; the taxon, to my knowledge, is known only from the holotype.

Touzalinia psilopteroides THY. s.str.

Touzalinia psilopteroides THÉRY 1922

Material examined:

?Paratype: "Paratype" "Pe-Yen-Tsin, Yunnan" "Touzalinia psilopteroides THÉRY, paratype, Théry det." [1 ex. (NHM)]

??Paratype: "TYPUS" "1870" "Koll.D^r.A.Fr.v.Hoscheck, Pe Yen Tsin, Yunnan" *Touzalinia psilopteroides* Théry, Det. Hoscheck. 192." [1♂ (ZIRAN)]

Additional material: 5♂ + 8♀

Characters:

Males [6] 23.5×9 - 25×10, females [8] 23.5×9.5 - 29.5×11.5 mm. Bright green to dark bluish-green, sometimes with cupreous reflections on elevated surfaces (especially of pronotum and underside); elytral interstriae predominantly black, interrupted with numerous, coarse, green punctures. Some (worn?) specimens are (especially on dorsal side) virtually glabrous, but most are covered with not dense but long, whitish, erect pubescence.

Epistome rather shallowly, arcuately emarginate. Front trapezoidal, not separated from epistome; very coarse sculpture consists of rather dense network of prominent, elevated, smooth ridges and very densely and coarsely punctured depressions between them; periocular stripes not distinctly developed; vertex wide; eyes prominent, *ca.* 2× longer than wider.

Pronotum wide; sides slightly, somewhat sinuately divergent in basal third and much rather strongly, roundedly convergent anteriorly (the two sections meet usually at obtuse angle, frequently with blunt denticle at junction); apical margin rather deeply, basal shallowly bisinuate. Disk convex, lateral carina not marked except at very base, sides viewed from above coarsely crenulate; basal depression shallow but distinct; pair of rather deep but very irregular and indefinite depressions at posterior third somewhat closer to sides than to midline, shallowly and still more irregularly obliquely extended to anterior angles; median line not distinguished, or with very irregular, indistinct longitudinal relief bordered with pair of densely punctured stripes; otherwise sculpture very coarse and irregular, especially dense towards sides. Scutellum very small, usually trapezoidal or rounded.

Elytra *ca.* 1.9× longer than wide; sides obliquely truncated at humeri, then subparallel to midlength, strongly arcuately convergent to ⁹/₁₀ and more or less deeply sinuate before apices; lateral margin crenulated due to interruption of marginal carina by coarse punctures; external apical denticle sharp but rather short, sutural not prominent. Striae deep, finely (medial) to very coarsely (lateral) densely punctured; interstriae equally convex, interrupted by coarse punctures.

Anterior margin of prosternum deeply arcuately emarginated between two prominent denticles; prosternal process with deep lateral striae, narrow convex lateral rims smooth, 4× wider median space sparsely but very coarsely punctured; proepisterna with narrow, densely punctured depressions among very coarse, irregular, strongly elevated reliefs. Metasternum deeply sulcate along median line, sparsely and finely punctured on median parts, coarsely and rather densely, irregularly on sides; hind margin of metacoxae with very distinct though obtuse tooth at medial third. Sculpture of abdomen consists of very coarse and rather dense, more or less longitudinally confluent punctures; 1. sternite broadly and deeply depressed along midline; apex of anal segment arcuately emarginate in male, roundedly truncate in female. Aedoeagus chestnut-brown.

Remarks:

In describing *Touzalinia belladonna* HOL. (HOLYŃSKI 1981) I had only one specimen of *T. psilopteroides* THY. for comparison; the study of more abundant material has shown, that some characters used then to distinguish the two forms from one another are in fact much less decisive or even simply invalid - for details see the "Remarks" on *T. p. belladonna* HOL..

The original description of *Touzalinia psilopteroides* THY. was based on one - apparently female ("Dernier segment arrondi au sommet") - specimen of 27×12 mm.; THÉRY (1922) mentioned also one "un peu plus petit" male, which could be regarded as a paratype. However, it is not clear which - if any - of the "types" listed above is just the specimen in question [the Petersburg (ZIRAN) "Typus" is indeed a male somewhat smaller (23.5×9.5 mm.) than the holotype; unfortunately, having 20 years ago the opportunity to examine the London (NHM) "paratype" I did not record either sex or measurements, but as that specimen has been labelled as paratype by THÉRY himself, the correctness of this identification seems more probable].

The specimens of this race examined by me come from three localities in Yunnan: Pe-Yen-Tsin, Tche-Ping-Tcheou, and Djo-Kou-La; unfortunately, I have been unable to locate any of them on available maps [some labels place Tche-Ping-Tcheou in S-Yunnan and Djo-Kou-La in NW-Yunnan; none states anything more precise about the type-locality, Pe-Yen-Tsin (or: Pe-Yen-Tsing)].

Touzalinia psilopteroides belladonna HOL.

Touzalinia belladonna HOLYŃSKI 1981

Material examined:

Holotype: "BURMA: Mishmi Hills. Lohit River. 1. iv. 1935." "*Touzalinia belladonna* HOL. det R. Holyński 1978" "*Touzalinia belladonna* HOLYŃSKI HOLOTYPE" [♀ (RBH: BPb-f)]

Characters:

29×11 mm. Bright purplish-red; elytral interstriae between interrupting punctures black; tibiae, tarsi, and some frontal, sternal and abdominal reliefs bluish-black; antennae purplish-black. Body throughout clothed with long, erect, white

pubescence. Elytra more distinctly "caudate": sides subparallel before apices (decidedly convergent in nominotypical subspecies). Subhumeral and external apical denticles of elytra, as well as those flanking the emargination of the anterior margin of prosternum, more prominent. Otherwise as the Yunnanese race.

Remarks:

Neither THÉRY (1922), nor DESCARPENTRIES & VILLIERS (1963) make any mention of dorsal pubescence in the races described by them, and the specimen then in my disposition was also dorsally glabrous, so in 1981 I quoted this character as diagnostic for *Touzalinia belladonna* HOL.; additional material examined later (especially the series from KBIN) has shown, however, that *T. psilopteroides* THY. *s.str.* is either highly variable in this respect, or (more probably) the lack of pubescence is only an effect of wearing: several specimens are almost as hairy as the holotype of *T. p. belladonna* HOL.! Some other "differences" listed in that paper have also proven either (*e.g.* colouration: distinct cupreous shine in many Yunnanese beetles) much less contrasting, or (dorsal convexity of the body, shape of scutellum) not exceeding the range of individual variability, and now I consider all the described forms of the subgenus *Touzalinia* THY. as geographical races of single species.

The subspecies is known only from the holotype, collected in the northernmost corner of Burma (map 18).

***Psiloptera* DEJ.**

Psiloptera DEJEAN 1833

Type-species: *Buprestis attenuata* FABRICIUS 1792

General characteristics:

Pantropical genus, with *ca.* 500 known species, traditionally divided into four big subgenera: *Psiloptera* "SOL." *s.str.* restricted to South America; "*Damarsila* THS." to subsaharan Africa; *Polybothris* "SPIN." to Madagascar area; and "*Lampetis* SPIN.", widely distributed in the Neotropical, Ethiopian, Indo-Pacific and southern parts of Nearctic and Palaearctic Regions. The nomenclature of, and taxonomic relations among, the taxa included in *Psiloptera* DEJ. have, however, not yet been fully clarified. KUROSAWA (1993) has shown, that the name *Lampetis* SPIN. refers in fact to what had been traditionally known as *Damarsila* THS., while the subgenus hitherto called *Lampetis* SPIN. [in fact, SPINOLA (1837) attributed the name to DEJEAN, who indeed was the first to publish it, and only later authors on flimsy - see BARBER & BRIDWELL (1940) for more detailed argumentation - grounds declared the "Catalogue..." a nomenclaturally invalid work] should be properly referred to as *Spinthoptera* CSY.; and BELLAMY (1997) recently demonstrated also the priority of *Psiloptera* DEJ. [in fact, he quotes the name as "*Psiloptera* Serville in Dejean 1833", but the author of the respective publication is evidently DEJEAN himself, who only - according to the widespread custom of his time - credited SERVILLE, MEGERLE &c. with the authorship of what they used *in litteris* or as collection names] over

Psiloptera SOL., and the same - despite BELLAMY's (1997) not easily understandable reservations - applies to *Polybothris* DEJ. vs. *Polybothris* SPIN. As to the taxonomy, *Polybothris* DEJ. is an extremely heterogeneous group, justly subdivided by THOMSON (1878b), whose action has, however, not been followed by later authors; Australian *Notobubastes* CART. has little to do with the **Bubastina** OBB., being in fact also a subgenus of *Psiloptera* DEJ. (HOLYŃSKI 1988); the same is the proper status of Neotropical *Pseudolampetis* OBB., while "*Dicercomorpha*" *cupreomaculata* SND. belongs in fact to *Tristria* g.n. Consequently, in the Indo-Pacific Region the genus is represented by the subgenera *Spinthoptera* CSY. and - if *P. preorientalis* sp.n. really belongs there - *Lampetis* DEJ.

Phylogenetic relations:

As explained in the discussion of intergeneric relations, taxonomic subdivisions within *Psiloptera* DEJ. are very poorly understood and seem to have been gravely misinterpreted in current classifications (recently summarized by KUROSAWA 1993); on the other hand, the procedure of phylogenetic reconstruction applied here (MICSEQ) is also still at rather early (in a sense, experimental) stage of development. In this situation it is not surprising, that the cladograms emerging from the present analysis are - as regards this genus - highly confused and incongruent as well among one another, as with the traditionally accepted groupings: certainly further research, including much more species from America and Africa, is needed to clarify the phylogenetic and taxonomic relations in *Psiloptera* DEJ. s.l. Such a study remains obviously by far out of the scope of the present work, but until it is done, it would be futile to attempt the detailed reconstruction of the phylogenetic and/or zoogeographic history of the genus as a whole. Fortunately, in practice only *Spinthoptera* CSY. occurs in the study area (*Psiloptera preorientalis* sp.n., although according to the current concepts should be included into *Lampetis* DEJ., has also been discussed under *Spinthoptera* CSY. - see below for argumentation), so I restrict the genealogic/distributional analysis to that subgenus.

Although some subgroups of what is currently called *Spinthoptera* CSY. should probably be excluded from the subgenus, the remainder seems to be a monophyletic, relatively ancient (many fossils dated as early as Eocene seem to be rather safely attributable to it) group. Its present distribution (South America, Africa, southern Asia, with but minor "excursions" into southernmost parts of Nearctic or Palaearctic Regions) might suggest Gondwanian origins, but presence in the Tertiary of Europe reminds that this may be the result of later dispersal as well. However, phylogenetic reconstruction (see fig. 10) seems to support the old southern supercontinent as the place of early development of *Spinthoptera* CSY.: among the analyzed taxa, the basalmost clade is represented by southern-Neotropical *P. torquata* DALM. and *P. aurifera* (OL.), showing some striking and possibly homologous similarities to (also exclusively Neotropical) *Psiloptera* DEJ. s.str.; the next two branches [*P. comorica* MNNH. and *P. alluaudi* (KERR.)], point to the Madagascan area and are followed by again Neotropical *P. tucumana* GUÉR., Burmese *P. comottoi* LSB., Ethiopian *P.*

funesta (F.), and evidently also Ethiopian by provenience (albeit now southern-Palaeartic) pair of sibling species *P. argentata* MNNH.-*P. mimosae* (KL.).

The true affinities of the above-mentioned *P. comottoi* LSB. remain unclear: in an earlier version of the cladogram it appeared as related to (also geographically close) *P. puncticollis* (SND.), to which indeed it shows several intriguing similarities (while the homologous nature of the characters in common with *P. tucumana* GUÉR. is certainly not beyond doubt).

The sister-group of the *argentata/mimosae*-clade was the ancestor - denoted in my reconstruction as Z (though, like other reconstructed ancestors, not named in the cladograms) - of two lineages. One of them (Y), after branching off of Ethiopian *P. rugulosa* (C.G.) [it should be remembered, that very few extralimital - non-Indopacific - representatives of the subgenus have been included in the analysis, so each such branch may consist in fact of many species], remains entirely within the Indian subcontinent, though the affinities of its next-basalmost "twig" are still African and very interesting from the taxonomic point of view, too. Namely, the species in question is *P. preorientalis* sp.n. which, having (even if unobscurely) bituberculate anterior margin of prosternum, should - according to the currently accepted definition - be classified as a representative of *Lampetis* DEJ. Indeed, *P. preorientalis* sp.n. shows some other "lampetoid" characteristics and is evidently a member of otherwise Ethiopian *Pupillata*-circle (see fig. 7), but its affinity to the above-mentioned, unambiguously spinthopteran group - the *Fastuosa*-circle - is also hardly questionable. This invasion of *Spinthoptera* CSY. into the Indo-Pacific was a rather recent event: most probably it occurred in the Middle or Late Pliocene, when - contrary to earlier periods of interchange - the migrations from Africa to Asia dominated over those proceeding in the opposite direction (HOLYŃSKI 1979).

Further history of the *Fastuosa*-circle seems to be that of repeated series of invasion-speciation-reinvasion events occurring between India and Ceylon (map 29). The ancestor of the circle inhabited India in the pre-Pleistocene or early Pleistocene time. Eustatic drop of the sea-level during glaciation enabled it to extend its distribution-area to Ceylon, but then the interglacial transgression separated it into two populations, of which the Ceylonese evolved into *P. jasienskii* sp.n., while the continental became almost identical to *P. orientalis* (C.G.). One of the later glaciations re-established the "bridge", providing this mainland form the opportunity to invade Ceylon, and the following period of high sea-level caused new speciation: *P. coerulescens* (HBST.) appeared. New cycle of regression-transgression led to the expansion of *P. coerulescens* (HBST.) to India and subsequent isolation of its newly established mainland population from the insular residue; the former, having found itself sympatric with very closely related *P. orientalis* (C.G.), "evolved away" ([competitive? reproductive?] character displacement) to become *P. fastuosa* (F), while the latter remained practically unchanged and at the next occasion (last glaciation?) invaded the continent again and outcompeted its sibling (or, rather, "daughter") in southern India (with, again, some divergent evolution in the invading populations).

The sister-taxon of Y might have lived somewhere in the present Middle East. It gave rise to two lineages, the only remnant of one of them being *P. scintillans* WATH., preserved in "splendid isolation" on Andaman Islands. The basalmost offshoot of the second lineage is the genus *Perotis* DEJ., presently inhabiting the Mediterranean area (map 24). Its sister-group seems to have lived and evolved in East Asia, sending (through - reasonably warm in preglacial and interglacial periods - Beringia) consecutively two branches - represented in the cladogram by Middle-American *P. geniculata* WATH. and *P. granulifera* (C.G.) - to what is now Canada and USA (from where they were subsequently displaced southwards by the Pleistocene glaciations), and ultimately splitting up into a northern (continental) and southern (insular) lineages. The northern gave rise to one more invasion of America (*P. chalconota* WATH., now inhabiting Mexico), and then - as the *Affinis*-circle - remained within the continental South-East Asia (with one species - *P. cupreosplendens* SND. - dispersed into India). Largely sympatric and, at that, poorly known distribution of members of this group does not allow to disclose the details of their zoogeographic history, in which the most important role has probably been played by repeated isolation on the opposite sides of mountain ranges.

The insular lineage has itself ramified into two branches - the *Alorensis*- and *Timoriensis*-circles - which further evolved in similar, "stepwise" manner: with one member of each pair of sister-taxa rapidly evolving and speciating, while the other remains almost unchanged. It is impossible to say with any certainty where the initial split between the two branches occurred - the most probable seems the division at the Wallace Line, with the ancestor of the *Alorensis*-circle inhabiting Sumatra, Java and Bali, and that of the *Timoriensis*-group extending from Lombok to the East. Later on, the former lineage - having left what is now *P. praeinsularis* sp.n. on Java and Sumatra (today it is known only from the latter) - also spread over Lesser Sundas, while an offshoot of the *Timoriensis*-circle (*P. baliana* KERR.) invaded Bali and Java; the present strictly allopatric "mosaic" distribution seems to be the result of mutual competitive exclusion between the members of both circles, but the exact sequence of colonizations and extinctions is now rather impossible to unravel.

Key to the Indo-Pacific subgenera of *Psiloptera* DEJ.

- 1 (2) Anterior margin of prosternum straight or slightly sinuate, without protruding tubercles *Spinthoptera* CSY.
- 2 (1) Anterior margin of prosternum emarginate between two tubercles [Lampetis DEJ.]

Sg. *Spinthoptera* CSY.

Spinthoptera CASEY 1909

=*Lampetis*: KERREMANS 1903 [nec DEJEAN 1833 non SPINOLA 1837]

Type-species: *Psiloptera valens* LÉCONTE 1858

[= *Buprestis drummondi* CASTELNAU & GORY 1837]

The largest [to be sure, with *ca.* 150 described species it yields precedence to *Polybothris* SPIN. *s.l.* including 250, but the latter is an evidently heterogeneous group to be split - as has already been done by THOMSON (1878a,b) - into several smaller taxa] and by far most widely distributed (occurring - except Australia - virtually all over the area inhabited by *Psiloptera* SOL. as a whole - map 7) subgenus. It is best represented in America - reaching from central Argentina to central USA (Colorado, Kansas - NELSON 1986) - from where more than 100 species are known; the remaining seem almost equally divided between Africa and South Asia, with three or four species of African provenience extending into Palearctic Region: *P. (S.) mimosae* (KL.) reaches to Caucasus and Kara-Kum, *P. (S.) argentata* (MNNH.) even to Beludjistan (RICHTER 1954). In the Indo-Pacific Region the subgenus is widely distributed all over the Indian and Indochinese Peninsulae, and then appears again in the Malay Archipelago: along the southern arc (from Sumatra to Timor) and in the Moluccas (Batjan); to my knowledge, it has not (yet?) been reported from Borneo, Celebes, or Philippines).

There are some distinctive, unmistakable species among the Indo-Pacific *Spinthoptera* CSY., but most are very similar and/or difficult to diagnose (differing in characters like coarseness of sculpture or convexity of interstriae, which are sometimes even striking to experienced eye, but refract exact definition), making proper identification of a specimen at hand, or - especially - interpretation of published description, by no means an easy task.

Key to the Indo-Pacific species of the subgenus *Spinthoptera* CSY.

- 1 (4) Abdomen coarsely and sparsely punctured, with narrow pubescent band of dfp punctulation at some distance from each lateral margin
- 2 (3) Each elytron with dfp lateral part of base, three obliquely arranged big round spots before middle, cuneate longitudinal lateroapical band, and few very small and indistinct foveae on 3., 5., and 9. interstriae *P. (S.) comottoi* LSB.
- 3 (2) Elytra with numerous, almost uniform (though denser and somewhat bigger lateroapically) dfp foveae on odd interstriae *P. (S.) puncticollis* (SND.)
- 4 (1) Abdomen without distinctive dfp band, or pubescent dfp stripes run at lateral margins
- 5(45) Elytra without costae (both even and odd interstriae flat) or intercostae also elevated (usually interrupted by dfp foveae)
- 6(17) Lateral margin of pronotum marked with distinct, regular, smooth carina reaching to at least two thirds of its length. Front relatively finely sculptured, smooth reliefs small and indistinct (fig. 45)

- 7(10) Elytral interstriae without any trace of dfp foveae
- 8 (9) Striae coarser, less regular; interstriae narrower, more convex. Sides of pronotum with finer but more confluent punctures, no apparent smooth interspaces wider than a puncture; punctulation of pronotal disk denser. Parameres dorsally separated in apical $\frac{2}{5}$ by parallelsided slit; tip of penis roundedly tapering *P. (S.) fastuosa (F.)*
- 9 (8) Striae finer, more regular; interstriae wider and less convex. Sides of pronotum coarser but less confluent punctured, with rather large, irregular, smooth reliefs; disk with less dense punctulation. Dorsal slit separating apical parts of parameres extends to their midlength, navicular; tip of penis sinuately tapering *P. (S.) coerulescens (HBST.)*
- 10 (7) Odd elytral interstriae interrupted with dfp foveae (sometimes apparent only on 9.interstria and/or represented only by coarse punctures)
- 11(12) Elytral foveae concentrated along suture [*P. (S.) melancholica (F.)*]
- 12(11) Interstitial foveae distributed over all elytral surface or only on sides
- 13(16) 9. interstria flat and wide (wider than 8.), clearly demarcated in posterior $\frac{4}{5}$
- 14(15) All elytral dfp foveae small, punctiform, occupying only the middle part of the width of their interstriae; undersurface (especially legs) bronzed
..... *P. (S.) orientalis (C.G.)*
- 15(14) At least some foveae on 9. interstria large, rectangular, occupying all its width; underparts and legs golden-green or golden-cupreous
..... *P. (S.) jasienskii sp.n.*
- 16(13) 9. interstria narrower than 8., distinctly elevated (costiform), somewhat confused in anterior half *P. (S.) praeorientalis sp.n.*
- 17 (6) Lateral carina of pronotum indistinct, broken, or disappears already in basal half among coarse punctures. Frontal sculpture very coarse, smooth reliefs large and prominent (figs. 46, 47)
- 18(29) Elytral interstriae not costiform: flat or but slightly convex; if - very rarely - subcostiform, then colouration bright green or cupreous and foveae on odd interstriae present but weakly developed, not or only slightly depressed, not much differing from those occasionally appearing on even interstriae (continental forms)
- 19(28) Elytral sides sometimes somewhat angular behind humeri, but without prominent denticular projection
- 20(27) Proepisterna without any trace of additional ridge parallel to lateral margin
- 21(26) Elevated, smooth reliefs on pronotum and elytra similar in colouration to depressed dfp areas
- 22(23) 9. interstria with large (much larger than those situated more medially) dfp spots contrasting with smooth elevated areas. Dorsal side green or dark-bronzed. Male genitalia yellowish-brown ... *P. (S.) cupreosplendens SND.*
- 23(22) Dfp foveae on 9. interstria similar to those on others, small, inconspicuous. Dorsal side (or at least pronotum: elytra sometimes duller coppery-bronzed) bright coppery-red. Male genitalia brownish-black

- 24(25) Median line of pronotum greenish, sides of disk more golden or cupreous. Male genitalia more than 4× longer than wide *P. (S.) viridicuprea (SND.)*
- 25(24) Median line of pronotum concolorous. Male genitalia less than 4× longer than wide [*P. (S.) holynskii (A.O.)*]
- 26(21) Elevated smooth reliefs on dorsal surface deep violaceous-black, sharply contrasting with mostly purplish-red or coppery, depressed dfp areas *P. (S.) nelsoni (A.O.)*
- 27(20) Proepisterna with usually very irregular, but always appreciable, row of smooth reliefs running parallel to lateral carina as additional, submarginal ridge *P. (S.) affinis (SND.)*
- 28(19) Elytral sides with laterally projecting denticle behind humeri *P. (S.) psilopteroides (SND.)*
- 29(18) Interstriae definitely costiform, strongly convex; if colouration bright metallic, then elytral foveae either totally absent or developed only on odd interstriae but there very distinct, regular, deeply depressed (insular forms)
- 30(38) Odd and even interstriae similar, continuous or (exceptionally) almost so, dfp foveae absent or sparse, small, inconspicuous
- 31(35) Body metallic green or cupreous. Abdomen almost uniformly, coarsely sculptured
- 32(33) Elytra green, concolorous with pronotum. Punctures in elytral striae coarse, deep, uniserial; superimposed finer punctulation inappreciable *P. (S.) eva (THS.)*
- 33(32) Elytra bronzed-cupreous, pronotum dull bluish; sculpture of elytral striae consists of coarse but shallow uniserial punctures obscured by dense and relatively coarse irregular punctulation *P. (S.) draconis sp.n.*
- 35(31) Body black with or without metallic shine. Sides of abdomen dfp
- 36(37) Frontal sculpture very coarse; elevated reliefs cover at least as much surface as depressed dfp spaces between them. Abdominal pubescence less dense, surface of sclerites clearly visible. Body black without distinct metallic shine. Metacoxal denticle obtuse, broadly rounded at tip, but distinct. Male genitalia yellowish-brown *P. (S.) baliana KERR.*
- 37(36) Frontal sculpture finer; elevated reliefs less extensive than depressed dfp background. Pubescence on sides of ventral surface (esp. of metacoxae and 1. sternite) very dense, making surface of sclerites practically invisible. Body black with strong (at least on front) metallic (violet or green) lustre. Metacoxae without appreciable denticle. Male genitalia brownish-black *P. (S.) timoriensis (C.G.)*
- 38(30) Odd interstriae (costae) unbroken, even (intercostae) interrupted with large dfp foveae
- 39(42) Lateral carina on pronotum somewhat irregular but distinct at least to midlength
- 40(41) Body bright cupreous *P. (S.) praeinsularis sp.n.*
- 41(40) Body black with only elytral foveae and tarsi bright metallic (green or blue) .
..... *P. (S.) alorensis THY.*

- 42(39) Lateral carina on pronotum practically absent
- 43(44) Dorsal side black with cupreous elytral foveae. Pronotal sides definitely rounded before midlength. Long prosternal pubescence extends to, or even slightly beyond, the almost totally obliterated lateral carina and is clearly visible from above *P. (S.) sumbana sp.n.*
- 44(43) Dorsal side greenish-cupreous. Pronotal sides almost straightly convergent from base to apex. Prosternal pubescence not extending to sides, and not visible from above *P. (S.) lombokiana sp.n.*
- 45 (3) Elytra very prominently costate, without intercostae (even interstriae flat)
..... *P. (S.) scintillans WATH.*

Comottoi-circle

***Psiloptera (Spinthoptera) comottoi* LSB.**

Psiloptera Comottoi VAN LANSBERGE 1885

Material examined:

Holotype: "Minhla, Birmania, D. Comotto 1883" "TYPUS" "Psiloptera Comottoi Lansbge." "det. J.W.van Lansberge" "HOLOTYPUS Psiloptera comottoi Lansberge, 1885" "Museo Civico di Genova" [MCGD]

Additional material (?paratype?): "Minhla, Birmania, D. Comotto 18....." "Psiloptera comottoi Lansb." "Museo Civico di Genova" [1 ex. (MCGD)]

Characters (fig. 27):

Males unknown; females 22.5-32×8-12.5 mm. Brownish-black with dfp depressions (partly greenish) and median parts of prosternum cupreous, front, lateral parts of sternum, and legs purplish-violet. Front with dense irregular network of elevated ridges and small depressed dfp spaces in between. Pronotal puncturation coarse, dense, irregularly confluent on sides, finer and much sparser on disc; no distinct smooth anterodiscal spots, impunctate space along midline poorly developed; lateral carina well marked, smooth in basal half, then either becomes irregular or disappears. Elytra without posthumeral denticle; striae consist of rows of fine punctures anteromedially, deeply depressed and coarsely punctured on sides and towards apices; interstriae almost flat, smooth, 3., 5., and 9. with some punctiform dfp foveae; transverse postbasal fascia (extending from humeri to 3. stria), obliquely arranged 3 spots on 3. (just before midlength), 5., and 7.-9. (at level of metacoxae - apparently representing the result of fusion of original two) interstriae, and cuneate stripe on what apically represents 6.-8. interstriae, dfp, densely pubescent and pulverulent. Prosternal process smooth or but very sparsely punctured; proepisterna covered with irregular, dense callosities emerging from dfp background, median part separated from lateral part by more or less conspicuous stripe of smooth reliefs forming submarginal ridge; median part of metasternum very finely and sparsely punctulate, sides dfp with numerous smooth reliefs; metacoxae with large dfp space covered with very dense and long whitish pubescence; 1. abdominal segment very sparsely and finely punctured, narrowly sulcate along median line; abdomen otherwise rather coarsely but sparsely punctured, with four (two on each side - both widely

removed from lateral margin; outer much narrower and less distinct than inner and not reaching anal segment) lines of dfp sculpture and dense long pubescence.

Remarks:

The label of the smaller specimen is the same as that of the holotype, except that it lacks the hand-written specification of the year ("83"). VAN LANSBERGE (1885) did not mention the number of specimens in the type-series (and the size given as "*Long.* 28 *mill.*" may suggest a single holotype), but he dedicated this species to Captain COMOTTO, "auquel le Musée Civique de Gênes est redevable *des exemplaires* qu'il en possède". On the other hand, KERREMANS (1910) gives the measurements as "*Long.* 23-23 [sic!]; *long.* [sic!] 8-13 mm.", so he evidently also saw more than one specimen. The size quoted in the original description does not agree with the specimen labelled as holotype in MCGD (there are some other minor discrepancies too), but this should be ascribed to inexactitude of the description rather than questioning the identity of the type-specimen; however, if we replace the "upper" 23 mm. with 32 and the second "long." with "larg." (what certainly was the intention of the author), the range given by KERREMANS (1910) agrees very well with the measurements of the two individuals examined by me. In view of these circumstances, it seems almost sure that the second specimen is a paratype.

A very distinctive species: elytral sculpture, and especially arrangement of dfp spots, make it unmistakable among (not only Indo-Pacific) *Psiloptera* DEJ.

Known only from the type-locality: Minhla in central Burma (map 12 - there are at least two localities of this name in Burma: one ca.140, the other ca.375 km NNW of Rangoon; in the XIX century the latter was apparently much larger and better known than the former, so I suppose the type-series to have been collected there).

***Puncticollis*-circle**

Psiloptera (Spinthoptera) puncticollis (SND.)

Lampetis puncticollis SAUNDERS 1867

Material examined:

Holotype: "Holotype" "Pach. Mouhot" "Saunders 74.18" "*puncticollis* (Type) Saund."
"Type" ♀ (NHM)]

Additional material: 1♀.

Characters:

Males unknown; females 30-32.5×11.5-12 mm. (AKIYAMA & OHMOMO 1994). Labrum, depressed parts of head, disc of pronotum, elytral foveae, almost all ventral side, femora, tibiae, and basal antennomeres cupreous; elevated parts of elytral interstriae cupreous-bronzed; prosternum medially purplish-bronzed; elevated frontal reliefs dull greenish-black; lateral (broadly), basal and apical (narrowly) margins of pronotum, marginal carina and epipleura of elytra, and some elevated smooth areas of undersurface green; tarsi greenish-blue. Front with irregular network of coarse, smooth elevated ridges emerging from deeply depressed dfp surface. Pronotal

punctuation coarse, dense, very irregular, confluent on sides, becoming much finer and sparser towards midline; smooth median and anterodiscal spaces hardly appreciable; lateral carina well developed in basal fourth, traceable to apical third. Elytra definitely angular behind humeri, but without posthumeral denticle; sides very coarsely, median parts rather finely striatopunctate; interstriae almost flat, smooth, 1. (sutural) with some punctures in apical third, 3. (in apical half only), 5., 7. and 9. interrupted with rather sparse but very distinct dfp foveae, which become larger towards sides (especially in 9. interstria). Prosternal process very sparsely punctured, laterally bordered with only partly confluent rows of rather fine punctures; median parts of proepisterna irregularly, densely granulate-punctate, separated from dfp lateral parts by stripe of small, smooth, elongated reliefs forming distinct submarginal ridge; 1. abdominal segment broadly and shallowly depressed along median line; sternites coarsely but sparsely punctured except for very irregular dfp spaces at anterior angles and longitudinal dfp stripe on each side halfway between median line and lateral margin; anal segment rounded apically.

Remarks:

Like in the case of *P. psilopteroides* (SND.), the material - two females - available for study [AKIYAMA & OHMOMO (1994) had only two females more: the third - that figured on their phot. A - is my specimen BPchi] is too scanty to allow a sound assessment of its variability (the specimen in my collection is practically identical with the holotype), but for the moment *P. puncticollis* (SND.) seems to be rather well differentiated species: distinct submarginal ridge on proepisterna suggest its affinities with *P. affinis* (SND.), but sculpture of abdomen and peculiar pattern of elytral foveae makes it unmistakable.

AKIYAMA & OHMOMO (1994) report it from "India", otherwise known only from northern Siam and Laos (BAUDON 1968).

Fastuosa-circle

Psiloptera (Spinthoptera) fastuosa (F.)

Buprestis fastuosa FABRICIUS 1775

= *Lampetis landeri* AKIYAMA et OHMOMO 1994

Material examined:

305 ex.

Characters:

Males [142] 13×4.5 - 25.5×9.5; females [115] 12.5×4 - 27.5×10.5 mm. Usually dull cupreous with green sides of elytra, sometimes pronotum also more or less green; in some specimens lateral elytral bands are very narrow or even totally disappear, in others green colouration extends almost to suture; very rarely all the body is green. Front relatively finely sculptured (fig. 45), elevated reliefs dense, irregular, rather uniformly distributed. Sides of pronotum arcuately narrowed to apex, slightly sinuate at basal angles; pronotal punctures moderately coarse and dense on disk, much more

so at sides; lateral carina distinct in basal half, sometimes extends beyond anterior third. Elytral striae very coarse and irregular, interstriae narrow and (at least at sides) strongly convex, costiform; no trace of dfp foveae. Anterior margin of prosternum straight; median part of prosternal process rather coarsely but sparsely punctured, in some specimens almost smooth; punctures of proepisterna very coarse but rather sparse medially, much finer and very dense just beneath lateral carina, both areas being more or less sharply delimited and sometimes marked by irregular "submarginal ridge". Abdomen coarsely, almost uniformly punctured on disk, with dfp band along lateral margins; anal sternite narrowly rounded at apex in female, truncated or shallowly emarginated in male. Male genitalia markedly variable in shape, but always rather elongate; parameres posterolaterally more or less angular, separated with rather short (opening at *ca.* apical $2/5$), narrow, parallelsided slit (fig. 81); these characters usually more accentuated in small specimens.

Remarks:

Closely resembling *P. coerulescens* (HBST.), but duller and much less variable in colouration, with front and underside almost invariably cupreous, coarser elytral sculpture, and slightly different male genitalia (fig.81). AKIYAMA & OHMOMO (1994) declared "*L. coerulescens*" to be "only a color variation of *L. fastuosa*", but this opinion is apparently based on misunderstanding: they seem to have compared a blue variety of *P. coerulescens* (HBST.) with much more common green specimens of the same species (all from South India!), and thence - understandably... - "have not been able to find any differences in body shape or male genitalia". Apparently the only representative of the genuine *P. fastuosa* (F.) (very rare in South India) in their disposition showed such differences, and... has been described as a new species, *Lampetis landeri* A.O. - a comparison of their description and figures with beetles from northern India leaves no serious doubt as to the identity of these two taxa.

P. fastuosa (F.) is widely distributed in northern and central parts of India (map 8), becoming very rare on the South, and being apparently absent on Ceylon (I have seen only one old specimen so [?mis]labelled).

Psiloptera (Spinthoptera) coerulescens (HBST.)

Buprestis coerulescens HERBST 1801

= *Buprestis coerulea* OLIVIER 1790 [nec THUNBERG 1789 (*Meliboeus*)]

= *Psiloptera japonensis* OBENBERGER 1914

Material examined:

Syntypes: "Syntype" "Type?" "Pondichéry, Olivier" "Collection Chevrolat" "Psiloptera coerulea Ol. Ent. 2. 3221, 13 pl. 4, ES Type, coerulescens Hbst., Ind. Or. Pondy., ex 191 in Oliv." "Kerremans 1903-59" "coerulea Oliv. Type" [1 ex. (NHM)]; "Syntype" "Type?" "Pondichéry, Olivier" "Collection Chevrolat" "Kerremans 1903-59" "coerulea Olivier Type" [2 ex. (NHM)]; "Syntype" "Type?" "Madras, Olivier" "Collection Chevrolat" "coerulea Olivier Type" "Kerremans 1903-59" [1 ex. (NHM)]

Additional material: 221 ex.

Characters (fig. 21):

Males [68] 12.5×4 - 22×8; females [55] 13.5×4.5 - 27×10.5 mm. Colouration variable, usually with striking contrast between green, golden, or cupreous sutural part of elytra (extending most often to 5., but sometimes only to 4. or even 3. stria) and bright green (most commonly) or dark blue, rarely cupreous or black lateral bands; front, pronotum and underside normally similar in colour to elytral sides. Structurally almost identical to *P. fastuosa* (F.), even the few appreciable differences (sculpture of pronotal sides less dense and less evenly distributed, elytral striae finer and more regular, interstriae wider and flat, median part of prosternal process almost always smooth, finer and denser punctured submarginal space on proepisterna usually indistinct, with no trace of "submarginal ridge") being only "statistical" (with not infrequent intermediates and overlaps) - the only reliable distinguishing character I am aware of is longer (extending to midlength), wider, navicular slit separating apical halves of parameres (fig. 82).

Remarks:

Similarity of the commonest colour varieties, lack of hiatus in external morphology, and parapatric distribution with relatively narrow zone of "transgression", initially suggested to me that *P. coerulescens* (HBST.) is a southern subspecies of *P. fastuosa* (F.), and so I have determined many specimens in various collections. Male genitalia seemed initially to support this opinion: in *P. fastuosa* (F.) they are variable, from very narrow with prominently angular lateroposterior angles of parameres [as described and figured by AKIYAMA & OHMOMO 1994 for *P. landeri* (A.O.)] to approaching *P. coerulescens* (HBST.) in robustness and "streamlined" shape. However, closer examination allowed to disclose the consistent difference in apical slit, and showed a discontinuity - albeit rather narrow - in general outline, what must be interpreted as evidence of specific status. The pattern of geographical variability - best explainable by competitive character displacement: the distinctive features of *P. coerulescens* (HBST.) are somewhat stronger developed in continental [sympatric with *P. fastuosa* (F.)] populations than in those from Ceylon [where the latter does not occur] - further corroborates this conclusion.

P. coerulescens (HBST.) occurs in southern India and Ceylon (map 8); *P. japonica* OBB. was described from "Japan" (OBENBERGER 1914), but KUROSAWA (1989) is certainly right in placing this record on the list of erroneous data.

[*Psiloptera (Spinthoptera) melancholica* (F.)]

Buprestis melancholica FABRICIUS 1798

Material examined:

None

Remarks:

I have never seen any specimen attributable to this form, which has apparently never been rediscovered. The original description offers only two characters of any value: black colouration and elytral foveae concentrated in sutural region - perhaps the name denotes a dark variety of *P. orientalis* (C.G.)?

Described from "Indes".

***Psiloptera (Spinthoptera) orientalis* (C.G.)**

Buprestis orientalis CASTELNAU et GORY 1836

? = *Lampetis crassicollis* THOMSON 1879b

Material examined:

85 ex.

Characters:

Males [12] 15×5 - 24×9; females [24] 17×6.5 - 26.5×10 mm. Head, pronotum, disk of elytra and ventral side bronzed-cupreous, elytral sides (from 6.-7. stria) graduating through green to dark blue; sometimes bronzed-cupreous is replaced with blackish-bronzed, green with cupreous and blue with green, or cupreous colour extends to the very lateral margins; one female ["? INDIA: Balasore, 7 VII 1938 ?" (RBH: BPgto)] is brownish-black with abdomen and inconspicuous lateral band (8.-10. interstriae) of elytra slightly more vivid, cupreous-brown. Frontal sculpture fine and irregular. Pronotum rather finely and sparsely punctured on disk, more coarsely and densely on sides; lateral carina long, reaching usually to anterior fourth. Interstriae flat, at least some of them (usually 3. or 9.) with small, frequently inconspicuous, dfp foveae. Prosternal process smooth between lateral striae; proepisterna rather coarsely sculptured, "submarginal ridge" none or indistinct; lateral dfp band on abdomen inconspicuous, separated with irregular smooth reliefs. Male genitalia (fig.) rather robust, parameres regularly arcuately tapering to apices, with no trace of angular preapical dilatation.

Remarks:

Deceptively similar to *P. coerulescens* (HBST.), but bronzed underside, wider discal patch of elytra, interstriae interrupted by small dfp foveae, and regularly arcuate sides of parameres allow unambiguous identification. The original description of

Lampetis crassicollis THS. offers no point to distinguish it from *P. orientalis* (C.G.). Widely distributed over all the Indian subcontinent, but apparently absent from Ceylon, where it is replaced by *P. jasienskii* sp.n.

The distribution of *P. orientalis* (C.G.) includes almost all the Indian Peninsula (map 10).

Psiloptera (Spinthoptera) jasienskii sp.n.

Material examined:

Holotype: "CEYLON: SOUTHERN PR.: Palatupana, 6°17'N; 81°24'E, 12.I.1981, leg. Exp. Univ. Cracov." [♂ (RBH: BPbnr)]

Paratypes: "CEYLON: SOUTHERN PR.: Palatupana, 6°17'N; 81°24'E, 8.I.1981, leg. M. Jasiński" [1♂ (RBH: BPbnq)]; "CEYLON: SOUTHERN PR.: Palatupana, 6°17'N; 81°24'E, 20.I.1981, leg. Exp. Univ. Cracov." [1♂ (RBH: BPbns)]; "CEYLON: SOUTHERN PR.: Palatupana, 6°17'N; 81°24'E, 20.I.1981, leg. E. Starszak" [1♀ (RBH: BPbnt)]; "CEYLON: SOUTHERN PR.: Palatupana, 6°17'N; 81°24'E, 24.I.1981, leg. Exp. Univ. Cracov." [1♀ (RBH: BPbnu)]; "Hambantote, litus Ceyloni mer., Казнаковъ 96" [1♀ (ZIRAN)]; "Hambantote, litus Ceyloni mer., Казнаковъ. 96" "Kasnakov" [1♀ (ZIRAN)]; "Ceylon, Candy, Coll. Semenov-Tian-Shansky" (3♂ + 1♀ (ZIRAN), 1♀ (RBH: BPhmy)]; "Coll. Nonfried, Ceylon" "*Psiloptera* Sol. fastuosa Fabr., G. Suvorov. det." [1♀ (ZIRAN)]; "Ceylon, Radde 90" "к. Г. Сиверса," [1♂ (ZIRAN)]; "CEYLON" "*Lampetis cupreosplendens* Snd. 51, V. Stepanov det." [1♀ (ZIRAN)]; "Koll.Df. A.Fr.v.Hoschek, Ceylon" "3425" "*cupreosplendens* Sd. Det. Hoscheck 192" [1♀ (KBIN)]; "Koll.Df.A.Fr.v.Hoschek, Ceylon" "3426" "*cupreosplendens* Sd. Det. Hoscheck 192" [1♂ (KBIN)]; "CEYLON" "*orientalis* CG, Det. Hoscheck 19?" [1♂ (RBH: BPgtu)]; "*Psiloptera fastuosa* (Ceylan)" [1♀ (RBH: BPgtt)]; "*Psiloptera fastuosa*, 50, Bengalen" [1♂ (ZIRAN)]; "Koll.Df.A.Fr.v.Hoschek, Java" "3422" "*orientalis* CG. Det. Hoscheck 192" [1♂ (KBIN)]; "Singapore, Dr. F.A.Phillips" [1♀ (KBIN)]. "3424" "*cupreosplendens* Sd. Det. Hoscheck 192" [1♀ (KBIN)]; "7921" "*cupreosplendens* Sd. Det. Hoscheck 192" [1♀ (KBIN)]

Additional material: 5 ex. from CEYLON: SOUTHERN PR.: Palatupana, 6°17'N; 81°24'E, 5 I - 1 II 1981 [these specimens had been sent as *P. orientalis* (C.G.) to Charles BELLAMY, PENG Zhong-liang, and Willi KRONBLAD before I recognized *P. jasienskii* sp.n. as a distinct species; I cannot consider them paratypes, but having previously measured three of them, I include these measurements in the description]

Holotype:

Male, 21.5×7.5 mm. Green, with narrow (1. and 2. interstria) sutural band on elytra, median part of prosternum, outer surface of tibiae, and tarsi cupreous; antennae piceous-black with greenish hue, basal joint cupreous.

Epistome broadly arcuately emarginate, not separated from front. Front trapezoidal, flat; rather fine sculpture consists of dense, sharply defined, mostly longitudinally oriented, confluent vermiculate reliefs on dfp background; pubescence long, recumbent, yellowish, denser laterally and anteriorly. Eyes rather prominent, twice longer than wide. V:H=0.47. Antennae reaching to midlength of pronotal sides; 1. joint egg-shaped, ca. 1.5× longer than wide; 2. spherical, distinctly narrower than 1.; 3. subcylindrical. ca. 1.5× longer than 2.; 4. elongately subtriangular with very broadly rounded external angle, as wide as 1. and 2× longer than 2.; 5. similar in shape and length to 4. but slightly wider; 6.-10. rhomboidal, progressively shorter and

slenderer (10. as long as 3. and as wide as 4.); 11. egg-shaped, as wide as 10. but slightly longer.

Pronotum wide (L:BW:AW=1:1.6:1.1); sides very slightly convergent in basal, much more strongly so in apical half, in both posterior and anterior part shallowly but distinctly sinuate; basal and apical margins bisinuate. Disk convex, with shallow transverse depression along base; lateral carina (in side view) bisinuate, almost reaching to apical angles; pronotal sculpture moderately coarse, rather irregularly distributed, dense and confluent on sides, much sparser (spaces between punctures subequal to their diameters) on disk; small triangular prescutellar, longitudinal medial, and two rounded discal (closer to anterior margin and median line than to sides and base) reliefs very irregular, smooth. Scutellum roundedly trapezoidal, as long as wide, strongly convex.

Elytra 2.1× longer than wide; base slightly wider than that of pronotum; sides subparallel in anterior fourth, then very slightly convergent to midlength, and much more strongly, cuneately so to obliquely truncate, sharply bidentulate apices. Only 1. (perisutural; scutellar not counted), 2. (less strongly), and 10 (marginal) striae distinctly depressed on posterior $\frac{3}{4}$, others represented by rows of coarse (finer towards apices), densely spaced punctures; all interstriae flat, only 10. slightly costiform; 3. with several small foveae consisting of depressed groups of fine punctures; 5. and 7. with some coarse punctures; 9. with very big, rectangular posthumeral dfp depression, elongately cuneate one occupying almost all apical $\frac{2}{5}$, and three smaller (but also very prominent) in between.

Prosternal process (fig. 65) very slightly widened behind procoxae, then sinuately narrowed to rounded apex; both lateral and median portions smooth; lateral striae deep, sparsely and rather finely punctured; proepisterna dfp, becoming a little more coarsely punctured just below lateral carinae. Metasternum medially furrowed (except anterior fourth), median parts finely and very sparsely, sides densely and much more coarsely punctured; hind margin of metacoxae with very obtuse, rounded tooth at median third. Abdomen densely and very coarsely punctured, with irregular smooth reliefs on sides of 3. and 4. segments; 1. sternite furrowed medially; anal sternite not distinctly depressed at sides, apically rounded, with shallow, very inconspicuous emargination at tip. Aedoeagus (fig. 83) yellowish-brown, with darker, piceous-black, apical $\frac{2}{3}$ of parameres.

Paratypes and additional specimens (fig. 44):

Vary in size (males [7] 15.5×5 - 22.5×8; females [9] 22×7.5 - 27.5×10.5 mm.), shape [some females are more robust, similar to *P. orientalis* (C.G.) in having both pronotum and elytra parallelsided in basal half, and more roundedly tapering apically; others are slenderer, with pronotum almost cuneate and elytra slightly but distinctly narrowed behind anterior fourth], colouration [sutural band of elytra occupies from one to five interstriae; rarely dorsal side may be dark green with lateral parts (from 5. interstria) of elytra blackish-blue; pronotum may be totally green, green graduating posteriorly into cupreous, or even almost totally (except at anterior angles) cupreous;

ventral surface green to greenish-cupreous], development of dfp foveae [in some specimens they are reduced to coarse punctures on 3. interstria, absent on 5. and 7., and - except the posthumeral - small and inconspicuous on 9. (very rarely even the posthumeral is not easily diagnostic)], sculpture [puncturation more or less coarse, pronotal reliefs sometimes hardly appreciable], &c.

Remarks:

The new species is very closely related to *P. orientalis* (C.G.), differing mainly in slightly more elongate body, more green and less bronzed (even on the ventral side) colouration, coarser sculpture, and especially in large elytral dfp foveae (at least the posthumeral one on 9. interstria). In shape of body and in sculpture it is similar to *P. preorientalis* sp.n., but the latter is totally brownish-black, shows prominent [like in *P. psilopterooides* (SND.)] subhumeral denticle on elytra, and has the foveae on 5. and 7. interstria slightly bigger, and those on 9. much smaller, than *P. jasienskii* sp. n..

The new species seems to be endemic to Ceylon (map 10): "Java", "Singapore", and even "Bengalen" are certainly mislabellings.

Psiloptera (Spinthoptera) praeorientalis sp.n.

Material examined:

Holotype: "Indes or." [♂ (RBH: BPgtn)]

Paratype: "Indes or." [1♀ (RBH: BPgtn)]

Holotype:

Male, 19.5×7. Both dorsal and ventral side (including legs, antennae and labrum) uniformly brownish-black with metallic bronzed bottoms of punctures mm.

Epistome very shallowly arcuately emarginate, not separated from flat; trapezoidal front. Moderately coarse frontal sculpture consists at vertex of dense, sharply defined, longitudinally oriented, confluent reliefs leaving little space for punctured depressions; towards epistome of similarly dense reticulate reliefs; and in between of prominent irregular longitudinal median carina and sparse small reliefs on dfp background. Pubescence rather short, recumbent, yellowish. Eyes moderately prominent, twice longer than wide. V:H=0.4. 1. antennal joint egg-shaped, ca. 1.5× longer than wide; 2. spherical, distinctly narrower than 1.; 3. similar to 2. but slightly longer; 4. club-shaped, as wide as 1. and as long as 2. and 3. together; 5. triangular, similar in length to 4. but slightly wider; 6.-7. rhomboidal, decidedly wider than 5. and as long as (6.), or slightly shorter than (7.) wide; distal part of left antenna, and almost all (3.-11. joints) right antenna missing.

Pronotum wide (L:BW:AW=1:2.0:1.1); sides distinctly convergent in basal ³/₅, much more strongly so in anterior part, lateral margin both basally and apically (except short "collar" just behind anterior angles) nearly straight; anterior margin very shallowly arcuately emarginate, base bisinuate. Disk convex, with shallow transverse depression along base; lateral carina reaching to apical fourth, arcuate basally, then nearly straight; pronotal sculpture moderately coarse, irregularly spaced, not markedly

denser on sides than on disk; longitudinal medial, two small irregular discal (closer to anterior margin and median line than to sides and base), obliquely elongate at each anterior angle, and several very irregular reliefs here and there, smooth. Scutellum roundedly trapezoidal, as long as wide, convex.

Elytra 1.9× longer than wide; base slightly wider than that of pronotum; sides obliquely truncated at humeri, with obtuse and rounded but prominent denticle at end of truncature, then parallel to above metacoxae, deeply sinuate just behind, and arcuately convergent to obliquely truncate apices; apical denticles not prominent. All elytral striae fine (coarser basally), continuous, finely and densely punctulate; medial interstriae flat, lateral progressively more convex, 9. and 10. distinctly costate; odd interstriae disrupted with rather large (occupying all the width of interval and as long as, or somewhat longer than, wide), rectangular dfp foveae (only on 1. and 9. and especially on 1. interstria foveae are smaller); even interstriae with rows of coarse punctures.

Anterior margin of prosternum (fig. 66) at middle straight between two indistinct tubercles, laterally very shallowly sinuate; prosternal process parallelsided to behind procoxae, then sinuately narrowed to rounded apex; both lateral and (definitely wider) median portions smooth; lateral striae deep, sparsely and very finely punctulate; proepisterna dfp. Metasternum flat with but indication of longitudinal furrow, median parts finely and sparsely, sides densely and coarsely, irregularly punctured; hind margin of metacoxae with obtuse, blunt tooth at median third. Abdomen densely and coarsely punctured medially, dfp laterally, with but very small smooth reliefs at sides of 3. and 4. sternite; 1. segment furrowed medially; anal sternite not distinctly depressed at sides, apically broadly truncated. Aedoeagus piceous-brown with paler, yellowish-brown penis.

Paratype (fig. 26):

Female, 24.5×9 mm. Virtually identical to the holotype, but ventral side and anterior part of front bronzed-cupreous, frontal sculpture more evenly distributed, median relief on the pronotum lacking, elytral foveae a little bit smaller, apex of anal sternite regularly rounded (sexual character).

Remarks:

This species seems to be related on the one hand to African *P. pupillata* (KL.), on the other to *P. orientalis* (C.G.) and *P. jasienskii* sp.n. The former has been classified as belonging to *Lampetis* DEJ., and *P. praeorientalis* sp.n. also shows the main distinctive characteristics of that subgenus: [very slightly] bituberculate anterior margin of prosternum. However, its similarity to the above-mentioned South Asian species is also striking, and the respective cladograms (figs. 7, 10) support the affinity of the *Pupillata*-circle to *Spinthoptera* CSY., thence I leave the question open for the moment, and for convenience treat *P. praeorientalis* sp.n. in this paper as belonging to the latter subgenus. *P. orientalis* (C.G.) differs in more rounded sides of pronotum, coarsely punctured proepisterna and usually bright metallic colouration; besides, its frontal sculpture is finer and more regular, without distinct median relief, pronotum

without smooth spaces at anterior angles, elytra without subhumeral denticles, elytral foveae much smaller and less conspicuous, 9. interstria wide and flat, apical denticles of elytra longer and sharper, no tubercles on apical margin of prosternum. *P. jasienskii* sp.n. is always bright metallic, has frontal sculpture, anterior margins of pronotum and prosternum, and shape of elytra similar to those in *P. orientalis* (C.G.), no smooth reliefs at apical angles of pronotum, and 9. interstria flat with very large dfp foveae (at least posthumeral one).

The geographical distribution of *P. preorientalis* sp.n. needs clarification: "India or." on old labels may mean anything from Pakistan, Sikkim and Burma to Ceylon [and - worse still - is one of the most notorious forms of crude mislabellings, so that even the possibility of its African (like that of the remaining members of the *Pupillata*-circle) rather than Asian provenience cannot be excluded].

Affinis-circle

***Psiloptera (Spinthoptera) cupreosplendens* SND.**

Psiloptera cupreosplendens SAUNDERS 1871

= *Psiloptera viridans* KERREMANS 1893b

Material examined:

Syntypes of *P. viridans* KERR.: "Syntype" "Silhet, Chevrolat" "Collection Chevrolat" "viridans Kerr. Type" "Kerremans 1903-59" [1 ex. (NHM)]; "Syntype" "Inde MÉR., Mus. Calc." "viridans Kerr. Type" "Kerremans 1903-59" [1 ex. (NHM)]

Additional material: 37 ex.

Characters:

Males [4] 14×4.5 - 16.5×5; females [5] 20×7 - 25×9 mm. Green with dfp foveae and very narrow (only suture) to broad (5 interstriae on each side) sutural stripe of elytra (reaching to apices, or but narrowly separated from them), sides of sternum, abdomen, antennae, and sometimes head and pronotum, golden- to bronzed-cupreous. Frontal sculpture consists of network of very coarse reliefs, with coarse foveolate punctures in meshes and narrow dfp stripe along at least lower half of oculo-frontal margin; no distinct median relief. Pronotum rather coarsely and (especially on sides) densely, irregularly punctured, with only median relief more or less distinct; lateral carina well developed only at basal angles, then disappears among coarse sculpture. Elytral interstriae shallowly depressed, coarsely and densely punctured; 2., 4., 6., 8., and 10. more or less distinctly elevated; 1., 3., 5. and 7. interstriae with small dfp foveae (often represented only by coarse punctures), those on 9. interval large, rectangular. Prosternal process smooth; proepisterna very coarsely sculptured, no appreciable "submarginal ridge"; abdomen uniformly punctured, without lateral dfp band or smooth reliefs. Male genitalia pale brownish-yellow, sides of parameres regularly arcuate in apical half.

Remarks:

Similar in colouration and pattern of elytral dfp foveae to *P. jasienskii* sp.n., but differs in coarse sculpture of front and proepisterna, short lateral carina of pronotum, lack of smooth reliefs on sides of abdomen, pale aedoeagus, &c. KERREMANS (1893b, 1910) separated *P. viridans* KERR. on grounds of colouration (green) and elytral sculpture (very coarse), but these characters show neither clear-cut difference (there are all intermediates between the extreme forms), nor correlation to one another or to geographic origin; as my efforts to find any other distinguishing feature have also remained unsuccessful, I consider this form as a mere colour variety of *P. cupreosplendens* SND.

This species seems to occur from Assam or even Burma to Ceylon (map 11), but I have never seen any recently collected specimen, while frequent mislabellings and notorious misidentifications make old labels and - especially - literature data not always reliable.

Psiloptera (Spinthoptera) viridicuprea (SND.)

Lampetis viridicuprea SAUNDERS 1867

? = *Lampetis cambodgiensis* THOMSON 1879b

? = *Psiloptera viridicuprea cambodgensis* [sic!] OBENBERGER 1932

Material examined:

Holotype: "Holotype", "Siam, Mouhot" "*Lampetis viridicuprea* (Type) Saund., Label written by C.O. Waterhouse" "Saunders 74.18" [NHM].

Additional material: 5 ex. [until the publication of AKIYAMA & OHMOMO (1994) I confused this species with *P. affinis* (SND.) so the present description is based on only few recently examined specimens].

Characters:

Males [2] 24×8.5 - 26.5×9; females [3] 17×6 - 27.5×10 mm. Cupreous (elytra sometimes bronzed) with usually green front; median line and lateral margins of pronotum, suture and sides of elytra, margins of some sclerites on ventral surface, 1. antennomere, and greater part of legs; antennae piceous-black with greenish tinge on outer surface. Frontal sculpture consists of elevated, smooth, confluent ridges, and deeply depressed spaces in between; in males these spaces are broader and more coarsely microsculptured than in females. Pronotal sculpture coarse and confluent on sides, finer and much sparser on disk; smooth spaces (median line, diskal spots) inconspicuous; lateral carina regular only just before basal angles, but traceable sometimes to near midlength.. Elytra without subhumeral denticle; striae rather deep. coarsely punctured; interstriae convex, odd ones interrupted by very shallow, inconspicuous foveae consisting of groups of rather coarse punctures. Apical margin of prosternum shallowly emarginate between two rounded protrusions; proepisterna very coarsely and irregularly punctured, without any trace of additional "submarginal" ridge; median part of prosternal process with very sparse to rather dense, moderately coarse punctures; abdomen coarsely and irregularly punctured but without distinct reliefs or dfp spaces; first sternite with but traces of median sulcus in females, deeply sulcate in males. Male genitalia elongated, roughly parallelsided, piceous-brown with

yellowish basal piece and sides of penis; sides of parameres apically roundedly narrowed to pointed tips.

Remarks:

Deceptively similar to *P. affinis* (SND.), the lack of "submarginal ridges" on proepisterna and shape of male genitalia seem to provide the only reliable distinguishing characters. THOMSON's (1879b) original description is not sufficient to form any sound opinion as to the taxonomic position of *Lampetis cambodgiensis* THS., and I place it in the synonymy of *P. viridicuprea* (SND.) after KERREMANS (1910); similarly, having not seen the type of *Psiloptera viridicuprea cambodgiensis* OBB., I must provisionally accept the opinion of its author, although his concept of *P. viridicuprea* SND. was not perfectly clear (I have seen in collections several specimens wrongly attributed by him to this species) and the "einförmig, wie bei *coerulea* etc. gestreift punktierten Flügeldecken, mit gleichartig gebildeten Zwischenräumen, die nirgends kettenförmig unterbrochen sind" seem extremely strange for any Indochinese species!

P. viridicuprea (SND.) seems to be rather widely distributed between Assam and Cambodia (map 11).

[*Psiloptera (Spinthoptera) holynskii* (A.O.)]

Lampetis holynskii AKIYAMA et OHMOMO 1994

Material examined:

None

Remarks:

The very brief and unconvincing - restricted, in fact, to length and width of body and short (two characters) comparison with *P. viridicuprea* (SND.) - original description does not allow to form a safe opinion on it. I suspect it to be a variety (or - less probable - subspecies) of *P. viridicuprea* (SND.): two small smooth anterodiscal spots on pronotum occur almost invariably in all species of the *P. affinis* (SND.) - group, and *P. viridicuprea* (SND.) is no exception [even the specimen on AKIYAMA & OHMOMO's (1994) photograph shows them - albeit somewhat less conspicuous than in the holotype of *Psiloptera (Spinthoptera) holynskii* (A.O.)]; the difference in male genitalia looks much less convincing on the photographs than on the apparently not too exact drawings and may easily represent intraspecific variability [see e.g. the remarks on *P. fastuosa* (F.) above]; and neither the pictures nor text of description suggests any other distinguishing character.

The holotype - the only specimen known - has been collected in Burma: Shan States: Thunggyi.

Psiloptera (Spinthoptera) nelsoni (A.O.)

Lampetis nelsoni AKIYAMA et OHMOMO 1994

Material examined:

Paratype: "Syntype" "Type" "Type" "Pach. Mouhot" "Saunders 74.18" "Lampetis affinis (Type) Saund." "Labelled by C.O.W." [1♀ (NHM) - examined by me in 1978 as a syntype of *Lampetis affinis* SND.; later designated by AKIYAMA & OHMOMO (1994) as paratype of *Lampetis nelsoni* A.O.]

Additional material: 3♀.

Characters:

Males 24-25.5×8.5-9.5 mm. (AKIYAMA & OHMOMO 1994), females [3] 20.5×7 - 26.5×8.5 (my specimens) or 23-30×8-11 mm. (AKIYAMA & OHMOMO 1994). Reddish-bronzed to purplish-red; front, lateral margins of elytra and abdomen, and legs greenish, antennae dark green to blackish-blue; median line of pronotum not differentiated in colour; smooth reliefs on front, pronotum, abdomen and - especially - of elytra bluish-black, sharply contrasting with surrounding surface. Front with relatively sparse, narrow, boldly elevated smooth reliefs, and wide, flat, finely punctured depressions between them. Pronotum coarsely and densely punctured, with more or less appreciable, irregular, smooth median ridge; a pair of small, round smooth discal elevations just before midlength; and some very irregular reliefs here and there; lateral carina very short, disappears among coarse punctures at *ca.* basal sixth. Elytral striae fine, densely and very finely punctulated; interstriae almost flat, covered with coarser (especially on sides) puncturation, odd (3., 5., 7., 9.) ones with very conspicuous, rectangular, very slightly convex, smooth reliefs. Median portion of prosternal process rather coarsely, regularly punctured; proepisterna with no trace of additional, submarginal ridge; 1. abdominal segment more or less distinctly sulcate along median line; sternites 2., 3., and 4. with small, rounded, laterodiscal smooth elevation on each side (2. also with relieved anterior angles); apex of anal sternite narrowly rounded. Male genitalia (according to the drawing in AKIYAMA & OHMOMO 1994) rather short and stout, with parameres narrowed almost from base to acutely pointed apices.

Remarks:

Very conspicuous and regular, contrasting, bluish-black reliefs on elytra (and, to a somewhat lesser degree, of front, pronotum and abdomen) make this species rather distinctive (but small number of examined specimens does not allow to assess its validity and limits of variability); from similar *P. affinis* (SND.) it differs in lacking submarginal ridges on proepisterna and "normal" shape of parameres, but I have not been successful in finding any - except for the above-mentioned dark reliefs - reliable character to distinguish *P. nelsoni* (A.O.) from *P. viridicuprea* (SND.); having only females in my disposition I am unable to check the shape of male genitalia, which looks quite promising on the Authors' drawing, but much less so on their photographs!

Almost all known specimens - the paratype from NHM labelled "Pach." [bon] (?=Muang Phetchabun in central Siam) being the only exception - have been collected in Laos (map 12).

Psiloptera (Spinthoptera) affinis (SND.)

Lampetis affinis SAUNDERS 1867

This species, well characterized by the shape of parameres (fig. 84) and presence of "submarginal ridge" on proepisterna, occurs in two geographical races (map 13):

Key to subspecies of *P. (S.) affinis (SND.)*

- a (b) Dorsal side predominantly green *P. (S.) a. cochinchinae ssp.n.*
b (a) Dorsal side predominantly bright purplish-red *P. (S.) affinis (SND.) s.str.*

Psiloptera (Spinthoptera) affinis cochinchinae ssp.n.

Material examined:

Holotype: "SAIGON, Cochinchina, COLLECTION LE MOULT" "Le Moul't vend. LAMPETIS psilopteroides Saund." "sec. J. Obenberger, Col. Cat.: Junk, xii, 1926-1935, p. 172, P. (LAMPETIS) psilopteroides Saund." "R. Mus. Hist. Nat. Belg. I.G. 12.595" [♂ (KBIN)]

Paratypes: "SAIGON, Cochinchina, COLLECTION LE MOULT" "Le Moul't vend. LAMPETIS psilopteroides Saund." "sec. J. Obenberger, Col. Cat.: Junk, xii, 1926-1935, p. 172, P. (LAMPETIS) psilopteroides Saund." "R. Mus. Hist. Nat. Belg. I.G. 12.595" [2♂ (KBIN)]; "SAIGON, Cochinchina, COLLECTION LE MOULT" "R. Mus. Hist. Nat. Belg. I.G. 12.595" "J. de Walsche det., 1943: P. *Lampetis psilopteroides* Saund." [1♀ (KBIN)]; "SAIGON, Cochinchina, COLLECTION LE MOULT" [3♂ (2 KBIN, 1 RBH:BPgta) + 3♀ (1 KBIN, 2 RBH: BPgsq, BPgt-)]; "Saïgon" "R.M.N.H.B. 15.962, coll. A. d'Orchymont" [1♂ + 1♀ (KBIN)]; "Saïgon" [1♀ (RBH: BPgtb)]; "Cap St. Jacques" "*Lampetis viridicuprea* Saund., Théry det" [1♀ (KBIN)]; "Cap St. Jacques, Coch. chine" [1♀ (RBH: BPgtd)]

Holotype:

Male, 23.5×8.5. Dorsal side green very broad cupreous-red spots on sides of pronotal disk (median line, as well as lateral and apical margins, green); ventral side green medially, cupreous on sides, tibiae cupreous, femora and tarsi green; antennae brown with bronzed-green shine. Front (fig. 46) with irregular network of elevated ridges and rather coarse, dense punctures in between; lower two thirds of each lateral margin depressed to form regular periorcular sulcus covered with very dense silky-white pubescence and separated from the rest of frontal surface by very prominent prolongation of supraantennal carina. Pronotal sculpture consists of irregular coarse punctures, becoming very coarse and confluent on sides, and leaving a smooth spot on each side of disk slightly before midlength; lateral carina distinct and smooth in basal fourth. Elytral striae rather deep, coarsely punctured; interstriae narrow, convex; dfp foveae very small and indistinct on 1., becoming larger and more conspicuous on 3., 5., 7., and especially on 9. interval. Prosternal process rather densely punctured between lateral striae; proepisterna with rather dense, coarse, smooth granulation on dfp background, and conspicuous (though very irregular) submarginal ridge parallel to lateral carina; first sternite deeply sulcate along median line; apex of anal sternite narrowly but distinctly emarginate. Tips of parameres obliquely truncated and deeply, broadly emarginate between two denticles.

Paratypes:

Males [6] 15.5×5 - 21×7.5; females [8] 20×7 - 27×10.5 mm. Some show distinct brownish-cupreous shine on front and elytra, and in two the colouration does not differ from the nominotypical subspecies. Discal smooth spots on pronotum are frequently indistinct, interstriae usually flatter than in holotype, submarginal ridge on proepisterna more or less regular, sulcus on first sternite sometimes rather shallow; in females apex of anal sternite is always narrowly rounded.

Remarks:

Markedly different colouration makes this subspecies distinctive, while apparent lack of other differences, and occasional occurrence of reddish specimens, point to its conspecificity with *P. affinis* (SND.) s.str.

This race seems confined to Cochinchina.

Psiloptera (Spinthoptera) affinis (SND.) s.str.
Lampetis affinis SAUNDERS 1867

Material examined:

Lectotype: "Syntype" "Type" "Type" "Camb. Mouhot" "Saunders 74.18" "Lampetis affinis (Type) Saund." "Labelled by C.O.W." [♀ (NHM) - examined by me in 1978 as a syntype, later designated by AKIYAMA & OHMOMO (1994) as **lectotype**]

Additional material: 28 ex.

Characters:

Males [17] 16×5.5 - 23.5×8.5, females [11] 16×5.5 - 30×11 mm.. Dorsal side usually bright red with golden-green to cupreous front and green median line, anterior margin and sides of pronotum and elytra, undersurface predominantly cupreous-red; in some specimens reddish colour is replaced with cupreous and green parts are much wider; otherwise seemingly identical to *P. a. cochinchinae* ssp.n.

Remarks:

Widely distributed all-over the Indochinese Peninsula (Burma, Siam, Laos, Cambodja - map 13); AKIYAMA & OHMOMO (1994) report it also from Sikkim and Malaysia.

Psiloptera (Spinthoptera) psilopteroides (SND.)

Lampetis psilopteroides SAUNDERS 1867

Material examined:

Holotype: "Holotype" "Type" "Siam, Mouhot" "Saunders 74.18" "psilopteroides (Type) Saund." [♀ (NHM)]

Additional material: 1♀.

Characters:

Males unknown to me; females 29.5-34.5×11-14 mm. (AKIYAMA & OHMOMO 1994). Dorsal side green with predominantly bronzed-cupreous pronotum and bronzed-brown elytral reliefs; sternum and abdomen medially cupreous, laterally green; legs green, antennae greenish-brown. Front with coarse, smooth elevated reliefs enclosing small, deeply depressed, irregular dfp foveae. Pronotum coarsely, densely, very irregularly punctured, without appreciable median ridge or anterodiscal spots; lateral carina very short, disappears among coarse punctures immediately before basal angles. Lateral margins of elytra with very distinct posthumeral denticle (fig. 64); striae rather coarsely punctured; interstriae almost flat, all with conspicuous (though poorly delimited), rectangular, smooth "mirrors". Median portion of prosternal process with moderately coarse, sparse puncturation; submarginal proepisternal ridge represented by indistinct, very irregular, coarsely punctured longitudinal elevation; 1. abdominal segment broadly and shallowly depressed along median line; laterodiscal smooth elevations on sternites very irregular, inconspicuous; apex of anal sternite rounded.

Remarks:

With no males and only five females studied by modern authors [one - that figured on their phot. B - of the three non-types examined by AKIYAMA & OHMOMO (1994) is the specimen BPchj from my collection], this species remains somewhat enigmatic: except size and conceivably size-correlated (allometric) features (posthumeral denticle on elytra, traces of submarginal ridge on proepisterna) I failed to find any reliable character to distinguish it from *P. viridicuprea* (SND.), and cannot exclude the possibility that the name *P. psilopteroides* (SND.) denotes simply very big females of the latter.

All specimens seen by AKIYAMA & OHMOMO (1994) and me have been collected in Upper Burma (Bhamo) and Siam (map 11); KERREMANS (1910) reported the species also from Laos.

Timoriensis-circle

Psiloptera (Spinthoptera) eva (THS.)

Lampetis Eva THOMSON 1881

Material examined:

1♀.

Characters:

Male unknown, females 24.5×9.5 (KERREMANS 1910) - 29×11 mm. Dorsal side dull green with slight bronzy shine on elytral disc; undersurface cupreous laterally, green (especially on abdomen) medially; legs green, antennae bronzed-brown. Front with dense network of coarse, smooth elevated ridges leaving but little space to rather coarsely punctured depressed surface; vertex finely punctulate, punctures confluent to form dense, obliquely transverse rugosity. Pronotum coarsely, densely, irregularly, confluent punctured on sides, somewhat less so at middle of disc; smooth median carina flat and irregular, totally disappears at anterior third; lateral carina developed only in basal fourth. Elytra with traces of posthumeral denticle; sides shortly but very distinctly sinuate before apex; striae coarsely and densely punctured; interstriae moderately convex (with no distinction between odd and even), somewhat higher laterally than towards suture; elytral foveae represented by rather fine punctured sparsely spaced on odd intervals. Prosternal process sparsely punctured, lateral striae deep and regular; punctulation of proepisterna rather fine and very dense, traces of submarginal ridge appreciable. Abdomen rather densely covered with coarse rasp-like punctures and rather sparsely with white, recumbent pubescence; 1. segment broadly, very shallowly depressed along median line; anal sternite rounded apically.

Remarks:

This species differs from the remaining representatives of the *Timoriensis*-circle in green dorsal side of the body. KERREMANS' (1910) synonymization of *P. eva* (THS.) with *P. curvipes* (CHVR.) is evidently erroneous [see **Remarks** under *P. timoriensis* (C.G.) – p. 83].

Apparently a very rare species, described from Flores; the NNHM specimen examined by me comes from Solor (map 14).

Psiloptera (Spinthoptera) draconis sp.n.

Material examined:

Holotype: "Indonesia, Komodo I. 19 08.1962" [♀ (RBH:BPhix)]

Paratype: "KOMODO isl, 20. 8. 1965, J.M.Štusák" "Coll. S.Bily" "Psiloptera (Lampetis) sp. cum baliana Kerr., det. Sv. Bílý" [♀ (SB)]

Holotype:

18.5×6.5 mm. Front cupreous with median relief green, depressed dfp surface golden-cupreous; pronotum bluish-black with green (disc) or cupreous (sides) bottom of punctures; elytra dull cupreous; ventral side, labrum, and legs bright cupreous-red;

antennae piceous; punctures on both dorsal and ventral side filled with whitish pulverulence.

Epistome rather deeply angularly emarginate, not separated from flat; trapezoidal front. Frontal sculpture consists of dagger-like median ridge and network of smooth reliefs (better defined anteromedially), leaving ample space (especially on sides) for depressed dfp areas; vertex covered with moderately fine, dense punctulation, somewhat confluent into rather indistinct transverse strigosity. Pubescence rather short, recumbent, yellowish. Eyes moderately prominent, twice longer than wide. V:H=0.5. 1. antennal joint egg-shaped, *ca.* 2× longer than wide; 2. spherical, distinctly narrower than 1.; 3. conical, much shorter and thinner than 1.; 4. club-shaped, almost as long as 2. and 3. together; 5. triangular, somewhat longer and wider; 6. still longer and wider, triangular with broadly rounded outer angle; 7.-10. rhomboidal, progressively shorter and narrower; 11. longer than 10., elongately and asymmetrically club-shaped.

Pronotum wide (L:BW:AW=1:1.5:1.3); sides almost straightly convergent from base to apex, slightly sinuate in basal third; anterior margin almost perfectly straight, base bisinuate with median lobe protruding much further back than posterior angles. Disk convex, with hardly appreciable transverse depression along base; lateral carina irregular, inconspicuous; pronotal punctures coarse, irregularly spaced, very dense and confluent on sides, dense but isolated on disk; smooth median carina flat, very inconspicuous and irregular; no anterodiscal reliefs. Scutellum small, trapezoidal, as long as wide, convex.

Elytra 2.0× longer than wide; sides obliquely truncated at humeri (with no trace of posthumeral denticle), then parallel to behind metacoxae, and arcuately convergent to obliquely truncate apices (slightly sinuate just before them); apical denticles not prominent. Striae continuous, with relatively coarse and dense irregular punctulation superimposed over coarser but shallow uniserial punctures; interstriae narrow, convex, more elevated on sides; without distinct foveae.

Anterior margin of prosternum at middle straightly truncate; prosternal process parallelsided to behind procoxae, then sinuately narrowed to rounded apex; lateral striae slightly convergent backwards, continuous, finely and rather sparsely punctured, smooth lateral portions twice narrower than sparsely punctured median space; proepisterna dfp. Metasternum convex, narrowly depressed along midline, punctulation on median parts fine and sparse, on sides coarser and much denser, irregular; hind margin of metacoxae with obtuse, blunt tooth at median third. Abdomen rather coarsely, almost uniformly punctured with irregular, shallow anterolateral depression on each segment; 1. segment shallowly but distinctly furrowed medially; anal sternite narrowly rounded at apex.

Paratype:

23×8.5 mm. Elytra somewhat duller, greenish-cupreous; otherwise very similar to the holotype.

Remarks:

P. draconis sp.n. is very closely related to (perhaps only a subspecies of) *P. eva* (THS.); it differs from the latter in elytral sculpture, from the remaining [*P. baliana* KERR., *P. timoriensis* (C.G.)] members of the superspecies in uniform (without lateral dfp bands) sculpture of abdomen, and from all of them in predominantly cupreous body.

P. draconis sp.n. seems to be endemic for Komodo (map 14).

***Psiloptera (Spinthoptera) baliana* KERR.**

Psiloptera baliana KERREMANS 1900

Material examined:

Holotype: "Holotype" "Bali, I.c., III-IV. 96, (W.Doherty)" "baliana Kerr. Type"
"Kerremans 1903-59" [♀ (NMH)]

Additional material: 2 ex. (♂ and ♀)

Characters:

Male [1] 17.5×6.5, females [2] 20.5×8.5 - 23.5×9 mm. Body black with faint (somewhat stronger on sides of ventral side, especially in female) bronzed shine; tarsi dark blue. Front with network of coarse reliefs emerging from depressed dfp surface; vertex with moderately coarse, not confluent puncturation; pubescence rather long, recumbent, yellowish along eye margins, otherwise inconspicuous. Pronotal puncturation coarse but rather sparse on disc, much denser and irregularly confluent on sides; median line almost undifferentiated, smooth anterodiscal spots well developed (male) or very inconspicuous (female); lateral carina distinct only at the very base. Elytral sides very obtusely angular behind homeri, but without posthumeral denticle; striae continuous, rather deep, coarsely and densely punctured; interstriae narrow, convex, more elevated on sides, odd and even alike except that the former are less regular, with traces of very irregular and inconspicuous foveae. Anterior margin of prosternum slightly arcuate; lateral rims of prosternal process narrow and smooth, median part twice wider and sparsely though rather coarsely punctured, lateral striae deep with row of coarse and dense punctures at bottom; proepisterna densely, very irregularly, rather finely punctured, with traces (more distinct in female) of submarginal ridge. First abdominal segment deeply (male) or shallowly (female) sulcate; disc of abdomen rather sparsely but very coarsely punctured (individual "punctures" are in fact foveae composed of depressed groups of several finer punctures), sides broadly dfp; pubescence of ventral side yellowish, recumbent, rather short and sparse medially, longer and dense (though leaving surface of sclerites clearly visible) on sides; anal sternite roundedly truncated (male) or narrowly rounded (female) at apex. Male genitalia brownish-yellow, becoming piceous-brown towards tips of parameres, with blackish streak along midline of penis; parameres obliquely truncate at apex.

Remarks:

P. baliana KERR. is apparently rather rare species, deceptively similar (differing only in fine details of colouration, sculpture and pubescence) and undoubtedly closely related to *P. timoriensis* (C.G.).

Described from Bali, both additional specimens have been collected on Java: male [RBH: BPchg] is labelled "Java" without any details, female [NHNM] "Banjuwangi, IV 1936, leg. Adj. L.b.C." (map 14).

***Psiloptera (Spinthoptera) timoriensis* (C.G.)**

Buprestis timoriensis CASTELNAU et GORY 1837

= *Lampetis curvipes* CHEVROLAT 1838

Material examined:

Holotype of *L. curvipes* CHVR.: "Holotype" "curvipes Chevr." "Type" "Saunders 74.18" [♀ (NHM)]

Additional material: 14 ex.

Characters:

Males [6] 18.5×6.5 - 25×10, females [9] 16.5×6 - 27×10.5 mm. Body black with faint to strong (always strong on front and tibiae) green, blue, or violet (sometimes bronzed or purplish on ventral side and elytral disk) shine; tarsi usually green or violet, rarely blue. Front (fig. 47) with three (one along midline and two periorcular) usually prominent longitudinal carinae and some small smooth reliefs between them, otherwise dfp.; periorcular stripes (between carinae and eye margins) densely pubescent, pubescence of remaining frontal surface inconspicuous (but all depressed dfp spaces distinctly pulverulent): vertex densely and relatively coarsely, but not confluent punctulate. Pronotal puncturation coarse and moderately dense on disc, much denser and irregularly confluent on sides; smooth median line and anterodiscal spots usually very inconspicuous; lateral carina distinct only at the very base (if at all). Elytra usually without, sometimes with traces of posthumeral denticle; striae continuous, rather deep, coarsely and densely punctured; all interstriae narrow, convex, almost equally elevated; foveae on odd intervals most often missing or hardly appreciable, only exceptionally well developed. Median part of prosternal process sparsely punctured, separated from much narrower smooth lateral rims by deep striae; proepisterna dfp without (or, exceptionally, with very fine trace of) submarginal ridge. First abdominal segment rather deeply sulcate; "secondary" (consisting of depressed dense groups of fine "primary" punctures) puncturation of abdominal disc coarse and moderately dense, sides of ventral sides dfp; pubescence of ventral side yellowish, recumbent, rather short and sparse (especially in females) medially, longer and very dense (almost totally covering surface of sclerites) on lateral dfp band; apex of anal sternite roundedly truncated with more or less distinct incision at middle (male) or narrowly rounded (female). Parameres, piceous-brown (slightly paler at base); penis yellowish-brown with dark median stripe.

Remarks:

The closest relative of *P. timoriensis* (C.G.) is evidently *P. baliana* KERR., from which it differs mainly in distinct metallic shine of the body (especially front and legs), dark male genitalia, much sparser frontal reliefs, and very dense pubescence on lateral band of ventral side. KERREMANS (1910) separates *P. curvipes* (CHVR.) on grounds of colouration ("Dessus noir ou noir bleuâtre ... *timoriensis*", "Dessus vert ... *curvipes*"), but CHEVROLAT (1838) described it as "Caput coeruleum, ... Thorax nigro coeruleus, ... Elytra violacea", what agrees with my notes on the holotype ("black with metallic - blue on head and pronotum, purplish on elytra, and bluish-violet on ventral side - shine" and fits *P. timoriensis* (C.G.) very well. The clue to the understanding of KERREMANS' (1910) misinterpretation is his remark, that "La description du *Lampetis Eva* Thoms. se rapporte exactement à un exemplaire que j'ai sous les yeux et que je considère comme une femelle du *curvipes* Chevrol." - apparently he had not seen the type of *Lampetis curvipes* CHVR. and based his concept of that taxon on a specimen belonging in fact to *P. eva* (THS.)! However, as well the geographical distribution as morphological details (colouration, elytral foveae, sculpture of vertex) clearly show, that *P. eva* (THS.) is not synonymous with *P. curvipes* (CHVR.) - instead, neither the original description nor the study of the holotype offers any point to separate the latter from *P. timoriensis* (C.G.): of the only two apparent differences, the presence in *P. curvipes* (CHVR.) of elytral foveae remains comfortably within the limits of individual variability, while the strongly inflected (like broken) metatibiae of the holotype - interpreted by KERREMANS (1910) as sexual character of male - look decidedly unnatural and most probably represent some developmental or genetical abnormality.

Both nominal taxa have been described from Timor, and indeed *P. timoriensis* (C.G.) is known only from that island (map 14).

Alorensis-circle

Psiloptera (Spinthoptera) praeinsularis sp.n.

Material examined:

Holotype: "Sumatra N.E.coast, Gedong Biara, 15-XII-1952, R.Straatman leg"
"Psiloptera sp., det. Sv. Bily" [♀ (RBH: BPhq)]

Holotype:

23.5×9 mm. Front, sides of prothorax, scutellum, epipleura, antennae and legs green (5. tarsal joint violet-blue), otherwise body dorsally and ventrally cupreous-red.

Epistome rather shallowly, roundedly-triangularly emarginate, with some coarse punctures concentrated on sides; not separated from generally flat; trapezoidal front. Frontal disc bordered on both sides with prominent smooth arcuate carina running roughly parallel to eye margin; space between these carinae covered with network of smooth reliefs enclosing rather broad depressed dfp foveae; periocular bands dfp, covered with short and dense yellowish pubescence - otherwise front but inconspicuously pubescent; vertex rather wide (V:H=0.5), covered with coarse and

dense puncturation; eyes moderately prominent, *ca.* 2.5× longer than wide. 1. antennal joint egg-shaped, *ca.* 1.5× longer than wide; 2. cylindrical, *ca.* as long as wide, distinctly narrower than 1.; 3. conical, as wide as, but 1.5× longer than, 2.; 4. club-shaped, similar in length to 1. but thinner; 5. similar in shape but somewhat longer and wider; 6. still longer and definitely wider, triangular; 7.-10. rhomboidal, progressively shorter and narrower; 11. as long as 9., elongately and asymmetrically club-shaped.

Pronotum wide (L:BW:AW=1:1.5:1.2), trapezoidal; sides strongly, almost straightly convergent from base to apex (minimally less so in basal fourth); anterior margin very shallowly trisinate, base bisinate with median lobe protruding about as far back as sharply acute posterior angles. Disk shallowly transversely depressed along median half of base, otherwise almost regularly convex, lateral carina somewhat irregular but distinct to slightly before midlength; pronotal punctures coarse, very dense, forming reticulate sculpture on sides, somewhat less dense (but still interspaces on average much narrower than diameters of punctures), irregularly spaced, also coarse on disc; pair of discal reliefs very irregular and indistinct. Spaces between these "primary" punctures covered with very fine, rather sparse "secondary" punctulation on background of distinct (under 12× magnification) microsculpture. Scutellum small, roundedly trapezoidal, as long as wide, convex.

Elytra 2.0× longer than wide; sides obliquely truncated at humeri (no posthumeral denticle), then parallel to metacoxae, slightly sinuate just behind, arcuately convergent from midlength to *ca.* apical $\frac{1}{12}$, and sinuately so to obliquely truncate apices; external apical denticle distinct but not prominent. Striae coarsely and densely punctured; interstriae smooth, convex, of equal elevation; odd ones (1., 3., 5., 7.) broken up into sections by well developed, depressed dfp foveae; basal portion of epipleural carina irregularly coarsely punctured, looking crenulated when seen from above.

Anterior margin of prosternum arcuately produced; prosternal process parallelsided to behind procoxae, then sinuately narrowed to broadly rounded apex; lateral striae indistinctly shallowly punctured anteriorly, cuneately tapering and smooth apically; median space wide, sparsely punctured anteriorly, with only irregular median row of punctures behind; smooth lateral portions less than half as wide; median parts of proepisterna densely and finely granulated, separated from coarsely reticularly sculptured lateral portions by distinct though irregular "additional ridge". Metasternum convex, narrowly furrowed along midline, finely and sparsely punctate medially, very densely, coarsely on sides; hind margin of metacoxae with but indication of tooth at median third. 1. sternite rather deeply depressed along median line; median parts of abdomen with coarse foveolate (consisting of depressed groups of fine punctures) sculpture, which laterally becomes much denser; no distinct dfp spaces or on sides of sternum or abdomen; lateral pubescence distinct but not forming appreciable bands or spots; anal sternite narrowly rounded at apex.

Remarks:

P. praeinsularis sp.n. seems to represent a link between continental (the *Affinis*-circle) and insular (the *Alorensis*-circle) groups. It is deceptively similar to *P. affinis* (SND.), from which it differs in uniformly (without green midline almost always appreciable in the latter species) reddish-cupreous pronotum; coarser and denser pronotal puncturation and more distinct microsculpture; definitely costiform interstriae [very rare in *P. affinis* (SND.)]; broad (wider than adjoining interstriae), irregularly punctured periscutellar stria; more regular and deeply depressed elytral foveae; "crenulated" basal section of epipleural carina; coarsely foveolate sculpture of abdomen; and some other minor details. However, similarities with *P. alorensis* THY. seem at least as convincing - dark colouration and much better developed lateroventral pubescence of the latter being apparently the only clear-cut distinguishing characters - and indeed this is probably the closest relative of the new species.

P. praeinsularis sp.n. is known only from the type-locality in NE-Sumatra (map 14).

Psiloptera (Spinthoptera) alorensis THY.

Psiloptera alorensis THÉRY 1901

= *Lampetis timoriensis* var *rossi* OBENBERGER 1939

Material examined:

3 ex. (1♂, 1♀, 1♂)

Characters:

Male [1] 23×9, female [1] 24×10 mm. Body black with green elytral foveae and blue to violet labrum, basal two antennomeres, and tarsi; tibiae with distinct violet shine. Front encircled with irregular, here and there interrupted carina, consisting of (least distinct) transverse part along epistomal border, short oblique supraantennal ridges, vertical periocular (at some distance from each eye) portions, and - again transverse - upper arch; conspicuous cross-shaped elevation at middle, short more or less distinct vertical ridge on each side of it, and network of irregular reliefs anterolaterally, emerge from dfp bottom of this enclosure; periocular stripe dfp; frontal pubescence short and inconspicuous, dfp depressions pulverulent; vertex finely and shallowly but very densely punctulate, with slight tendency to form transverse rugae. Pronotum coarsely, at sides very densely and confluent punctured, smooth median line rather distinct, other reliefs very irregular; lateral carina well marked and reaching to anterior fifth, though smooth only at basal and apical end: otherwise somewhat obliterated by dense puncturation. Elytra with distinct posthumeral denticle; striae rather shallow, consist of rows of deep, coarse, dense punctures; all interstriae convex, odd intervals ("intercostae") - broken up by large dfp foveae into short (not much longer near suture, definitely shorter on sides, than foveae) sections - look lower than "costae", though in fact there is no appreciable difference in elevation. Median part of prosternal process sparsely punctured, lateral rims smooth, striae deep; proepisterna dfp with traces of submarginal ridge. First sternite rather deeply sulcate (male) or almost flat (female); puncturation of abdominal disc coarse (consisting in

fact of depressed dense groups of fine "primary" punctures) and moderately dense; sides of sternum and of 1. abdominal segment broadly dfp, 2. - 5. sternites with only very narrow lateral border and two to four small spots on each side dfp; pubescence of ventral side yellowish, recumbent, medially short and inconspicuous, on lateral dfp areas longer and dense; apex of anal sternite narrowly rounded in female (tip of abdomen damaged in male specimen examined by me).

Remarks:

P. alorensis THY. has been usually considered a synonym of *P. timoriensis* (C.G.), but in fact represents a distinct species. It differs from *P. baliana* KERR. and *P. timoriensis* (C.G.) mainly in large elytral foveae and in broad lateral dfp band of ventral side not (or in but rudimentary form) extending beyond 1. abdominal segment; of its two apparently closest relatives, *P. sumbana* sp. n. is recognizable by details of colouration, lack of lateral carina of pronotum, prosternal pubescence visible from above, elytra without subhumeral denticle, etc., while good distinguishing characters of *P. (S.) lombokiana* sp. n. are bright colouration and absence of clearly developed lateral dfp band on sternum and abdomen. I have not seen the type of *Lampetis timoriensis* var. *rossi* OBB., but the allegedly distinctive colouration (the only distinguishing character quoted) is in fact quite typical, and as the type-locality is Alor, that form certainly belongs to *P. alorensis* THY.: the genuine *P. timoriensis* (C.G.) occurs only on Timor.

P. alorensis THY. is endemic of Alor (map 14).

Psiloptera (Spinthoptera) sumbana sp.n.

Material examined:

Holotype: "Sumba Is., Indonesia, XII 1992" "Akiyama Collection" [♀ (RBH: BPhuq)]

Paratype: "Sumba" [♀ (RBH: BPgtp)]

Holotype:

22×8.5 mm. Relieved parts of body black with very slight bluish (dorsally) or strong golden-green (on ventral side) shine; depressed dfp areas cupreous; apical parts of epipleura, labrum and legs bluish-green; two basal antennomeres blue, remaining joints piceous-black.

Epistome rather shallowly, roundedly-triangularly emarginate, coarsely and densely punctured, not separated from generally flat; trapezoidal front. Frontal disc bordered on both sides with prominent smooth arcuate carina running parallel to eye margin; between these carinae some small (mostly longitudinal) reliefs emerge from dfp depression; periocular bands dfp, covered with short and dense yellowish pubescence - otherwise front but inconspicuously pubescent; vertex rather wide (V:H=0.5), covered with moderately coarse, dense but not confluent punctulation; eyes moderately prominent, ca. 2.5× longer than wide. 1. antennal joint egg-shaped, ca. 1.5× longer than wide; 2. cylindrical, shorter than wide, distinctly narrower than 1.; 3. conical, as wide as, but 1.5× longer than, 2.; 4. club-shaped, similar in length to

1. but slightly thinner; 5. similar in shape but somewhat longer and wider; 6. still longer and definitely wider, triangular; 7.-10. rhomboidal, progressively shorter and narrower; 11. as long as 8., elongately and asymmetrically club-shaped.

Pronotum wide (L:BW:AW=1:45:1.1); sides strongly convergent in basal $\frac{1}{7}$, then subparallel to near midlength, and regularly arcuately narrowed to apex; anterior margin almost straightly truncated, base bisinuate with median lobe protruding further back than posterior angles. Disk convex, with four (a pair at basal $\frac{1}{4}$, nearly as far from median line as from sides, and another at midlength, slightly inwards) rather deep foveolate depressions; prebasal depression inconspicuous, lateral carina absent, notosternal border broadly rounded off and densely punctured; pronotal punctures coarse, irregularly spaced, dense and somewhat confluent on sides, rather sparse and isolated on disc; no distinct discal reliefs appreciable. Scutellum small, trapezoidal, as long as wide, slightly convex.

Elytra $2.0\times$ longer than wide; sides obliquely truncated at humeri (no posthumeral denticle), then parallel to metacoxae, slightly sinuate just behind, arcuately convergent from midlength to *ca.* apical $\frac{1}{12}$, and sinuately so to obliquely truncate apices; external apical denticle distinct but not prominent. Striae coarsely and densely punctured; interstriae smooth, convex, of similar elevation - though "intercostae" look lower than "costae" as a result of being broken up into short (mostly shorter than large dfp foveae between them) sections.

Anterior margin of prosternum straightly truncate; prosternal process parallelsided to behind procoxae, then sinuately narrowed to broadly rounded apex; lateral striae slightly convergent backwards, continuous, rather densely punctured; median space wide, sparsely punctured anteriorly, with only irregular median row of punctures behind; smooth lateral portions twice narrower; proepisterna dfp, laterally intergrading without distinct border into coarse pronotal sculpture. Metasternum convex, narrowly furrowed along midline, sparsely punctulate medially, very densely on sides; hind margin of metacoxae with but indication of tooth at median third. 1. sternite broadly but shallowly depressed along median line; median parts of abdomen with coarse foveolate (consisting of depressed groups of fine punctures) sculpture, which laterally becomes much finer but definitely denser; sides of 1. and progressively smaller spaces at anterior angles of 2.-4. sternites, dfp; lateral dfp spaces of sternum and abdomen covered with long and dense yellowish pubescence, extending so far on sides of prothorax as to be visible from above; anal sternite narrowly rounded at apex.

Paratype:

22×8.5 mm. Virtually identical to the holotype: slightly differs only in duller colouration of labrum and legs (especially of femora, which are concolorous with rest of ventral side), distinct (though weakly developed) frontoclypeal ridge, less prominent periocular carinae, lack of appreciable discal foveae on pronotum, its sides definitely convergent also in basal half, somewhat denser pronotal sculpture, deeper median groove on metasternum and 1. sternite, and more extensive lateral dfp areas on sternum and abdomen.

Remarks:

P. sumbana sp.n. is apparently very closely related to *P. alorensis* THY. and *P. lombokiana* sp.n. - see the key and remarks on *P. alorensis* THY. for differences.

The species apparently occurs only on Sumba I. (map 14).

Psiloptera (Spinthoptera) lombokiana* sp.n.*Material examined:**

Holotype: "Lombok Is., Indonesia, I 1989" "Akiyama Collection" [♀ (RBH: BPhur)]

Holotype:

24×9 mm. Front and legs green, pronotum and elytra green with strong cupreous reflexions, labrum and ventral side cupreous, antennae piceous-brown with cupreous - strong on basal joints, slight otherwise - shine.

Epistome rather shallowly, triangularly emarginate, coarsely and densely punctured. Front generally flat; trapezoidal, not separated from epistome; discal part ornamented with network of prominent smooth ridges (including well marked median cruciform and pair of lateral carinae), leaving not much space to depressed dfp bottom; periocular stripes dfp, densely covered with rather long yellowish pubescence - discal part virtually glabrous; vertex rather wide (V:H=0.5); eyes moderately prominent, *ca.* 2.5× longer than wide. 1. antennal joint egg-shaped, *ca.* 1.5× longer than wide; 2. cylindrical, shorter than wide, distinctly narrower than 1.; 3. slightly conical, distinctly wider and 1.5× longer than 2.; 4. club-shaped, again markedly longer; 5. angularly clavate, still longer and wider; 6. of similar length, triangular, widest of all (almost as wide as long); 7.-11. rhomboidal, progressively shorter and narrower.

Pronotum wide (L:BW:AW=1:1.5:1.1); sides strongly convergent in basal $\frac{1}{7}$, then somewhat less so to near midlength, and again a little stronger to apex; anterior margin almost straightly truncated, base bisinuate with median lobe protruding further back than posterior angles. Disk convex, prebasal depression shallow but distinct, lateral carina virtually absent, notosternal border broadly rounded off and densely covered with coarse and very irregular sculpture (making pronotal sides look irregularly crenulate in dorsal aspect); pronotal punctures coarse, irregularly spaced, rather dense and confluent even on disc, very strongly so on sides (this sculpture extending far to ventral side); median line almost undifferentiated, smooth anterodiscal reliefs rather well developed, another pair at anterior angles also appreciable. Scutellum small, trapezoidal, as long as wide, slightly convex.

Elytra 2.0× longer than wide; sides obliquely truncated at humeri, with small but rather distinct posthumeral denticle, then subparallel to midlength, and arcuately convergent almost to apices (very shallowly sinuate just before); external apical denticle distinct but not prominent. Striae coarsely and densely punctured; interstriae smooth, convex, not differing in elevation but "intercostae" broken up into short (mostly - except on 3. interval - shorter than large dfp foveae between them) sections.

Anterior margin of prosternum broadly rounded; prosternal process parallelsided to behind procoxae, then sinuately narrowed to broadly rounded apex; deep and coarsely punctured lateral striae also parallel, lateral rims smooth, twice wider median space coarsely and rather densely punctured anteriorly, very sparsely (with irregular row of punctures along median line) on middle and apical parts; proepisterna medially dfp, laterally covered with coarse sculpture similar to, and not clearly demarcated from, that of pronotal sides. Metasternum convex, deeply grooved apically, sparsely punctured on median parts, very densely on sides; hind margin of metacoxae with but broadly rounded indication of tooth at medial third. 1. sternite broadly depressed along median line; median parts of abdomen with coarse, elongately foveolate (consisting of depressed groups of fine punctures) sculpture, which laterally becomes much finer and very dense, but without typically dfp spaces; median parts of sternum and abdomen virtually glabrous, sides covered with long but sparse yellowish pubescence; apex of anal sternite narrowly rounded.

Remarks:

The closest relatives of *P. lombokiana* sp.n. are undoubtedly *P. sumbana* sp.n. and *P. alorensis* THY.; it differs from both in bright colouration, lack of clearly developed dfp band on ventral side, and some other details.

The species is known only from its type-locality, Lombok I. (map 14).

Scintillans-circle

Psiloptera (Spinthoptera) scintillans WATH.

Psiloptera scintillans WATERHOUSE 1877

= *Lampetis costata* THOMSON 1878a

Material examined:

Holotype: "Holotype" "Andaman Is., 81-61" "*Psiloptera scintillans* (Type) C. Waterh." [♀ (NHM)]

Syntype[?] of *L. costata* THS.: "Th, TYPE" "Ex Musaeo James Thomson" "Costata Thomson, ex typis, =scintillans Waterh., Théry" [1 ex. (NHM)]

Additional material: 36 ex.

Characters:

Males [3] 15.5×5.5 - 17.5×6, females [4] 22×8 - 25×9.5 mm. Labrum and front green; pronotum and elytra dull cupreous with green bottoms of punctures and piceous-black elytral costae; ventral side greenish-cupreous; tarsi bluish-green. Epistome shallowly arcuately emarginate, coarsely and densely punctured, not separated from front; frontal sculpture consists of rather dense network of smooth reliefs encircling coarse, regular (of virtually identical shape and size) ocelliform punctures; supraantennal ridges short, median ridge irregular and not conspicuous, no individualized clypeofrontal or periocular carinae; periocular band less coarsely punctured, but neither clearly demarcated nor conspicuously pubescent; 6. to 11. antennomeres similar in shape and size: rhomboidal, very slightly diminishing in length. Pronotum strongly convex, prebasal depression very shallow; puncturation

coarse and rather dense on disc, still coarser and very dense, irregularly confluent on sides; smooth median line inconspicuous, other reliefs very irregular; lateral carina well marked, smooth in basal $\frac{2}{3}$, traceable still somewhat further. Elytra without posthumeral denticle; striae consist of rows of not or but very shallowly depressed rows of deep, coarse punctures; odd intervals (costae) smooth, continuous, markedly elevated; intercostae (even interstriae) flat, finely and sparsely punctulate. Median part of prosternal process smooth, not wider than lateral rims; striae deep, parallel; proepisterna densely covered with very coarse ocelliform punctures. Metasternum flat, grooved along midline, puncturation finer and sparser, simple at middle, coarse and very dense, irregularly ocelliform on sides; metacoxal tooth represented by broadly rounded lobe. First sternite rather deeply sulcate along median line; abdominal sculpture foveolate (consisting of depressed dense groups of fine "primary" punctures) on disc, finer and very dense, irregularly granular laterally; anal segment with rather sparse but coarse, ocellate punctures; pubescence (even on sides of sternum and abdomen) inconspicuous; apex of anal sternite truncated in males, rounded in females. Male genitalia (fig.) ferrugineous, sides of parameres regularly rounded to tips, penis sharply pointed.

Remarks:

Regularly elevated costae and depressed intercostae make *P. scintillans* WATH. unmistakable. Its affinities are unclear [*"Dicercomorpha" alluaudi* (KERR.) from Seychelles - belonging in fact undoubtedly to *Psiloptera* DEJ., as evidenced by striatomarginate prosternal process, lack of prehumeral sulci on pronotum or pubescent spots on elytra, &c. - shows somewhat similar elytral structure, but profound differences in other characters leave no doubt as to convergent nature of this similarity], but seem to remain within the Indo-Pacific Region: joining some peculiarities of the "continental" lineage (e.g. frontal and abdominal sculpture) with costate interstriae closer to those in the "insular" group, it seems to represent an ancient offshoot of the common ancestral stem.

Also its distribution (map 12) is intermediate: it is endemic to Andaman Is. (one specimen in NNHM is labelled "Nepal", one in MCGD "Imalaja" - certainly mislabellings).

[Sg. *Lampetis* DEJ.]

Lampetis DEJEAN 1833

= *Damarsila*: KERREMANS 1903 [nec THOMSON 1878a]

Type-species: *Buprestis bioculata* OLIVIER 1790

Large subgenus, comprising some 100 described species known, until now, only from Africa (map 7). This group has traditionally been characterized by the anterior margin of prosternum emarginated at middle and flanked by a pair of sometimes prominent, sometimes only indicated denticles; however, the same can be observed not only in several other genera (e.g. *Ectinogonia* SPIN., *Oedisterna* LAC., *Dicercomorpha* DEYR., *Tristria* g.n., *Touzalinia* THY.), but even within *Psiloptera*

SOL.: in one species [*P. (P.) weddelli* LUC.] of the nominotypical subgenus, in many representatives of *Polybothris* SPIN. (*s.l.*), &c. Truly unambiguous differential diagnosis of *Lampetis* DEJ. vs. *Psiloptera* DEJ. *s.str.* or *Polybothris* DEJ. has, to my knowledge, never been formulated, and is evidently out of the scope of the present work (it would demand careful examination of several hundred species, none of which occurring in the Indo-Pacific).

The subgenus does not seem to occur in the Indo-Pacific Region: the specimen in my collection labelled "Borneo ?" is very close to, or identical with, West African *P. (L.) zona* (THS.), and has evidently been mislabelled; on the other hand, *P. praeorientalis* sp.n. belongs to the *Pupillata*-circle which shows striking affinities to *Spinthoptera* CSY. (esp. the *Fastuosa*-circle) and is provisionally treated as belonging there.

Archepsila g. n.

General characteristics:

Monotypic genus, known only from the unique holotype of its type-species, found unexpectedly on Batjan I. in North Moluques, but apparently related to Neotropical *Pseudolampetis* OBB. and *Ectinogonia* SPIN.

Phylogenetic relations:

While phylogenetic affinities of this genus seem relatively well defined (it appears consistently near *Spinthoptera* CSY., *Ectinogonia* SPIN. and *Pseudolampetis* OBB. - fig. 1, 3), its zoogeographical roots are rather nebulous: I cannot think of any scenario, which would plausibly explain how and wherefrom [the ancestor of] *Archepsila* g.n. arrived to Moluccas. Perhaps the answer will emerge from further palaeographic studies on small terranes supporting islands of this region: "... the terranes in the Moluccas are predominantly of continental (probably Australian) origin ... Many of these continental fragments (e.g., ... Bacan and Obi; ... are supposed to be slivers that have become detached from the northern craton of the Australian continent ..." (DE BOER 1995). There is much controversy about the timing of these events, the opinions vary between early Jurassic and middle Eocene. If the latter assessment is closer to the truth (and, of course, if the drifting "microcontinent" has never been submerged), then *Archepsila cordicollis* sp.n. might perhaps represent the last survivor of some ancient Gondwanian group of [or: related to] *Spinthoptera* CSY., that persisted in northern part of Australia during early Tertiary and then travelled on the Obi-Batjan terrane to its present position. This, however, is no more than a speculation.

[S g. *Archepsila* s g. n.]

Type-species: *Archepsila cordicollis* sp.n.

***Cordicollis*-circle**

***Archepsila cordicollis* sp.n.**

Material examined:

Holotype: "Bacan Is., Indonesia, 1 - 1991" [♂ (RBH: BPgrb)]

Holotype:

17.5×5.5 mm. Body dorsally and ventrally of rather uniform bronzed colouration with slight cupreous tinge.

Epistome short, deeply arcuately emarginate at apex, coarsely and densely punctured. Front trapezoidal, not separated from epistome, broadly and rather deeply transversely depressed in anterior half; supraantennal carinae very prominent anteriorly, disappearing behind midlength of front among coarse longitudinal punctate-rugose sculpture; frontal pubescence rather short and inconspicuous, almost uniformly distributed, whitish. Vertex wide (V:H=0.45); eyes prominent, not quite twice longer than wide. 1. antennal joint egg-shaped, *ca.* 1.5× longer than wide; 2. globular, shorter than wide, distinctly narrower than 1.; rest of antennae missing.

Pronotum wide (L:BW:MW:AW=1:1.5:1.4); base bisinuate, basal angles acute (*ca.* 70°); sides deeply sinuate in posterior third, strongly rounded at middle (here attaining maximum width) and somewhat less strongly so in apical third; anterior angles right; anterior margin deeply bisinuate, laterally bordered with shallow but distinct, coarsely punctures stria. Disk convex, with broad (*ca.* 1/3 of pronotal width) and rather deep depression in basal half, and shallow oblique one at midlength of each side; lateral carina virtually absent, notosternal border broadly rounded off and densely covered with coarse and very irregular sculpture (making pronotal sides look coarsely irregularly crenulate in dorsal aspect); pronotum coarsely punctured, punctures irregularly spaced, sparse on both sides of median depression, rather dense otherwise on disk, very dense and confluent near lateral margins (this sculpture extending to ventral side); prescutellar pits deep, elongate, separated by *ca.* their diameter. Scutellum small, trapezoidal, *ca.* 1.5× wider than long, convex.

Elytra 2.4× longer than wide; sides slightly divergent behind humeri (no trace of posthumeral denticle), then very shallowly sinuately subparallel to midlength, arcuately convergent to apical fifth, again slightly sinuate, and again somewhat more strongly tapering just before apices obtuse, sutural much more prominent. Epipleural carina coarsely crenulate in humeral part and slightly uneven apically. Striae shallow, rather coarsely and densely punctured (much more so at sides); interstriae flat, their puncturation almost as coarse and dense as that in striae, becoming very coarse and confluent laterally; 3., 5., 7., and 9. interstria with series of elongated, convex, smooth, darker cupreous reliefs.

Anterior margin of prosternum very shallowly, almost inappreciably emarginated; prosternal process parallelsided to behind procoxae, then cuneately narrowed to broadly rounded apex; lateral striae deep, parallel; lateral rims smooth, twice wider median space with sparse and moderately coarse punctures; proepisterna covered with very coarse, dense, punctate-foveolate sculpture not clearly demarcated from that of pronotal sides. Metasternum convex, shallowly grooved, sparsely and rather finely punctured on median parts, densely, coarsely and irregularly on sides; hind margin of metacoxae with obtuse and blunt, but very prominent tooth at median third. 1. sternite broadly depressed along median line; median parts of abdomen with coarse, rather sparse, elongate punctures, which laterally become finer but denser, without typically dfp spaces; median parts of sternum and abdomen virtually glabrous, sides covered with long but sparse yellowish pubescence; apex of anal sternite broadly roundedly truncated.

Remarks:

P. cordicollis sp.n. is known only from its type-locality, Batjan I. (map 23).

***Dicerca* ESCH.**

Dicerca [erratum] ESCHSCHOLTZ 1829

General characteristics:

Large genus, widely distributed (map 19) throughout the Palaearctic (11 sp.) and Nearctic (27 sp. - NELSON 1975) Regions; 3 species have been reported from the Indo-Pacific (Taiwan, S-China, N-Vietnam) and, besides, 4 of the essentially Palaearctic representatives occur also within the limits of the area under study. A combination of bronzed colouration, small scutellum, "caudate" elytra with more or less clearly developed rows of small smooth elevated "mirrors" on densely punctured background, longitudinally depressed prosternal process without marginal stria, &c., make the genus rather distinctive. The systematic relations are poorly understood; in Eurasia three subgenera have been described, of which only the nominotypic *Dicerca* ESCH. s.str. certainly occurs within the study area: "sg. *Argante* GISTL" is considered to contain two very rare, relict species in Europe, one of which has been once recorded from China (prov. Shantung); the distribution of the monotypic "sg. *Hemidicerca* RICHT." is restricted to areas around the southern end of the Caspian Sea. Beyond serious doubt, these groupings - based on evident overestimation of the importance of few characters in few (exclusively Palaearctic: to my best knowledge inclusion of the American representatives of the genus into this scheme has ever been attempted) species of somewhat aberrant morphology - do **not** warrant taxonomic recognition: the "diagnostic" (mostly sexual, so notoriously unreliable as evidence of evolutionary relationship - see below [CONCLUSIONS: **genitalic characters**] for discussion of the point) features of *Argante* GISTL or *Hemidicerca* RICHT. are but extremal "states" of highly variable characters, whose development in particular species shows no apparent correlation either to one another or to anything else, and anyway seems to have nothing to do with phylogenetic affinities (cf. fig. 12).

Phylogenetic relations:

According to the intergeneric tree (fig. 1), the genus is the sister-taxon of *Poecilonota* ESCH. and *Scintillatrix* OBB., together sharing a common ancestor with the large *Psiloptera* DEJ. - group. This arrangement is definitely supported by the cladogram for *Ovalisia* KERR. s.l. (fig. 15), and partly by those for *Poecilonota* ESCH. (fig. 13) and *Scintillatrix* OBB. (fig. 14), and *Dicerca* ESCH. itself (fig. 12), being definitely refuted by none.

The *leitmotiv* of the distributional evolution of *Dicerca* ESCH. seems to be the repeating cycle of separation and reunion between Palaearctic and Nearctic part of its vast area. Already the lowest branch of the cladogram (fig. 12) is composed by Eurasian relict *D. moesta* (F.) (*nb.* the type-species of *Argante* GISTL) and American *D. punctulata* (SCHH.); their common ancestor almost certainly inhabited both continents. Of the two branches making the main lineage none is purely Eurasian or entirely American, though one most probably originated on the western side of the Pacific. This western branch bifurcated into the south-eastern (Yunnano-Tibetan *D. corrugata* FRM. and Japanese *D. tibialis* LEW.) and Euro-Siberian ramification, of which the basalmost offshoot is now very rare though widely (from Hercegovina to the Japan Sea) distributed relict, *D. amphibia* MARS., followed by inhabiting almost all the northern part of Eurasia (from Morocco to Japan) *D. furcata* (THB.) and another Euro-American pair: *D. herbsti* (KSW.) (Middle Europe, Caucasus) and *D. tenebrosa* (KBY.) (Canada, USA).

The area of origin of the second lineage is much less clear. The basalmost clade consists again of Persian *D. fritillum* MÉN. ("sg. *Hemidicerca* RICHT.") and *D. horni* CROTCH from western USA; the next [*D. obscura* (F.), *D. lurida* (F.), *D. pugionata* (GRM.)] is entirely American, and the third predominantly Eurasian. The first to branch off is here Palaearctic *D. aenea* (L.); its sister-taxon gave rise to Taiwanese *D. unokichii* HRI. and a clade consisting of two pairs of siblings: European *D. alni* (F.-W.) and *D. berolinensis* (HBST.), and American *D. divaricata* SAY and *D. tenebrica* (KBY.).

The general picture is rather obscure: the species seem to disperse chaotically from East to West and from West to East, with no clear pattern discernible (this lack of clarity may, however, be partly due to the fact, that I concentrated on Asian species and included in the analysis only relatively few of numerous American representatives of the genus; as Palaearctic species make a highly polyphyletic assemblage, such bias must have negatively influenced the clarity of the obtained results). Anyway the Indo-Pacific fauna developed from several (at least two) separate "invasions": 1) *D. moesta* (F.) (of course if its presence in Shantung is natural); 2) the ancestor of *D. tibialis* LEW., *D. corrugata* FRM. and probably *D. latouchei* FRM.; 3) perhaps independent *D. furcata* (THB.) (though it may also be an "autochthonous" descendant of the former group); 4) the ancestor of *D. aenea* (L.), *D. unokichii* HRI., and probably *D. nishidai* TMA.

Sg. *Dicerca* ESCH. s. str.

Dicerca [erratim] ESCHSCHOLTZ 1829
= *Argante* GISTL 1834
= *Stenuris* KIRBY 1837
= *Hemidicerca* RICHTER 1952

Type-species: *Buprestis aenea* LINNAEUS 1761

Key to the Indo-Pacific species of the subgenus *Dicerca* ESCH. s. str.

- 1 (4) Outer denticle on elytral apex totally obliterated
- 2 (3) Apex of anal sternite in female simply rounded; male mesotibiae simple
..... *D. (s.str.) moesta* (F.)
- 3 (2) Anal sternite in female with two deep apical notches; male mesotibiae with
long inwardly directed spine at proximal third.....
..... *D. (s.str.) furcata* (THB.)
- 4 (1) Elytral apex distinctly emarginate and bidenticulate
- 5(10) Pronotum with 4 or 5 smooth stripes or elevated carinae; elytra costate
- 6 (9) Pronotum glabrous
- 7 (8) Median line of pronotum carinate; posterior angles acute
..... *D. (s.str.) corrugata* FRM.
- 8 (7) Median line of pronotum sulcate without carina; basal angles right
..... *D. (s.str.) latouchei* FRM.
- 9 (6) Pronotum with long erect pubescence *D. (s.str.) tibialis* LEW.
- 10 (5) Pronotum without smooth stripes or carinae; elytral interstriae equally
elevated
- 11(14) Elytral interstriae strongly convex
- 12(13) Elytra only slightly caudate, sides strongly convergent also just before apex,
without distinct spots *D. (s.str.) unokichii* HRI.
- 13(12) Elytra strongly caudate, parallelsided before apex, with large aeneoaceous
spots at posterior third *D. (s.str.) nishidai* TMA.
- 14(11) Elytral interstriae flat *D. (s.str.) aenea* (L.)

Moesta-circle

Dicerca (s.str.) moesta (F.)
Buprestis moesta FABRICIUS 1792
= *Buprestis quadrilineata* HERBST 1801

Material examined:
None

Characters:

Length 12-17 mm. (RICHTER 1952) Dorsally brownish-black with cupreous bottoms of punctures, ventral side cupreous. Front depressed, divided at middle into two parts by very irregular transverse elevation; surface very densely punctured, with pair of small smooth tubercles at vertex. Pronotum widest at middle, sides deeply sinuate towards base, roundedly narrowed to apex; apical margin shallowly bisinuate,

anterior angles but slightly produced, base bisinuate, prescutellar lobe produced slightly further back than distinctly acute hind angles; four longitudinal ridges (and sometimes more or less distinct traces of mediaal carina) irregular, smooth, convergent apically; remaining surface very densely, confluent punctured; oblique laterobasal depression well defined but short; prescutellar pits shallow, widely separated; lateral carina entire but densely punctured throughout. Elytral striae distinct except lateral 3 or 4, which are only apically traceable; interstriae flat, uniformly and very densely punctured, with sparse smooth, elongated, somewhat more convex "mirrors". Anterior margin of prosternum shallowly emarginate; prosternal process densely uniformly punctured; proepisterna with very irregular rugose-reticulate sculpture; sternum and 1. sternite broadly depressed along midline; metasternum rather densely punctured even at middle; metacoxal dent obtuse but distinct; puncturation of abdomen dense on sides, somewhat sparser medially; no distinct smooth relief on sternites; apex of anal segment broadly emarginate in male, rounded in female. Mesotibiae simple even in male (fig. 73).

Remarks:

To some degree this species resembles a small and short *D. furcata* (THB.), differing however at glance in basally much more deeply sinuate pronotal sides, more prominent pronotal reliefs, shorter and less divaricate tips of elytra, lack of smooth lateral rims on prosternal process, and external sexual characters: simply rounded apex of anal sternite in female and simple mesotibiae in male.

KUROSAWA (1954) reported to have examined "a couple of specimens of this species from Laoshan, Shantung, Eastern China, captured by Y. Yano on June 26th, 1937"; otherwise *D. moesta* (F.) is known to occur only in Middle and Eastern Europe and West Siberia (map 19).

Furcata-circle

Dicerca (s.str.) *furcata* (THB.)

Buprestis furcata THUNBERG 1787

= *Buprestis acuminata* PALLAS 1782 [nec DEGEER 1774 (*Melanophila*)]

= *Buprestis calcarata* FABRICIUS 1801

= *Dicerca aino* LEWIS 1893

Material examined:

Syn[?]type (of *D. aino* LEW.): "Type" "Japan, G. Lewis, 1910-320" "Yezo, Tujer [?], 1883" "*Dicerca aino* Lewis, Type" [♂ (NHM)]

Additional material: 8 ex.

Characters (fig. 23):

Males [2] 18.5-20×6.5-7, females [2] 18-19.5×6-6.5 mm. Body elongated, convex. Dorsally brownish-black with cupreous bottoms of punctures, on head and ventral side cupreous colour dominates. Pubescence in female practically lacking, in male on ventral side appreciable but short and sparse, erect. Front flat, covered with dense, longitudinally confluent punctures. Pronotum widest at middle, slightly

sinuately narrowed to base, more abruptly roundedly or almost straightly so to apex; apical margin shallowly arcuately or somewhat bisinuately emarginate between prominent anterior angles, basal bisinuate, prescutellar lobe produced slightly further back than distinctly acute hind angles; three pairs of longitudinal elevations, progressively more disrupted and irregular towards sides, sparsely but coarse punctured; otherwise pronotal puncturation very dense, confluent; oblique laterobasal depression broad, distinct; punctiform pits on bottom of inconspicuous prescutellar fovea rather broadly separated; lateral carina only just at base distinct, otherwise almost totally obliterated. Elytral apices (fig. 58) narrow, elongated, strongly "caudate", lateroapical angle obliterated; striae distinct though fine in sutural part, become very inconspicuous or totally disappear towards sides; all interstriae flat, uniformly and very densely punctured, odd (1., 3., 5., &c.) with regular rows of dark smooth "mirrors". Anterior margin of prosternum very shallowly but perceptibly arcuately emarginate; prosternal process densely punctured between very sparsely punctured lateral rims; proepisterna with dense ocellate sculpture; prosternum and metasternum deeply, 1. sternite rather shallowly sulcate along midline; metasternal puncturation fine and sparse medially, coarse and very dense at sides; punctures on median parts of abdomen rather sparse and confluent into longitudinal strigae, laterally very dense and mostly simple; anterior angles of sternites usually with indistinct elevated reliefs, anal segment with pair of smooth carinae bordering shallow median sulcus; apex of anal sternite in both sexes trilobate: in male incisions separating lobes broad and median lobe wide and short (more than twice shorter than lateral pair), in female (fig. 70) incisions narrow and median lobe as long as laterals. Inner margin of male mesotibia at basal third with long, thin spine, almost isodiametric in section, directed obliquely backwards.

Remarks:

This species is distinctive among the Eurasiatic representatives of the genus [resembling rather the American *D. tenebrica* (KBY.) - group] by its remarkably long, narrow, divergent elytral apices with fully roundedly obliterated external angle. *D. aino* LEW. was described as distinct species, then (KUROSAWA 1946, 1970; AKIYAMA & OHMOMO 1997) treated as subspecies of *D. furcata* (THB.), but the alleged distinguishing characters (shorter elytra with laterally obliterated striae and less divaricate apices) are well within the range of individual variability of the continental populations, and as I have been not successful in finding any other differences, I consider the two names as synonymous. The status of the "type" examined by me in London is uncertain: I found only one so labelled specimen in the NHM, but LEWIS (1893) gives the size as "18-20 mm.", suggesting that he had more than one specimen before him; so I treat it provisionally as a syntype.

D. furcata (THB.) is the widest distributed (map 20) species of *Dicerca* ESCH.: its geographical area extends from France to Japan (Hokkaido); in China it reaches as far south as the vicinities of Peking.

Corrugata-circle

Dicerca (s.str.) corrugata FRM.

Dicerca corrugata FAIRMAIRE 1902b

With its heavy sculpture [resembling European *D. (Argante) herbsti* (KSW.) or - especially - American *D. (?Argante?) tenebrosa* (KBY.)] this species is unmistakable among East-Asian representatives of the genus. Inhabiting the extensive area between Thibet and Laos, it is also distinguished geographically, reaching further South than any other *Dicerca* ESCH. Two taxa described as separate species are probably but geographic races; Thibetan population is also subspecifically distinct (map 22).

Key to subspecies of *D. (s.str.) corrugata FRM.*

- a (d) Pronotum about as wide at middle as at base
- b (c) Median pair of pronotal reliefs less regular, narrower, apically almost linear
..... *D. (s.str.) c. thibetana ssp.n.*
- c (b) Median pair of pronotal reliefs rather broad even apically
..... *D. (s.str.) c. corrugata FRM. s.str.*
- d (a) Pronotum distinctly narrower at middle than at base
..... *D. (s.str.) c. vitalisi D.V.*

Dicerca (s. str.) corrugata thibetana ssp. n.

Material examined:

Holotype: "Thibet, Nuanatong" "R. Mus. Hist. Nat. Belg. I. G. 12.595" [♂ (KBIN)]

Paratypes: "Thibet, Nuanatong" [1♂ (RBH: BPgc), 1♀ (RBH: BPdst)]; "THIBET, Coll. Le Moul" "Le Moul vend., DICERCA corrugata Fairm." "R. Mus. Hist. Nat. Belg. I. G. 12.595" [1♂, 2♀ (KBIN)]

Additional material: 5 ex.

Characters:

Males 15.5-18×6-7 mm. [3], females 15.5-18.5×6-7 [4]. Differs from the nominotypic race in the development of longitudinal smooth ridges on pronotum: the inner (immediately neighbouring the median carina) pair is much narrower and less regular, touching anterior margin as very narrow point; the external (usually disrupted into several fragments, sometimes present only as traces) pair does not reach the anterior margin at all. Neither of these differences is absolutely consistent, thence the Tibetan population must be considered a subspecies of widely distributed *D. corrugata FRM.*

Remarks:

The geographical distribution of this race remains unclear: it inhabits (probably eastern part of) Tibet, but I have not been successful in finding the only specifically named locality (Nuanatong) on maps.

Dicerca (s. str.) corrugata FRM. s.str.
Dicerca corrugata FAIRMAIRE 1902b

Material examined:
49 ex.

Characters:

Males 15-20.5×5.5-8 mm. [18], females 14.5-22×5.5-8.5 [28]. Dorsal side black with dull cupreous bottoms of punctures, ventral cupreous; pronotum and elytra glabrous, head and undersurface with rather long, erect pubescence. Front irregularly, coarsely and densely punctured, with usually more or less distinct narrow median carina and pair of longitudinal smooth reliefs on vertex. Pronotal sides subparallel, more or less distinctly sinuate in basal half (basal angles acute), roundedly convergent apically; surface overall coarsely and very densely punctured, with 5 or 7 smooth longitudinal reliefs: very narrow but usually entire median carina, pair of rather broad regular ridges parallel to it, another (more external) narrow and less regular pair placed more externally, and sometimes traces of prehumeral carina visible (if at all) only in basal half; oblique depression deep, running from anterior third of lateral margins to base of median pair of ridges; prescutellar pits deep, punctiform, narrowly separated placed in broader depression making proximal end of median sulcus; lateral carina entire but very irregular, densely punctured. Elytra definitely "caudate" (fig. 59), covered with coarse and very dense puncturation similar to that on pronotum; costae disrupted into sections (long and close to one another near suture, short and widely spaced on sides); intercostal interstriae flat to very slightly convex, here and there with small anastomosing callosities. Anterior margin of prosternum straight, without any trace of lateral tubercles; puncturation of median part of prosternal process coarse and rather dense, lateral rim broad; proepisterna with dense irregular network of elevated callosities, densely punctured in between; broad and rather deep longitudinal depression runs along median line of prosternum, metasternum and 1. sternite; base of each sternite with smooth relief at middle; anal sternite medially sulcate between pair of indistinct smooth longitudinal elevations; otherwise ventral side covered with dense jumble of small callosities and coarse ocellate punctures; anal sternite rounded with pair of small but deep notches in female, broadly emarginate between two denticles in male. Mesotibiae in male (fig. 75) with long spine at upper third, strongly flattened frontocaudally, directed inwards and somewhat upwards.

Remarks:

This is the best-known form, occupying central position between the remaining two races: I have seen specimens from several localities in NW-, E-, SE-, and S-Yunnan, but it has been reported also from Szechuan (DESCARPENTRIES & VILLIERS 1963), Tonkin (OBENBERGER 1930), and even Formosa (MIWA & CHÛJÔ 1940); some years ago I saw in the collection of S. BÍLÝ a specimen determined as *Dicerca vitalisi* D.V. from Kuei-chou, which probably also belonged to the nominotypical subspecies (see below).

Dicerca (s. str.) corrugata vitalisi D.V.
Dicerca vitalisi DESCARPENTRIES et VILLIERS 1963

Material examined:
None

Characters:

"- Long. 16 mm. - Très proche de précédent [*D. corrugata* FRM.], en diffère, outre les caractères indiqués au tableau, par sa coloration plus cuivreuse, sa sculpture générale plus effacée, les bandes longitudinales lisses du pronotum moins saillantes, les interstries élytraux non caréniformes, moins grossièrement ponctués, cette sculpture effacée latéralement, les interstries caréniformes interrompus et ne formant, en arrière, que de petits reliefs isolés, les apex plus étroitement et plus profondément échancrés, la dent latérale plus aiguë.

LAOS: Xieng-Khouang (*Vitalis*), holotype au Muséum de Paris." (DESCARPENTRIES & VILLIERS 1963).

Remarks:

This form is not known to me in nature: my attempts to borrow material from MNHN, or even to arrange my visit to this museum, remained totally unsuccessful. To be sure, I saw so identified specimen in the collection of S. BÍLY, but it was several years ago, when I had not even planned the present work; my very brief notes from the rather superficial, routine examination of this beetle ("16×5.5 mm.; elytra distinctly caudate; lateral margin very coarsely, irregularly crenulated; apices emarginate; dorsal side rather brightly cupreous; head with median carina; pronotum narrower and elytral tips longer [than in Yunnanese specimens of *D. corrugata* FRM.]") - though partly (more cupreous colouration, narrower pronotum) in agreement with the original description - are rather inconclusive, and the locality (China: Kuei-chou) strongly suggests that it belonged more probably to *D. corrugata* FRM. s.str. DESCARPENTRIES & VILLIERS (1963) distinguish *D. vitalisi* D. V. mainly by the shape of pronotum, but their drawing is evidently somewhat "idealized", and this character (like colouration and details of sculpture, also mentioned in the original description) is highly variable in both the Yunnanese and Tibetan races of *D. corrugata* FRM., so I prefer to treat the Laotian form as another subspecies of the latter.

Described apparently from unique holotype; BAUDON (1966) reports two other specimens, collected also in Laos (Muong Panh) on *Pinus khasya* ROYLE. Like the remaining races, it occupies mountainous areas: Xieng-Khouang lies at 1000 m., Muong Panh at 1200 m. a.s.l. (BAUDON 1966).

Dicerca (s.str.) latouchei FRM.

Dicerca Latouchei FAIRMAIRE 1899

Material examined:

None

Characters:

"Long. 12 mill. - Oblonga, parum convexa, postice attenuata, tota aeneo-metallica, cupreo-mixta, sat nitida, glabra; capite brevi, densissime subtiliter ruguloso-punctulata, cupreo-micans, inter oculos plagulis 2 leviter convexis, minus rugosis et obscuro-aeneis, clypeo profunde et arcuatim emarginata, labro rugoso, cupreo; prothorace transverso, longitudine duplo latiore, antice a medio paulo angustato, fortiter punctato-rugoso, inaequali, medio canaliculato et cupreo, utrinque vitta convexa fusco-metallica, fere polita, lateribus late impressis et plagula polita fusco-metallica signatis, extus magis rugatis, margine postico medio reflexo, polito, utrinque minus, angulis rectis; scutello minuto, rotundato, medio impresso, obscuro; elytris oblongo-ovatis, ad humeros obtusis, postice vix sensim ampliatis, apice angustatis et subproductis, apice ipso truncato, leviter bispinoso, spina interna minutissima, sutura anguste elevata, utrinque costulis aliquot sat irregularibus, 1 fere integra sed post medium oblitterata, 2^a basi et post medium distincta, ceteris valde interruptis, intervallis valde punctato-rugosis, plagulis leviter virescentibus impressiusculis; subtus cum pedibus cuprea, nitida, rugosa, prosterno lato, cum meso- et metasterno medio paulo concavo et virescente, tarsis coeruleis." (FAIRMAIRE 1899).

Remarks:

Unknown to me in nature, and difficult to interpret from the description: it can as well be a close relative (or even a subspecies - perhaps identical to *D. c. vitalisi* D.V.) of *D. corrugata* FRM. [in describing the latter, FAIRMAIRE (1902) compared it to "*D. Delatouchii* F a i r m."] or *D. tibialis* LEW., as a completely different species of no apparent affinities.

Described from probably unique specimen of unknown sex, collected in south-eastern China: Amoy (map 22).

Tibialis-circle

Dicerca (s.str.) tibialis LEW.

Dicerca tibialis LEWIS 1893

Material examined:

Holotype: "Type" "Japan, G.Lewis, 1910-320" "Kashiwagi, 15.VI.-24.VI.81" "*Dicerca tibialis* Lewis Type" [♂ (NHM)]

Additional material: 2 ex.

Characters:

Male [1] 12×4.5, female [1] 12×5 mm. Body rather short, flattened. Depressed parts cupreous, reliefs bronzed-black. Head, pronotum and ventral side with rather

sparse but long, erect pubescence;. elytra glabrous. Front shallowly depressed along midline, covered with dense, longitudinally confluent punctures. Pronotum as wide at middle as at base, sides distinctly sinuate in basal half, then roundedly narrowed to prominent anterior angles; apical margin rather deeply, basal shallowly bisinuate, prescutellar lobe produced further back than acute hind angles; rather indistinct longitudinal median relief, pair of very prominent smooth elevations to both sides of it, pair of interrupted and less regular ridges still further outwards, and traces of yet another pair close to lateral margin, emerge from almost uniformly, coarsely and very densely punctured surface; oblique laterobasal depression deep and broad; prescutellar fovea deep, with pair of punctiform, narrowly separated pits on its bottom; lateral carina entire, strongly S-shaped, smooth in basal half but progressively less distinct before middle and almost obliterated anteriorly. Elytral costae smooth, disrupted into long sections, wide and convex suturally, very narrow and sharply carinate on sides; intercostal interstriae broad, flat, covered with coarse and very dense puncturation similar to that on pronotum. Anterior margin of prosternum straight; prosternal process coarsely but rather sparsely punctured, with smooth lateral rim; proepisterna covered with dense ocellate punctures; prosternum, metasternum and 1. sternite distinctly, rather narrowly sulcate along midline; median parts of metasternum very finely and sparsely, sides and abdomen coarsely and densely punctured; no distinct smooth reliefs on sternites; anal sternite emarginate at apex in male, rounded with minute denticle between pair of equally minute incisions in female. Male mesotibia with long spur at middle.

Remarks:

Small size, short and flat form, and well developed smooth elevations on pronotum and elytra, make this species easily distinguishable from its East-Asiatic congeners. Contrasting dorsal sculpture, straight anterior margin of prosternum, and coniferous host-plant suggest the affinity to sg. *Argante* GISTL, but long mesotibial spine of male places *D. tibialis* LEW. nevertheless in the nominotypic subgenus.

The area of distribution (fig. 22) includes Japan (Honshu, Shikoku, Kyushu); the species has also been recorded from "China" (AKIYAMA & OHMOMO 1997). Develops on *Abies firma*.

Unokichii-circle

Dicerca (s.str.) unokichii HRI.

Dicerca unokichii HATTORI 1991

Material examined:

Paratype: "Kukuang (1300 m.), Taichung-hsuen, (TAIWAN), 9. Sep. 1989., T. Hattori leg." "*Dicerca unokichii* HATTORI, 1991, DET. K. AKIYAMA, 1993" "PARATYPE" [1♂ (RBH: BPfk)]

Characters:

Male [1] 16×5.5 mm. Body very slender, brownish-black on relieved parts, brassy-green (dorsally) or cupreous (on head and underside) in punctures. White soft, semierect to erect pubescence appreciable only on ventral side. Front broadly depressed from side to side, covered with reticulate jumble of dense ocellate punctures and narrow anastomosing reliefs separating them; vertex occupying more than half of total width of head; eyes very prominent. Pronotum as wide at middle as at sharply acute hind angles, sides conspicuously sinuate in basal half and roundedly narrowed to distinctly bisinuate apex; pronotal punctures very coarse: on disc sparse and elongated, laterally very dense, confluent into groups, with network of irregular ridges between them; oblique laterobasal depression very irregular but rather deep and distinct; two dense rows of coarse elongated punctures, representing pair of perimedial sulci and separated at midlength by very inconspicuous smooth median relief, merge at basal (prescutellar fovea) and apical third; prescutellar pits well developed, narrowly separated; lateral carina, except at basal fifth, totally obliterated by coarse and dense puncturation. Six medial striae on elytra very coarse and prominent, lateral ones barely traceable; interstriae evenly convex; interstrial smooth "mirrors" less distinct medially (due to coarser and sparser surrounding puncturation) than on sides (where punctures are finer but very dense); costa separating disc from epipleura sparsely interrupted by very distinct dfp foveae, what makes lateral margin (especially on apical half) prominently denticulate; apices slightly caudate, tips sinuate between two denticles. Anterior margin of prosternum straight; prosternal process at middle coarsely and densely punctured, lateral rims wide, impunctate; proepisterna covered with coarse ocellate punctures within network of narrow smooth ridges; prosternum, metasternum and 1. sternite deeply sulcate along midline; median parts of metasternum finely and sparsely punctulated, punctures of abdomen coarse and much denser, sides covered with very densely arranged dfp foveolae encircled by anastomosing network of narrow elevated ridges; metacoxal dent almost right-angled but blunt, separated by deep incision from more medial part; sides of sternites with very irregular smooth reliefs; anal sternite in male broadly and deeply emarginate at apex. Male mesotibia (fig. 74) with very obtuse dentiform protuberance at basal $2/5$.

Remarks:

Narrow (narrower than in any other species of *Dicerca* ESCH. known to me) body with but slightly caudate elytra, very coarse (but in quite different way than in e.g. *D. corrugata* FRM.) sculpture, brassy-green colouration, &c. make *D. unokichii*

HRI. one of the most distinctive representatives of the genus. Phylogenetically it seems to be an offshoot of the lineage that eventually gave rise to the Palaearctic *D. alni* (F.-W.) - group, but morphologically it does not closely resemble any Eurasian species.

D. unokichii HRI. is the only representative of the genus occurring on Formosa (map 22).

Aenea-circle

Dicerca (s.str.) nishidai TMA.

Dicerca nishidai TÔYAMA 1986b

Material examined:

None

Characters:

Male [1] 21×7.5 mm. "Body large and robust"; "head and pronotum black distinctly tinged aeneo-aureous; elytra black, very sparsely and not uniformly inlaid with inconspicuous aeneo-aureous spots, each with two distinct aeneo-aureous markings, the small one near the side at the anterior third, and the large and transverse one between the fourth costa and the side at the posterior third; ventral surface entirely black with aeneo-aureous tinge; antennae and legs black". "Front ... coarsely and strongly rugose, sparsely clothed with long, inconspicuous, silver-whitish hairs". "Pronotum ... widest at base; sides arcuately expanded from anterior to posterior angles, ... very slightly sinuate near all the angles; anterior margin broadly and arcuately emarginate, ... posterior margin bisinuate, with median lobe arcuately produced; anterior angles subrectangular and produced in dorsal aspect; posterior angles slightly acute ...; marginal carinae absent; disc convex, with three, very shallow and longitudinal depressions at middle, two small and profound pores just before scutellum; surface rather densely punctated in the depressions, sparsely punctate in the areas along depressions, densely and coarsely punctate in the broad area along the sides". "Elytra ... sinuously and strongly convergent to the tips; apices slightly separated, each with an arcuate emargination between short spines; ... lateral margins unarmed ...; disc densely, strongly and longitudinally punctate, the punctures becoming denser towards the sides, and forming nine distinct longitudinal rows, longitudinally costate between the rows, the costae becoming more inconspicuous towards the sides, very sparsely clothed with silver-whitish hairs". "Ventral surface evenly and coarsely punctate, and rather sparsely clothed with fine, silver-whitish hairs. Prosternum ... with the anterior margin arcuately emarginate throughout; prosternal process ... longitudinally depressed at middle. Meetasternum with a distinct median groove. Abdomen with the first visible ventral segment shallowly depressed at middle, the anal one roundly emarginate at apex". "Middle tibia with a distinct tooth at the basal third" (TÔYAMA 1986b).

Remarks:

Unknown to me in nature. According to the colour photograph (pl. 1: fig. 2) in the original description, elytra are very strongly caudate, with sides not appreciably diverging but subparallel in apical tenth; interstriae rather strongly but evenly elevated, without distinguished costae (those mentioned in the original description mean simply convex interstriae); lateroapical margins seem coarsely crenulated; apices look relatively very wide; mesotibial denticle stout, cuneate (or laterally flattened, triangular). The species may be distantly related to *D. aenea* (L.), but is anyway highly distinctive.

Described from the unique holotype, collected in "Kusuki, Nakanoshima Is., Tokara, Kagoshima Pref.", Japan (map 22).

***Dicerca (s.str.) aenea* (L.)**
Buprestis aenea LINNAEUS 1761

This species - characterized by evenly sculptured (without distinct longitudinal bands or sulci) pronotum, short but distinctly caudate elytra, flat interstriae with but very inconspicuous "mirrors" &c. - is besides *D. furcata* (THB.) the widest distributed representative of the genus, reaching from Morocco and Portugal to the Sea of Japan (apparently with disjunction in Middle Siberia - map 21). On this vast area it shows some geographic variability: four subspecies of rather doubtful validity have been distinguished.

Key to subspecies of *D. (s.str.) aenea* (L.)

- a (d) Abdomen very sparsely and inconspicuously pubescent
- b (c) Pronotum relatively narrow (W:L<1.45). Colouration bright cupreous
..... [*D. (s.str.) a. bella* AB.]
- c (b) Pronotum wider (W:L>1.55). Colouration dull brown or brownish-black
..... [*D. (s.str.) a. aenea* (L.) s.str.]
- d (a) Abdomen very distinctly and rather densely pubescent
- e (f) Pronotum narrower (W:L<1.65) [*D. (s.str.) a. validiuscula* SEM.]
- f (e) Pronotum wider (W:L>1.65) *D. (s.str.) a. chinensis* OBB.

[*Dicerca (s. str.) aenea bella* AB.]
Dicerca aenea bella ABEILLE DE PERRIN 1891

Poorly known race occupying a restricted area in Syria and South Turkey.

[*Dicerca* (*s. str.*) *aenea* (L.) *s.str.*]

Buprestis aenea LINNAEUS 1761

Mordella cuprea SCOPOLI 1763

Buprestis austriaca SCHRANK 1781

Buprestis oxyptera PALLAS 1781

Buprestis reticulata FABRICIUS 1794

Buprestis subrugosa PAYKÜLL 1799

Buprestis carniolica FABRICIUS 1801

Dicerca scabrosa MANNERHEIM 1837

Western Palaearctic subspecies, distributed from Morocco to Altai.

[*Dicerca* (*s. str.*) *aenea validiuscula* SEM.]

Dicerca validiuscula SEMENOV 1895

Middle-Asian subspecies, occurring from Georgia and Armenia through North Persia, Turkmenia and Uzbekistan, to Kirghizia.

Dicerca (*s. str.*) *aenea chinensis* OBB.

Dicerca aenea chinensis OBENBERGER 1929

Material examined:

None

Characters:

Length 17-22 mm. [RICHTER 1952]. Brown to brownish-black, ventral surface cupreous. White soft pubescence semirecumbent abd very conspicuous on head and undersurface, recumbent and shorter but still distinct on pronotum and elytra. Front shallowly and indistinctly depressed along midline, covered with coarse and very dense confluent punctures. Pronotum widest at middle, hind angles sharply acute, sides conspicuously sinuate in basal half and roundedly narrowed to distinctly bisinuate apex; oblique laterobasal depression very broad, deep and distinct; no trace of longitudinal smooth bands or depressed sulci; prescutellar pits transverse, deep, very narrowly separated; pronotal punctures coarse, moderately dense on disc, very dense and confluent at sides; lateral carina entire but densely punctured and blunt. Elytral striae traceable throughout, but rather indistinct in coarse and dense puncturation of anterolateral parts; interstriae flat, with but few and hardly discernible smooth "mirrors"; costa separating disc from epipleura totally obliterated, epipleura convex, with dense row of small dfp foveae, making lateroapical margin of elytra serrulate in dorsal aspect; apices distinctly caudate, tips sinuate between two denticles. Anterior margin of prosternum very shallowly, almost inappreciably emarginate; prosternal process coarsely and rather densely punctured at middle, lateral rims impunctate; proepisterna covered with coarse, very irregular, dense ocellate punctures within network of narrow smooth ridges; prosternum, metasternum and 1. sternite deeply sulcate along midline; median parts of metasternum finely, sides very densely and irregularly punctured; metacoxal dent nearly right-angled, but broadly rounded at tip; punctures of 1.-4. abdominal segments coarse, very dense and irregularly confluent on sides, sparser and elongated at middle; anal segment covered with dense,

coarse, elongate punctures throughout, apex in male broadly and rather shallowly emarginate, in female truncate with pair of small but deep notches. Male mesotibia with very broad obtuse dent at basal third.

Remarks:

This race occupies the eastern part (map 21) of the species area: southern part of East Siberia and North China (to the vicinities of Pekin).

***Poecilonota* ESCH.**

Poecilonota ESCHSCHOLTZ 1829

= *Descarpentriesina* LERAUT 1983

Type-species: *Buprestis conspersa* GYLLENHAL 1801

[= *Buprestis variolosa* PAYKÖLL 1799]

General characteristics:

Mostly holarctic genus (map 25), including eight (EVANS 1957, BRIGHT 1987) species in North America and three (one of them highly polytypic) in Eurasia - all of the latter occur in the study area. In the general appearance (colouration, sculpture, shape of pronotum and elytra, &c.) the representatives of this genus resemble species of *Dicerca* ESCH., differing from them principally in transverse scutellum, well developed smooth median ridge on pronotum, simple median incision of anal sternite in female, and lack of mesotibial modifications in male; from *Ovalisia* KERR. it can be distinguished by the combination of distinctly caudate elytra, sharply defined smooth median carina on pronotum, very wide scutellum, and - at least in the area of sympatry - colouration (all species of the latter genus occurring North of the Isthmus of Kra are bright green or - rarely - cupreous).

Phylogenetic relations:

In good agreement with current concepts and intuitive assessment, *Poecilonota* ESCH. consistently appears on the cladograms (fig. 1, 13, 14, 15) as a close relative of *Dicerca* ESCH. and *Scintillatrix* OBB. General distribution of the genus is similar to that of *Dicerca* ESCH., but history of its development seems different: while various lineages of *Dicerca* ESCH. have crossed the Bering Strait several times in both directions, making the picture rather obscure and the sequence of events very difficult to disentangle, the evolution of *Poecilonota* ESCH. (fig. 13) has apparently been centered throughout in Nearctis, with Eurasian members making only one well defined, holophyletic group: a single superspecies. The analysis of the American branches is beyond the scope of this paper, thence only few species representing various morphological tendencies were considered, and I will not discuss this matter any further. There is also not very much to say about the Palaearctic lineage: its ancestor [common, as it seems, with the Nearctic *P. thureura* (SAY) - *P. salicis* CHAMB. clade] has probably crossed Beringia at the beginning (when the "bridge" was already sufficiently warm but yet subaerial) of the last-but-one interglaciation (Mindel-Riss - the timing is of course only tentative, the more so that according to the

present knowledge the "traditional" four glacials and interglacials were in fact further subdivided into up to 30 alternate cold and warm phases), dispersed over the East Siberia, and then displaced by advancing glaciation southwards, where it survived in three [Sinotibetan, Mandjurian and Japanese according to DE LATTIN's (1967) scheme] refugia and there differentiated into - respectively - *P. semenovi* OBB., *P. variolosa* (PK.) and *P. yanoi* KUR.; the former and the latter remained "stationary", but *P. variolosa* (PK.) used the next interglacial to expand all-over the Eurasian temperate forest zone; the last glacial pushed it again southwards, where the isolated populations further differentiated to become the modern *P. v. populialbae* RICH. (Atlantomediterranean refugium), *P. variolosa* (PK.) s.str. (?Pontomediterranean?), *P. v. dicercoides* RTT. (?Mongolian?) and *P. v. chinensis* THY. (Mandjurian); postglacial dispersal has led to the presently observed distribution.

Sg. *Poecilonota* ESCH.

Poecilonota ESCHSCHOLTZ 1829
= *Descarpentriesina* LERAUT 1983

Type-species: *Buprestis conspersa* GYLLENHAL 1801
[= *Buprestis variolosa* PAYKÜLL 1799]

Key to the Indo-Pacific species of the subgenus *Poecilonota* ESCH.

- 1 (4) Elytral interstriae of equal width
- 2 (3) 1. sternite distinctly sulcate *P. variolosa* (PK.)
- 3 (2) 1. sternite without median sulcus *P. semenovi* OBB.
- 4 (1) 2., 4., and 6. elytral interstria twice narrower than others, not wider than striae *P. yanoi* KUR.

***Variolosa*-circle**

***Poecilonota variolosa* (PK.)**
Buprestis variolosa PAYKÜLL 1799

Very widely - from Morocco and France, through Europe and Siberia, to Japan and Southern China (map 26) - distributed species of considerable geographical variability: five subspecies have been distinguished, two of them occurring in the area under study:

Key to subspecies of *Poecilonota variolosa* (PK.)

- a (f) Sides of pronotum broadly rounded at middle
- b (e) Dfp spots on elytra irregularly distributed, more or less confluent into larger patches
- c (d) Apical denticles on elytra longer, sharp; body more lustrous; dorsal dfp areas bright cupreous [*P. v. populialbae* RICH.]
- d (c) Denticles of elytral apex very short, indistinct; body less shining; dfp areas on dorsal side duller, cupreous-bronzed [*P. v. variolosa* (PK.) s.str.]
- e (b) Elytral dfp spots uniformly distributed, not confluent into patches; prosternal process more densely pubescent [*P. v. dicercoides* RTT.]
- f (a) Sides of pronotum angular, almost straightly convergent towards apex and towards base .
..... *P. v. chinensis* THY.

[*Poecilonota variolosa populialbae* RICH.]

Poecilonota Conspersa var. *P. albae* RICHARD 1889

African (Morocco, Algeria, Tunisia) race inhabiting also southern Spain (COBOS 1986).

[*Poecilonota variolosa* (PK.) s.str.]

Buprestis variolosa PAYKÜLL 1799

= *Buprestis plebeia* HERBST 1801

= *Buprestis conspersa* GYLLENHAL 1808

= *Poecilonota tremulae* ABEILLE DE PERRIN 1896

= *Poecilonota setulosa* FLEISCHER 1896

Western Palaearctic subspecies, distributed from northern Spain to East Siberia (Yakoutia).

[*Poecilonota variolosa dicercoides* RTT.]

Poecilonota dicercoides REITTER 1888

Southern part of East Siberia, Manchouria; as a result of poor morphological differentiation from the nominotypic race, western limits of the distribution of this subspecies remain unclear: e.g. OBENBERGER (1930) includes here all the southern-Siberian and even Transcaucasian populations, while RICHTER (1952) leaves only those from the easternmost area (Amur distr., southern part of Chabarovsk distr., Maritime Prov.).

Poecilonota variolosa chinensis THY.

Poecilonota chinensis THÉRY 1926

? = *Poecilonota cupreomaculata* MIWA et CHŪJŌ 1935

Material examined:

1♂

Characters:

Male [1] 13.5×5.5 mm. (male/female 15×6.5 mm. - THÉRY 1926). Brownish-black with cupreous punctures and most part of undersurface. Soft whitish pubescence distinct on head and ventral side (very long and dense on median parts of sternum in

male), inconspicuous on pronotum and elytra. Front broadly depressed along midline, coarsely and densely punctured with some small elevated smooth reliefs. Pronotum (fig. 54) widest at middle, where straight posterior and anterior sections of lateral margin meet at obtuse (*ca* 130°) but very well marked angle; apical margin very shallowly emarginate, apical angles not prominent; base bisinuate, prescutellar lobe produced further back than right or slightly obtuse hind angles; oblique depression directed from middle of base to anterior third of sides (but not reaching either) shallow, inconspicuous; median carina smooth, narrow, somewhat ill-defined; some irregular, slightly elevated and sparser punctured spaces and narrow anastomosing ridges on sides of disc; otherwise puncturation coarse and very dense; lateral carina entire, apical section densely punctured, basally sharp and smooth. Elytral striae (fig. 62) rather coarse, distinct throughout; interstriae convex, disrupted with numerous dfp spots which frequently join together to form irregular transverse patches; costa separating disc from epipleura with very small dfp foveae, thence lateroapical margin of elytra finely but distinctly serrulate; apices distinctly caudate, tips truncate with barely appreciable sutural and lateral denticles. Anterior margin of prosternum very shallowly emarginate; smooth lateral rims of prosternal process very narrow, separated from coarsely and rather densely punctured middle with distinct stria; proepisterna covered with coarse and dense ocellate punctures; prosternum and metasternum broadly and deeply depressed along midline, depression on 1. sternite only anteriorly marked; puncturation of ventral side rather dense on sides, less so on median parts; metacoxal dent small, obtuse, blunt, inconspicuous; apex of anal segment in male broadly arcuately emarginate, in female "échancrure du dernier segment abdominal ... faible" (THÉRY 1926).

Remarks:

As noticed by THÉRY (1926), 3. antennomere (fig. 50) in *P. v. chinensis* THY. is but slightly longer than 2. (and much shorter than 4.), while it is *ca.* twice longer than 2. and subequal to 4. in Eurosiberian races. *P. cupreomaculata* M.C. remains unknown to me; it was described as separate species and then variously treated as a synonym (KUROSAWA 1962; also A. DESCARPENTRIES determined the type-specimen as "*P. chinensis* Thery = *cupreomaculata* Miwa et Chûjô" - CHÛJÔ & CHÛJÔ 1998) or subspecies (KUROSAWA 1970, AKIYAMA & OHMOMO 1997) of *P. v. chinensis* THY. [traditionally considered by these authors to be specifically different from *P. variolosa* (PK.)]. *P. cupreomaculata* M.C. has been described from Hokkaido (Sapporo), and then reported from northern Honshu; the "nominotypic" *P. chinensis* THY. (map 26), described from Pekin, is said to occur in N-China, Korea, and "Far East of Russia" (AKIYAMA & OHMOMO 1997 - but neither RICHTER 1952 nor ALEXEEV 1989 mention its occurrence in the former Soviet Union).

***Poecilonota semenovi* OBB.**

Poecilonota semenovi OBENBERGER 1934

Material examined:

1♀

Characters:

Male 13.2×5.3 mm. (OBENBERGER 1934); female [1] 12.5×5 mm. Front with conspicuous elevated reliefs. Pronotum widest at anterior third; median carina is wide, regular, finely furrowed along midline; anterior margin deeply, bisinuate emarginate, with protruding apical angles; scutellum very wide (fig. 56). Elytra strongly caudate; interstriae very convex, cariniform; anterior margin of prosternum almost straight; prosternal process flat. 3. antennomere, like in *P. v. chinensis* THY., relatively short. Lateroapical margin of elytra with long, semierect, white setae. Incision of anal sternite broadly arcuately emarginate in male (OBENBERGER 1934), more deeply but narrowly so in female.

Remarks:

Having only one specimen in my disposition, I cannot say whether long pubescence on apical half of elytral margin is a character of taxonomic importance or merely an individual (?sexual) variant, but other [sub]species of *Poecilonota* ESCH. available to me for study show there at most very short, hardly appreciable setulae. *P. semenovi* OBB. was described from apparently unique holotype collected in southern China (prov. Fukien: Kiulung), and I am not aware of any other published record; the specimen before me (UN: 2344) is labelled: "CHINA - YUNNAN, ZONGDIAN, 17.6.-19.6.1995, E. KUČERA leg." (map 26).

***Poecilonota yanoi* KUR.**

Poecilonota yanoi KUROSAWA 1962

Material examined:

1♂

Characters:

Male [1] 13.5×5 mm. (holotype: 12.8×6 mm. - KUROSAWA 1962); female, to my knowledge, has not yet been described. Brownish-black with undersurface and depressed, densely punctured areas on dorsal side bright copperous. Pubescence whitish, sparse on head, long and very dense on prosternal process, virtually none otherwise. Front shallowly depressed, very densely punctured, vertex with distinct medial carina. 1. antennomere (fig. 51) twice longer than 2. Pronotum (fig. 55) widest at middle, sides slightly roundedly convergent to base and shallowly sinuate so to apex; apical margin very shallowly bisinuate, apical angles not prominent; basal angles right, somewhat protruding; prescutellar lobe at middle with smooth, transversely trapezoidal protruding process, "pushing" scutellum somewhat backwards; oblique lateromedian depression hardly appreciable; median carina smooth, well defined slightly widened at middle; sides of disc with some irregular,

slightly elevated and sparser punctured spaces; otherwise puncturation coarse and very dense (leaving but very narrow carinulae to separate punctures from one another; lateral carina entire but only just before base smooth. Elytral striae (fig. 63) very coarse, continuous, distinct throughout; interstriae convex, uneven: 2., 4., 6., and 10. very narrow, remaining at least twice wider; dfp spaces as a rule developed only on wide intervals; lateroapical margin very finely serrulate due to punctures and dfp foveolae on discoepipleural costa; apices slightly caudate, tips shallowly and somewhat obliquely between obtuse lateral and acute sutural angles. Anterior margin of prosternum straight; prosternal process flat, rather densely punctured; smooth lateral rims narrow, sharply delimited but without distinct bordering stria; proepisterna covered with coarse but rather sparse ocellate punctures; metasternum medially sulcate, 1. sternite regularly convex; abdominal puncturation coarse and moderately dense, elongate medially, somewhat denser and isodiametric on sides; metacoxa with no appreciable dent; apex of anal segment deeply arcuately emarginate.

Remarks:

P. yanoi KUR. was described as distinct species, but later (KUROSAWA 1970) considered by its author a subspecies of *P. chinensis* THY.; in my opinion, very special structure of elytral interstriae, together with other differences (rounded pronotal sides, flat prosternal process, &c.), strongly supports the originally attributed status. Known from southern Honshu (map 26): the type-locality is Mie Pref., the specimen studied by me comes from Okayama Pref.

Ovalisia KERR.

Ovalisia KERREMANS 1900

General characteristics:

The second largest genus of the **Psilopterina** LAC., containing some 70 species widely (map 27) distributed throughout the Palaearctic (ca. 15 sp.) and Indo-Pacific (ca. 55 sp.) Regions. For the reasons mentioned in the introduction, *Ovalisia* KERR. will be considered in this work only at the generic/subgeneric level. Three traditionally recognized subgenera - *Ovalisia* KERR. s. str., *Palmar* SCHF., and *Scintillatrix* OBB. - have often been considered distinct genera, but the differences between them (mainly the pattern of colouration) are rather trivial; indeed, even the separation of *Ovalisia* KERR. from *Poecilonota* ESCH. at more than subgeneric level may not be easy to defend on purely morphological grounds (but see the results of phylogenetic analysis below!). On the other hand, some Indo-Pacific species do not naturally fit in any of the above-mentioned taxa, so ZYKOV (1998) established the new taxon (genus in his interpretation) *Erialata* ZYK. for *O. auripilis* (OBB.), and I feel necessary to erect further four subgenera.

Phylogenetic relations:

The distinction between *Scintillatrix* OBB. and the remainder of *Ovalisia* KERR. s.l. has been much debated since long time, but the point in question was only the rank

of the taxa (the majority has treated them as subgenera, but some students prefer to speak of "full" genera, while several others deny their taxonomic validity whatsoever), not their affinity. On the other hand, close systematic - and, implicitly, phylogenetic - relationships between these taxa and *Poecilonota* ESCH. (as well as between *Poecilonota* ESCH. and *Dicerca* ESCH.) have also never been seriously questioned. So, wide separation between *Scintillatrix* OBB. (together with *Poecilonota* ESCH. and *Dicerca* ESCH.) and *Ovalisia* KERR. on the intergeneric cladogram of the **Psilopterina** LAC. (fig. 1) - at least not incompatible with the trees obtained for *Poecilonota* ESCH. (fig. 13), for subgenera of *Ovalisia* KERR. (fig 15) and for sg. *Palmar* SCHF. (fig. 16) - is certainly one of the most intriguing feature of these reconstructions. Of course, due to the - already mentioned at several occasions - present state of development of both the applied procedure (MICSEQ) and phylogenetic study of the **Psilopterina** LAC., these results must not be taken as decisive, but two facts suggest that they could not be outright disregarded, either. Firstly, the separation between *Scintillatrix* OBB. and the remaining subtaxa of *Ovalisia* KERR. s.l. was very distinct throughout the analysis: already in the initial distance-matrix the distance between *Scintillatrix* OBB. and *Poecilonota* ESCH. was 50, while that between *Scintillatrix* OBB. and the closest member of the *Ovalisia* KERR.-group (*Cinyrisia* sg.n.) amounted to more than 1.5 times as much (76); the distance separating the ancestor of the *Dicerca/Poecilonota/Scintillatrix*-complex from that of *Ovalisia* KERR. did not so greatly exceed the distance between the former and ancestor of the *Psiloptera* DEJ.-group [sister-lineages according to the cladogram], but the difference (75 vs. 64) was nevertheless considerable, so that the degree of support for the "unorthodox" arrangement seems relatively strong. Secondly, the so "truncated" *Ovalisia* KERR. appeared at the very base of the tree, as the sister-group of all the remaining **Psilopterina** LAC. (including the **Pseudoperotina** TMA., **Hypoprasina** HOŁ. and **Chalcophorina** LAC.!), what may suggest that it does not belong to this subtribe at all. This gives a new meaning to the recent (BÍLÝ 1997) synonymization of *Pagdeniella* THY. (traditionally considered close to *Philanthaxia* DEYR. and classified in the composite "tribe **Buprestini** LEACH"; included by me - HOŁYŃSKI 1993b - in the subtribe **Bubastina** OBB. of **Anthaxiini** C.G.) with *Ovalisia* KERR.: may be the "diceroid/psilopteroid" features of these taxa are only convergent, superficial similarities, and *Ovalisia* KERR. is in fact a member (or close relative) of the **Bubastina** OBB.? The question is certainly worth exploration, the more so that BÍLÝ (1997) apparently based his conclusion solely on the obvious affinity of what was known as *Pagdeniella* THY. to *Ovalisia* KERR. s.str. and *Palmar* SCHF., but has not mentioned any difference which would substantiate its removal from the **Bubastina** OBB.

As to the relations within the *Ovalisia* KERR. - complex, the monophyly of the subgenera is well supported, but the *intersubgeneric* affinities vary considerably between cladograms. Closer examination shows, however, that the inconsistencies concern almost exclusively two taxa: nominotypical *Ovalisia* KERR. s.str. and *Poecilisia* sg.n.: the former sometimes appears as the basalmost branch in the complex (figs. 1, 16) and sometimes at the "top" of the clade as the sister-group of *Palmar*

SCHF. (fig. 15); the latter "travels" between the sister position to *Palmar SCHF.* (fig. 16) and that of *Scintillatrix OBB.* (fig. 13), occupying "by the way" various intermediate (fig. 15) or ambiguous (fig. 14) sites. Certainly further research is needed to clarify the phylogenetic affinities of these taxa.

Recently ZYKOV (1998), discovered three hitherto unnoticed characters to distinguish *Ovalisia KERR. s.str.* from the remaining subgenera, and proposed to consider it as a "full" genus (like his simultaneously erected *Erialata ZYK.*), separate from *Palmar SCHF.* (in his interpretation a complex of all the remaining groups, including *Scintillatrix OBB.*), and comprising - besides the type-species, *O. auricollis (DEYR.)* - also *O. jakobsoni (OBB.)*. His assessment of the taxonomic importance of these "stable diagnostic characters" is evidently exaggerated [they occur - not always congruently: e.g. in *O. semperi (SND.)* or *O. siamensis D.V.* the structure of mandibulae and labrum agree with those in *Ovalisia KERR. sensu ZYKOV*, but elytral sculpture is "normally" rugosopunctate] in several species unquestionably (according to all other features) belonging to *Palmar SCHF.* and showing very little in common with the genuine *Ovalisia KERR. s.str.* [good example is just *O. jakobsoni (OBB.)* - very close to, or perhaps synonymous with, well-known *O. leoparda (DEYR.)*]; thence, my classificatory conclusions are different: I prefer to consider the respective species as two subgenera of *Ovalisia KERR. s.l.* (see below) rather than one separate genus. However, the characters used by ZYKOV (1998) are mostly (even if not strictly) correlated to one another (and to some other features, e.g. shape of 4.-5. antennal joints) and almost certainly homologous, what makes them useful in phylogenetic reconstructions. Unfortunately, ZYKOV's (1998) paper appeared (or, at least, came to my attention) too late to include these characters in the analysis by MICSEQ, but they evidently point to close affinity of *Palmar SCHF. (s.str.)*, through *Zykovisia sg.n.*, to *Ovalisia KERR. s.str.*, supporting the phylogenetic pattern (and, thence, the resulting reconstruction of the common ancestor) like that on the cladogram for *Ovalisia KERR.* (fig. 15) rather than that for **Psilopterina LAC.** in general (fig. 1), and - as a consequence - weakening the case for wide separation between *Ovalisia KERR. s.l.* and the *Scintillatrix/Poecilnota/Dicerca*-complex.

Key to the subgenera of *Ovalisia KERR.*

- 1 (2) Elytral interstriae with numerous small (not extending to neighbour interstriae), irregularly distributed, smooth, blackish rectangular spots ("mirrors" - fig. 28); body green, usually with reddish-cupreous lateral band .
..... *Scintillatrix OBB.*
- 2 (1) Elytra with larger, not confined to one interstria, symmetrically distributed patches (fig. 30) or without any; if patches irregular (fig. 29), then colouration bronzed or brown
- 3 (6) Dorsal and at least lateral parts of ventral side uniformly (except for blackish spots) bronzed; if median parts of ventral side green, then scutellum scarcely wider than long and anal sternite with long, sharply carinate lateroapical spines

- 4 (5) Scutellum at least twice wider than long, trapezoidal, with acute lateroposterior angles; lateral denticles of apex of anal sternite short and not carinate *Poecilisia* *sg.n.*
- 5 (4) Scutellum less than twice wider than long, cordiform, with roundedly obliterated lateroposterior angles; apex of anal sternite with pair of long, sharply carinate spines, carinae extend to at least apical fourth of sternite (fig. 71) *Cinyrisia* *sg.n.*
- 6 (3) Ventral side predominantly bright cupreous, green, or blue; if dorsal side bronzed, then scutellum much wider than long. Spines of anal sternite (if present) short and not carinate (fig. 72)
- 7(10) Elytra conspicuously pubescent; elytral apices sharply tridenticulate (fig. 60)
- 8 (9) Lower half of front broadly depressed between long, strongly elevated supraantennal carinae (fig. 49). Elytral pubescence sparse. Prosternal process very sparsely punctured, striatomarginate. Apex of anal sternite with prominent median lobe, separated from lateral denticles by deep incisions. 6.-10. antennomeres not much wider than long (fig. 49c)
..... *Mabomisia* *sg.n.*
- 9 (8) Front anteriorly narrowly depressed along midline, supraantennal carinae short and inconspicuous (fig. 48a). Elytral surface concealed by very dense pubescence. Prosternal process densely punctured, without bordering striae. Apex of anal sternite without distinct median lobe, rectangularly emarginate. Antennal joints *ca.* 2.5× wider than long (fig. 48c)
..... *Erialata* *ZYK.*
- 10 (7) Elytra glabrous or but very indistinctly pubescent; apices rounded or with blunt, indistinct denticles (fig. 61)
- 11(12) Outer margins of mandibles regularly rounded. Labrum not divided, with nearly straight anterior margin *Palmar* *SCHF.*
- 12(11) Outer margins of mandibles sharply angular. Labrum divided by transverse ridge or furrow, its anterior portion semicircular or triangular
- 13(14) Elytra green or cupreous (very rarely bronzed) with several relatively small bluish-black spots *Zykovisia* *sg.n.*
- 14(13) Elytra without dark spots, uniformly dark blue or violet, or with large oval patch of this colour along suture *Ovalisia* *KERR. s.str.*

Sg. *Scintillatrix* OBB.

Scintillatrix OBENBERGER 1956

Type-species: *Buprestis rutilans* FABRICIUS 1777

Fig. 28. Very homogeneous group (in fact, a single circle), containing some 25, mainly palaeartic (map 27) species. Besides the "diceroid" (in fact, even better developed in, and more characteristic of, *Scintillatrix* OBB. than *Dicerca* ESCH.) pattern of small rectangular dark "mirrors" on elytral interstriae there is little to distinguish this subgenus from *Palmar* SCHF., but this pattern is so peculiar and stable feature of the "*Rutilans*-circle" that the warrantness of its separation at the subgeneric level has seldom been questioned. Pronotum in *Scintillatrix* OBB. is usually

ornamented with smooth, dark median ridge and some more or less irregular reliefs; elytral apex rounded or truncated with several denticles (sometimes suggesting tridentate condition, but the denticles are never sharp and prominent); prosternal process sometimes densely punctured, sometimes almost smooth, bordered with distinct lateral furrows, in males often covered with conspicuously long and dense pubescence; apex of anal sternite bi- or (rarely) quadridentate, denticles in some species prolonged into (not carinate) spines, in others almost obliterated. Species of this subgenus develop on various deciduous trees (*Ulmus*, *Alnus*, *Tilia*, *Betula*, &c.).

Sg. *Poecilisia* sg. n.

Type-species: *Poecilonota nigrofasciata* SAUNDERS 1867

Fig. 29. Small group including - besides the type-species described from Penang - only two others known to me: Bornean *O. gebhardti* (OBB.) and Malaccan *O. apicalis* (DEYR.) (map 27). The subgenus is well characterized by the combination of dark-bronzed colouration; irregularly distributed - but confluent into patches or fasciae extending onto several interstriae - dark spots on elytra; transverse, sharp-angled scutellum; tridenticulate (with median denticle usually blunt or obliterated) elytral apex; densely punctured prosternal process with no distinct marginal stria; lateroapical denticles of anal sternite short, without carinulae.

Sg. *Cinyrisia* sg. n.

Type-species: *Poecilonota psilopteroides* DEYROLLE 1864

Another small subgenus, distributed on Sumatra, Malay Peninsula and Borneo (map 27). Here belong, as far as I can establish now, three species: *O. psilopteroides* (DEYR.), *O. aenea* (DEYR.), and *O. pantherina* (DEYR.) [*O. subornata* (OBB.) seems to be identical with the latter]; judging from the descriptions, *O. perakensis* (FISH.) and *O. pendleburyi* (FISH.) should also be placed in *Cinyrisia* sg. n. Long carinate apical spines of the anal sternite are the best distinguishing feature of this taxon, but the combination of bronzed colouration, small irregular dark (but usually not contrasting, brown rather than bluish-black) elytral spots, broad supraepistomal depression (between prominent, reaching far upwards supraantennal carinae and transversely triangular relief at middle of front), scutellum at most twice wider than long, its lateroposterior angles blunt or fully obliterated, &c., also substantially contributes to its distinctiveness.

Sg. *Mabomisia* sg. n.

Type-species: *Chalcophora (Evides) sex-spinosa* THOMSON 1857

Monotypic Bornean (map 27) subgenus, characterized by distinctive colouration (pronotum and elytra cupreous-bronzed with four small dark spots on each elytron; head, anterior angles and narrow apical margin of pronotum, and ventral side green),

long and highly elevated supraantennal carina, conspicuously angular sides of pronotum, blunt-angled scutellum, sharply tridentate elytral apex, laterally furrowed prosternal process with sparsely punctured median part, and tripartite apex of anal sternite with broad median lobe and sharp lateral denticles.

Sg. *Erialata* ZYK.

Erialata ZYKOV 1998

Type-species: *Lampra auripilis* OBENBERGER 1922

This subgenus - containing Bornean *O. auripilis* (OBB.) and Malayan *O. pubescens* (FISH.) (map 27) - is very well characterized by its strikingly wide antennal joints and dense orange pubescence covering elytra and (though somewhat less densely) pronotum. Body dorsally golden, ventrally green; pronotum with 2 - 5, each elytron with 5 dark spots; supraantennal ridges not prominent; vertex occupies much less than $\frac{1}{3}$ of total width of head; sides of pronotum rounded at middle; elytral apices tridentate; prosternal process densely punctured, without lateral striae; apex of anal sternite with broad rectangular emargination between short but sharply spinose denticles; femora longitudinally furrowed on inner surface.

Sg. *Palmar* SCHF.

Palmar SCHAEFER 1949

= *Lampra* DEJEAN 1833 [nec HÜBNER 1821]

Type-species: *Buprestis festiva* LINNAEUS 1758

Figs. 24, 30. Largest (ca. 35 species), variable group, widely distributed in the Indo-Pacific Region - only two [or four if *O. holzschuhi* (HELLR.) and *O. cretica* (ZABR.) are truly separable at the species level - what seems doubtful: apparently none of the characters quoted by ZABRANSKY (1994) does exceed the limits of variability of *O. festiva* (L.)] species inhabit western (Mediterranean countries) and other two reach the peripheries (Japan, N-China, southeasternmost Siberia) of eastern Palaearctis. Colouration predominantly green or bright cupreous, only exceptionally dorsal side bronzed; elytra (and usually also pronotum) with regularly, symmetrically arranged [bluish-]black spots; elytral apices rounded or truncated, sometimes bluntly and indistinctly tridenticulate; otherwise rather variable. Some species develop on deciduous (*Quercus*, *Malus*), some others on coniferous (*Chamaecyparis*, *Cryptomeria*, *Juniperus*) trees, but the biology of the majority remains unknown.

Sg. *Zykovisia* s.g.n.

Type-species: *Lampra Jacobsoni* OBENBERGER 1926a

Poorly known group, distributed - as far as currently known - from Sumatra [*O. jacobsoni* (OBB.)] and Borneo [*O. leoparda* (DEYR.)] to Siam [*O. siamensis* D.V.] and Philippines [*O. semperi* (SND.)], but probably several other species, not represented in my collection and consequently not available now to me for checking the diagnostic

characters, also belong here. Superficially not differing from *Palmar* SCHF., but the structure of mandibulae, labrum, and usually also antennae and elytra, are characteristic rather of *Ovalisia* Kerr. s.str.

Sg. *Ovalisia* KERR. s.str.

Ovalisia KERREMANS 1900

= *Pagdenia* THÉRY 1934 [nec MILLER 1934]

= *Pagdeniella* THÉRY 1935a

Type-species: *Ovalisia insularis* KERREMANS 1900

?= *Poecilonota auricollis* DEYROLLE 1864

Southeasternmost (Morotai in Moluques, Aru, New Guinea, Solomon Is.) subgenus, comprising 5 [or 6, if the synonymy of Solomonese *O. insularis* KERR. with Moluccan *O. auricollis* (DEYR.) is false] rare and poorly known species. The identity of *Ovalisia* KERR. and *Pagdeniella* THY. has been established only recently (BÍLÝ 1997), until this time the latter was considered to belong to different tribe [Buprestini LEACH or - according to my (HOLYŃSKI 1993b) classification - Anthaxiini C.G.]. *Ovalisia* KERR. most conspicuously differs from *Zykovisia* sg.n. and *Palmar* SCHF. in non-spotted pattern of colouration, and from the latter also in sharply angular outer margin of mandibulae, transversely divided labrum with semicircular anterior margin, antenna distinctly serrate only from 5. joint, and granulated lateral interstriae of elytra.

CONCLUSIONS

Three basic factors determine the course and results of a scientific study: the object, theoretical premises, and methods - in the case of this work all of them contain a significant element of novelty or at least unorthodoxy: the Indo-Pacific **Psilopterina** LAC. have never been the target of special, comprehensive study; my taxonomic, zoogeographic, evolutionary concepts are frequently different from those accepted by the majority of my colleagues; newly invented procedure of phylogenetic analysis was being developed and improved simultaneously with the progress of research. In such situation the risk of error is inevitably rather great, the conclusions must be taken with special caution, but the reward - increased likelihood of obtaining truly interesting, original results, discovering unexpected facts or phenomena - is worth this price. In the following I try to evaluate the adopted concepts and procedures in the light of the obtained results, and main results in relation to conceptual and methodological premises.

THE OBJECT

The starting assumptions justifying the choice and delimitation of the object of this work were: (a) that the Indo-Pacific **Psilopterina** LAC. represent few natural, monophyletic (though not necessarily strictly holophyletic) groups plus some phylogenetically independent peripheral invaders; (b) that the subtribe as currently (HOLYŃSKI 1993b) conceived is monophyletic as well; and (c) that *Ovalisia* KERR. s.l.

is one of holophyletic terminal clades (and thence its - coerced by the inaccessibility of important material - more superficial treatment should not distort the conclusions concerning other taxa).

(a). At the end of the work, this point seems fully confirmed: even though the subgenus *Spinthoptera* CSY. as a whole is almost certainly an unnatural assemblage of not directly related lineages, its Indo-Pacific representatives (with possible exception of *P. comottoi* LSB.) make a well defined, monophyletic (even if apparently not holophyletic: with some offshoots "sent" to the Mediterranean and America) group; the *Dicercomorpha/Tristria/Touzalina*-complex, *Archepsila* g.n., *Dicerca corrugata/tibialis/amphibia/furcata*, *D. aenea/nishidai/unokichii*, *Poecilonota variolosa*-superspecies, and *Ovalisia* KERR. (without *Scintillatrix* OBB.) form other monophyla, while few "strangers" of extralimital affinities (*Cyphonota turcomanicum* (Kr.), *Capnodis* spp., *Dicerca moesta* (F.), and *Scintillatrix* spp.) enter but peripheries of the studied area.

(b). Two unexpected features of the cladogram of the **Psilopterina** LAC. (fig. 1) may influence the definition and content of this subtribe: the "deeply ingroup" position of the **Chalcophorina/Hypoprasina/Pseudoperotina**-lineage would - if confirmed - render the **Psilopterina** LAC. paraphyletic and thence unacceptable for strictly cladistic classifications, whereas the appearance of *Ovalisia* KERR. (without *Scintillatrix* OBB.) as the basalmost branch reinforces the suggestion of its affinity to the **Anthaxiini** C.G.: **Bubastina** OBB. rather than to the **Buprestini** LEACH: **Psilopterina** LAC.

(c). At the starting-point of this study I - like all my predecessors - "took for granted" that *Ovalisia* KERR. s.l. is holophyletic and represents one of the "uppermost" twigs on the phylogenetic tree of the **Psilopterina** LAC. The results of analysis - though not fully congruent - suggest that both assumptions may be wrong: *Scintillatrix* OBB. is perhaps a separate, not even closely related genus, and the "extralimital" affinities of the remainder seem a real possibility too. Fortunately, also in such arrangement the omission of *Ovalisia* KERR. and *Scintillatrix* OBB. from the detailed consideration at specific level is unlikely to have confused other results.

THE PREMISES

I have applied in this work some "unorthodox" concepts (not always, strictly speaking, theoretical: e.g. the category of circle or working definition of species are rather but practical solutions, facilitating discussion and enabling more exact presentation of the taxonomic conclusions), which might have influenced the results of study and have themselves been tested against them; some of them are widely known but currently out of vogue, some others were introduced by me in earlier publications, but have not [yet?] been widely accepted by other workers, and some are published for the first time.

"Working definition" of species

Many years ago (HOLYŃSKI 1977) I formulated - and then (HOLYŃSKI 1992d) further developed - a definition of species based on unequivocally discernible phenotypic divergence (stable difference in at least one character), and thus applicable to all (including allopatric and allochronic) populations of sexually reproducing organisms [the later (CRACRAFT 1983) proposed "phylogenetic species concept" is virtually identical to this "working definition", though - as the terminology ("working definition" vs. "species concept") already suggests - the new approach is seen by me as but a practical improvement rather than principal revolution]. Theoretical soundness of such ideas cannot be directly tested in works like the present one, but their practical consequences can, and extensively insular character of the studied area provides especially good opportunity to such testing. The advocates of the "rule of single fixed difference" argue, that it gives the only chance to arrive at considerable agreement as to the "rank" of insular taxa (what would make zoogeographic or evolutionary discussions much more meaningful): the criterion of "potential interbreeding" ("biological definition") is rarely applicable, while - frequently resorted to - comparison of the degree of differentiation between allopatric populations with those observed among sympatric species is extremely subjective and almost never conclusive. Opponents say, it will destabilize classifications and nomenclature by multiplication of the number of "superfluously" named insular "pseudospecies", and promote confusion by creating "two radically different kinds" of species: true, well differentiated sympatric and biologically invalid, in fact equivalent to varieties, insular. The present study does not support these misgivings: neither has the application of my "working definition" dramatically increased the number of insular species (only in two cases - *Psiloptera alorensis* THY. and *Dicercomorpha argenteoguttata* THS. - what had been traditionally considered an allopatric variety "became" a species in my interpretation), nor are members of insular groups on the average less differentiated than their continental, extensively sympatric relatives (cf. *Alorensis*- and *Timoriensis*- vs. *Fastuosa*- and *Affinis*- circles of *Psiloptera* DEL., or *Dicercomorpha* DEYR. vs. *Dicerca* ESCH.).

Circles

The concept of circle - nomenclaturally informal, but otherwise perfectly "normal" taxon between species and subgenus - was introduced by me seven years ago (HOLYŃSKI 1992c); while one of my colleagues (Tieri LANDER *i.l.*) accepted it almost enthusiastically as very useful, another (Charles BELLAMY *i.l.*) criticized it as superfluous, synonymous with either group or superspecies. In fact, "group" is (and should remain) a neutral term to denote - according to the context - anything from a pair of sibling species to a superkingdom and from perfectly valid taxon to ecologically ("leaf-mining group"), morphologically ("green-fronted group") or otherwise defined assemblage; as to the superspecies, some of them are indeed equivalent to the respective circles [e.g. the *Dicercomorpha javanica* (C.G.) - superspecies contains all members of the *Javanica*-circle], but generally the two concepts have not much to do with one another: superspecies is defined by allopatric

distribution of its members, circle by degree of their differentiation - thus *e.g.* the *Affinis*-circle of *Psiloptera* DEJ. does not contain any (or, in more exact formulation, contains six monotypic) superspecies.

"Synthetic" classification

"Synthetic" (or "evolutionary") approach to biological classification - once overwhelmingly dominant - is now rather out of fashion, the "stamp of orthodoxy" having been transferred to cladistic ("phylogenetic") taxonomy. The dispute between adherents of both schools concerns, in fact, the fundamental question of what is the main (or even the only) purpose of classification, and thence what - maximum predictive power or exact translation of one aspect (branching sequence) of phylogenetical history - is the hallmark of good classification (some cladists argue, that predictive power is also maximized in cladistic classifications, but their argumentation is based on drastic restriction - only synapomorphies being left! - of the scope of characters to be predictable). A good example of the consequences of the choice between synthetic and cladistic classification is provided *e.g.* by the genus *Dicercomorpha* DEYR.: *D. farinosa* THS. is a highly distinctive beetle, strikingly different from all its congeners, thence I have separated it into a monotypic subgenus (*Mirolampetis* *sg.n.*). Phylogenetically, however, it belongs to the *dammarana/multiguttata/albosparsa*-lineage (fig. 11), what for a strict cladist leaves only two possibilities: either to renounce from the creation of the subgenus (and thence from direct increasing of predictive power), or to include *D. dammarana* *sp.n.*, *D. multiguttata* DEYR., and *D. albosparsa* (C.G.) to *Mirolampetis* *sg.n.* (so **decreasing** the predictive power by creation of false signals: these species have evidently much more in common with *D. mutabilis* SND. or *D. argenteoguttata* THS. than with *D. farinosa* THS.!). Similarly, even if - as seems highly probable - the "ingroup position" of the **Chalcophorina** LAC. (with or without the **Hypoprasina** HOŁ. and/or **Pseudoperotina** TMA.) is confirmed, their eventual inclusion into the **Psilopterina** LAC. (or the exclusion of *Touzalinia* THY., *Dicercomorpha* DEYR., *Oedisterna* LAC., *Sororcula* HOŁ., &c. from the subtribe) would certainly be a wrong solution.

Indo-Pacific Region

Although the term has been consistently used by me since several years (*e.g.* HOŁYŃSKI 1994c, 1998), I have never published its definition or justification. This concept differs principally from that of the traditional Oriental Region in its south-eastern border, running through Torres Strait, Coral Sea and eastern Pacific rather than along the WALLACE's, WEBER's or LYDEKKER's Line; in other words, New Guinea and Oceania **do** belong to Indo-Pacific but **do not** make a part of Oriental. As can be seen from the maps (esp. map 7, 15, 16, 27) the distribution of **Psilopterina** LAC. supports the warranty of such distinction, conforming to the pattern predicted for the Indo-Pacific: New Guinea and Solomon Is. have been populated exclusively by groups of north-western origin (*Dicercomorpha* DEYR., *Ovalisia* KERR.), while the only known Australian taxon (*Notobubastes* CART.) - of apparently Neotropical (surely not Asian) affinities - has not crossed the Torres Strait. On the other hand, the western and

northern limits of the Indo-Pacific Region coincide with those of the Oriental, and this is also reflected in the distribution of the **Psilopterina LAC.**: the westernmost group of South Asian *Psiloptera DEJ.*, the *Fastuosa*-circle, is not represented to the West of the Thar Desert, while members of Saharo-Mediterranean *Argentata*-circle or *Cyphonota DEJ.* do not occur to the East of it, and only two species of *Capnodis ESCH.* have been able to enter the Indian subcontinent along Himalayas; except for few species of polycentric sg. *Palmar SCHF.* of *Ovalisia KERR.*, no representative of any Indo-Pacific taxon (*Diceromorpha DEYR.*, *Tristria g.n.*, *Touzalinia THY.* or *Psiloptera DEJ.*) extends beyond the Yang-tse-kiang and Tokara Strait, while *Dicerca ESCH.*, *Poecilonota ESCH.*, and *Scintillatrix OBB.* only exceptionally cross them to the South, with but one species of *Dicerca ESCH.* (*D. corrugata FRM.*) reaching as far as Indochina and one (*D. unokichii HRI.*) having been recorded from Taiwan.

THE METHODS

The most important methodical innovation in this paper is certainly MICSEQ, but one particularity of my approach to taxonomic/phylogenetic work seems worth mentioning here as differing from currently most popular practice.

Genitalic characters

I refer to genitalia only in exceptional cases in keys and taxonomic descriptions, and totally ignore them in phylogenetic reconstructions. Genitalic characters are frequently very useful as diagnostic features to distinguish between closely related species, which sometimes do not apparently differ in anything else. However - contrary to the common belief - in virtually all other situations they are *less* informative than others *even as tools for identification*: they are restricted to one sex only; [thence] they are unknown in many species; [like other "internal" characters] they demand time-consuming preparation; [thence] their intraspecific variability has been studied - at least in **Buprestidae LEACH** - for but very few species (none of the Indo-Pacific **Psilopterina LAC.**), &c. As indicators of phylogenetic affinity genitalic characters are especially unreliable: the very function of their interspecific differentiation - to serve as [a component of] specific mate recognition system [SMRS] - causes their frequent involvement in reproductive character displacement what, however, may be easily achieved by simple "variations on few themes" (switching at each speciation - or secondary contact - between robust and slender, pointed and truncated, glabrous and setulose, &c.), leading to the commonly observed pattern of striking genitalic dissimilarity in closely allied species and near-identity in non-relatives. This is exactly that attribute of genitalia, which makes them so useful in identification of siblings, but the price is drastic reduction of their suitability for phylogenetic reconstructions [of course, such erratic, phylogenetically almost useless (though highly valuable in some cases of identification) type of interspecific variability is characteristic of any (not only genitalic) character involved in SMRS (or otherwise "socially selected" - WEST-EBERHARD 1983): nuptial plumage in birds, pheromones in insects, pattern of spinules in some copepods (HOLYŃSKA in press), courtship behaviour in various animals, &c.; among the **Psilopterina LAC.** a

particularly demonstrative example is the development of prosternal pubescence, male mesotibial armature, or apical notches on female abdomen in *Dicerca* ESCH.]. I have frequently observed this phenomenon in **Buprestidae** LEACH - sg. *Thymedes* WATH. (HOLYŃSKI 1994b) and *Smaragdula*-circle in *Chrysodema* C.G., *Indica*-circle in *Sphenoptera* DEL., several groups of *Agrilus* CURT., &c.), and the present study revealed similar situations in Indo-Pacific **Psiloptera** LAC. So, e.g., the most reliable distinguishing feature of *Psiloptera affinis* (SND.), truncated tips of parameres, is (among the Indo-Pacific congeners) most closely approached by a representative of another circle, *P. fastuosa* (F.) [and still closer by completely unrelated African *Oedisterna livida* PÉR. (BELLAMY 1988)], while their respective nearest - otherwise hardly distinguishable - relatives, *P. viridicuprea* (SND.) and *P. coerulescens* (HBST.) [as well as *Oedisterna bisulcata* (C.G.)], have normally pointed parameres. At least in this case the degree of differentiation of genitalia would be evidently misleading as a component of "distance-matrix"; as theoretical considerations strongly suggest - and observed examples confirm - that this is a rule rather than exception, it seems prudent to exclude genitalic characters from phylogenetic analysis.

MICSEQ

"The first step is intuition – it comes suddenly, difficulties appear later. Now this fails, then something else: 'bugs' (as we call such trifling errors) emerge, and it takes months of strenuous effort, observations, studies to acquire certainty of success – or defeat... [...] I have a good idea and proceed in right direction, but time, hard work and a bit of luck are also indispensable".

Thomas Alva EDISON

It follows from the very nature of data, that phylogenetic reconstructions at "deeper" (more inclusive) levels will be less reliable than results of analysis of "terminal twigs": what we really observe are individuals, our conclusions concerning species are already somewhat speculative (and thence possibly erroneous), and the degree of uncertainty increases as we pass to subgenera, genera, subtribes, &c.; wrong choice of character-states presumed (or simply selected) to represent a subgenus (equivalent to wrong reconstruction of its ancestor) naturally diminishes the probability of proper identification of sister-group relations within (and, thence, correct reconstruction of the ancestor of) the genus; this, in turn, confuses the analysis at the subtribal level; &c. - errors accumulate "downwards", making the results less and less veracious. Moreover, also convergences - the main confusing factor in phylogenetic reconstructions - accumulate: similarities between sister-species are almost by definition homologous; but some of those between circles, subgenera, genera, &c. may have evolved convergently, and of course the "longer" the lineage, the greater proportion of its (true) autapomorphies will have convergently "symmorphous" counterparts in other clades. This is a characteristic of basic data, encountered in any phylogenetic study irrespective of which particular procedure is employed; however, programs based on "overall parsimony" simply ignore it by treating character-transformations at various levels as equally weighed "steps", the number of which determines the primary criterion of "goodness" of a cladogram: its "length"; in this way, their credibility is "averaged" (or rather "levelled down") and

the revealed sister-group relations between terminal "OTU"-s become indeed no more reliable than those between basal branches. This has been one (though not the only) reason of my dissatisfaction with such programs (other students go still further, denying the very applicability of cladistic analysis at deeper phyletic levels, "where ... convergence seems to have been far more common than a practising cladist would care to admit, or can bear to contemplate" - WILLMER 1990) and incentive to think about a different approach: the result is MICSEQ. By constructing the tree "from the top", starting with closest - in terms of "corrected distance", thence presumably also in those of phylogeny - pairs of terminal taxa, MICSEQ assures them greater influence on the final tree, making a good use of their superior reliability (instead of neglecting it) to maximize the likelihood of correct reflection of true affinities by the resulting cladogram; this likelihood is "by definition" greater for "upper" branches than for those near the base of tree, but correct reconstruction of relations at the top reduces also the danger of confusion towards the bottom.

The general idea of the new procedure was invented just at the beginning of the work on this paper, and developed together with it: MICSEQ served as a tool to reconstruct the evolutionary relations between the studied taxa, and was itself continuously modified according to the experiences accumulated in the course of these reconstructions; so it has been improved tremendously in the course of the work, but (especially its computerized form) still remains in rather experimental stage. It might perhaps seem better to renounce from publishing the results obtained by admittedly immature program and wait until the final, perfect version becomes available, but - in my opinion - it would be a specious stipulation: on the one hand, nothing in this world can ever be "finally perfect", thence waiting for perfection is an inherently hopeless endeavour; on the other, there is no more efficient way to test a procedure than to work with it, apply it to real problems and real data, and make it available to others for evaluation and criticism.

Of course, both this "unpolished" state and the differences in details among the algorithms employed in the construction of particular cladograms, have some consequences even beyond the direct reduction of credibility of results. One of them is the above-mentioned experimental character of the work, the need of "reciprocal evaluation" of the method and obtained results: the aim of the phylogenetic analyses by MICSEQ has been not only to disclose the evolutionary relationships between the studied taxa, but also to reveal the strong and weak points of the procedure - its sensitivity to our decisions concerning data (*e.g.* selection of characters and taxa, linearity of transformation-chains, weighing) and solutions in the course of reconstruction (*e.g.* criteria of choice between equal "corrected distances"), its "robustness" to incomplete or uncertain (thence possibly wrong) informations, &c. This, in turn, forced me to choose simpler (more uniform, "objective", "orthodox") options even if differentiated - though less straightforward and thence subjective - approach would have better assured the reliability of conclusions. So *e.g.*, for the sake of objectivity and comparability (obviously necessary in the phase of testing) I tried to keep the differentiation of weights at minimum (as can be seen in the example analysis of *Dicercomorpha DEYR.* - see Appendix - most transformations have been

equally weighed), define the characters uniformly for all taxa (thus *a priori* assuming homology even in cases of evident convergence), &c.

“Rigorous” phylogenetic “algorithms” are often featured as fully objective, unfailing way to disclose the truth, and their results as incontestable Last Word of Science; in the absence of convergences such claims would perhaps be legitimate (though then no rigorous methodologies would be necessary...), but convergences do occur, and striking disparities between cladograms obtained by different authors, with different procedures, and/or based on different material (to say nothing about the notoriously more than one - usually very many... - “equally parsimonious trees” resulting from a single analysis...) impressively illustrate the distinction between theoretical soundness and practical reliability. The remedy is typically hoped for from further “considering the ‘rules of the game’” and “laying out some guidelines that may allow” still “more rigorous conclusions to be drawn from cladistic analyses” (JENNER & SCHRAM 1999) - and in many cases this may indeed be the way to minor improvements.

However, contrary to the widespread belief, objectivity (or methodological “rigour”) and truth are *not always* good friends (the most objective algorithm is often just that least likely to produce correct results), and thence (however paradoxical may it seem to many “modern” students) it is just this strive for objectivity that - apart from some factors independent of the procedure [poor background taxonomic knowledge (subgenera of *Psiloptera* DEJ., intergeneric relations), strongly restricted number of included species (extralimital groups, *Ovalisia* KERR.)] - has apparently been responsible for most contradictions and incongruencies between the cladograms! For one example (cf. Appendix), in both *Dicercomorpha subcincta* DEYR. and *D. farinosa* WATH. character 24 (“elytral dfp [=densely and finely punctured depressed areas] – spot size”) has been coded as [4] (“continuous bands”); however, character 23 (“elytral dfp - arrangement”) is [b] (“transverse”) in the former and [z] (“longitudinal”) in the latter, and already this fact strongly suggests that “continuous bands” are of different origin (dfp spots became confluent independently), and thence represent convergent rather than homologous - as suggested by the coding - features.

The distinction between cases of homology and those of convergence is fundamental for any phylogenetic procedure, thus such errors - though MICSEQ seems relatively resistant to them [e.g. in this particular case the “miscoding” remained without damaging effect: elimination of the false symmorphism would lead to the same cladogram, even strengthening the support for it] - may nevertheless induce serious distortions in the results of analysis; evidently, the longitudinal “continuous bands” of *D. farinosa* WATH. might (and, in a routine work with sufficiently tested procedure, should) be coded as a character-state different from the transverse ones in *D. subcincta* DEYR. Unfortunately, independent criteria of homology vs. convergence (like disparate arrangement in the case of dfp in *Dicercomorpha* DEYR.) do not always exist - tufts of white, soft, long hairs on the elytra of *Touzalinia psilopteroides* THY. (unique in the *Dicercomorpha/Tristria/Touzalinia*-complex) are virtually identical to those in *Psiloptera (Polybothris) sumptuosa* (KL.) (unique in *Psiloptera* DEJ.); highly elevated, smooth, continuous elytral costae of *Psiloptera scintillans* WATH. do not

essentially differ from those in *Dicercomorpha farinosa* WATH. (elytral structure in their respective relatives being strikingly different) - and nevertheless convergent origin of such features in but remotely related taxa is obvious, their coding as different character-states would certainly reduce the likelihood of erroneous conclusions, and therefore objectivity should be compromised in favour of verity.

However, incontestably subjective nature ("evident homologies" and "evident convergences" are but extremal cases of continuous chain of intermediate situations) and distinct flavour of circularity (characters for reconstruction of phylogenetic affinities are defined according to the degree of relatedness - *i.e.* phylogenetic affinities ... - of respective taxa) of such criteria make them clearly unsuitable for **testing** the procedure. So, the particularities of coding and weighing applied in this work are very often a compromise between what I consider optimal (for reconstruction of a given taxon's phylogeny) and the objectivity or uniformity (needed at the present - still somewhat experimental - stage of development of MICSEQ). This form of testing is not yet really "intercommunicable" (at least by the way of published paper) between me and other workers, thence I find unwarranted (except in the "example reconstruction" of *Dicercomorpha* DEYR. - see Appendix) to present here all the character-matrices and character-state definitions: I would like to direct the discussion (which I hope my paper will provoke) primarily to the general assumptions and theoretical foundations of the procedure (and to the comparison of the results - phylogenetical trees - with those obtained by other students working with different procedures) rather than to specific questions of whether a given character has been properly coded or not, and whether the particular transformation should be attributed the weight of 2 - or perhaps rather 12 - instead of 4 chosen by me.

In my - certainly subjective... - estimation MICSEQ, despite its immaturity with all the imperfections and inconsistencies discussed above, performs remarkably well: evident contradictions (or hardly acceptable discrepancies from current classifications) mostly concern some (not all!) poorly represented (*Ovalisia* KERR., several extralimital taxa) or probably polyphyletic (subgenera of *Psiloptera* DEJ.) groups, while those studied in reasonable detail (*Cyphonota* DEJ., *Capnodis* ESCH., *Dicercomorpha* DEYR., Indo-Pacific lineage of *Spinthoptera* CSY.) show good agreement between the reconstructions done by MICSEQ and expectations based on current knowledge and/or intuitive evaluation [of course, degree of agreement with results of other - no matter whether intuitive or algorithmic - analyses is not a "measure of reliability" of a procedure (disagreement may mean that **the other** is wrong), but congruent conclusions obtained by essentially different methods are anyway a **serious evidence** that **both** performed well].

THE RESULTS

As I have frequently emphasized, due to the still insufficient amount of testing available for MICSEQ, the majority of the results obtained in this work must be considered preliminary; however, some are apparently reliable, and some others so interesting even as but a suggestion for further research that I find it worthwhile to mention them here.

Taxonomy

No “taxonomic revolution” has been proposed in this paper: albeit phylogenetic analyses would suggest some profound changes in classification, introduction of such changes on grounds of single (not supported by other data or independent analyses) reconstruction is - in my opinion - always risky and rather unwarranted; this is, of course, especially true of MICSEQ at its present stage of “testedness”. Thus, I have made only some minor taxonomic modifications based on direct morphological evidence, not dependent upon the correctness of phylogenetic conclusions: I have described two (*Tristria g.n.*, *Archepsila g.n.*) new genera, five (*Mirolampetis sg.n.* in *Dicercomorpha DEYR.*; *Poecilisia sg.n.*, *Cinyrisia sg.n.*, *Mabomisia sg.n.*, *Zykovisia sg.n.* in *Ovalisia KERR.*) new subgenera, eight (*Dicercomorpha dammarana sp.n.*, *Psiloptera praeorientalis sp.n.*, *P. jasienskii sp.n.*, *P. draconis sp.n.*, *P. praeinsularis sp.n.*, *P. sumbana sp.n.*, *P. lombokiana sp.n.*, *Archepsila cordicollis sp.n.*) new species and two (*Psiloptera affinis cochinchinae ssp.n.*, *Dicerca corrugata thibetana ssp.n.*) new subspecies; I have also introduced some corrections as to the synonymy and/or rank of some taxa.

Of the new genera, only *Archepsila g.n.* is really “new”, *i.e.* has been established to include a hitherto unknown beetle. It is certainly the most intriguing taxonomic discovery of this work, potentially (if its provenience from Moluccas is true) very important from phylogenetical and zoogeographical viewpoints. *Tristria g.n.* has been based on a species hitherto considered to belong to *Dicercomorpha DEYR.*; my - expressed *in litteris* to some colleagues - opinion that it should be placed in *Spinthoptera CSY.* is not confirmed by the results of phylogenetic analysis (which consistently show it as close to *Dicercomorpha DEYR.* and *Touzalinia THY.*), but anyway it is sufficiently distinct to warrant the generic rank. Also all the new subgenera contain already known species, and only my evaluation of the degree of their distinctiveness is new.

The most interesting among the new species (besides *Archepsila cordicollis sp.n.*, commented upon under the genus) is *Psiloptera praeorientalis sp.n.*, evidently a member of the African *Pupillata*-circle (traditionally included into, and showing the “key characteristic” - [slightly] bituberculate anterior margin of prosternum - of, the subgenus *Lampetis DEJ.*) yet apparently very close to the Indian *Fastuosa*-circle of *sg. Spinthoptera CSY.*; unfortunately, also in this case the reliability of the [old] labels [“India or.”] is not beyond doubt. Sumatran *P. praeinsularis sp.n.* provides the important “missing link” between continental and insular groups of *Spinthoptera CSY.*; the characteristics and distribution of *Dicercomorpha dammarana sp.n.* make it helpful in understanding the evolution of main lineages of the *Multiguttata*-circle; the significance of the remaining new taxa does apparently not extend beyond increasing our (still very poor) knowledge of biodiversity.

Distribution

The potentially most important, though - due to old and inexact labels - not satisfactorily certain, distributional “discovery” of the present work is the apparent

occurrence of *Psiloptera praeorientalis* sp.n., a representative of the otherwise exclusively African *Pupillata*-circle, in India. Interesting are also: first record of the genus *Cyphonota* DEJ. from the periphery of the studied area (*C. turcomanicum* KR. from Baluchistan); probable (if my identification of the "Dammar I." has been correct) extension of the range of *Dicercomorpha* DEYR. to [easternmost] Lesser Sundas; filling the disjunction between continental and insular areas of sg. *Spinthoptera* DEJ. (*Psiloptera praeinsularis* sp.n. on Sumatra); finding of a member of apparently ancient psilopterine lineage in Moluccas (*Archeopsila cordicollis* sp.n. on Batchian); and second - more than 1500 km. to the West from the first - known locality for *Poecilonota semenovi* OBB. (the only representative of the genus in South China).

Zoogeography

Some evidently [sub-]tropical taxa (among the **Buprestidae** LEACH e.g. the genera *Paratrachys* SND., *Chrysochroa* SOL., *Chrysodema* C.G., *Toxoscelus* DEYR., *Endelus* DEYR., &c.) extend very far to the North (Honshu, Manchuria); on the other hand, many species of obviously northern (or western) origin reach as far south (or east) as Indochina, southern subhimalayan ranges, or Rajasthan. The "line of equilibrium" between the southern and northern elements is different for different groups, and thence the opinions as to the position of the Palaearctic/Indo-Pacific (or Palaearctic/Oriental) border vary considerably. The pattern of distribution of the **Psilopterina** LAC. supports the narrowest delimitation of the Indo-Pacific Region: all the "contestable" areas are inhabited almost exclusively by representatives of Palaearctic genera (Indus Valley and foothills of Himalaya by *Capnodis* ESCH., southern China by *Dicerca* ESCH., *Poecilonota* ESCH. and *Scintillatrix* OBB.), while the genuine Indian and Indochinese taxa only peripherally enter Kumaon [*Psiloptera orientalis* (C.G.)] and southwesternmost Yunnan [*Touzalinia psilopteroides* THY.] (the polycentric subgenus *Palmar* SCHF., of uncertain origin, is not reliably informative without detailed study at the species-level, and thence has been left here out of consideration).

Phylogeny

As I repeatedly emphasized, the results of phylogenetic analyses - especially at deeper (generic, subtribal) levels - presented here must be treated with caution greater than usual; however, at least as suggestions for further studies, some of them seem very interesting and valuable.

So, e.g., while the close affinity between the **Pseudoperotina** TMA., **Hypoprasina** HOL., and [represented in the analyses by *Chalcophorella stigmatica* (SCHH.)] **Chalcophorina** LAC. is not surprising (it was postulated - in various combinations - e.g. by TÔYAMA 1987, BELLAMY 1988, and HOLYŃSKI 1993b), and their more "terminal" placement in relation to the **Psilopterina** LAC. was also already suggested (HOLYŃSKI 1997), the position of this complex well within the latter subtribe has been rather unexpected. Certainly further study is needed to confirm the arrangement suggested by the present analysis, but here it emerges as a remarkably stable feature, supported by all the relevant cladograms (fig. 1, 2, 3). Poorly known

Neotropical genus *Cordillerita* OBB. seems to be a sister-group of Ethiopian *Pseudoperotis* OBB.

Still more intriguing is the wide separation between *Scintillatrix* OBB. and the remaining taxa traditionally included in *Ovalisia* KERR., as well as the appearance of the latter as the basalmost branch of the **Psiloptera** LAC. (in this case the support is not so unambiguous, but anyway none of the relevant trees clearly contradicts the relationships suggested by the "general" cladogram). Among the conceivable taxonomic consequences of eventual (partial or full) confirmation of this arrangement are transfer of *Ovalisia* KERR. (of course without *Scintillatrix* OBB.) from the **Buprestini** LEACH: **Psiloptera** LAC. to **Anthaxiini** C.G.: **Bubastina** OBB. (or - much less likely - of the *Philanthaxia* DEYR. and related genera in the opposite direction), and general reassessment of the relationships between and within these tribes (with - perhaps dramatic - rearrangements in the classification at the subtribal/tribal levels).

The position of Neotropical *Hilarotes* THS. close to Indo-Pacific *Dicercomorpha* DEYR. and *Touzalinia* THY. is a corroboration of my earlier (HOLYŃSKI 1993b) conclusion, while my suggestions concerning *Notobubastes* CART. (HOLYŃSKI 1988) and *Sororcula* HOL. (HOLYŃSKI 1993a) have been confirmed only in part: the former seems indeed to belong to the **Psiloptera** LAC., yet its claimed close affinity to *Spinthoptera* CSY. has not been supported; the latter is evidently not a member of the *Polybothris* DEJ.-group, its relationships to *Lampetis* DEJ. being, however, also remote. Evidently refuted has been the transfer (HOLYŃSKI 1993b) of *Chalcopocila* THS. to the **Pseudoperotina** TMA.: it consistently appears as the sister-group of *Achardella* OBB., within the **Psiloptera** LAC. *Archeopsila* g.n. seems closely related to *Pseudolampetis* OBB.; *Perotis* DEJ. (as expected) remains within the *Psiloptera* DEJ. - clade, and also *Latipalpis* SOL. is apparently closer to it than to *Dicerca* ESCH.; *Capnodis* ESCH. and *Cyphonota* DEJ. are obviously sister-groups; *Poecilonota* ESCH. and *Scintillatrix* OBB. - despite claims (ALEXEEV & BEBKA 1970, VOLKOVITSH in press) of profound (at the tribal level!) differences - make a common clade with *Dicerca* ESCH.

The traditional subgenera of *Psiloptera* DEJ. are (at least in part) almost certainly unnatural, but the Indo-Pacific species (with possible exception of *P. comottoi* LSB.) seem to make a monophyletic group (with some subbranches having dispersed into America); the ancestor of this group apparently invaded South Asia from Africa through Arabia and Persia. *Cyphonota* DEJ. and *Capnodis* ESCH. are Mediterranean elements entering only the westernmost peripheries of the Indo-Pacific area; *Archeopsila* g.n. and the *Dicercomorpha*/*Tristria*/*Touzalinia*-lineage seem autochthonous (the former of probably Gondwanian, the latter of rather Laurasian origin); *Dicerca* ESCH., *Poecilonota* ESCH. and *Scintillatrix* OBB. are northern (Holarctic resp. Palaearctic) invaders; the distributional history of *Ovalisia* KERR. remains unclear until the uncertainties concerning its internal and external (to *Scintillatrix* OBB. [through *Palmar* SCHF.]? to *Poecilonota* ESCH. [through *Poecilisia* sg.n.]? to the **Bubastina** OBB. [through *Ovalisia* KERR. s.str.]?) phylogenetic relationships are clarified, what demands much more detailed analysis.

As a by-product of the study of Indo-Pacific **Psilopterina** LAC. phylogenetic reconstructions for some largely extralimital groups (*Cyphonota* DEJ., *Capnodis* ESCH., *Dicerca* ESCH., *Poecilonota* ESCH. - the latter two with not all, especially American, species included) have also been performed, showing - among others - interestingly dissimilar patterns of Palaearctic-Nearctic dispersal in, respectively, *Dicerca* ESCH. and *Poecilonota* ESCH.

Evolution

General problems of evolution were, of course, not among the direct targets of this study, but nevertheless some of the obtained results may be interpreted in terms of the underlying processes, and serve as a contribution to more detailed knowledge of these.

One of the frequently debated questions is the significance (or even the very existence) of sympatric character-displacement. However, in the **Buprestidae** LEACH - to my knowledge - nobody has ever paid any special attention to this phenomenon, and I am aware of but one paper (HOLYŃSKI 1994b) where it has been mentioned at all. This study had revealed several cases of sympatric character-displacement; those concerning genitalia have been discussed above (see **THE METHODS: Genitalia**), but in at least one instance external morphology is also involved: the features of *Psiloptera coerulescens* (HBST.) - finer sculpture, brighter colouration - distinguishing it from *P. fastuosa* (F.) are appreciably more accentuated in southern India (where both species occur) than in Ceylon (where only the former is present). *Psiloptera coerulescens* (HBST.) seems to have invaded India from Ceylon twice, the effect of the first invasion being just *P. fastuosa* (F.); such "multiple invasions" are well known to be frequently accompanied with divergence of characters (having - unlike the case of genitalia - probably not much to do with sexual isolation, but rather helping to avoid ecological competition).

Some groups exhibit the opposite phenomenon: sympatric character-convergence. Several explanations have been proposed, including "social mimicry" to promote formation of mixed flocks (MOYNIHAN 1968) or to evade direct competition by induction of interspecific territorial behaviour (CODY 1969), but in most cases concerning insects only two - "classic" (BATESIAN or MÜLLERIAN) mimicry and parallel response to specific (usually unknown: functional significance of most characters in jewel-beetles remains a mystery) environmental conditions - seem plausible. The Indo-Pacific area provides many interesting examples of sympatric convergence, from the peculiar shape of wings in many unrelated Celebesian butterflies reported already by WALLACE (1869) to remarkable "local specialities" in the **Buprestidae** LEACH: deceptively similar shape and colouration (green dorsally, cupreous-red on underside) in various Malayan *Chrysochroa* SOL., *Callopistus* DEYR., *Micropistus* THY., *Iridotaenia* DEYR., *Chrysodema* C.G. (KUROSAWA 1982); very smooth, shining surface and purplish- to violet-bronzed colouration in several species of *Cyphogastra* DEYR. and *Chrysodema* C.G. from Key Is.; or yellow legs and antennae in many *Iridotaenia* DEYR., *Metataenia* THY., *Cyphogastra* DEYR., *Paracupta* DEYR., *Chrysodema* C.G., &c. from Pacific Islands. Among the Indo-Pacific

Psilopterina LAC. such situation occurs in two places: the Andaman Is. [where only one species of *Psiloptera* DEJ. (*P. scintillans* WATH.) coexists with single representative of *Dicercomorpha* DEYR. (*D. farinosa* THS.), and both strikingly differ from all their Asian congeners in strongly, regularly costate elytra without any trace of intercostal foveae], and Masbate I., (Philippines) [inhabited by a local form of *Dicercomorpha argenteoguttata* THS., whose peculiar colouration and pattern of spotting is almost perfect replication of (or perhaps model for) similar in size and shape, also Masbatean, *Chrysochroa sororismiae* HOL. - (cf. phot.3 in HOLYŃSKI 1994c)]. Though some specific environmental demands would be difficult to exclude, [MÜLLERian] mimicry seems more likely explanation. KUROSAWA (1982) quotes the VANE-WRIGHT's concept of "numerical mimicry" (convergent similarity of several species, all "uniformly attractive" to predators; "having too many attractive objects in sight, birds may be bewildered in selecting their foods, and may end in catching none or only a very few of them") as best explaining the case of the Malayan mimetic group, because "*Chrysochroa holstii* WATERHOUSE, 1890, of the Bonin Islands, which is closely related to a member of this converging group, *C. purpureiventris*, is often preyed by birds" what - in his opinion - implies that all the involved species are "attractive". It is difficult to accept this argumentation: even if *Chrysochroa holsti* WATH. is indeed not protected (e.g. by toughness of its exoskeleton) from predation by Bonin birds (what is by no means sure: protection is always a *relative* property, even the best protected animals are "often preyed" by some predators), this does *not* necessarily mean that *different* (even if similar and/or related) species in *different* locality are "attractive" to *quite different* predators; members of all the above-mentioned mimetic groups (like most big jewel-beetles) are so heavily armoured, that certainly very strong beak is needed to crush them! Moreover, the "uniform attractiveness" may perhaps offer some protection to animals occurring in large, dense, mixed swarms (like some migrating birds), but I can hardly imagine how solitary (even if locally common) buprestids could "bewilder" predators with their similarity to other solitaires... KUROSAWA (1982) conceived also a theory of "circulation and phases" [*i.e.* cyclic changes in composition of mimetic groups and in relative frequency of their members] "apparently recognized in mimicry, especially in numerical mimicry", which serves him "to reconstruct the process of formation of this converging group in the Malay Peninsula"; he concludes, among others, that "the establishment of the mimicry seem to have been accomplished within a short geological time, and this convergent group may have been formed in [...] less than ten thousand years after the glacial age". Unfortunately, he has not supported the "circulation theory" with any evidence, while his argumentation purportedly justifying the scenario and timing is obscure and unconvincing, so I find it impossible to accept the conclusions.

As seen *e.g.* from lengths of particular branches of cladograms, the tempo of evolution (as measured by the amount of morphological changes) vary considerably between lineages. The most striking example of practically total stasis is *Capnodis porosa* (KL.) (fig. 5), differing in but a single "weak" character (elytral striae very fine rather than moderate) from the reconstructed common ancestor ("ground-pattern") of the genus - in the other clades the rate of evolution was *ca.* 20-30 times greater! This

is an extreme, but numerous cases of transformations several times faster in one lineage than in another may be seen on any cladogram (comparisons *between* cladograms are obviously *not* legitimate, especially because of different number of characters considered).

The old dispute between the proponents of what can be termed “centroactive” (which “predicts that the peripheral populations [...] would be the most plesiomorphic” - BRIGGS 1999) and “frontoactive” (“we should expect to find the primitive types of a group persisting in the area of its origin and the specialised forms in districts remote therefrom” - NELSON & PLATNICK 1984) [some authors use, respectively, the - in my opinion misleading - terms “centrifugal” and “centripetal”] evolution does not seem likely to be solved unambiguously in favour of one of them: apparently both (as well as many intermediate, geographically irregular patterns) do occur; however, their relative frequencies and - especially - the circumstances promoting one or another remain to be disclosed, and “case-studies” like this may be helpful in achieving this goal. I (HOLYŃSKI 1994b) have already touched the problem in connection with KUROSAWA’s (1979) interpretation of distributional history of the subgenus *Thymedes* WATH. in *Chrysodema* C.G.: while the Japanese author based his scenario on the assumption that “it is usual that the most primitive species of a genus survives in areas most distant from the centre of dispersal”, I showed that the observed pattern did not corroborate his hypothesis, and argued that even on theoretical grounds “I can hardly imagine any plausible mechanism, which could cause the species having moved farthest, having crossed numerous barriers [...], having inevitably passed a great variety of environments and so been exposed to a great variety of selection pressures, having at last lived under the conditions different from those in the ‘centre of dispersal’, [...] change less than its congener remaining all the time in the same area”. The results of the present study seem to confirm my standpoint, the evolution of dispersing lineages of both *Dicercomorpha* DEYR. and [Indo-Pacific] *Psiloptera* DEJ. having apparently followed the “frontoactive” way: the most plesiomorphic taxa (*Dicercomorpha vitalisi* BRG., *Psiloptera fastuosa*-circle) occupy the presumed “fatherland” (Indochina, India), while those representing more “terminal” clades inhabit progressively more and more distant areas, marking the “dispersal tracks” with the most derived forms [*Dicercomorpha multiguttata* DEYR., *D. javanica* (C.G.), *Timoriensis*- and *Alorensis*-circles of *Psiloptera* DEJ.] at the ends; the only exception from this rule seems to be *Psiloptera scintillans* WATH., a peripheral (Andaman Is.) species representing a relatively ancient, “basal” branch. In my opinion, the frontoactive and centroactive patterns may be interpreted as (expansive and territorially static, respectively) stages of - not always regular and often hardly discernible, to be sure - “dispersal-cycles”. When a “new-born” taxon spreads (especially in “discontinuous” - insular, montane, &c. - regions), each barrier-crossing means “population-bottleneck” (with associated founder-effect, genetic drift, &c.), each new environment (with different climate, different predators, different parasites, different competitors, different varieties - or even species - of host-plants) means change in strength and direction of selection-pressure, the obvious consequence being rapid genotypic and phenotypic rebuilding of the “foremost” populations, *i.e.* *frontoactive* evolution (of course, if the taxon expands through a continuous,

environmentally homogeneous country, the - usually slow - “phyletic transformation” may proceed more or less uniformly over all its territory). However, as the distribution-area increases and ultimately reaches its maximum extent (delimited by - at least temporarily - impassable barriers), more and more occasions for [sub-] speciation arise within it while simultaneously its frequency at “frontiers” dwindles; thus, the most apomorphous species emerge “inside”: *centroactive* evolution takes place. If the new form proves competitively superior (as it usually does: otherwise the selection would probably prevent its creation), it can eventually invade the territory inhabited by its “mother” and eliminate it; the previously “frontoactively” evolved taxa - specially adapted to their peripheral environments and thus relatively immune to competition - have better chances to resist the invasion and frequently survive, but now *they* are relatively plesiomorphous as predicted by the “centrifugal” hypothesis (this seems to have been the case of *Psiloptera scintillans* WATH.). Of course, this cycle may be repeated several times, “stages” may overlap (e.g. a centroactively created taxon may itself frontoactively evolve during expansion), the direction of dispersal may change or even reverse (e.g. a peripheral isolate may reinvade the “original motherland”), “central” species may turn out to be sufficiently different to establish itself in the “frontier” area without competitive exclusion of earlier settlers, &c. [all these situations apparently occurred in the history of *Psiloptera fastuosa*-circle] - the result is almost infinite variety of observed patterns, often (as e.g. in the case of *Psiloptera affinis*-circle in Indochina) very difficult to disentangle.

It is well known since DARWIN’s times, that evolution *sometimes* proceeds according to what ELDREDGE & GOULD (1972) described as “punctualistic” model (rapid change in one - *only* one! - of sister-species at the speciation event, then stasis until the following speciation), but in the extremal form (as originally proposed and defended in later publications by its authors - e.g. ELDREDGE 1989: a species as such is unalterable, gradual phyletic transformation [anagenesis] does not exist, spacial and temporal variability “*never* [emphasis mine - RBH] seems to get anywhere”) the theory of punctuated equilibria has been seriously criticised since its first publication. It was proposed and then evaluated almost exclusively either on purely theoretical grounds, or from the palaeontological perspective; however, fossil record is notoriously imperfect and - at least in overwhelming majority of actual cases - badly unconvincing as a test for punctualism. Fortunately, various possibilities exist to test the validity of the hypothesis against neontologic material: some years ago, in an unpublished (only few-sentences-long abstract - HOLYŃSKI 1994a - appeared in print) lecture I suggested several taxonomic/zoogeographic approaches, and phylogenetic reconstructions can also serve as a convenient base for such tests. Applied to Indo-Pacific **Psilopterina** LAC., these lines of reasoning cogently support the traditional “opportunistic” view: marked morphological transformations occur sometimes in only one daughter lineage, but frequently in both or occasionally in none; they are usually - though by no means always - faster immediately at the speciation event than later, but [nearly] total stasis between speciations is rather exception than rule. To be sure, the above-mentioned strikingly different rate of changes in various lineages, the nearly perfect stasis in *Capnodis porosa* (KL.), or frontoactive mode of evolution with consecutive parental species left almost unchanged at “stopovers” before each barrier,

could seem to corroborate the punctualistic hypothesis, but its acceptance on these grounds would be evidently unjustified. Closer examination of the cladograms immediately shows that albeit the amount of change from the ancestor to its immediate descendant varies considerably, the variability is continuous rather than of "all [in one daughter species] or nothing [in the other]" type: some "sister-pairs" show vast disparity in the degree of transformation, some others differ but moderately, and in many cases the rate of evolution was nearly equal. Likewise, frontoactive mode of evolution is (as predicted by the "dispersal cycle" hypothesis) virtually restricted to the expansive phase, and even then in but few cases [*Dicercomorpha interrupta* DEYR., *Psiloptera baliana* KERR.] the "parental" population remained apparently unchanged, while e.g. *Dicercomorpha vitalisi* BRG., *D. fasciata* WATH., or *Psiloptera eva* (THS.) have evolved not - or not much - less than their farther expanding sister-species; *Capnodis porosa* (KL.) is an evidently exceptional "living fossil". The strikingly distinctive morphology of all three taxa inhabiting small isolated islands (*Dicercomorpha dammarana* sp.n. on Dammar, *D. farinosa* THS. and *Psiloptera scintillans* WATH. on Andamans) has apparently also been the result of phyletic transformation, but punctualistic interpretation - though much less likely - cannot be fully excluded.

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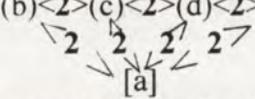
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Appendix

Commented example of phylogenetic reconstruction by MICSEQ (the genus *Dicercomorpha* DEYR.)

Dicercomorpha DEYR. is a small (14 subspecies in 12 species), exclusively Indo-Pacific (distributed between Siam, Andamans, Java and New Guinea) genus belonging to the subtribe **Psilopterina** LAC. Phylogenetic relationships among the **Psilopterina** LAC. (like in most other groups of the **Buprestidae** LEACH) are unknown, and we cannot *a priori* exclude the possibility that *Dicercomorpha* DEYR. is paraphyletic in relation to one or more other genera; therefore I decided to include in the analysis as many as 4 outgroups: *Tristria* sg.n. [*T. cupreomaculata* (WATH.)], *Spinthoptera* CSY. [represented by *S. timoriensis* (C.G.)], *Archepsila* g.n. [*A. cordicollis* sp.n.], and *Capnodis* ESCH. [represented by reconstructed ancestor].

For the analysis I have selected 33 characters showing more or less clear-cut interspecific differences [symbols of character-states in parentheses ("terminal" - at the start of the analysis - ones in square brackets]; values of differences in **bold**):

1. **Proportions of the body (L:W):** 2.5-3.0 [3]; 3.0-3.5 [4]
[3]<2>[4]
2. **Colouration of pronotum:** black [a]; bronzed (b); coppery (c); green (d); blue [e]
(b)<2>(c)<2>(d)<2>[e]

3. **Frontal depression:** none/indistinct [0]; on lower half (1); nearly all-over [2]
[0]<2>(1)<2>[2]
4. **Frontal sculpture:** dense punctures [b]; dense mixture of punctures and reliefs (x); narrow reliefs [y]
[b]<2>(x)<2>[y]
5. **Frontal pubescence:** short and sparse [a]; long and dense [z]
[a]<4>[z]
6. **Vertex width (VW:HW):** 0.2-0.3 [2]; 0.3-0.4 [3]
[2]<2>[3]
7. **Pronotal proportions (MW:BW):** 0.85-0.95 [2]; 0.95-1.05 (3); 1.05-1.15 [4]
[2]<2>(3)<2>[4]
8. **Pronotal sides basally:** sinuate [0]; straight [1]
[0]<2>[1]
9. **Pronotal prescutellar pits:** widely separated [0]; narrowly separated (1); fused (2); single [3]
[0]<1>(1)<1>(2)<1>[3]
10. **Pronotal laterobasal foveae:** none [0]; rounded (1); longitudinal slits (2); doubled [3]
[0]<2>(1)<2>(2)<2>[3]
11. **Pronotal prescutellar depression:** none [a]; small fovea (2); moderately broad (c); very broad [d]
[a]<2>(b)<2>(c)<2>[d]

12. **Pronotal midline:** impunctate [b]; undifferentiated (c); shallowly depressed (d); deeply sulcate [e]
[b]<2>(c)<2>(d)<2>[e]
13. **Pronotal irregular callosities:** none [0]; few (1); numerous [2]
[0]<2>(1)<2>[2]
14. **Pronotal sculpture - density:** very sparse [0]; moderate (1); very dense [2]
[0]<2>(1)<2>[2]
15. **Number of pronotal dfp spots:** none [0]; 3 (1); 5 [2]
[0]<2>(1)<2>[2]
16. **Pronotal lateroapical dfp spots:** none/single/2 separate [0]; confluent into transverse fascia [1]
[0]<2>[1]
17. **Pronotal lateral carina - length:** none/very short [0]; <midlength (1); >midlength (2); entire [3]
[0]<2>(1)<2>(2)<2>[3]
18. **Pronotal lateral carina - structure:** smooth [0]; punctured (1); crenulate (2); obliterated [3]
[0]<2>(1)<2>(2)<2>[3]
19. **Elytral striae - structure:** none [0]; puncture rows (1); continuously furrowed [2]
[0]<2>(1)<2>[2]
20. **Elytral interstriae - elevation relations:** equal [0]; alternately unequal (1); strikingly disparate [2]
[0]<2>(1)<2>[2]
21. **Elytral intercostate interstriae - convexity:** flat/depressed [0]; slightly convex (1); subcareniform [2]
[0]<1>(1)<1>[2]
22. **Elytral dfp - type:** none [a]; interstitial foveae (b); extensive patches [m]
[a]<2>(b)<2>[m]
23. **Elytral dfp - arrangement:** none/irregular [a]; transverse [b]; oblique [m]; longitudinal [z]
[b]<2>[a]<2>[z]
 $\begin{matrix} \uparrow \\ \downarrow \\ [m] \end{matrix}$
24. **Elytral dfp - spot size:** none/few punctures [0]; small foveae (1); large spots (2); partly confluent (3); continuous bands [4]
[0]<2>(1)<2>(2)<2>(3)<2>[4]
25. **Elytral epipleural pubescence:** as dorsal [0]; strikingly denser/longer [1]
[0]<2>[1]
26. **Prosternal apical margin:** truncated [1]; emarginated (2); bituberculate [3]
[1]<2>(2)<2>[3]
27. **Prosternal process - sculpture:** [smooth [a]; sparsely punctured [b]
[a]<2>[b]
28. **Prosternal process - border:** undifferentiated [0]; smooth rim (1); stria [2]
[0]<2>(1)<2>[2]

29. **Metacoxal denticle:** none [0]; broadly obliterated (1); well marked [2]
 [0]<2>(1)<2>[2]
30. **Ventral dfp - arrangement:** none [a]; margins of sternites [b]; 1 longitudinal band (x); 2 longitudinal bands [y]
 [a]<2>[b]<2>(x)<2>[y]
31. **1. sternite - structure:** flat/inconspicuously depressed [1]; sulcate [2]
 [1]<2>[2]
32. **Metafemur - posterior surface:** regularly convex [0]; indefinitely depressed (1); sulcate [2]
 [0]<1>(1)<2>[2]
33. **Elytral transverse fasciae:** none [0]; >5 (1); 3 (3); 1 [5]
 [0]<2>(1)<2>(3)<2>[5]

The differences are considered additive, so e.g. that between (2) and (4) in the character 7 equals 4, between (0) and (2) in character 21 - 2, between (0) and (4) in character 24 - 8 [if the change between given pair of character-states could have occurred on several ways, we accept the smallest possible total difference - thence in the case of character 2 we assume that the course of transformation between (b) and (e) has been (b)>(a)>(e) rather than (b)>(c)>(d)>(e), and the distance is 4 instead of 6].

The character-matrix for the analysed taxa is as follows [automorphous (terminal, unique to single taxa) character-states are marked as ***bold underlined italics***]:

	12345	67890	12345	67890	12345	67890	123
SPINTHOPTERA	3a0ya	33110	<i>ab</i> 020	01220	0 <i>az</i> 10	2a22x	200
subcincta	3a1xa	24032	bd200	03011	0mb40	3a10a	<i>225</i>
interrupta	3a0xa	24032	bd200	03011	0mb40	3a10a	223
fasciata	<i>3e</i> 0xa	24032	bd200	12011	0mb30	3b10a	221
mutabilis	3d0xa	24032	bd200	02011	0bz20	3b10b	220
argenteoguttata	3a1xa	24032	bd201	12011	0bz20	3b10b	220
dammarana	3b1xa	24033	be202	03011	0bz21	3b20a	220
saundersi	3d0xa	24133	ce202	03011	0bz20	3b00b	220
multiguttata	3a0xa	24133	ce202	03011	0bz20	3b00b	220
grosseguttata	3a0xa	24133	ce202	03011	0bz20	3b00b	220
albosparsa	3a0xa	24133	ce202	03011	0bz10	3b00b	220
farinosa	<i>3b2yz</i>	23133	ce202	030 <i>02</i>	0mz41	3b00b	220
javanica	4b0xa	23131	ce210	03121	1bz11	3b01b	220
viridisparsa	4d0xa	23131	cd210	03121	<i>2</i> bz11	3b00b	220
vitalisi	4d0xa	23031	bd210	02112	0bz11	3b00b	220
TRISTRIA	4d0xa	331 <i>03</i>	ae110	03011	0ba10	3a21b	110
ARCHEPSILA	4b0xa	330 <i>10</i>	<i>de</i> 210	0 <i>03</i> 10	0bz10	<i>1b</i> 21 <i>y</i>	200
CAPNODIS	3b0 <i>ba</i>	34020	ac220	03110	0ba10	2b12a	<i>000</i>

Having the character-matrix, it is easy to calculate the corrected distances between taxa. As an example let us do it for *D. farinosa* and *D. albosparsa*. As can be seen from the character-matrix, they differ in the characters 2, 3, 4, 5, 7, 19, 20, 22, 24 and 25; the overall (not corrected) phenetic distance is 2+4+2+4+2+2+2+6+1=27. However, the respective states of characters 3, 5, and 19 are automorphies of *D. farinosa* (*D. albosparsa* shows no unique character-state), thence the differences in

these characters must be accordingly modified, and the corrected distance becomes $2+2+2+0+2+0+2+2+6+1=19$ [note that the difference between the character-states 3:(0) in *D. albosparsa* and 3:(2) in *D. farinosa* has been reduced to 2 rather than to 0: the total (not corrected) distance is composed of two sections - (0)<2>(1) and (1)<2>(2) - of which only that between the automorphic (2) and its closest neighbour (1) has been ignored, while the distance separating non-automorphic states (1) and (0) is normally counted; in other words, in the calculation of distance we replace the automorphic feature with its closest (in the case of branched or circular transformation-series - closest in the direction of the just compared taxon) neighbour on the transformation chain]!

Performing the calculations for all pairs of taxa we arrive at the following distance-matrix:

	SP	su	in	fs	mb	ar	da	sa	mt	gr	al	fr	ja	vs	vt	TR	AR	CA
SPINTHOPTERA	0																	
subcincta	69	0																
interrupta	70	2	0															
fasciata	66	12	10	0														
mutabilis	58	23	21	13	0													
argenteoguttata	62	23	25	15	8	0												
dammarana	67	28	30	26	21	17	0											
saundersi	70	35	33	29	16	20	17	0										
multiguttata	68	33	31	29	18	18	15	2	0									
grosseguttata	68	33	31	29	18	18	15	2	<u>0</u>	0								
albosparsa	66	35	33	31	20	20	17	4	<u>2</u>	2	0							
farinosa	77	34	36	36	35	31	22	19	17	17	19	0						
javanica	54	47	45	41	32	36	35	28	26	26	24	33	0					
viridisparsa	54	43	41	37	24	32	39	24	26	26	24	37	8	0				
vitalisi	55	40	38	30	17	25	36	29	31	31	29	38	19	11	0			
TRISTRIA	44	45	43	43	34	42	39	34	36	36	34	49	34	34	35	0		
ARCHEPSILA	28	61	59	51	46	50	47	54	52	52	50	61	34	42	39	40	0	
CAPNODIS	31	50	48	44	43	47	48	55	53	53	51	66	43	47	44	41	31	0

The lowest [of course not counting the zero distances between each taxon and itself] value (marked as ***bold underlined italic***) - **0** - is that of the corrected distance between *D. m. multiguttata* and *D. m. grosseguttata*. Their last common ancestor (*A*) can be reconstructed as follows:

multiguttata	3a0xa	24133	ce202	03011	0bz20	3b00b	220
grosseguttata	3a0xa	24133	ce202	03011	0bz20	3b00b	220

A	3a0xa	24133	ce202	03011	0bz20	3b00b	220

As all the [included in the analysis] character-states of *D. multiguttata s.str.* and *D. m. grosseguttata* are identical, the reconstructed ancestor (*A*) does also not differ from them. Replacing the originally terminal taxa with this ancestor, we obtain a new character- and distance-matrices:

	12345	67890	12345	67890	12345	67890	123
SPINTHOPTERA	3a0ya	33110	ab020	01220	0az10	2a22x	200
subcincta	3a1xa	24032	bd200	03011	0mb40	3a10a	225
interrupta	3a0xa	24032	bd200	03011	0mb40	3a10a	223
fasciata	3e0xa	24032	bd200	12011	0mb30	3b10a	221
mutabilis	3d0xa	24032	bd200	02011	0bz20	3b10b	220
argenteoguttata	3a1xa	24032	bd201	12011	0bz20	3b10b	220
dammarana	3b1xa	24033	be202	03011	0bz21	3b20a	220
saundersi	3d0xa	24133	ce202	03011	0bz20	3b00b	220
A	3a0xa	24133	ce202	03011	0bz20	3b00b	220
albosparsa	3a0xa	24133	ce202	03011	0bz10	3b00b	220
farinosa	3b2yz	23133	ce202	03002	0mz41	3b00b	220
javanica	4b0xa	23131	ce210	03121	1bz11	3b01b	220
viridisparsa	4d0xa	23131	cd210	03121	2bz11	3b00b	220
vitalisi	4d0xa	23031	bd210	02112	0bz11	3b00b	220
TRISTRIA	4d0xa	33103	ae110	03011	0ba10	3a21b	110
ARCHEPSILA	4b0xa	33010	de210	00310	0bz10	1b21y	200
CAPNODIS	3b0ba	34020	ac220	03110	0ba10	2b12a	000

	SP	su	in	fs	mb	ar	da	sa	A	al	fr	ja	vs	vt	TR	AR	CA
SPINTHOPTERA	0																
subcincta	69	0															
interrupta	70	2	0														
fasciata	66	12	10	0													
mutabilis	58	23	21	13	0												
argenteoguttata	62	23	25	15	8	0											
dammarana	67	28	30	26	21	17	0										
saundersi	70	35	33	29	16	20	17	0									
A	68	33	31	29	18	18	15	2	0								
albosparsa	66	35	33	31	20	20	17	4	2	0							
farinosa	77	34	36	36	35	31	22	19	17	19	0						
javanica	54	47	45	41	32	36	35	28	26	24	33	0					
viridisparsa	54	43	41	37	24	32	39	24	26	24	37	8	0				
vitalisi	55	40	38	30	17	25	36	29	31	29	38	19	11	0			
TRISTRIA	44	45	43	43	34	42	39	34	36	34	49	34	34	35	0		
ARCHEPSILA	28	61	59	51	46	50	47	54	52	50	61	34	42	39	40	0	
CAPNODIS	31	50	48	44	43	47	48	55	53	51	66	43	47	44	41	31	0

The lowest value - 2 - figures thrice in the matrix, as the corrected distance between: 1) *D. subcincta* and *D. interrupta*; 2) *A* and *D. m. saundersi*; and 3) *A* and *D. albosparsa*. In this case, it does probably not matter whether we choose to analyze first the pair *subcincta/interrupta* or the triad *saundersi/A/albosparsa*, but in certain circumstances - through changing some (in each case different) symmorphous character-states into apomorphous - the choice may influence the results. The situation within the *saundersi/A/albosparsa*-complex is still more problematic: *A* is involved in both possible pairings, and MICSEQ - at least at this stage - does not accept polytomies, so we must make a choice though no truly reliable criterion seems to be available. The rule adopted by me is to analyse this pair first, whose members are - according to the distance-matrix - most different from any other taxon. Such pair in the present case is obviously that of *subcincta/interrupta*: the minimal distance between one of them and one of the remaining taxa is 10 (*D. interrupta* vs. *D. fasciata*), while for any pair from the *saundersi/A/albosparsa*-complex it is naturally 2 (separating *A* from the third member of the triad) [the rationale behind the "rule of the

most distant" is, that the greater the distance between, in this case, *subcincta/interrupta* and all the remaining taxa, the better "corroborated" is the naturalness of the pair, *i.e.* the less probable is that true phylogenetic relations between either *D. subcincta* or *D. interrupta* and an "outsider" (say, *D. fasciata*) are in fact closer than those within the pair]. So:

```
subcincta      3a1xa 24032 bd200 03011 0mb40 3a10a 225
interrupta     3a0xa 24032 bd200 03011 0mb40 3a10a 223
-----
B              3aBxa 24032 bd200 03011 0mb40 3a10a 22B
```

D. subcincta and *D. interrupta* are not identical, they differ in two characters. There is no generally applicable criterion to resolve unambiguously the ancestral state in cases like that of the character (3) above; however, to calculate the next distance-matrix, we must specify the states for each character and each taxon. The best solution seems to be to choose one of the descendant taxa (*D. subcincta* or *D. interrupta*) as the *ad hoc* substitute of the reconstructed ancestor (as if the other member of the pair were unknown). Again, none of the conceivable criteria to choose one of them seems easily defensible, but perhaps the most reasonable is to select that *less* distinct from its next-closest (according to the distance-matrix) relative [on the assumption that this reflects less differentiation from the substituted common ancestor]. In the present case the preferred substitute is *D. interrupta* (the distance between *D. interrupta* and *D. fasciata* is 10, while that between *D. subcincta* and *D. fasciata* is 12). In the case of character 33, neither the state (5) nor (3) are represented in any of the other taxa, only (1) is, so the state closer to (1), *i.e.* (3), must be postulated for *B*! Generally, while - without additional knowledge - it is not possible to decide, which of the two *non-automorphous* character-states of the descendant taxa has been inherited from their ancestor, it can be parsimoniously done if one state is automorphous: the ancestral state is most probably the "proximal" (closer to the remaining) one (and this frequently - as in this case - becomes the "new" automorphy).

Thence:

```
B              3a0xa 24032 bd200 03011 0mb40 3a10a 223
```

and the next character-matrix:

	12345	67890	12345	67890	12345	67890	123
SPINTHOPTERA	3a0ya	33110	a b 020	01220	0a z 10	2a22x	200
B	3a0xa	24032	bd200	03011	0mb40	3a10a	22 3
fasciata	3e0xa	24032	bd200	12011	0mb30	3b10a	221
mutabilis	3d0xa	24032	bd200	02011	0bz20	3b10b	220
argenteoguttata	3a1xa	24032	bd201	12011	0bz20	3b10b	220
dammarana	3b1xa	24033	be202	03011	0bz21	3b20a	220
saundersi	3d0xa	24133	ce202	03011	0bz20	3b00b	220
A	3a0xa	24133	ce202	03011	0bz20	3b00b	220
albosparsa	3a0xa	24133	ce202	03011	0bz10	3b00b	220
farinosa	3b2yz	23133	ce202	03002	0mz41	3b00b	220
javanica	4b0xa	23131	ce210	03121	1bz11	3b01b	220
viridisparisa	4d0xa	23131	cd210	03121	2bz11	3b00b	220
vitalisi	4d0xa	23031	bd210	02112	0bz11	3b00b	220
TRISTRIA	4d0xa	33103	ae110	03011	0ba10	3a21b	110
ARCHEPSILA	4b0xa	33010	de210	00310	0bz10	1b21y	200
CAPNODIS	3b0ba	34020	ac220	03110	0ba10	2b12a	000

Now the state (3) of the character 33 became terminal and automorphous [until now, with the existence of (5), (3) was intermediate and thence - though unique to single taxon - not considered as automorphous], and in the calculation of distances must be substituted by its nearest neighbour (1) [note that if we choose *D. subcineta* rather than *D. interrupta* to represent *B* in calculations, the situation for the character 33 would be the same: the character-state in the matrix would be (5), but it is also automorphous, and as (3) would be already eliminated, the nearest neighbour of (5) would also be (1)!].

	SP	B	fs	mb	ar	da	sa	A	al	fr	ja	vs	vt	TR	AR	CA
SPINTHOPTERA	0															
B	65	0														
fasciata	65	8	0													
mutabilis	58	19	13	0												
argenteoguttata	62	23	15	8	0											
dammarana	67	28	26	21	17	0										
saundersi	70	31	29	16	20	17	0									
A	68	29	29	18	18	15	2	0								
albosparsa	66	31	31	20	20	17	4	2	0							
farinosa	77	34	36	35	31	22	19	17	19	0						
javanica	54	43	41	32	36	35	28	26	24	33	0					
viridisparisa	54	39	37	24	32	39	24	26	24	37	8	0				
vitalisi	55	36	30	17	25	36	29	31	29	38	19	11	0			
TRISTRIA	44	41	43	34	42	39	34	36	34	49	34	34	35	0		
ARCHEPSILA	28	57	51	46	50	47	54	52	50	61	34	42	39	40	0	
CAPNODIS	31	46	44	43	47	48	55	53	51	66	43	47	44	41	31	0

Now we have to "dismember" the complex *saundersi/A/albosparsa*. *A* is common to both possible pairs, so we must look for the least distance between either *D. m. saundersi* or *D. albosparsa* and a taxon not belonging to the triad; it turns out, that for *D. m. saundersi* it is 16 and for *D. albosparsa* 17 - the difference is certainly trifling, but for lack of better criterion we select *D. albosparsa* for the next pairing:

A	3a0xa	24133	ce202	03011	0bz20	3b00b	220
albosparsa	3a0xa	24133	ce202	03011	0bz10	3b00b	220

C	3a0xa	24133	ce202	03011	0bzC0	3b00b	220

The nearest (according to the current distance-matrix) relative of both *D. albosparsa* and *A* is *D. m. saundersi*; as the respective distances are 4 and 2, the unresolved character-state of the ancestor (*C*) will be represented by that of *A*:

	12345	67890	12345	67890	12345	67890	123
SPINTHOPTERA	3a0ya	33110	<u>a</u> b020	01220	0 <u>a</u> z10	2a22x	200
B	3a0xa	24032	bd200	03011	0mb40	3a10a	22 <u>3</u>
fasciata	3 <u>e</u> 0xa	24032	bd200	12011	0mb30	3b10a	221
mutabilis	3d0xa	24032	bd200	02011	0bz20	3b10b	220
argenteoguttata	3a1xa	24032	bd201	12011	0bz20	3b10b	220
dammarana	3b1xa	24033	be202	03011	0bz21	3b20a	220
saundersi	3d0xa	24133	ce202	03011	0bz20	3b00b	220
C	3a0xa	24133	ce202	03011	0bz20	3b00b	220
farinosa	3b <u>2</u> yz	23133	ce202	030 <u>0</u> 2	0mz41	3b00b	220
javanica	4b0xa	23131	ce210	031 <u>2</u> 1	1bz11	3b01b	220
viridisparsa	4d0xa	23131	cd210	031 <u>2</u> 1	<u>2</u> bz11	3b00b	220
vitalisi	4d0xa	23031	bd210	02112	0bz11	3b00b	220
TRISTRIA	4d0xa	331 <u>0</u> 3	ae110	03011	0ba10	3a21b	110
ARCHEPSILA	4b0xa	33010	<u>d</u> e210	0 <u>0</u> 310	0bz10	<u>1</u> b21 <u>y</u>	200
CAPNODIS	3b0 <u>b</u> a	34020	ac220	03110	0ba10	2b12a	<u>0</u> 00

	SP	B	fs	mb	ar	da	sa	C	fr	ja	vs	vt	TR	AR	CA
SPINTHOPTERA	0														
B	65	0													
fasciata	65	8	0												
mutabilis	58	19	13	0											
argenteoguttata	62	23	15	8	0										
dammarana	67	28	26	21	17	0									
saundersi	70	31	29	16	20	17	0								
C	68	29	29	18	18	15	<u>2</u>	0							
farinosa	77	34	36	35	31	22	19	17	0						
javanica	54	43	41	32	36	35	28	26	33	0					
viridisparsa	54	39	37	24	32	39	24	26	37	8	0				
vitalisi	55	36	30	17	25	36	29	31	38	19	11	0			
TRISTRIA	44	41	43	34	42	39	34	36	49	34	34	35	0		
ARCHEPSILA	28	57	51	46	50	47	54	52	61	34	42	39	40	0	
CAPNODIS	31	46	44	43	47	48	55	53	66	43	47	44	41	31	0

Now the lowest value represents the distance between *D. m. saundersi* and *C*. However, unlike *A* involved in the previous reconstruction, not all character-states of *C* are resolved, and the substitution of the ancestor by one of its descendants should, of course, be applied **only** to the calculation of the distance-matrix: to reconstruct the next ancestor we must take the unresolved character-states into consideration as such! In this case, (C) in the character 24 means "(1) or (2)", and as the respective feature in *D. m. saundersi* is (2), that in the ancestor must also be reconstructed as (2).

saundersi	3d0xa	24133	ce202	03011	0bz20	3b00b	220
C	3a0xa	24133	ce202	03011	0bzC0	3b00b	220

D	3D0xa	24133	ce202	03011	0bz20	3b00b	220

Now, in *D*, the character 2 is unresolved [(a) or (d)], and must be substituted by that of *C*: the next-lowest value in the distance-matrix for *C* is 15, for *D. m. saundersi* 17. Thus:

	12345	67890	12345	67890	12345	67890	123
SPINTHOPTERA	3a0ya	33110	a b 020	01220	0a z 10	2a22x	200
B	3a0xa	24032	bd200	03011	0mb40	3a10a	22 3
fasciata	3e0xa	24032	bd200	12011	0mb30	3b10a	221
mutabilis	3d0xa	24032	bd200	02011	0bz20	3b10b	220
argenteoguttata	3a1xa	24032	bd201	12011	0bz20	3b10b	220
dammarana	3b1xa	24033	be202	03011	0bz21	3b20a	220
D	3a0xa	24133	ce202	03011	0bz20	3b00b	220
farinosa	3b2y z	23133	ce202	030 0 2	0mz41	3b00b	220
javanica	4b0xa	23131	ce210	03121	1bz11	3b01b	220
viridisparsa	4d0xa	23131	cd210	03121	2 b z11	3b00b	220
vitalisi	4d0xa	23031	bd210	02112	0bz11	3b00b	220
TRISTRIA	4d0xa	331 0 3	ae110	03011	0ba10	3a21b	110
ARCHEPSILA	4b0xa	330 1 0	d e 210	0 0 310	0bz10	1b21 y	200
CAPNODIS	3b0 b a	34020	ac220	03110	0ba10	2b12a	0 00

	SP	B	fs	mb	ar	da	D	fr	ja	vs	vt	TR	AR	CA
SPINTHOPTERA	0													
B	65	0												
fasciata	65	8	0											
mutabilis	58	19	13	0										
argenteoguttata	62	23	15	8	0									
dammarana	67	28	26	21	17	0								
D	68	29	29	18	18	15	0							
farinosa	77	34	36	35	31	22	17	0						
javanica	54	43	41	32	36	35	26	33	0					
viridisparsa	54	39	37	24	32	39	26	37	8	0				
vitalisi	55	36	30	17	25	36	31	38	19	11	0			
TRISTRIA	44	41	43	34	42	39	36	49	34	34	35	0		
ARCHEPSILA	28	57	51	46	50	47	52	61	34	42	39	40	0	
CAPNODIS	31	46	44	43	47	48	53	66	43	47	44	41	31	0

Now again the lowest value - **8** - occurs thrice (*B/fasciata*, *mutabilis/argenteoguttata*, and *javanica/viridisparsa*). The next-lowest distance for the latter pair is 11 (*viridisparsa/vitalisi*), while for both former pairs it is 13 (*fasciata/mutabilis*); as however both this and the immediately higher value (15 - *fasciata/argenteoguttata*) involve representatives of both pairs, it is only the third in order - 17 (*argenteoguttata/danmarana*) - which allows to discriminate between them: as the respective value for the pair *B/fasciata* is higher (26 - *fasciata/danmarana*; 19 and 23 involve again members of both groups), it is this pair which should be considered first:

```

B          3aBxa 24032 bd200 03011 0mb40 3a10a 22B
fasciata  3e0xa 24032 bd200 12011 0mb30 3b10a 221
-----
E          3a0xa 24032 bd200 EE011 0mbE0 3E10a 221

```

Three points are worth mentioning here. Firstly, the character-state 2(e) [*i.e.* the state (e) of character 2] was an automorphy of *D. fasciata*, thence - as (a) is its nearest neighbour in the transformation-series - character 2 need not be considered as unresolved in *E*. Secondly, according to our "rule of thumb" unresolved characters of *E* will be represented by features of *D. fasciata*, and thus the state 24(4) of *B* remains no longer "in game", what makes this feature in *D. farinosa* - not directly involved in the reconstruction of *E*! - automorphous. Thirdly, automorphous becomes also - having 33(3) of *B* "run out" - the state 33(1) in *E*.

```

                12345 67890 12345 67890 12345 67890 123
                -----
SPINTHOPTERA  3a0ya 33110 ab020 01220 0az10 2a22x 200
E              3a0xa 24032 bd200 12011 0mb30 3b10a 221
mutabilis     3d0xa 24032 bd200 02011 0bz20 3b10b 220
argenteoguttata 3alxa 24032 bd201 12011 0bz20 3b10b 220
dammarana     3b1xa 24033 be202 03011 0bz21 3b20a 220
D              3a0xa 24133 ce202 03011 0bz20 3b00b 220
farinosa      3b2yz 23133 ce202 03002 0mz41 3b00b 220
javanica      4b0xa 23131 ce210 03121 1bz11 3b01b 220
viridisparsa  4d0xa 23131 cd210 03121 2bz11 3b00b 220
vitalisi      4d0xa 23031 bd210 02112 0bz11 3b00b 220
TRISTRIA     4d0xa 33103 ae110 03011 0ba10 3a21b 110
ARCHEPSILA   4b0xa 33010 de210 00310 0bz10 1b21y 200
CAPNODIS     3b0ba 34020 ac220 03110 0ba10 2b12a 000

```

```

                SPI  E mut arg dam  D  far jav vir vit TRI ARC CAP
                -----
SPINTHOPTERA  0
E              62  0
mutabilis     58 12  0
argenteoguttata 62 12  8  0
dammarana     67 25 21 17  0
D              68 26 18 18 15  0
farinosa      75 33 33 29 20 15  0
javanica      54 40 32 36 35 26 31  0
viridisparsa  54 36 24 32 39 26 35  8  0
vitalisi      55 29 17 25 36 31 36 19 11  0
TRISTRIA     44 42 34 42 39 36 47 34 34 35  0
ARCHEPSILA   28 50 46 50 47 52 59 34 42 39 40  0
CAPNODIS     31 43 43 47 48 53 64 43 47 44 41 31  0

```

The relations between *mutabilis/argenteoguttata* and *javanica/viridisparsa* have not changed (the lowest value in both cases 8, the distance to next-nearest relative 12 vs. 11) so now it is the former pair's turn:

```

mutabilis     3d0xa 24032 bd200 02011 0bz20 3b10b 220
argenteoguttata 3alxa 24032 bd201 12011 0bz20 3b10b 220
-----
F              3FFxa 24032 bd20F 02011 0bz20 3b10b 220

```

Three "next-lowest" values (12, 17 and 18) for *D. mutabilis* and *D. argenteoguttata* are identical, so it is only the fourth (21) which makes *D. mutabilis*

the preferred substitute for *F* (again, this is almost purely formal decision, but we have no better criterion, and fortunately in such cases it is practically of no importance which of the descendant taxa is chosen).

	12345	67890	12345	67890	12345	67890	123
SPINTHOPTERA	3a0ya	33110	a b 020	01220	0a z 10	2a22x	200
E	3a0xa	24032	bd200	12011	0m b 30	3b10a	22 <u>1</u>
F	3d0xa	24032	bd200	02011	0bz20	3b10b	220
dammarana	3b1xa	24033	be202	03011	0bz21	3b20a	220
D	3a0xa	24133	ce202	03011	0bz20	3b00b	220
farinosa	3b2yz	23133	ce202	03002	0mz41	3b00b	220
javanica	4b0xa	23131	ce210	03121	1bz11	3b01b	220
viridisparsa	4d0xa	23131	cd210	03121	2bz11	3b00b	220
vitalisi	4d0xa	23031	bd210	02112	0bz11	3b00b	220
TRISTRIA	4d0xa	33103	ae110	03011	0ba10	3a21b	110
ARCHEPSILA	4b0xa	33010	de210	00310	0bz10	1b21y	200
CAPNODIS	3b0ba	34020	ac220	03110	0ba10	2b12a	000

	SPI	E	F	dam	D	far	jav	vir	vit	TRI	ARC	CAP
SPINTHOPTERA	0											
E	60	0										
F	58	10	0									
dammarana	67	23	21	0								
D	68	24	18	15	0							
farinosa	75	31	33	20	15	0						
javanica	54	38	32	35	26	31	0					
viridisparsa	54	34	24	39	26	35	<u>g</u>	0				
vitalisi	55	27	17	36	31	36	19	11	0			
TRISTRIA	44	40	34	39	36	47	34	34	35	0		
ARCHEPSILA	28	48	46	47	52	59	34	42	39	40	0	
CAPNODIS	31	41	43	48	53	64	43	47	44	41	31	0

javanica	4b0xa	23131	ce210	03121	1bz11	3b01b	220
viridisparsa	4d0xa	23131	cd210	03121	2bz11	3b00b	220
G	4G0xa	23131	cG210	03121	1bz11	3b0Gb	220

The preferred substitute for unresolved character-states (characters 2, 12 and 29) of *G* are those of *D. viridisparsa*, but note that the character 21 does not, in fact, belong to this category: like in the case of the character 33 in reconstruction of *B*, neither the state (1) nor (2) are represented in any of the other taxa, so the state (1) - as closer to (0) - must be postulated for *G* (even though it was characteristic of *D. javanica*, not of *D. viridisparsa*!).

	12345	67890	12345	67890	12345	67890	123
SPINTHOPTERA	3a0ya	33110	<u>ab</u> 020	01220	0 <u>az</u> 10	2a22x	200
E	3a0xa	24032	bd200	12011	0m <u>b</u> 30	3b10a	<u>221</u>
F	3d0xa	24032	bd200	02011	0bz20	3b10b	220
dammarana	3b1xa	24033	be202	03011	0bz21	3b20a	220
D	3a0xa	24133	ce202	03011	0bz20	3b00b	220
farinosa	3b <u>2yz</u>	23133	ce202	030 <u>02</u>	0mz <u>41</u>	3b00b	220
G	4d0xa	23131	cd210	03121	<u>1bz</u> 11	3b00b	220
vitalisi	4d0xa	23031	bd210	02112	0bz11	3b00b	220
TRISTRIA	4d0xa	331 <u>03</u>	ae110	03011	0ba10	3a21b	110
ARCHEPSILA	4b0xa	33010	<u>de</u> 210	0 <u>03</u> 10	0bz10	<u>1b21y</u>	200
CAPNODIS	3b0 <u>ba</u>	34020	ac220	03110	0ba10	2b12a	<u>000</u>

SPI E F dam D far G vit TRI ARC CAP

SPINTHOPTERA	0										
E	60	0									
F	58	<u>10</u>	0								
dammarana	67	<u>23</u>	21	0							
D	68	24	18	15	0						
farinosa	75	31	33	20	15	0					
G	53	33	23	38	25	34	0				
vitalisi	55	27	17	36	31	36	<u>10</u>	0			
TRISTRIA	44	40	34	39	36	47	<u>33</u>	35	0		
ARCHEPSILA	28	48	46	47	52	59	41	39	40	0	
CAPNODIS	31	41	43	48	53	64	46	44	41	31	0

Again the lowest value (10) appears twice (*E/F* and *G/vitalisi*), and again the "next-lowest" (17 for *F/vitalisi*) is common to both of them, so that only the third in the order (23 vs. 18) gives precedence to the latter. Choosing *D. vitalisi* to represent unresolved character-states in *H* makes 19(2) automorphous in *Spinthoptera*.

G	4G0xa	23131	cG210	03121	1bz11	3b0Gb	220
vitalisi	4d0xa	23031	bd210	02112	0bz11	3b00b	220

H	4d0xa	23H31	Hd210	0H1HH	0bz11	3b00b	220
	12345	67890	12345	67890	12345	67890	123

SPINTHOPTERA	3a0ya	33110	<u>ab</u> 020	012 <u>20</u>	0 <u>az</u> 10	2a22x	200
E	3a0xa	24032	bd200	12011	0m <u>b</u> 30	3b10a	<u>221</u>
F	3d0xa	24032	bd200	02011	0bz20	3b10b	220
dammarana	3b1xa	24033	be202	03011	0bz21	3b20a	220
D	3a0xa	24133	ce202	03011	0bz20	3b00b	220
farinosa	3b <u>2yz</u>	23133	ce202	030 <u>02</u>	0mz <u>41</u>	3b00b	220
M	4d0xa	<u>23031</u>	bd210	0211 <u>2</u>	0bz <u>11</u>	3b <u>00b</u>	220
TRISTRIA	4d0xa	331 <u>03</u>	ae110	03011	0ba10	3a21b	110
ARCHEPSILA	4b0xa	33010	<u>de</u> 210	0 <u>03</u> 10	0bz10	<u>1b21y</u>	200
CAPNODIS	3b0 <u>ba</u>	34020	ac220	03110	0ba10	2b12a	<u>000</u>

	SPI	E	F	dam	D	far	H	TRI	ARC	CAP
SPINTHOPTERA	0									
E	58	0								
F	56	<u>10</u>	0							
dammarana	65	23	21	0						
D	66	24	18	15	0					
farinosa	73	31	33	20	15	0				
H	53	27	17	36	31	36	0			
TRISTRIA	42	40	34	39	36	47	35	0		
ARCHEPSILA	26	48	46	47	52	59	39	40	0	
CAPNODIS	29	41	43	48	53	64	44	41	31	0
E		3a0xa	24032	bd200	EE011	0mbE0	3E10a	221		
F		3FFxa	24032	bd20F	02011	0bz20	3b10b	220		
I		3a0xa	24032	bd200	02011	0IzI0	3b10I	220		

The character 24 in *E* was unresolved with the possibilities (3) or (4); the respective feature in *F* was (2), so it remains unresolved in *I*; however, only one - closest to (2), *i.e.* (3) - of the states possible in *E* remains as a possibility also for *I* [*i.e.* the possibilities for *I* are (2) or (3), but not (4)]!

	12345	67890	12345	67890	12345	67890	123
SPINTHOPTERA	3a0ya	33110	<u>ab</u> 020	012 <u>20</u>	0 <u>az</u> 10	2a22x	200
I	3d0xa	24032	bd200	02011	0bz20	3b10b	220
dammarana	3b1xa	24033	be202	03011	0bz21	3b20a	220
D	3a0xa	24133	ce202	03011	0bz20	3b00b	220
farinosa	3b <u>2yz</u>	23133	ce202	030 <u>02</u>	0 <u>mz</u> 41	3b00b	220
H	4d0xa	23031	bd210	02112	0bz11	3b00b	220
TRISTRIA	4d0xa	331 <u>03</u>	ae110	03011	0ba10	3a21b	110
ARCHEPSILA	4b0xa	33010	<u>de</u> 210	0 <u>03</u> 10	0bz10	<u>1b</u> 21y	200
CAPNODIS	3b0 <u>ba</u>	34020	ac220	03110	0ba10	2b12a	<u>000</u>

	SPI	I	dam	D	far	H	TRI	ARC	CAP
SPINTHOPTERA	0								
I	54	0							
dammarana	65	19	0						
D	66	16	15	0					
farinosa	69	27	16	<u>11</u>	0				
H	53	19	36	31	32	0			
TRISTRIA	42	36	39	36	43	35	0		
ARCHEPSILA	26	44	47	52	55	39	40	0	
CAPNODIS	29	41	48	53	60	44	41	31	0
D		3D0xa	24133	ce202	03011	0bz20	3b00b	220	
farinosa		3b <u>2ye</u>	23133	ce202	030 <u>02</u>	0 <u>mz</u> 41	3b00b	220	
J		3JJJa	2J133	ce202	0301J	0bz2J	3b00b	220	

Here we have an especially instructive example of the significance of distinguishing between auto- and symmorphies. *D. farinosa* is morphologically by far the most distinctive species, and on the grounds of "overall similarity" its phylogenetic position could not be correctly resolved: it shows no specific similarity to any other species (or group of species) in the genus. Accordingly, it differs in unusually many

(10) characters from *D* (while, e.g., *D. dammarana* differs from *D* in only 7 characters). However, five - 3(2), 5(e), 19(2), 22(m) and 24(4) - of the differing pairs of character-states are represented in *D. farinosa* by automorphies (note that at the beginning of analysis only three automorphies were identified!), and having introduced the respective corrections (replacing "overall distances" by "corrected distances") it becomes clear that *D. farinosa* rather than *D. dammarana* is the closest relative of *D* (and thence of its descendants, *D. multiguttata* and *D. albosparsa*), while the striking disparity between them is the result of rapid divergent evolution of *D. farinosa*.

Unresolved character 2 in *D* allows for (a) or (d), in *D. farinosa* the respective character-state is (b); as (a) is closer to (b) in the transformation-series than (d), the possibilities for *J* are (a) or (b). 3(2) is an automorphy in *D. farinosa*, but (1) still (in *D. dammarana*) remains "in game" so this character in *J* is unresolved as (0) or (1) [choosing features of *D* to represent those unresolved in *J* makes 3(1) apomorphous for *D. dammarana*]. 5(e), 19(0), 22(m) and 24(4) are also apomorphous, what leaves 5(a), 19(1), 22(b) and 24(2) as the only possibilities for *J*. 4(y) becomes automorphous in *Spinthoptera*, and 20(2) in *H*.

	12345	67890	12345	67890	12345	67890	123
SPINTHOPTERA	3a0 <u>y</u> a	33110	a <u>b</u> 020	012 <u>2</u> 0	0 <u>a</u> z10	2a22x	200
I	3d0xa	24032	bd200	02011	0bz20	3b10b	220
dammarana	3b <u>1</u> xa	24033	be202	03011	0bz21	3b20a	220
J	3a0xa	24133	ce202	03011	0bz20	3b00b	220
H	4d0xa	23031	bd210	0211 <u>2</u>	0bz11	3b00b	220
TRISTRIA	4d0xa	331 <u>0</u> 3	ae110	03011	0ba10	3a21b	110
ARCHEPSILA	4b0xa	33010	<u>d</u> e210	0 <u>0</u> 310	0bz10	<u>1</u> b21 <u>y</u>	200
CAPNODIS	3b0 <u>b</u> a	34020	ac220	03110	0ba10	2b12a	<u>0</u> 00

	SPI	I	dam	J	H	TRI	ARC	CAP
SPINTHOPTERA	0							
I	52	0						
dammarana	61	17	0					
J	66	18	<u>11</u>	0				
H	49	17	32	31	0			
TRISTRIA	40	36	37	38	33	0		
ARCHEPSILA	24	44	45	50	37	40	0	
CAPNODIS	25	41	46	51	42	41	31	0

dammarana	3b <u>1</u> xa	24033	be202	03011	0bz21	3b20a	220
J	3J <u>J</u> xa	2J133	ce202	0301J	0bz2J	3b00b	220
K	3b <u>1</u> xa	24K33	Ke20 <u>2</u>	03011	0bz21	3bK0K	220

2(a), hitherto present in *J* as a result of substitution of its unresolved features with those of *D* (and there "inherited" from *C*), now is automorphous in *Spinthoptera*; 15(2) does not occur in any other taxon, so it becomes automorphy in *K*.

	12345	67890	12345	67890	12345	67890	123
SPINTHOPTERA	3a0ya	33110	ab020	01220	0az10	2a22x	200
I	3d0xa	24032	bd200	02011	0bz20	3b10b	220
K	3b1xa	24033	be202	03011	0bz21	3b20a	220
H	4d0xa	23031	bd210	02112	0bz11	3b00b	220
TRISTRIA	4d0xa	33103	ae110	03011	0ba10	3a21b	110
ARCHEPSILA	4b0xa	33010	de210	00310	0bz10	1b21y	200
CAPNODIS	3b0ba	34020	ac220	03110	0ba10	2b12a	000

SPI I K H TRI ARC CAP

SPINTHOPTERA	0						
I	52	0					
K	57	<u>13</u>	0				
H	47	15	26	0			
TRISTRIA	40	36	33	31	0		
ARCHEPSILA	22	42	39	33	38	0	
CAPNODIS	25	41	42	40	41	29	0

I	3a0xa	24032	bd200	02011	0IzI0	3b10I	220
K	3b1xa	24K33	Ke202	03011	0bz21	3bK0K	220

L	3b0xa	2403L	bL200	0L011	0bz2L	3b10L	220
---	-------	-------	-------	-------	-------	-------	-----

12345 67890 12345 67890 12345 67890 123

	12345	67890	12345	67890	12345	67890	123
SPINTHOPTERA	3a0ya	33110	ab020	01220	0az10	2a22x	200
L	3d0xa	24032	bd200	02011	0bz20	3b10b	220
H	4d0xa	23031	bd210	02112	0bz11	3b00b	220
TRISTRIA	4d0xa	33103	ae110	03011	0ba10	3a21b	110
ARCHEPSILA	4b0xa	33010	de210	00310	0bz10	1b21y	200
CAPNODIS	3b0ba	34020	ac220	03110	0ba10	2b12a	000

SPI L H TRI ARC CAP

SPINTHOPTERA	0					
L	46	0				
H	44	<u>14</u>	0			
TRISTRIA	36	34	28	0		
ARCHEPSILA	20	34	32	36	0	
CAPNODIS	23	33	39	39	29	0

L	3b0xa	2403L	bL200	0L011	0bz2L	3b10L	220
H	4d0xa	23H31	Hd210	0H1HH	0bz11	3b00b	220

M	MM0xa	2M03M	bd210	0MM11	0bz11	3b10b	220
---	-------	-------	-------	-------	-------	-------	-----

12345 67890 12345 67890 12345 67890 123

	12345	67890	12345	67890	12345	67890	123
SPINTHOPTERA	3a0ya	33110	ab020	01220	0az10	2a22x	200
M	4d0xa	<u>23031</u>	bd210	02111	0bz11	3b10b	220
TRISTRIA	4d0xa	33103	ae110	03011	0ba10	3a21b	110
ARCHEPSILA	4b0xa	33010	de210	00310	0bz10	1b21y	200
CAPNODIS	3b0ba	<u>34020</u>	ac220	03110	0ba10	2b12a	000

	SPI	M	TRI	ARC	CAP														
SPINTHOPTERA	0																		
M	37	0																	
TRISTRIA	32	17	0																
ARCHEPSILA	20	<u>25</u>	32	0															
CAPNODIS	19	28	31	25	0														
M	MM0xa	2M03M	bd210	0MM11	0bz11	3b10b	<u>220</u>												
TRISTRIA	4d0xa	33103	ae110	03011	0ba10	3a21b	<u>110</u>												
N	4d0xa	33NN2	NNN10	03011	0bN10	3b11b	210												
								12345	67890	12345	67890	12345	67890	123					
SPINTHOPTERA	<u>3a0ya</u>	<u>33110</u>	<u>ab020</u>	<u>01220</u>	<u>0az10</u>	<u>2a22x</u>	200												
N	<u>4d0xa</u>	<u>33022</u>	bd210	<u>03011</u>	0bz10	<u>3b11b</u>	<u>210</u>												
ARCHEPSILA	4b0xa	33010	<u>de210</u>	<u>00310</u>	0bz10	<u>1b21y</u>	200												
CAPNODIS	3b0 <u>ba</u>	<u>34020</u>	ac220	03110	0b <u>a10</u>	2b12 <u>a</u>	<u>000</u>												

Here, in fact, ends the reconstruction of genealogical relations: only outgroups remained, which have been included only in order to "root" the cladogram of *Dicercomorpha*; the extension of the analysis to them would not influence the topology of relations *within* the genus, while attempt to reconstruct the relations *among* them would be abortive: the features used in the character-matrices above have been selected as those appropriate for the analysis of the *internal* relations among the *species* of *Dicercomorpha*, i.e. variable within the genus [or different in *more than one* outgroup: character-states specific to single outgroup would be its automorphies, and as such unhelpful in phylogenetic analysis of *Dicercomorpha*]; those useful at the higher level (differentiated *between* genera, but relatively stable within them) have naturally been mostly omitted as uninformative for our purpose.

We have left the characters of reconstructed ancestral taxa (*A - J*) in the state of resolution resulting from the comparison of their immediate *descendants*; however, we can further resolve them using the reconstruction of further *ancestors*. Starting from the "bottom", we can see that e.g. character 1 in *N*, resolved as (4), determines that it should be also (4) in *M* [hitherto unresolved as (3) or (4)]; similarly resolved can be characters 2, 7, 10, 17 and 18, so that there remains no ambiguity as to the characters of *M* [now ***bold underlined italic*** means a new character-state, different from that in the immediate ancestor, i.e. a synapomorphy of the lineage (though, to be sure, some of them revert in further evolution); note that all the features identified previously as automorphies turn out now as synapomorphies, but - due to convergences - by far not all synapomorphies were automorphies at any stage of the analysis]:

M:	MM0xa	2M03M	bd210	0MM11	0bz11	3b10b	<u>220</u>	→											
								→	4d0xa	<u>23032</u>	bd210	03011	0bz1 <u>1</u>	3b1 <u>0</u> b	<u>220</u>				
N:	4d0xa	33NN2	NNN10	03011	0bN10	3b11b	210												

So reconstructed *M* enables us to resolve the hitherto ambiguous characters in *L* and *H*:

L: 3b0xa 2403L bL200 0L011 0bz2L 3b10L 220 →
 → 3b0xa 24032 bd200 03011 0bz21 3b10b 220
 H: 4d0xa 23H31 Hd210 0H1HH 0bz11 3b00b 220
 → 4d0xa 23031 bd210 03111 0bz11 3b00b 220

M: 4d0xa 23032 bd210 03011 0bz11 3b10b 220

&c.:

I: 3a0xa 24032 bd200 02011 0IzI0 3b10I 220 →
 → 3a0xa 24032 bd200 02011 0bz20 3b10b 220
 K: 3b1xa 24K33 Ke202 03011 0bz21 3bK0K 220 >
 → 3b1xa 24033 be202 03011 0bz21 3b10b 220

L: 3b0xa 24032 bd200 03011 0bz21 3b10b 220

Character-state 28(1), though not represented in either (*D. dammarana* or *J*) of the immediate descendants of *K*, as intermediate between (0) and (2) cannot be excluded from the possibilities for *K* - and indeed, the respective feature in *L* being just (1), this is the most parsimonious option! The same is the situation with the character 3 in *J*.

J: 3JJxa 2J133 ce202 0301J 0bz2J 3b00b 220 →
 → 3b1xa 24133 ce202 03011 0bz21 3b00b 220

K: 3b1xa 24033 be202 03011 0bz21 3b10b 220

D: 3D0xa 24133 ce202 03011 0bz20 3b00b 220 →
 → 3a0xa 24133 ce202 03011 0bz20 3b00b 220

J: 3b1xa 24133 ce202 03011 0bz21 3b00b 220

The feature 2(b) in *J* differs from both possible states [(a) or (d)] in *D*, so we must choose the nearer of the two *i.e.* (a) [note that in this case it is more parsimonious to consider not (b) as intermediate between (a) and (d), but rather (a) as intermediate between (b) and (d): the distance from (b) through (a) to (d) is shorter than from (a) through (b) and (c) to (d)!].

E: 3a0xa 24032 bd200 EE011 0mbE0 3E10a 221 →
 → 3a0xa 24032 bd200 02011 0mb30 3b10a 221
 F: 3FFxa 24032 bd20F 02011 0bz20 3b10b 220 →
 → 3a0xa 24032 bd200 02011 0bz20 3b10b 220

I: 3a0xa 24032 bd200 02011 0bz20 3b10b 220

As we can see, *F* is - on grounds of the characters included in the analysis - indistinguishable from *I*, so we have here, in fact, an "unresolved trichotomy": the seemingly clear resolution (much greater - 12 vs. 8 - distance between *D. mutabilis* or *D. argenteoguttata* and *E* than between one another) at earlier stage of the analysis having resulted from camouflaging of relatively numerous automorphies in *E* by convergences.

G: 4G0xa 23131 cG210 03121 1bz11 3b0Gb 220 →
→ 4d0xa 23131 cd210 03121 1bz11 3b00b 220

H: 4d0xa 23031 bd210 03111 0bz11 3b00b 220
B: 3aBxa 24032 bd200 03011 0mb40 3a10a 22B →
→ 3a0xa 24032 bd200 03011 0mb40 3a10a 223

E: 3a0xa 24032 bd200 02011 0mb30 3b10a 221
C: 3a0xa 24133 ce202 03011 0bzC0 3b00b 220 →
→ 3a0xa 24133 ce202 03011 0bz20 3b00b 220

D: 3a0xa 24133 ce202 03011 0bz20 3b00b 220

As in the case of *F* vs. *I*, *C* is identical (as far as the analyzed characters are concerned) to *D*; moreover, indistinguishable remains also *A* (and both its descendants, *D. multiguttata s.str.* and *D. m. grosseguttata*).

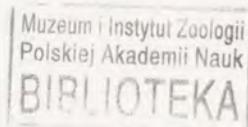
A: 3a0xa 24133 ce202 03011 0bz20 3b00b 220

C: 3a0xa 24133 ce202 03011 0bz20 3b00b 220

Thus, final (including reconstructed ancestors) character-matrix for *Dicercomorpha* looks as follows:

	12345	67890	12345	67890	12345	67890	123
SPINTHOPTERA	3a0ya	33110	ab020	01220	0az10	2a22x	200
subcincta	3a1xa	24032	bd200	03011	0mb40	3a10a	22 <u>5</u>
interrupta	3a0xa	24032	bd200	03011	0mb40	3a10a	22 <u>3</u>
fasciata	3e0xa	24032	bd200	12011	0mb30	3b10a	221
mutabilis	3d0xa	24032	bd200	02011	0bz20	3b10b	220
argenteoguttata	3a1xa	24032	bd201	12011	0bz20	3b10b	220
dammarana	3b1xa	24033	be202	03011	0bz21	3b20a	220
saundersi	3d0xa	24133	ce202	03011	0bz20	3b00b	220
multiguttata	3a0xa	24133	ce202	03011	0bz20	3b00b	220
grosseguttata	3a0xa	24133	ce202	03011	0bz20	3b00b	220
albosparsa	3a0xa	24133	ce202	03011	0bz10	3b00b	220
farinosa	3b2yz	23133	ce202	03002	0mz41	3b00b	220
javanica	4b0xa	23131	ce210	03121	1bz11	3b01b	220
viridisparsa	4d0xa	23131	cd210	03121	2bz11	3b00b	220
vitalisi	4d0xa	23031	bd210	02112	0bz11	3b00b	220
TRISTRIA	4d0xa	33103	ae110	03011	0ba10	3a21b	110
ARCHEPSILA	4b0xa	33010	de210	00310	0bz10	1b21y	200
CAPNODIS	3b0ba	34020	ac220	03110	0ba10	2b12a	000
A	3a0xa	24133	ce202	03011	0bz20	3b00b	220
B	3a0xa	24032	bd200	03011	0mb40	3a10a	22 <u>3</u>
C	3a0xa	24133	ce202	03011	0bz20	3b00b	220
D	3a0xa	24133	ce202	03011	0bz20	3b00b	220
E	3a0xa	24032	bd200	02011	0mb30	3b10a	22 <u>1</u>
F	3a0xa	24032	bd200	02011	0bz20	3b10b	220
G	4d0xa	23131	cd210	03121	1bz11	3b00b	220
H	4d0xa	23031	bd210	03111	0bz11	3b00b	220
I	3a0xa	24032	bd200	02011	0bz20	3b10b	220
J	3b1xa	24133	ce202	03011	0bz21	3b00b	220
K	3b1xa	24033	be202	03011	0bz21	3b10b	220
L	3b0xa	24032	bd200	03011	0bz21	3b10b	220
M	4d0xa	23032	bd210	03011	0bz11	3b10b	220

The resulting genealogical tree (showing branching pattern and approximate length of branches: weighed distances between each ancestor and its immediate descendants - fig.11), together with the character-matrix, allows to trace the evolution of particular characters, and evaluate the degree of support for particular clades.



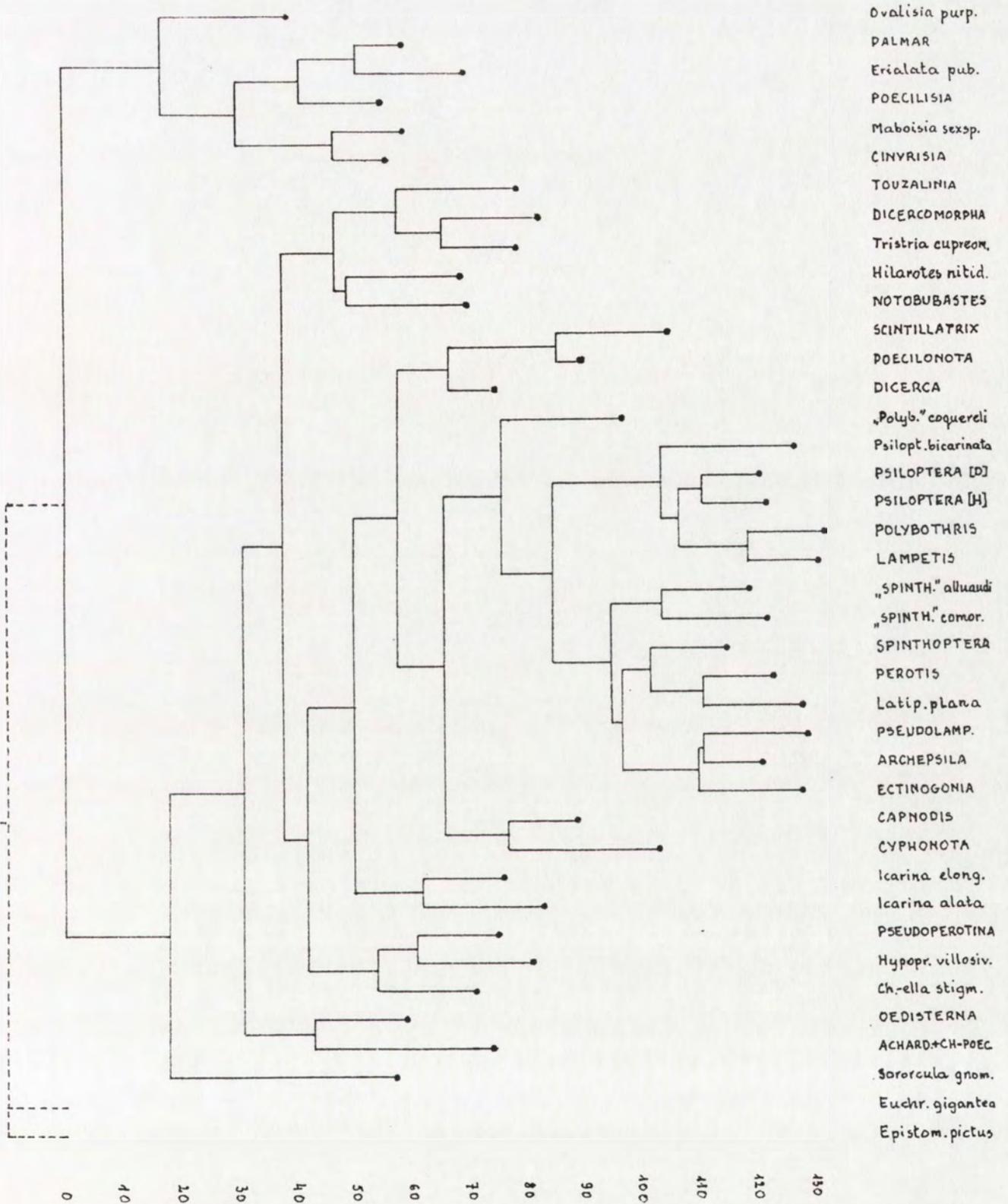


Fig. 1. General intergeneric cladogram of the subtribe Psilopterina LAC.

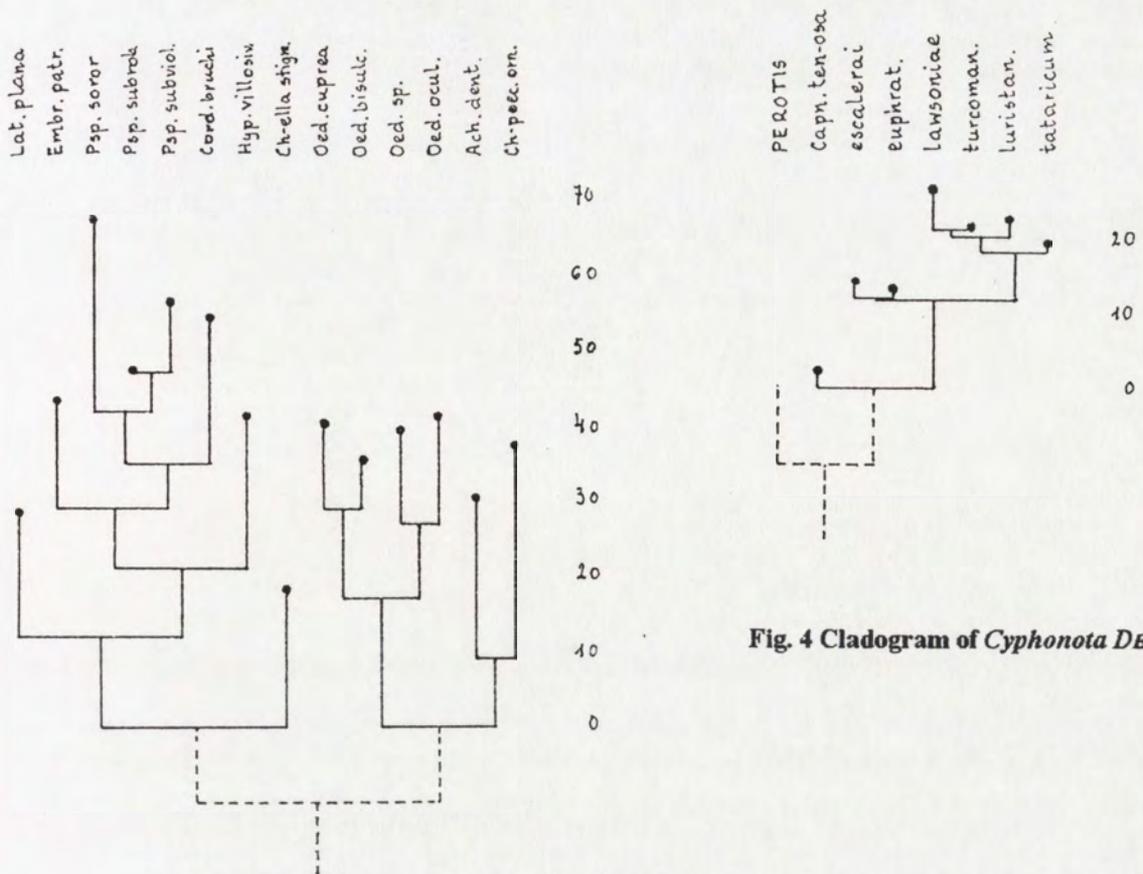


Fig. 4 Cladogram of *Cyphonota* DEJ.

Fig. 2 Cladogram of the Pseudoperotina TMA. and *Oedisterna* LAC.

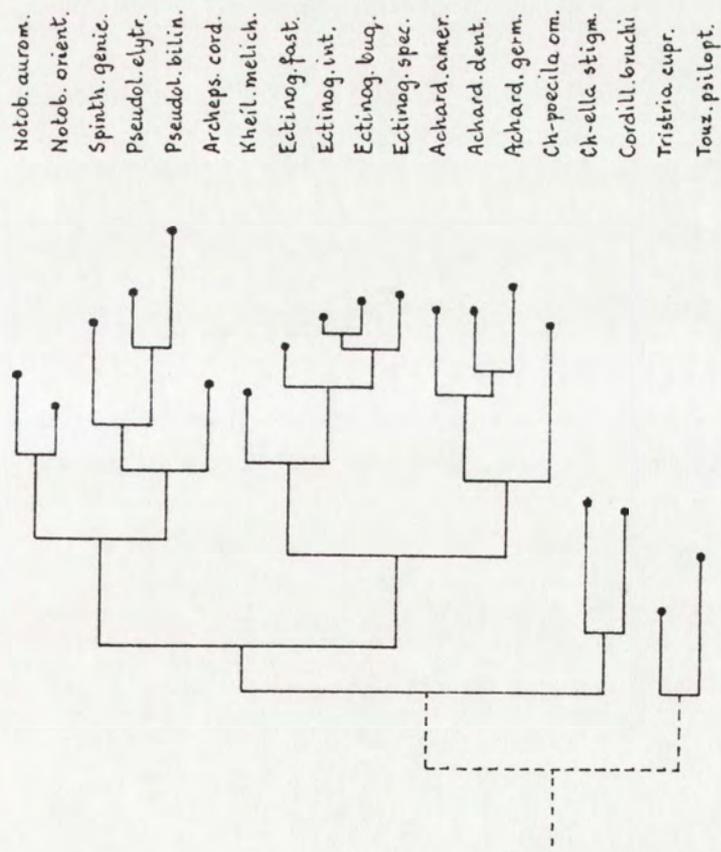


Fig. 3. Cladogram of *Chalcopyocila* THS., *Achardella* OBB., *Ectinogonia* SPIN., *Pseudolampetis* OBB. and *Notobubastes* CART.

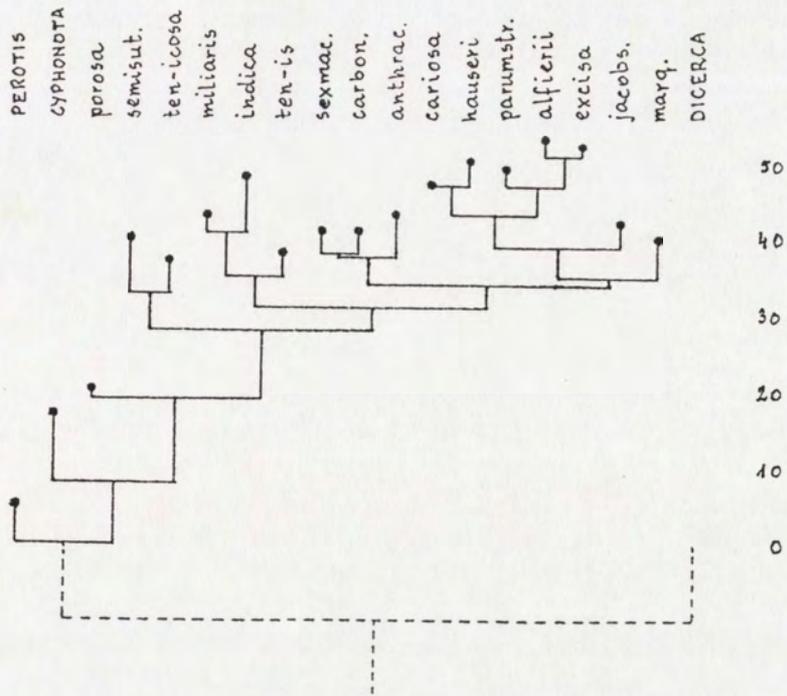


Fig. 5. Cladogram of *Capnodis* Esch.

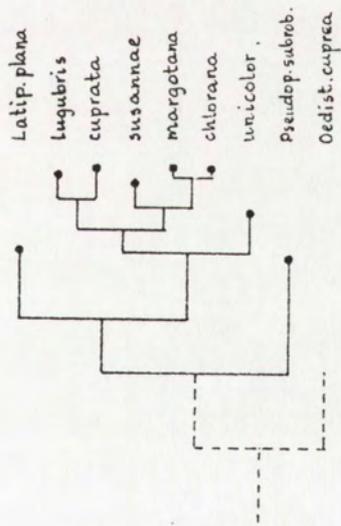


Fig. 6. Cladogram of *Perotis* Dej.

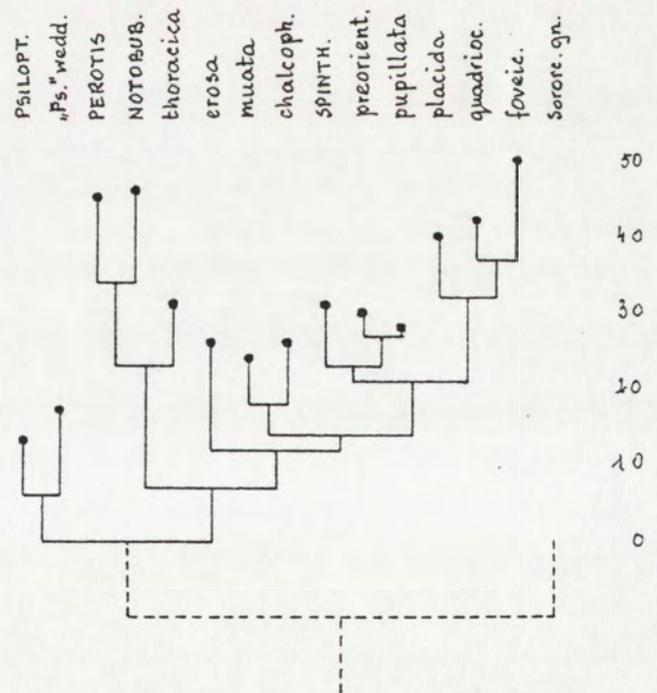


Fig. 7. Cladogram of sg. *Lampetis* Dej.

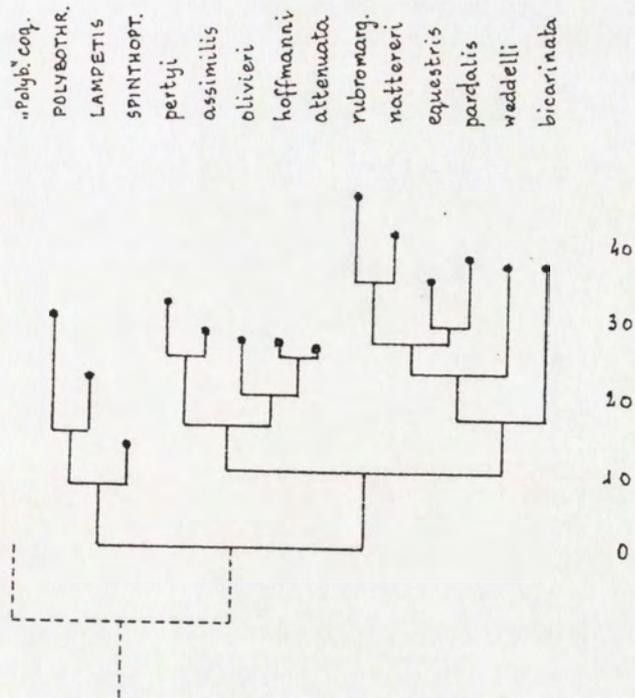


Fig. 8. Cladogram of sg. *Psiloptera* DEJ. s.str.

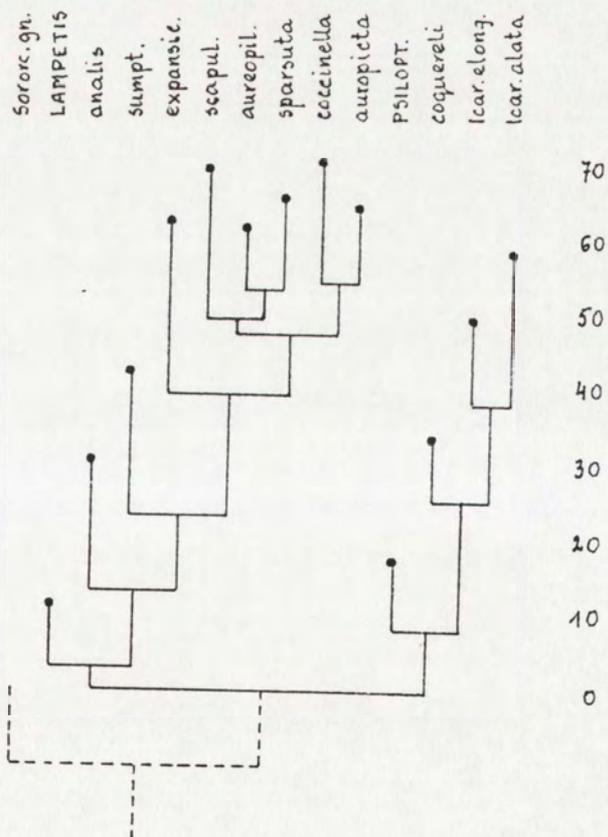


Fig. 9. Cladogram of sg. *Polybothris* DEJ.

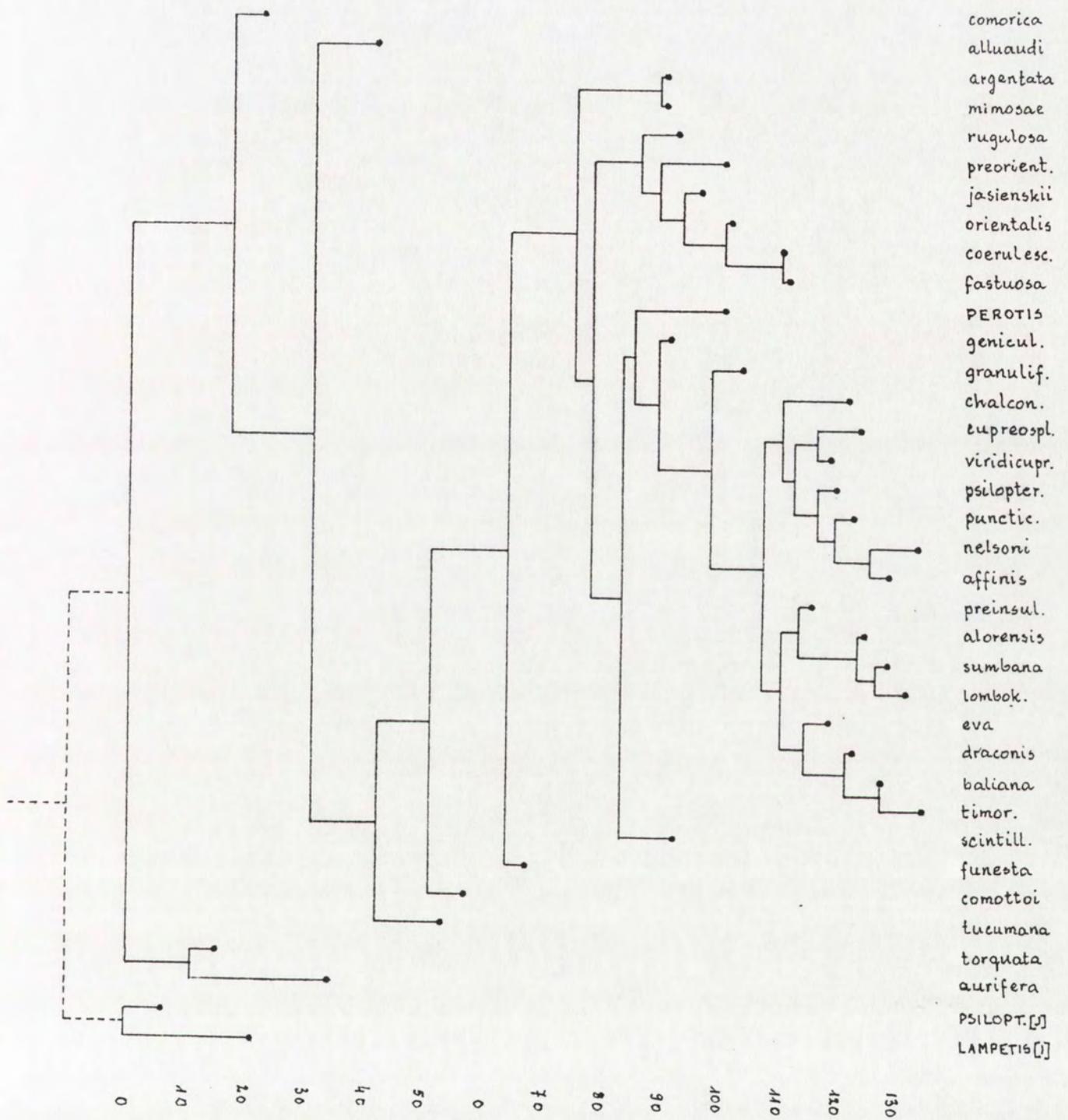


Fig. 10. Cladogram of sg. *Spinthoptera* DEJ.

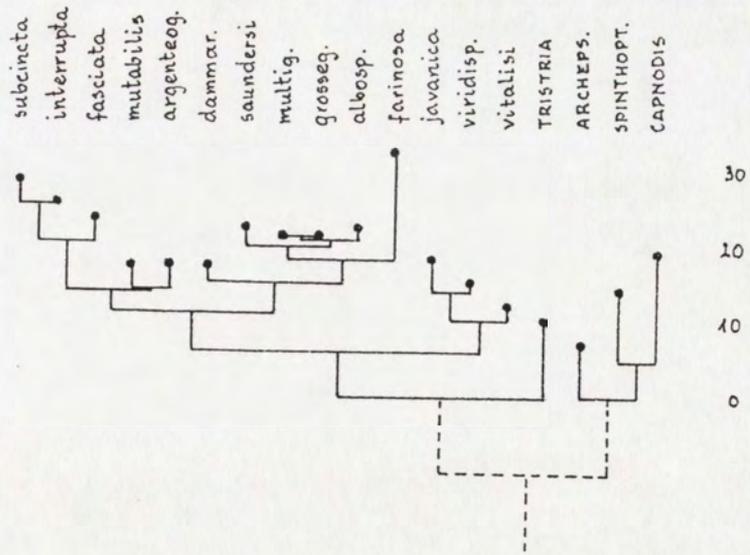


Fig. 11. Cladogram of *Dicercomorpha* DEYR.

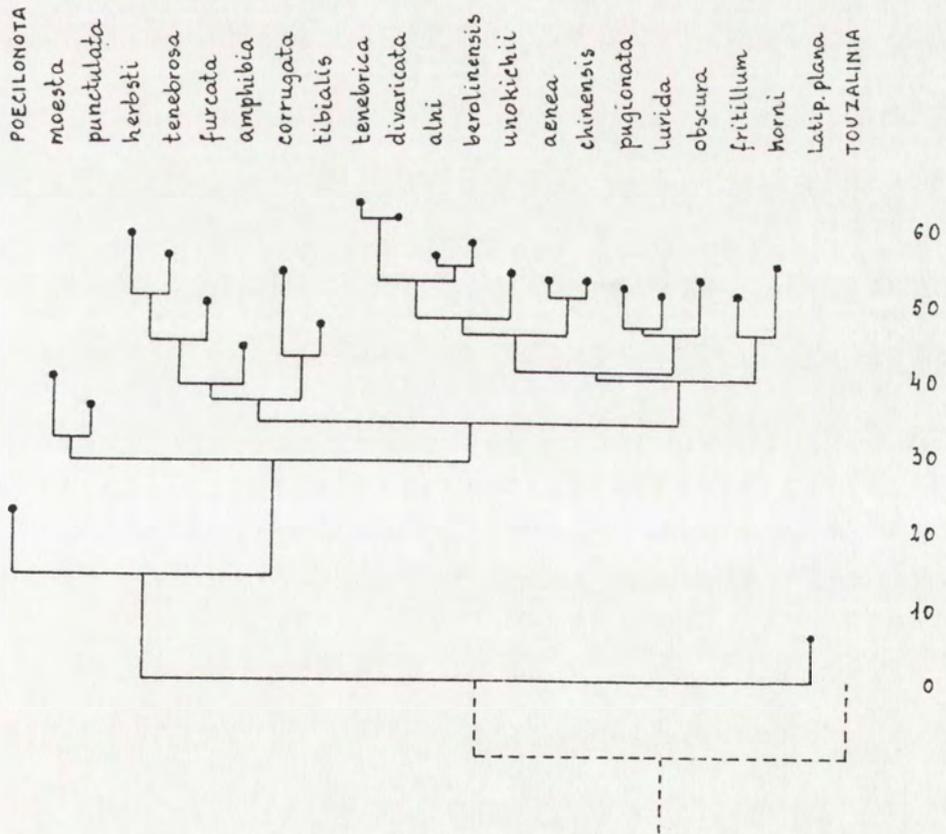


Fig. 12. Cladogram of *Dicerca* Esch.

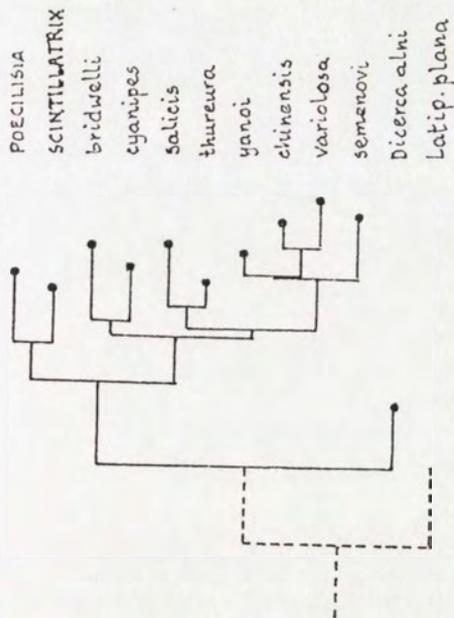


Fig. 13. Cladogram of *Poecilonota* ESCH.

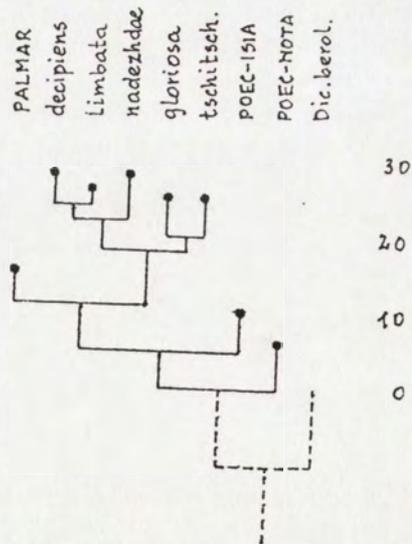


Fig. 14. Cladogram of sg. *Scintillatrix* OBB.

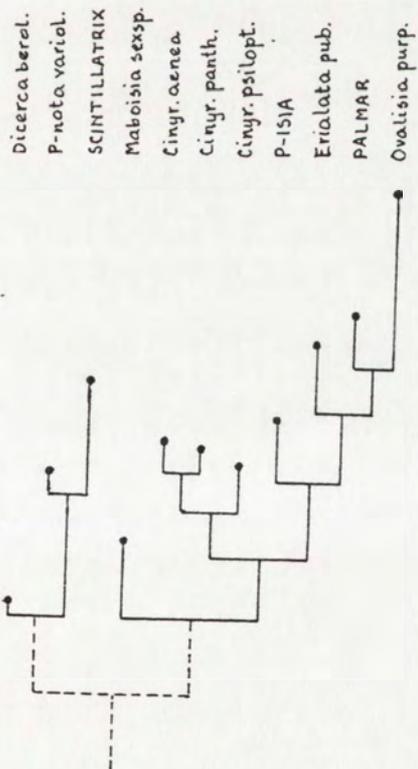


Fig. 15. Cladogram of *Ovalisia* KERR. s.l

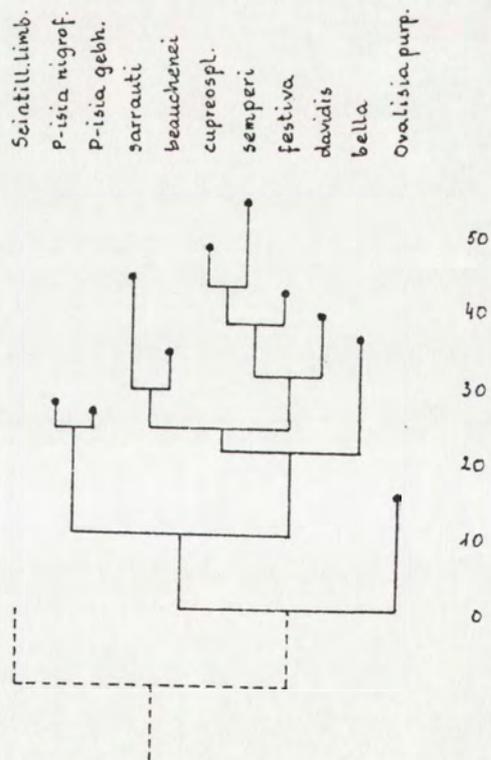


Fig. 16. Cladogram of sg. *Palmar* SCHF.

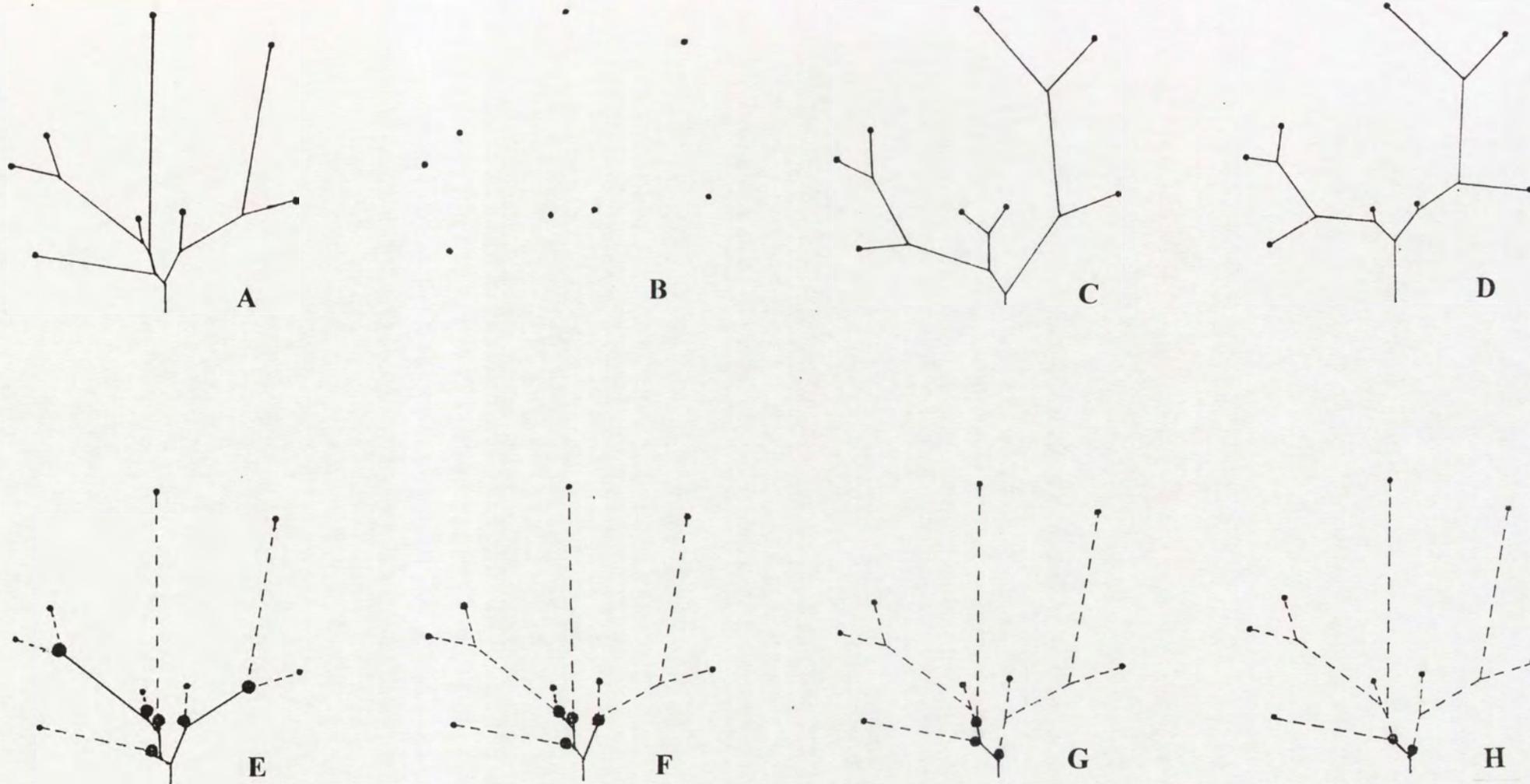
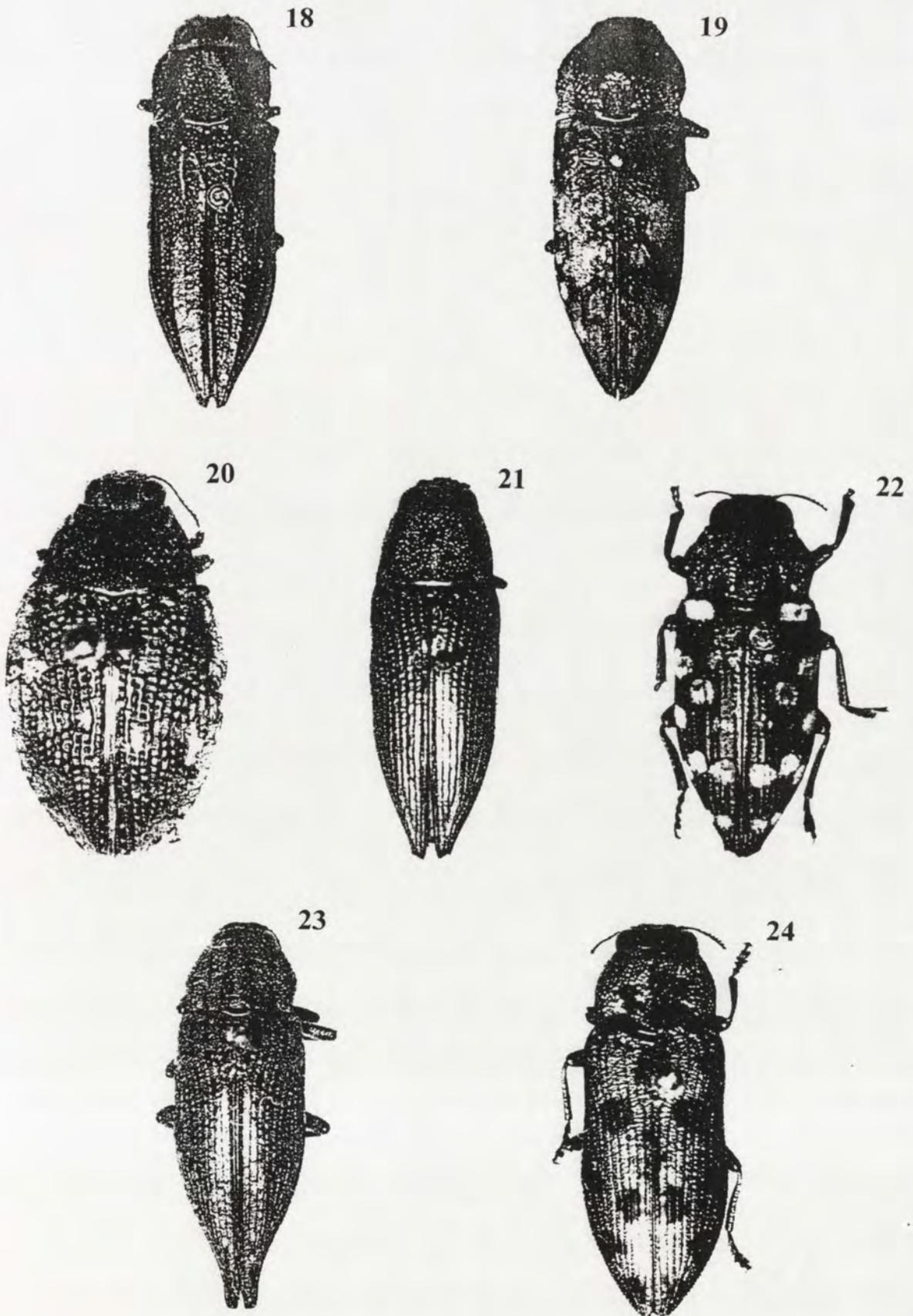


Fig. 17. Basic idea of phylogenetic reconstruction by MICSEQ
 A. Original ("true") tree; B. Only tops of twigs (terminal taxa) "visible";
 C. Result of reconstruction based on "overall similarity"; D. result of reconstruction based on "overall parsimony"; E-H. Stages of reconstruction by MICSEQ



Figs. 18-24. Some representatives of the subtribe Psilopterina LAC.

18. *Ectinogonia (Kheiliella) melichari* OBB.

19. *Achardella* sp.

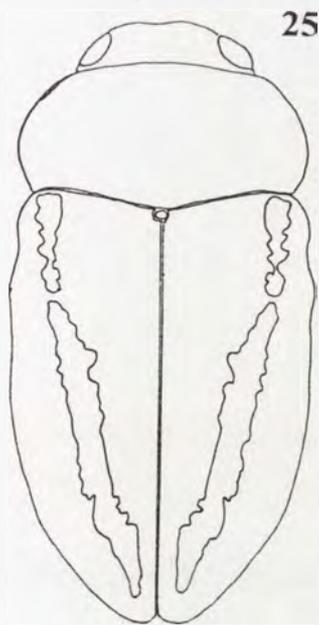
20. *Psiloptera (Polybothris) circularis* (C.G.)

22. *Dicercomorpha (s.str.) argenteoguttata* THS.

21. *Psiloptera (Spinthoptera) coeruleascens* (HBST.)

Fig. 23. *Dicerca (s.str.) furcata* (THB.)

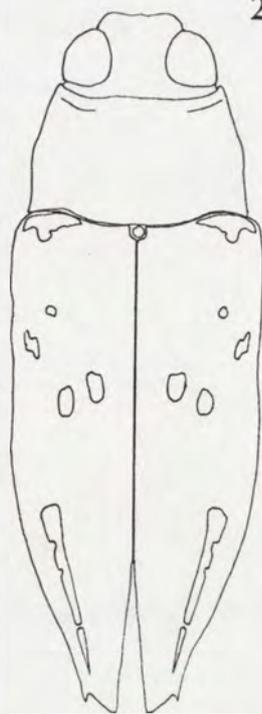
24. *Ovalisia (Palmar) beauchenei* (FRM.)



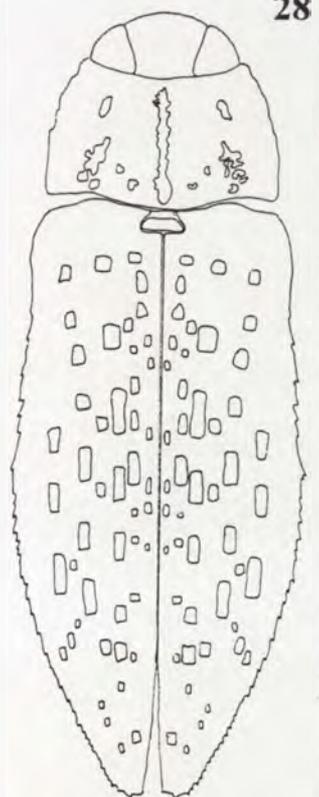
25



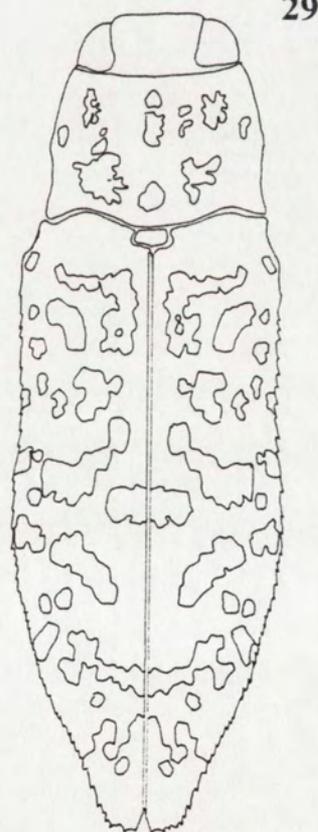
26



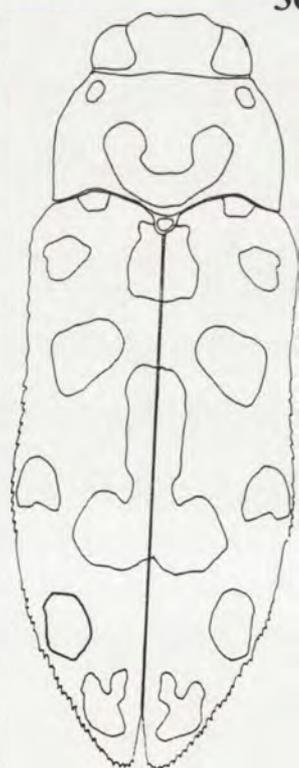
27



28



29



30

Figs. 25-30. Some representatives of Indo-Pacific Psilopterina LAC.

25. *Cyphonota (s.str.) turcomanicum (KR.)*

27. *Psiloptera (Spinthoptera) comottoi LSB.*

26. *Psiloptera (?Spinthoptera) preorientalis sp.n.*

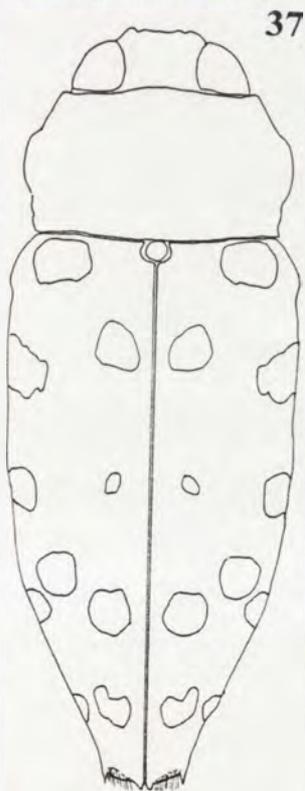
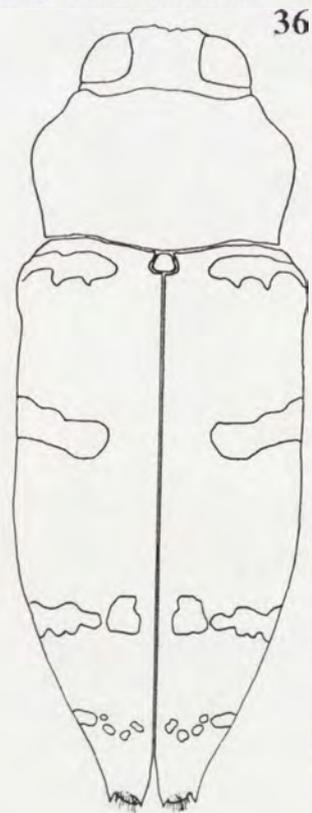
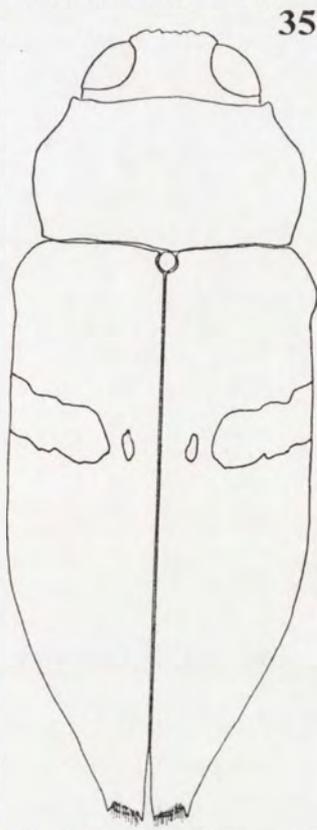
28. *Ovalisia (Scintillatrix) tschitscherini SEM.*

30. *Ovalisia (Palmar) beauchenei (FRM.)*

29. *Ovalisia (Poecilisia) gebhardti (OBB.)*

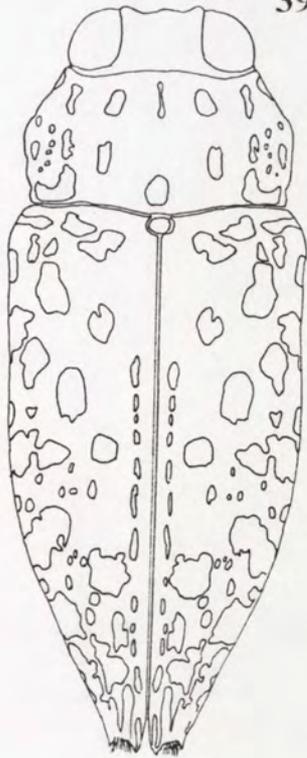


Figs. 31-34. Indo-Pacific representatives of the genus *Capnodis* ESCH.
 31. *C. carbonaria sexmaculata* BALL. 32. *C. indica* THS.
 33. *C. parumstriata* BALL. 34. *C. excisa* MËN.

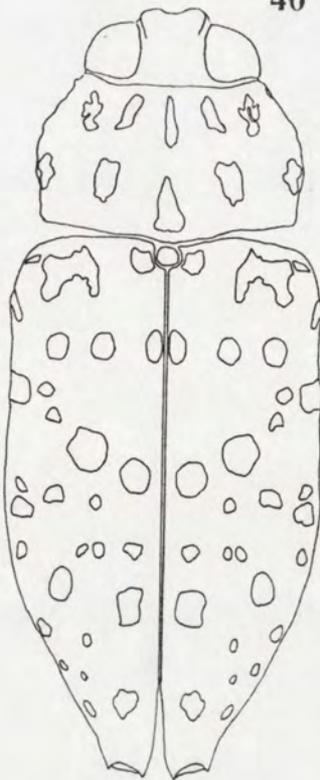


Figs. 35-38. Representatives of the genus *Dicercomorpha* DEYR.
35. *D. subcincta* DEYR. 36. *D. interrupta* DEYR.
37. *D. mutabilis* SND. 38. *D. argenteoguttata* THS.

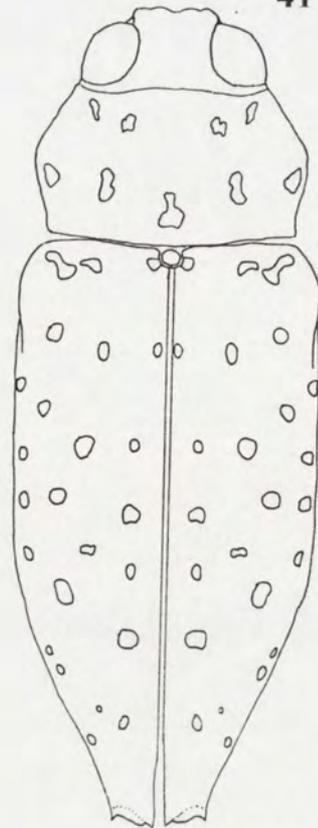
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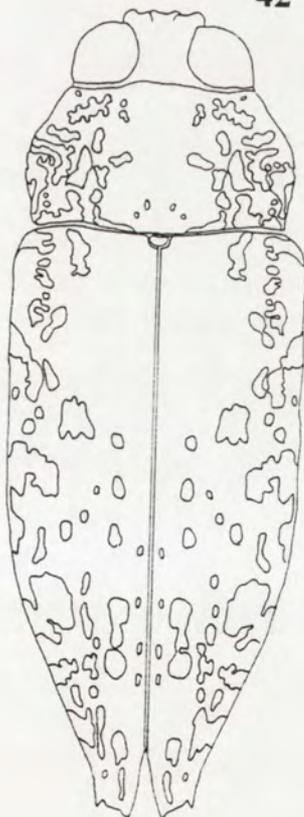
40



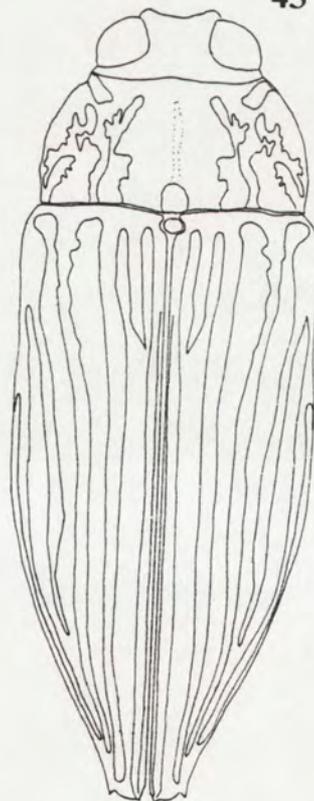
41



42



43



Figs. 39-43. Representatives of the genus *Dicercomorpha* DEYR.

39. *D. (s.str.) dammarana* sp.n. 40. *D. (s.str.) multiguttata* DEYR. 41. *D. (s.str.) albosparsa* (C.G.)
 42. *D. (s.str.) javanica* (C.G.) 43. *D. (Mirolampetis) farinosa* THS.

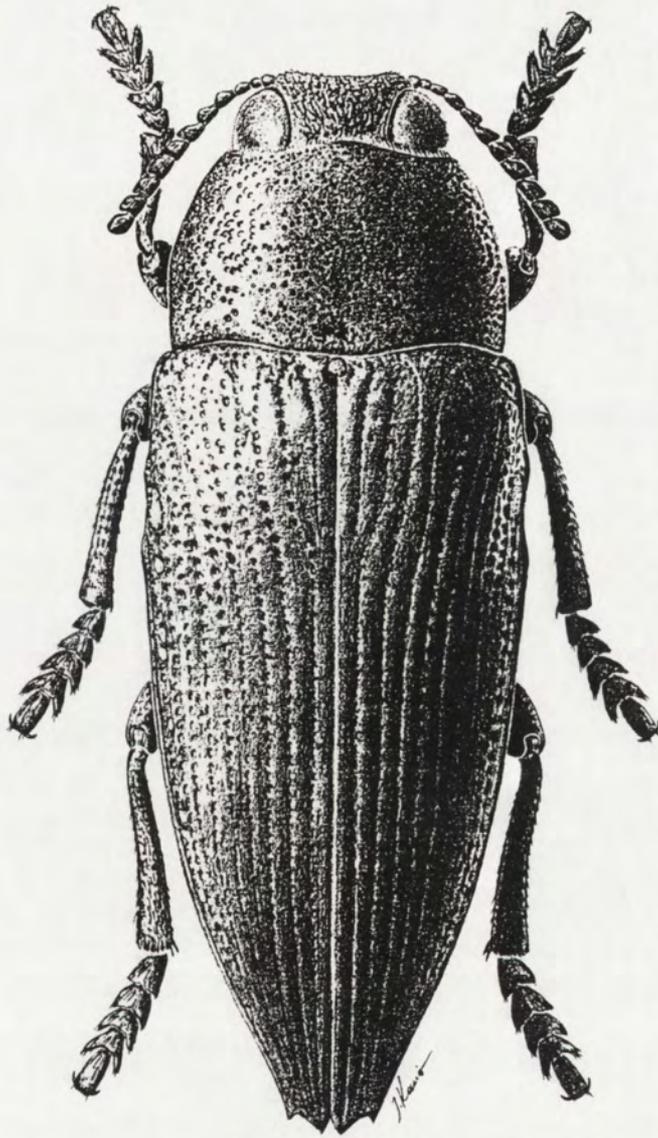
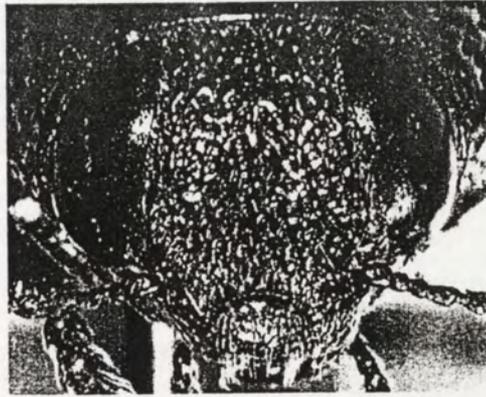
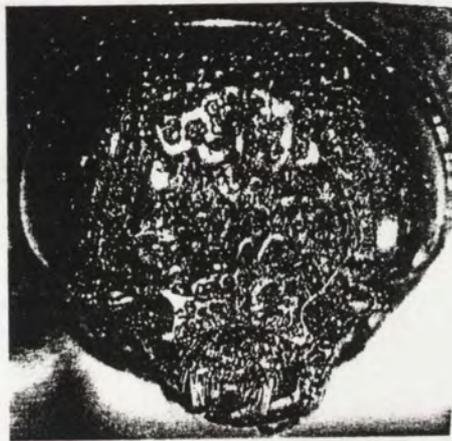


Fig. 44. *Psiloptera (Spinthoptera) jasienskii* sp.n.



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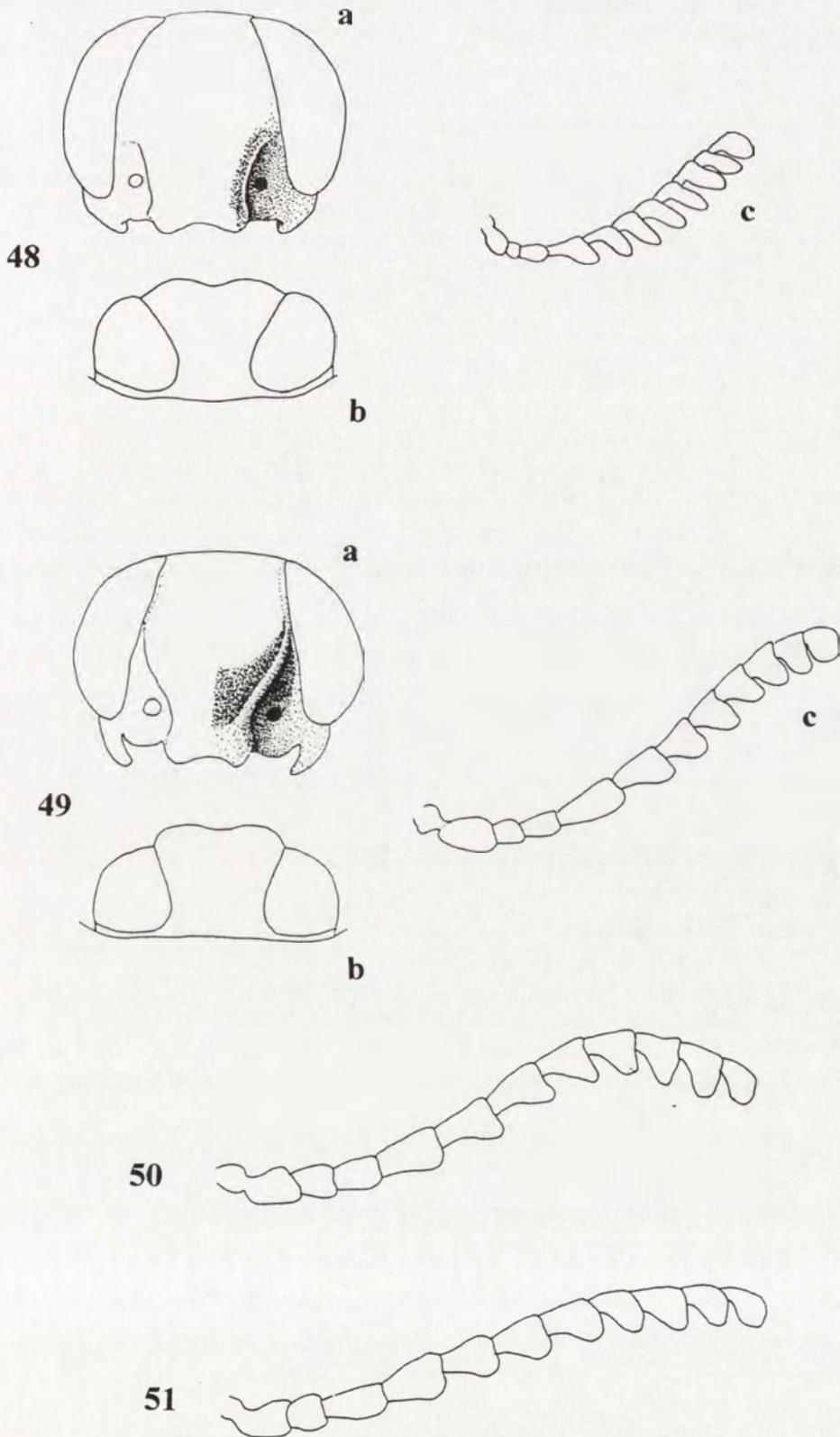


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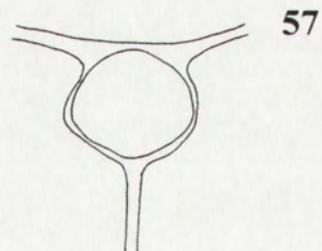
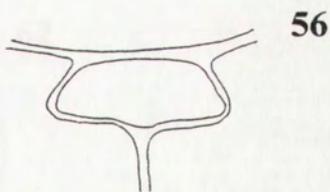
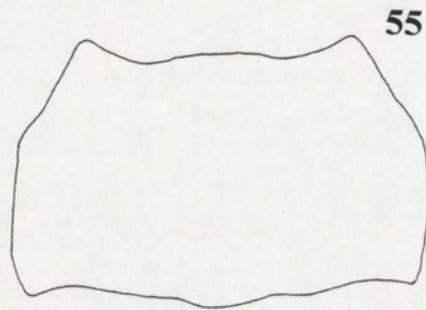
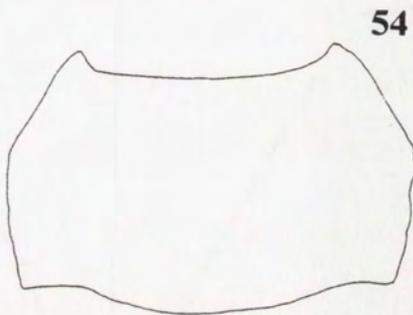
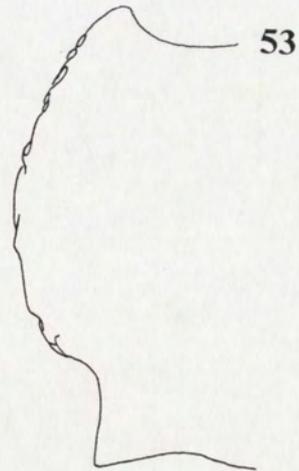
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Figs. 45-47. Frontal sculpture of Indo-Pacific *Psiloptera* DEJ.
45. *P. fastuosa* (F.); 46. *P. affinis* (SND.); 47. *P. timoriensis* (C.G.)



Figs. 48-51. Heads and antennae

48. *Ovalisia (Erialata) pubescens* (FISH.): a - front; b - vertex; c - antenna
 49. *Ovalisia (Mabomisia) sexspinosa* (THS.): a - front; b - vertex; c - antenna
 50. *Poecilonota variolosa chinensis* THY. - antenna
 51. *Poecilonota yanoi* KUR. - antenna



Figs. 52-57. Shape of pronotum and scutellum

52. *C. carbonaria sexmaculata* BALL. - lateral margin of pronotum

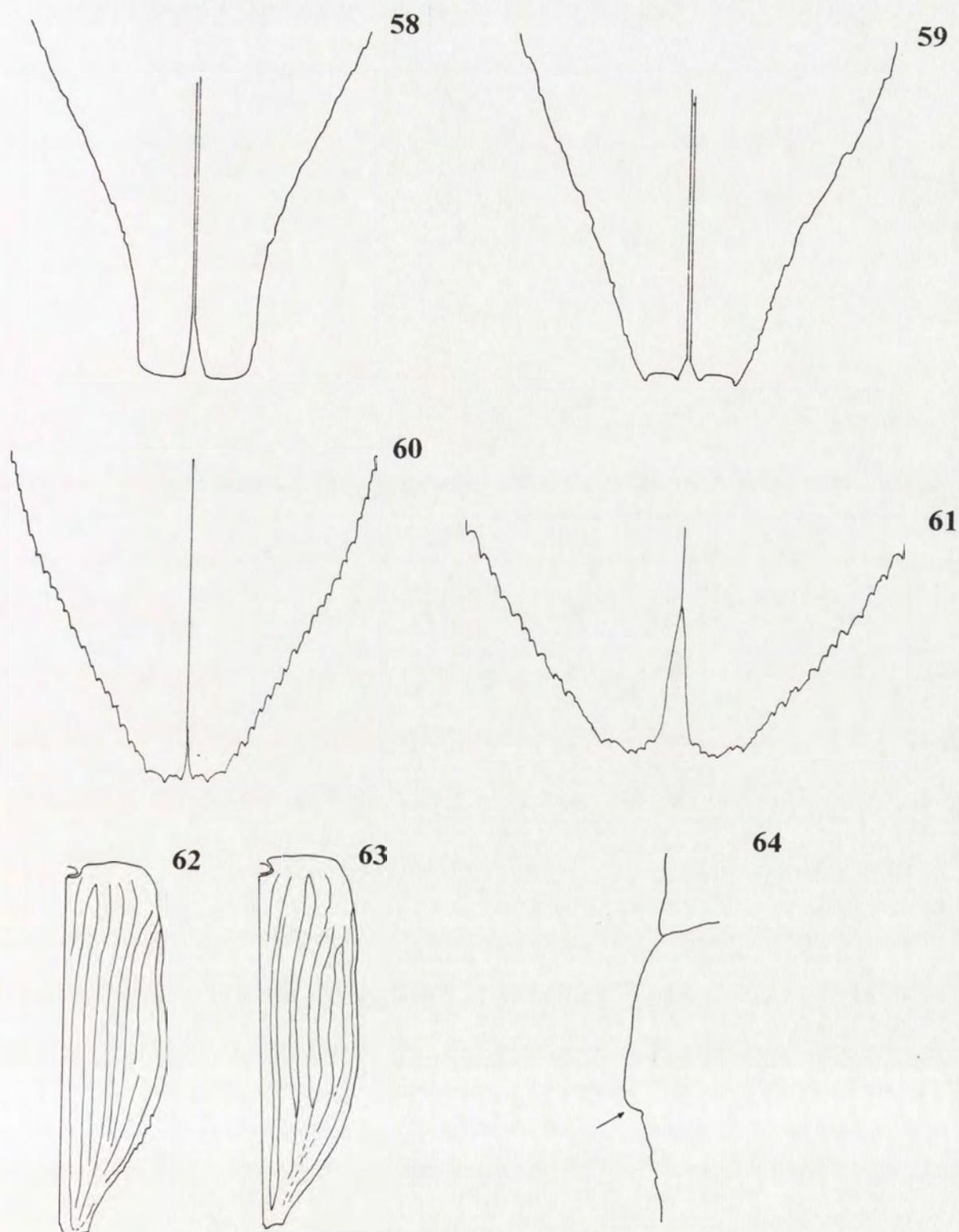
53. *C. excisa* MÉN. - lateral margin of pronotum

54. *Poecilonota variolosa chinensis* THY. - pronotum

55. *Poecilonota yanoi* KUR. - pronotum

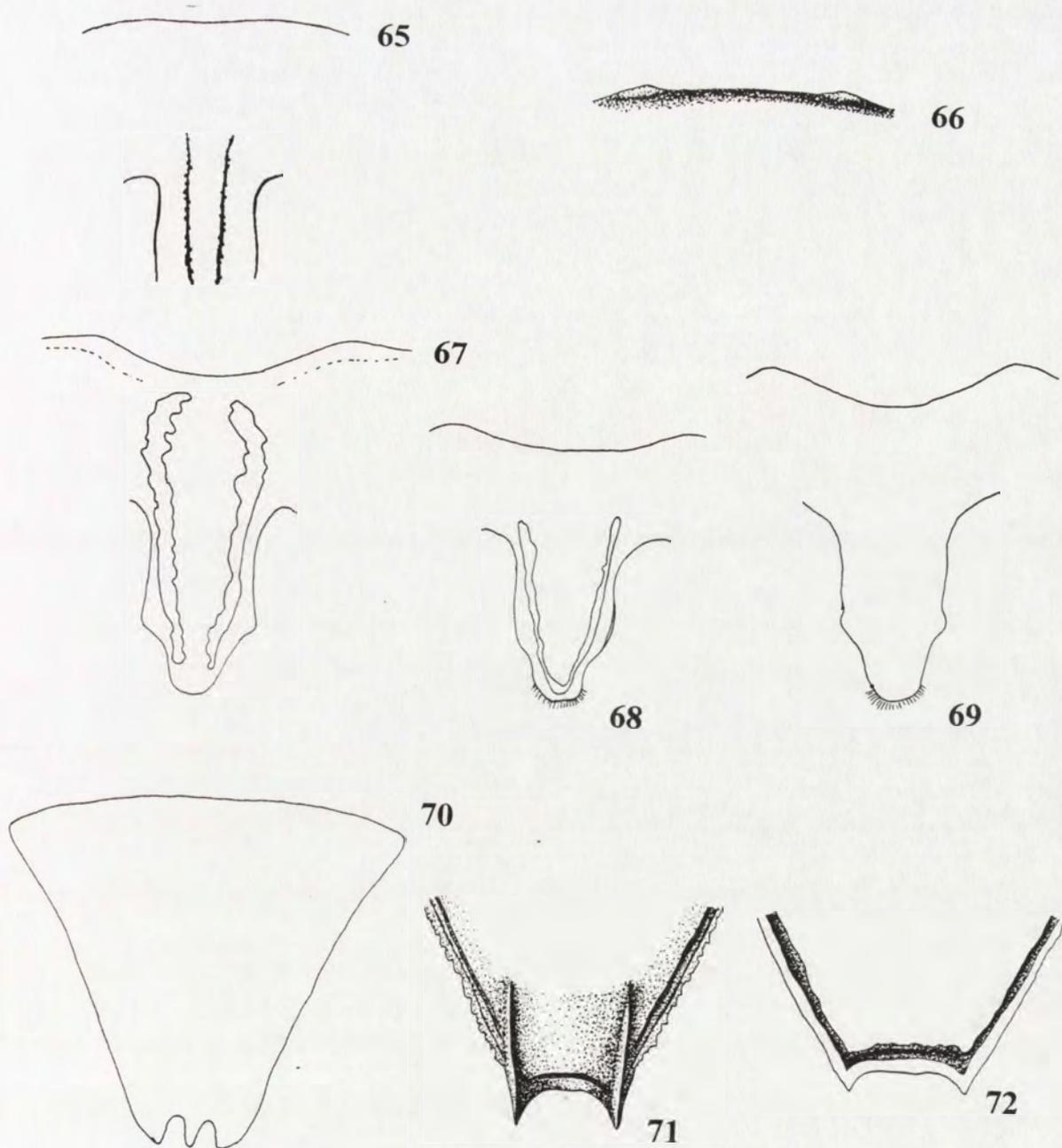
56. *Poecilonota semenovi* OBB. - scutellum

57. *Dicerca corrugata* FRM. - scutellum



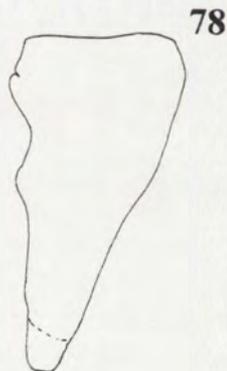
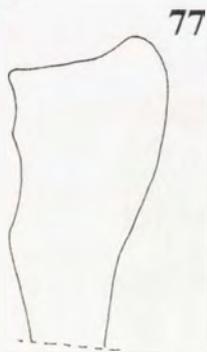
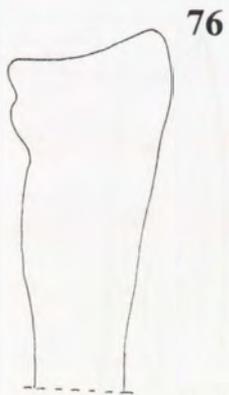
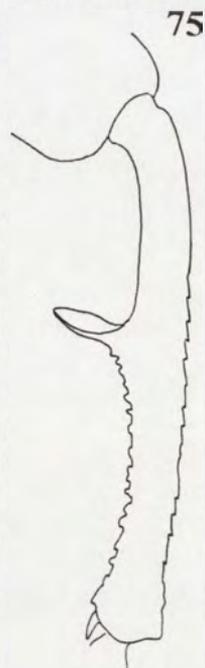
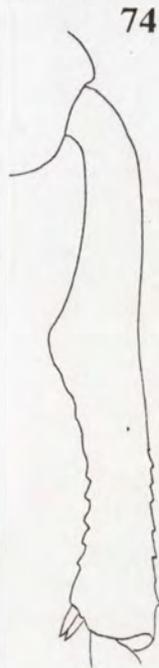
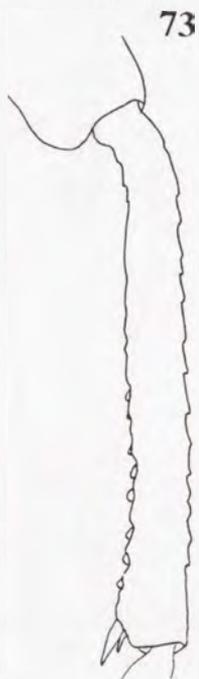
Figs. 58-64. Elytral features

58. *Dicerca furcata* (THB.) - Elytral apices
 59. *Dicerca corrugata* FRM. - elytral apices
 60. *Ovalisia (Erialata) pubescens* (FISH.) - elytral apices
 61. *Ovalisia (Palmar) bella* (C.G.) - elytral apices
 62. *Poecilonota variolosa chinensis* THY. - pattern of elytral striae
 63. *Poecilonota yanoi* KUR. - pattern of elytral striae
 64. *Psiloptera psilopteroides* (SND.) - subhumeral denticle



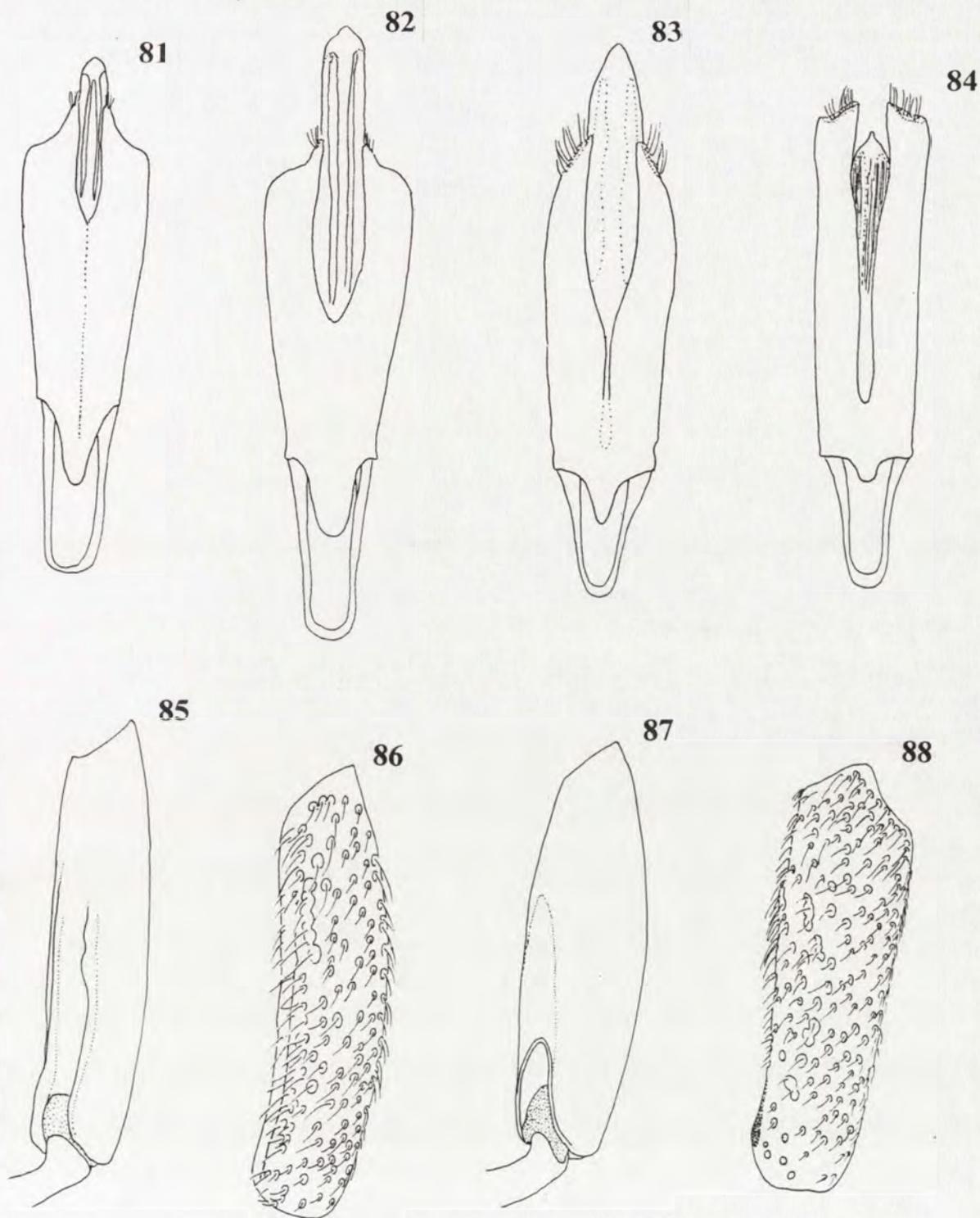
Figs. 65-72. Features of ventral side

65. *Psiloptera (Spinthoptera) jasienskii sp.n.* - anterior part of prosternum
 66. *Psiloptera (?Spinthoptera) preorientalis sp.n.* - anterior margin of prosternum
 67. *Tristria cupreomaculata (SND.)* - prosternal process
 68. *Dicercomorpha dammarana sp.n.* - prosternal process
 69. *Dicercomorpha vitalisi BRG.* - prosternal process
 70. *Dicerca furcata (THB.)*: female - anal sternite
 71. *Ovalisia (Cinyrisia) psilopteroides (DEYR.)* - apex of anal sternite
 72. *Ovalisia (Palmar) bella (C.G.)* - apex of anal sternite



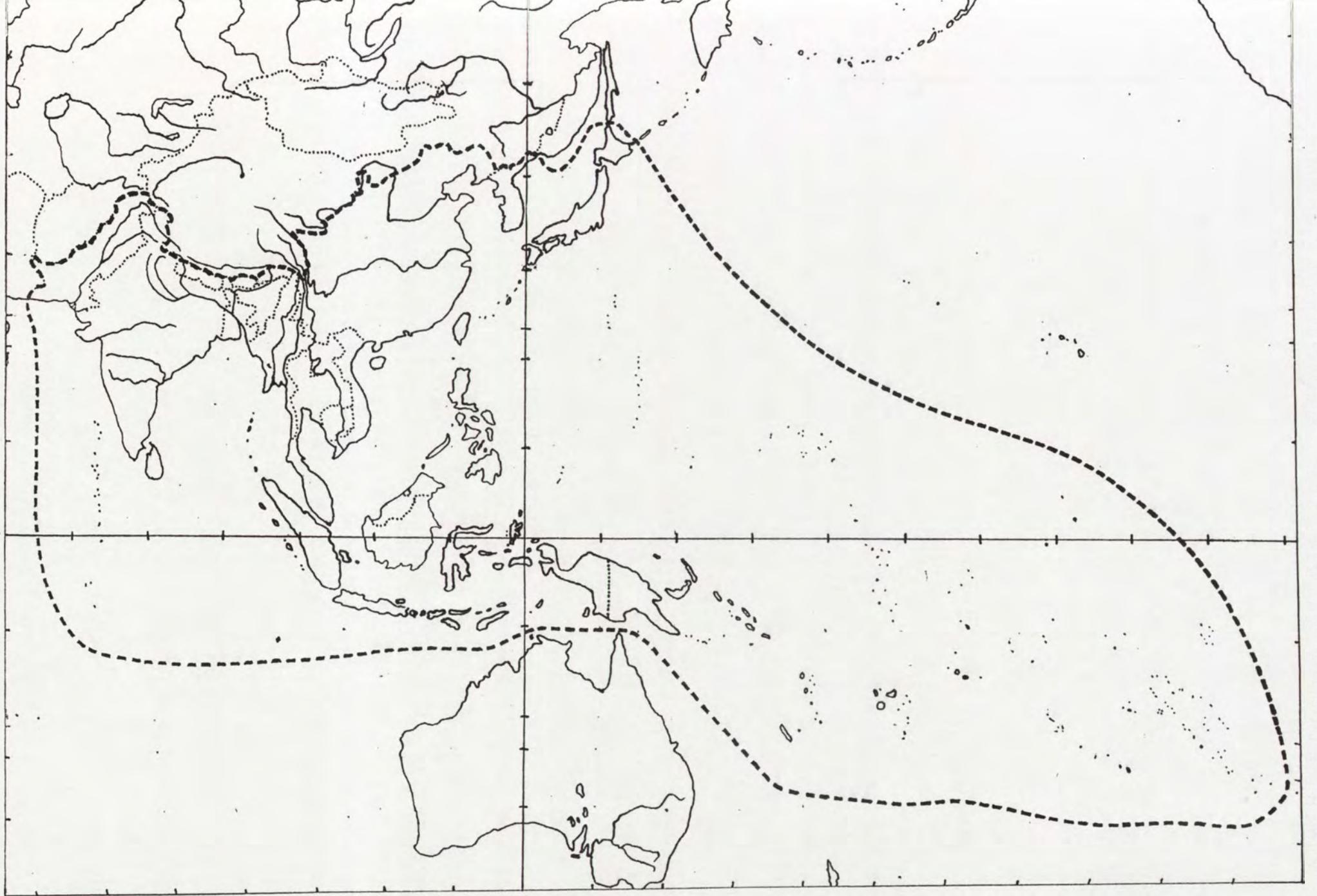
Figs. 73-80. Mesoibiae and metacoxae

73. *Dicerca (Argante) moesta* (F.): male mesotibia
 74. *Dicerca (s.str.) unokichii* HRI.: male mesotibia
 75. *Dicerca corrugata* FRM.: male mesotibia
 76. *Dicercomorpha vitalisi* BRG. - metacoxa
 77. *Dicercomorpha dammarana* sp.n. - metacoxa
 78. *Capnodis indica* THS. - metacoxa
 79. *Capnodis carbonaria sexmaculata* BALL. - metacoxa
 80. *Capnodis parumstrata* BALL. - metacoxa

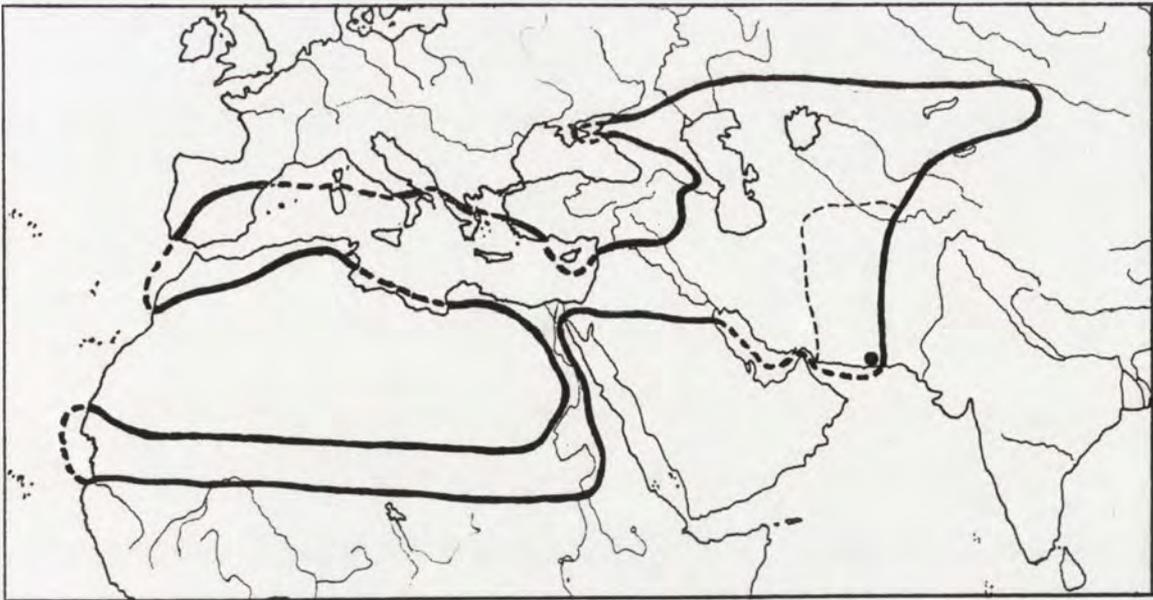


Figs. 81-88. Male genitalia and metafemora

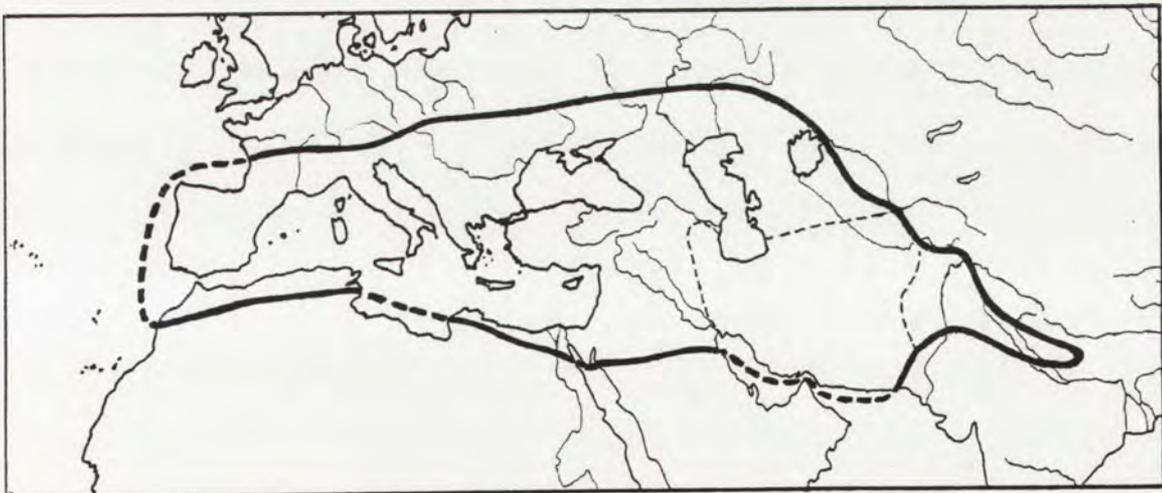
81. *Psiloptera fastuosa* (F.) - male genitalia
 82. *Psiloptera coerulescens* (HBST.) - male genitalia
 83. *Psiloptera jasienskii* sp.n. - male genitalia
 84. *Psiloptera affinis* (SND.) s.str. - male genitalia
 85. *Dicercomorpha vitalisi* BRG. - metafemur: posteroventral view
 86. *Dicercomorpha vitalisi* BRG. - metafemur: ventral view
 87. *Psiloptera psilopteroides* (SND.) - metafemur: posteroventral view
 88. *Psiloptera psilopteroides* (SND.) - metafemur: ventral view



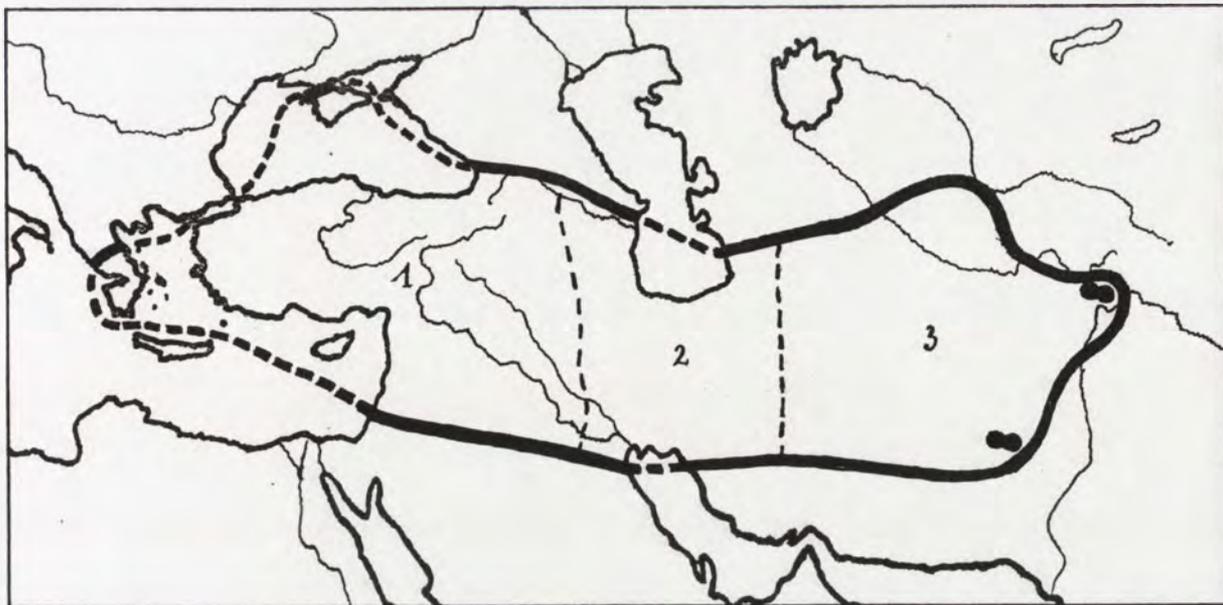
<http://rcin.org.pl>
Map 1. Limits of the study area



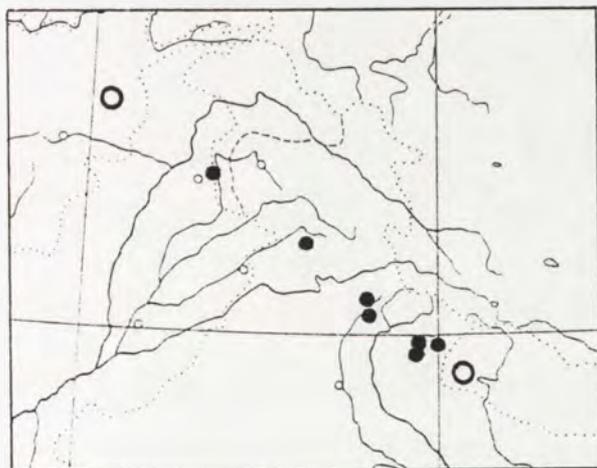
Map 2. Distribution of the genus *Cyphonota* DEJ.
 --- ● *C. turcomanicum* (KR.)



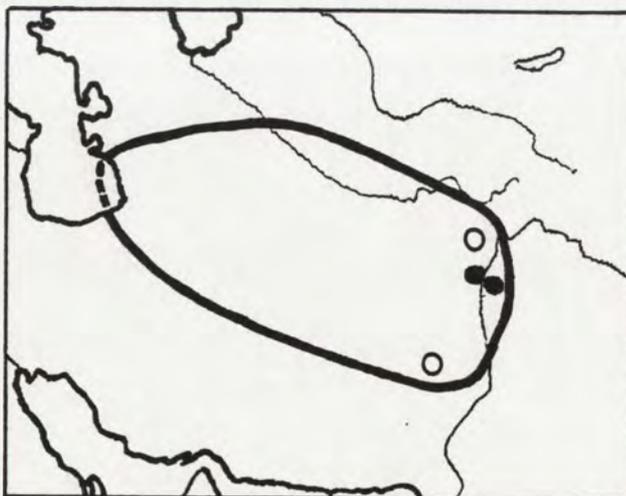
Map 3. Distribution of the genus *Capnodis* ESCH.
 --- *C. excisa* MËN.



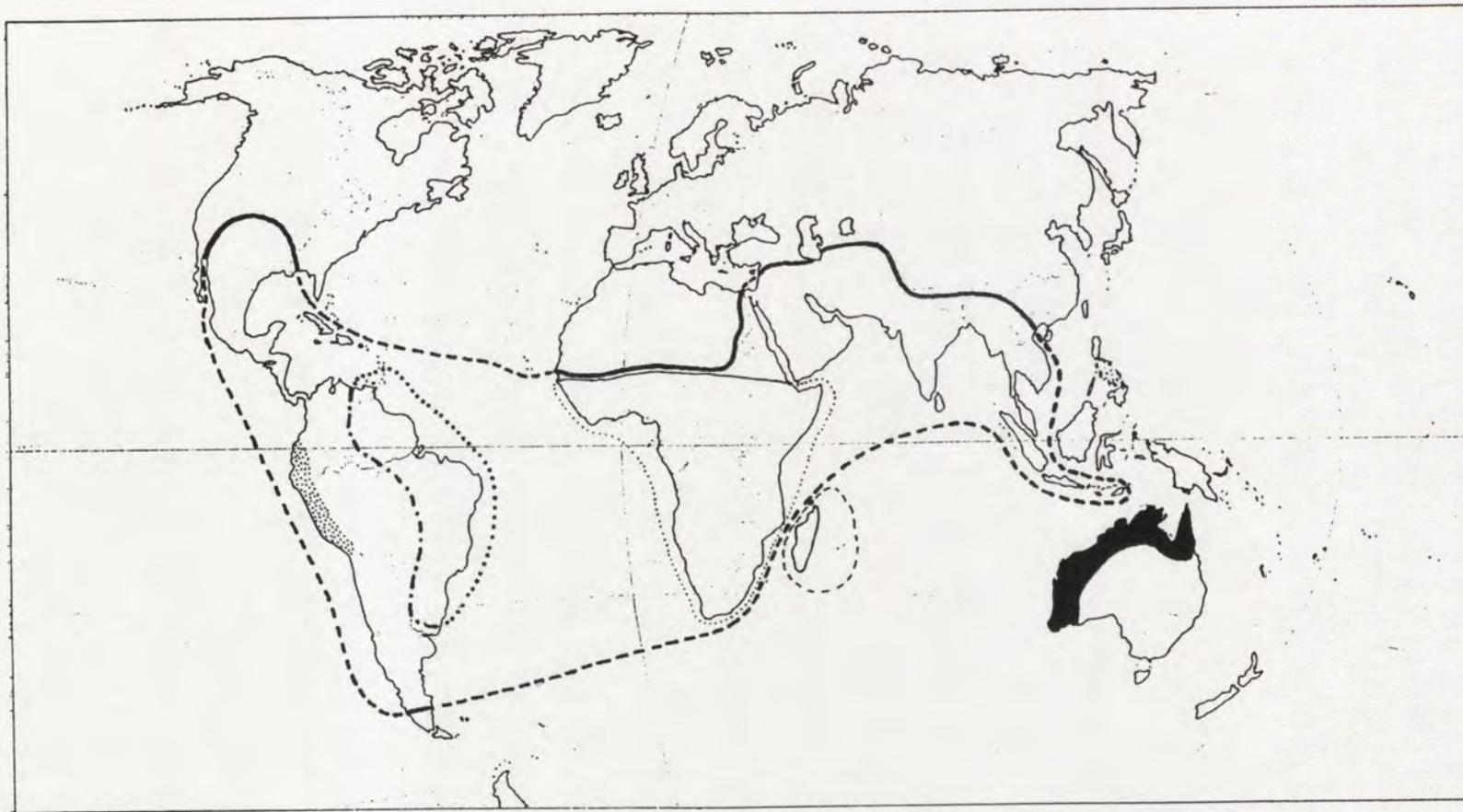
Map 4. Distribution of *Capnodis carbonaria* (KL)
 1 - *ssp. carbonaria s.str.*; 2 - *ssp. henningi* FALD.; 3 - *ssp. sexmaculata* BALL.



Map 5. Distribution of *Capnodis indica* THS.
 [open symbol denotes imprecise locality]

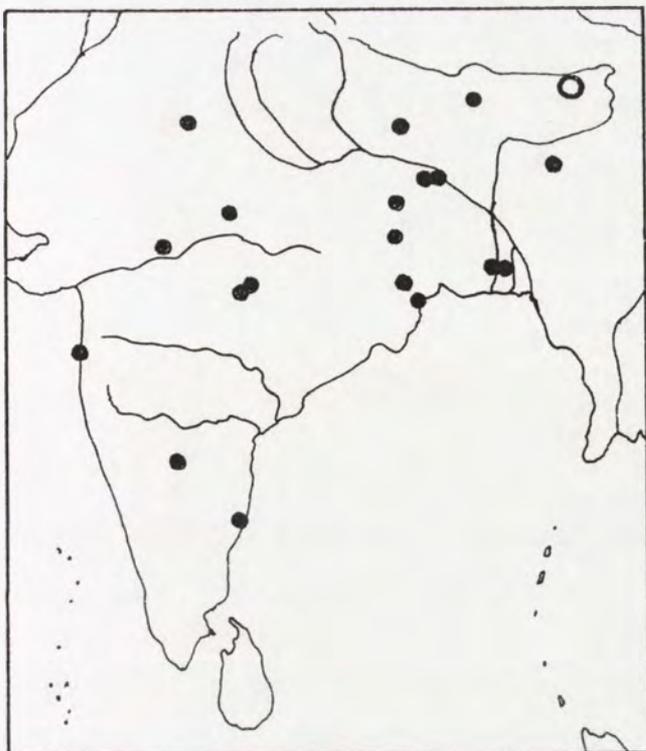


Map 6. Distribution of *Capnodis parumstriata* BALL.

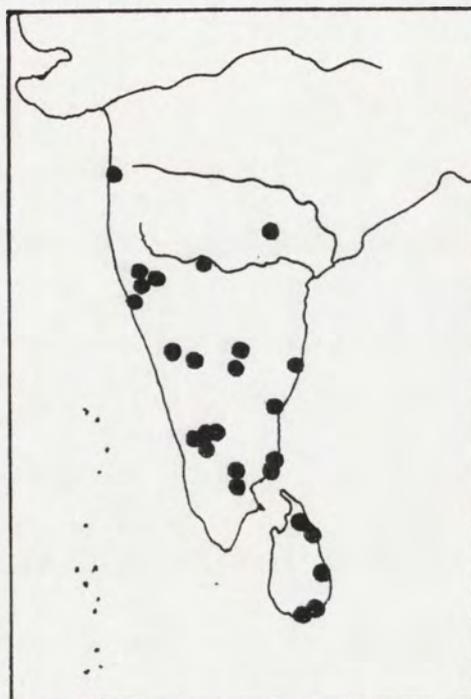


Map 7. Distribution of the genus *Psiloptera* DEJ.

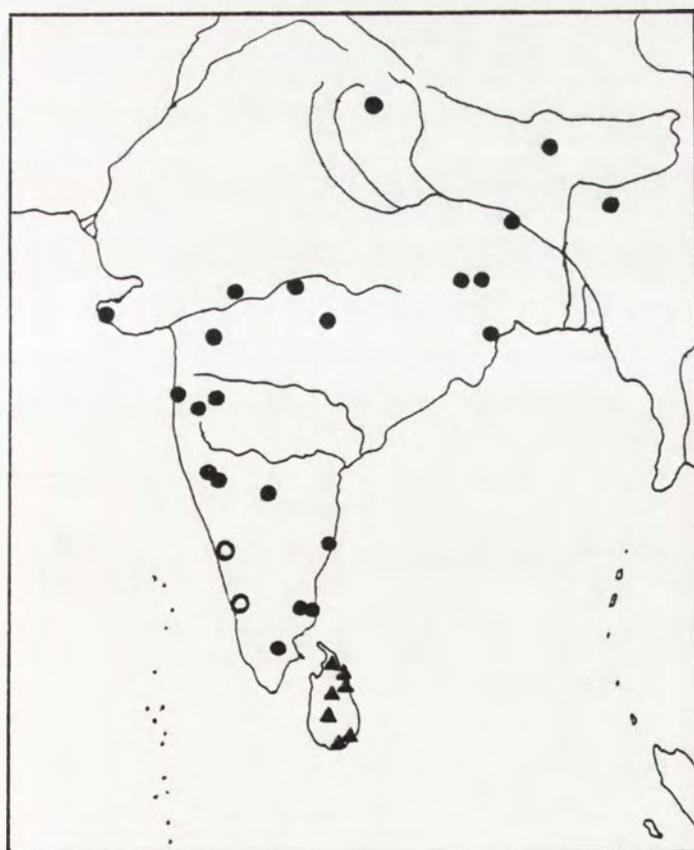
- . - . . . *sg. Psiloptera* DEJ; - - - *sg. Polybothris* DEJ. s.l.; --- *sg. Lampetis* DEJ.;
 ● *sg. Pseudolampetis* OBB.; - - - - *sg. Spinthoptera* CSY.; ● *sg. Notobubastes* CART.



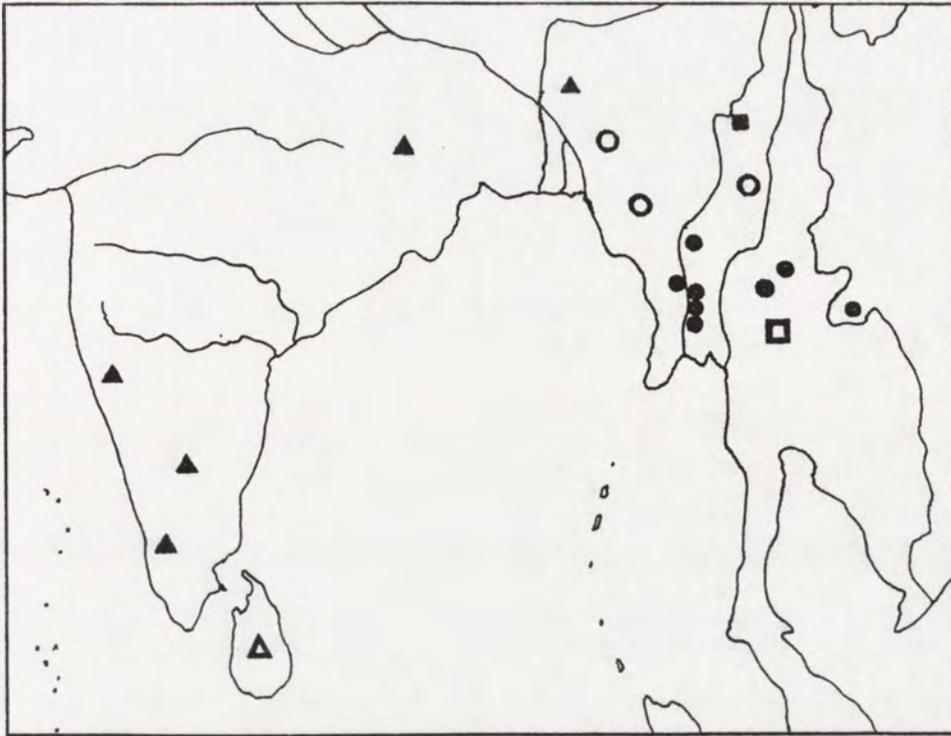
Map 8. Distribution of *Psiloptera fastuosa* (F.)



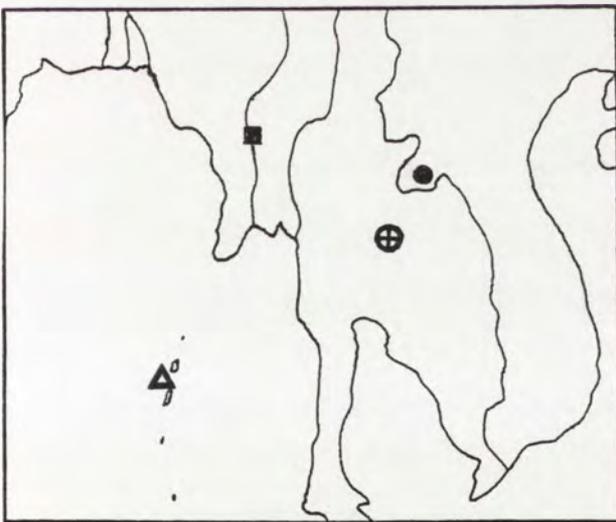
Map 9. Distribution of *Psiloptera coerulescens* (HBST.)



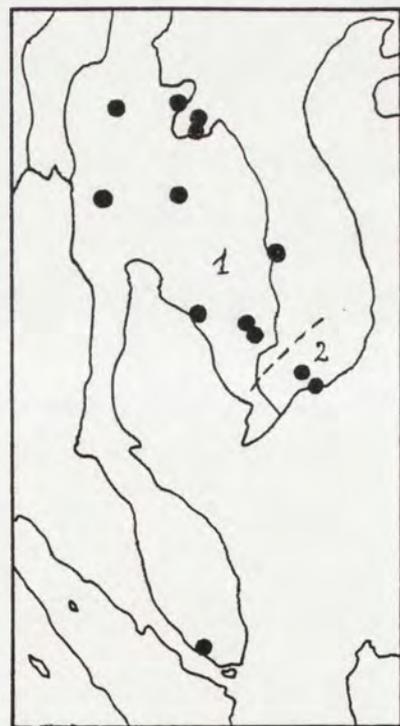
Map 10. Distribution of :
 ●○ *Psiloptera orientalis* (C.G.)
 ▲ *P. jasienskii* sp.n.
 [open symbols denote imprecise localities]



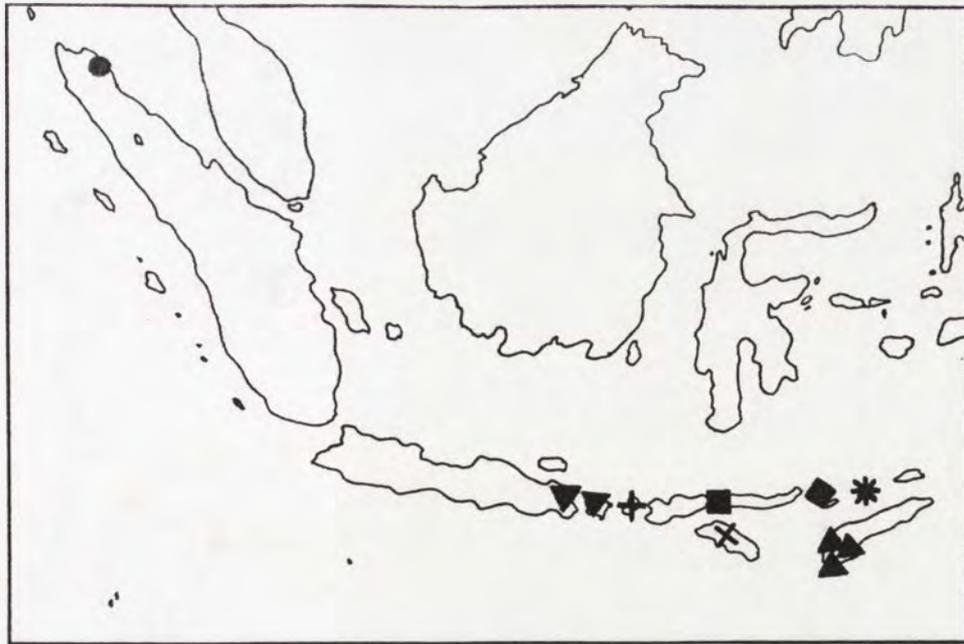
Map 11. Distribution of:
 ▲▲ *Psiloptera cupreosplendens* SND.; ●○ *P. viridicuprea* (SND.);
 ■□ *P. psilopteroides* (SND.)
 [open symbols denote imprecise localities]



Map 12. Distribution of:
 ● *Psiloptera nelsoni* (A.O.); ■ *P. comottoi* LSB.
 [⊕ - type locality of both]; ▲ *P. scintillans* WATH.

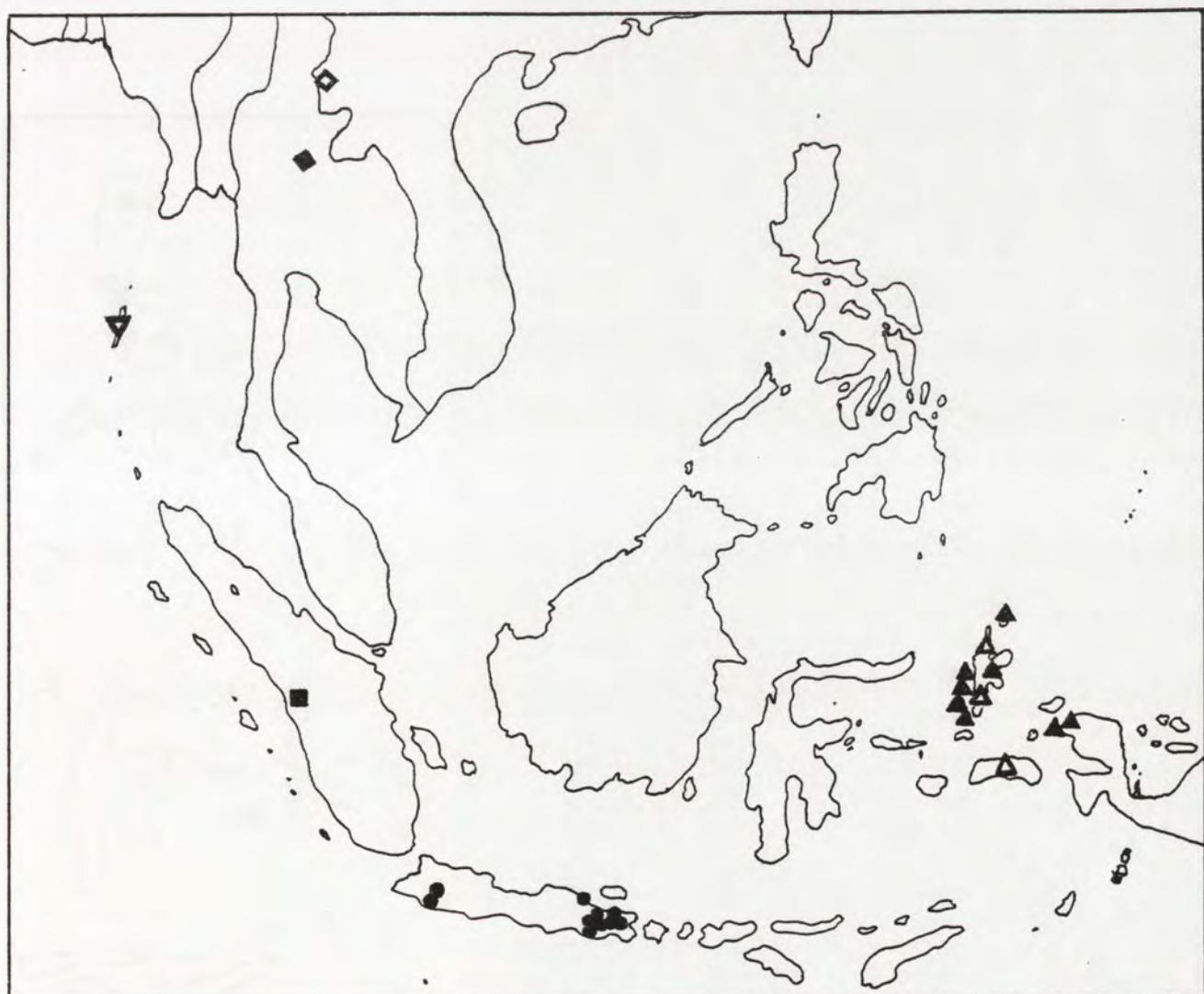


Map 13.
 Distribution of *Psiloptera affinis* (SND.)
 1 - *ssp. affinis s.str.*; 2 - *ssp. cochinchinae ssp.n.*



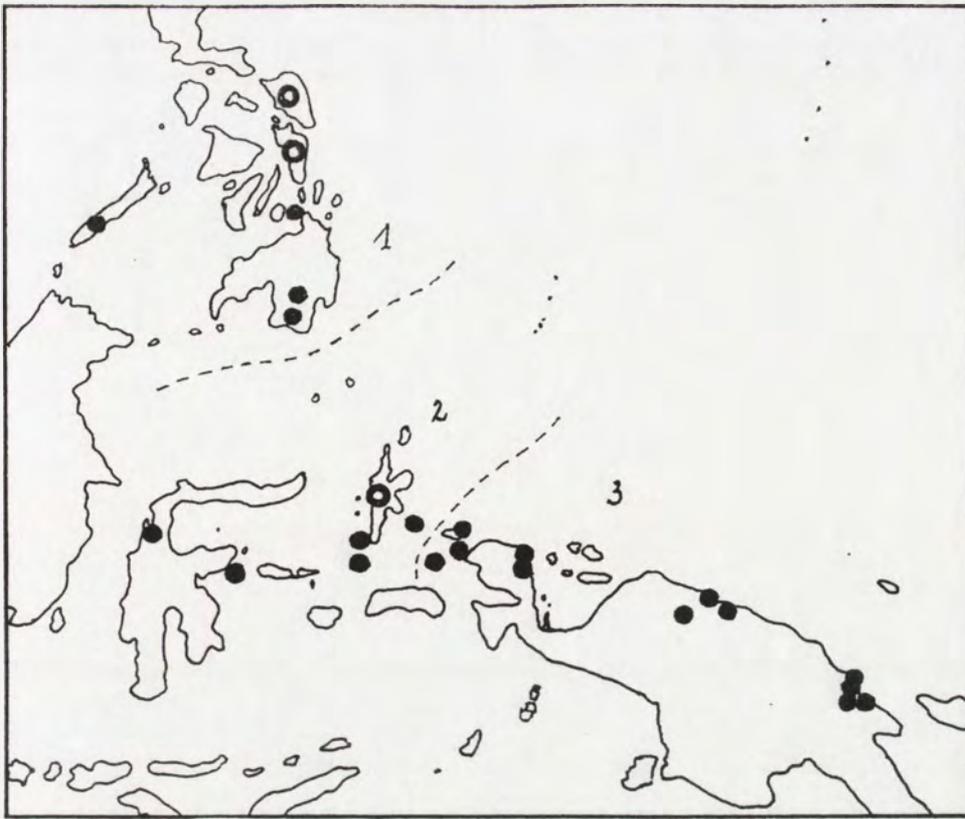
Map 14. Distribution of:

- *Psiloptera praeinsularis* sp.n.; * *P. aloreensis* THY.; × *P. sumbana* sp.n.;
- + *P. lombokiana* sp.n.; ▲ *P. timoriensis* (C.G.); ▼ *P. baliana* KERR.;
- *P. draconis* sp.n.; ◆ *P. eva* (THS.)



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Map 15. Distribution of:

- ▼ *Diceromorpha farinosa* THS.; ◆ *D. vitalisi* BRG.; ■ *D. viridisparva* THY.; ● *D. javanica* (C.G.);



Map 16. Distribution of *Dicercomorpha multiguttata* DEYR.

1 - *ssp. saundersi* KERR.; 2 - *ssp. multiguttata* s.str.; 3 - *ssp. grosseguttata* THS.



Map 17. Distribution of:

---■ *Tristria cupreomaculata* (SND.) [x - data from literature];

—●○ *Touzalinia psilopteroides* THY.

[1 - *ssp. belladonna* HOE.; 2 - *ssp. psilopteroides* s.str.;

3 - *ssp. siamensis* D.V.]; [open symbols denote imprecise localities]

Map 18. Distribution of:

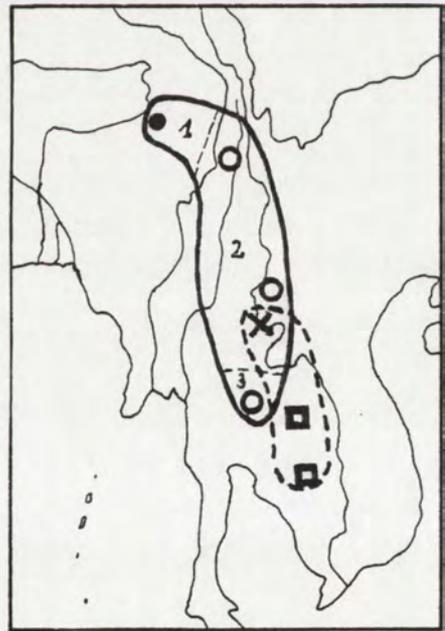
▼▼ *Dicercomorpha dammarana* sp.n.

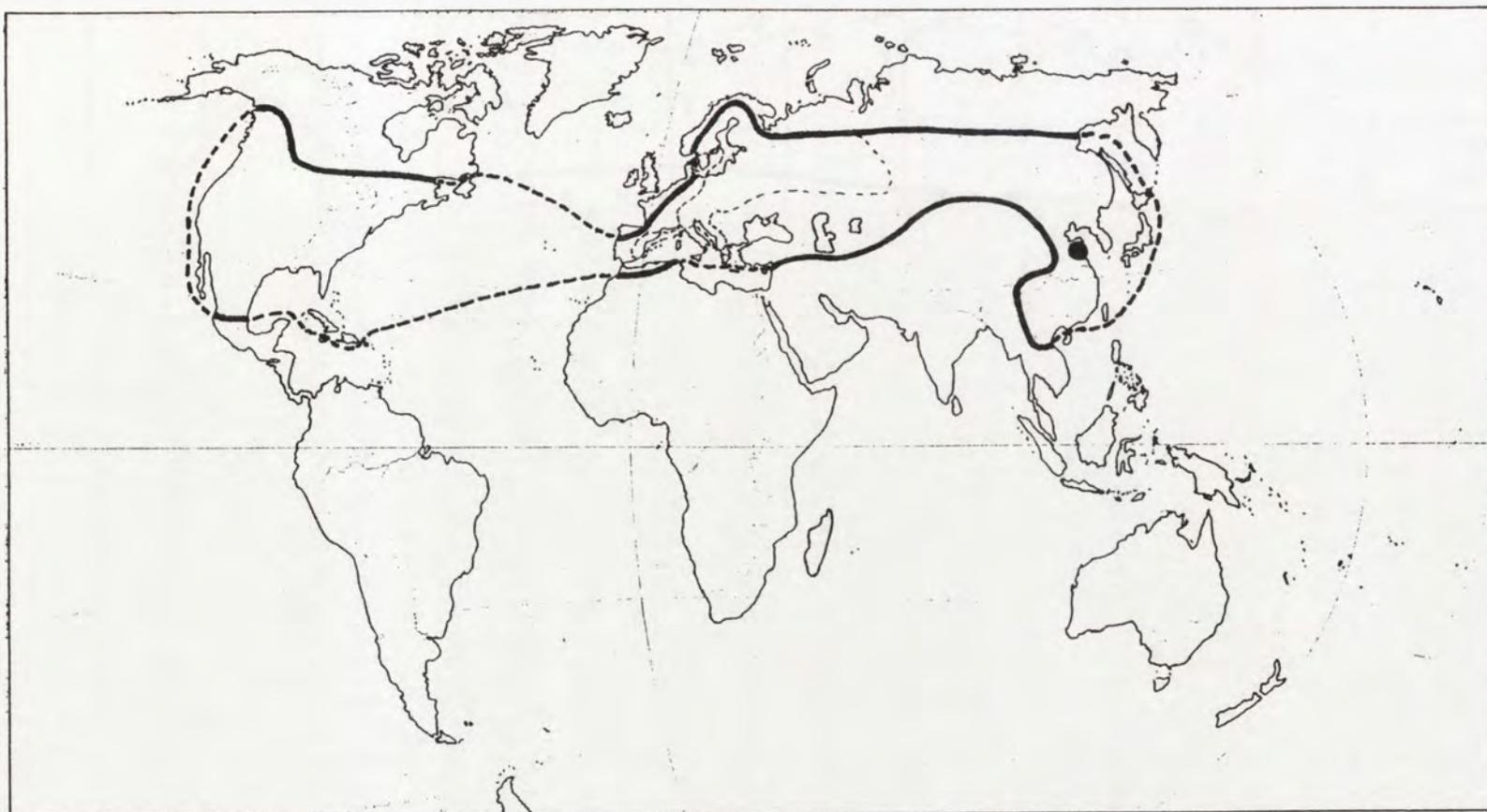
[open symbol: less probable identification of type locality - see text];

◆◇ *D. argenteoguttata* THS.; ■ *D. mutabilis* SND.;

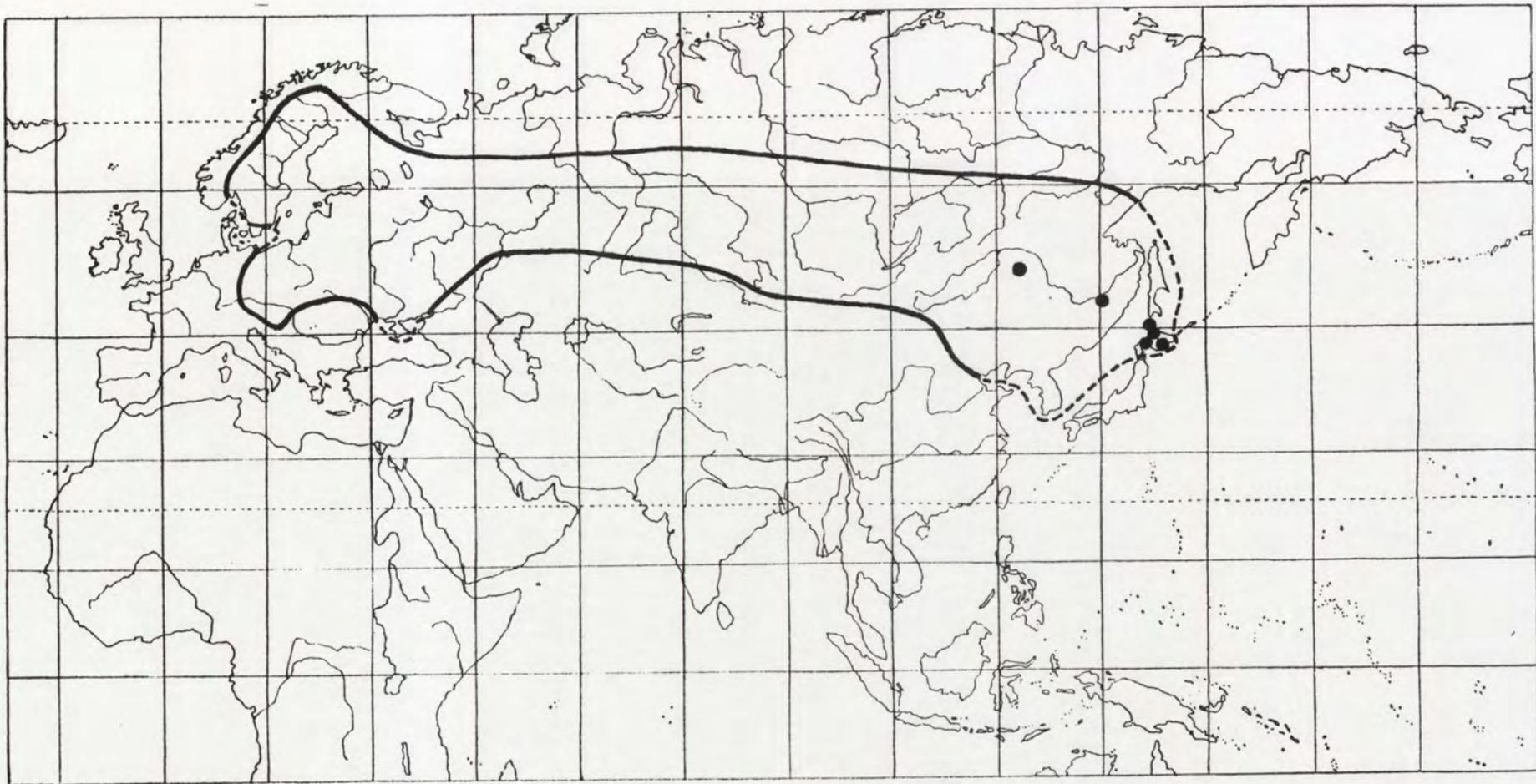
● *D. interrupta* DEYR.; ▲ *D. subcincta* DEYR.

<http://rcin.org.pl>

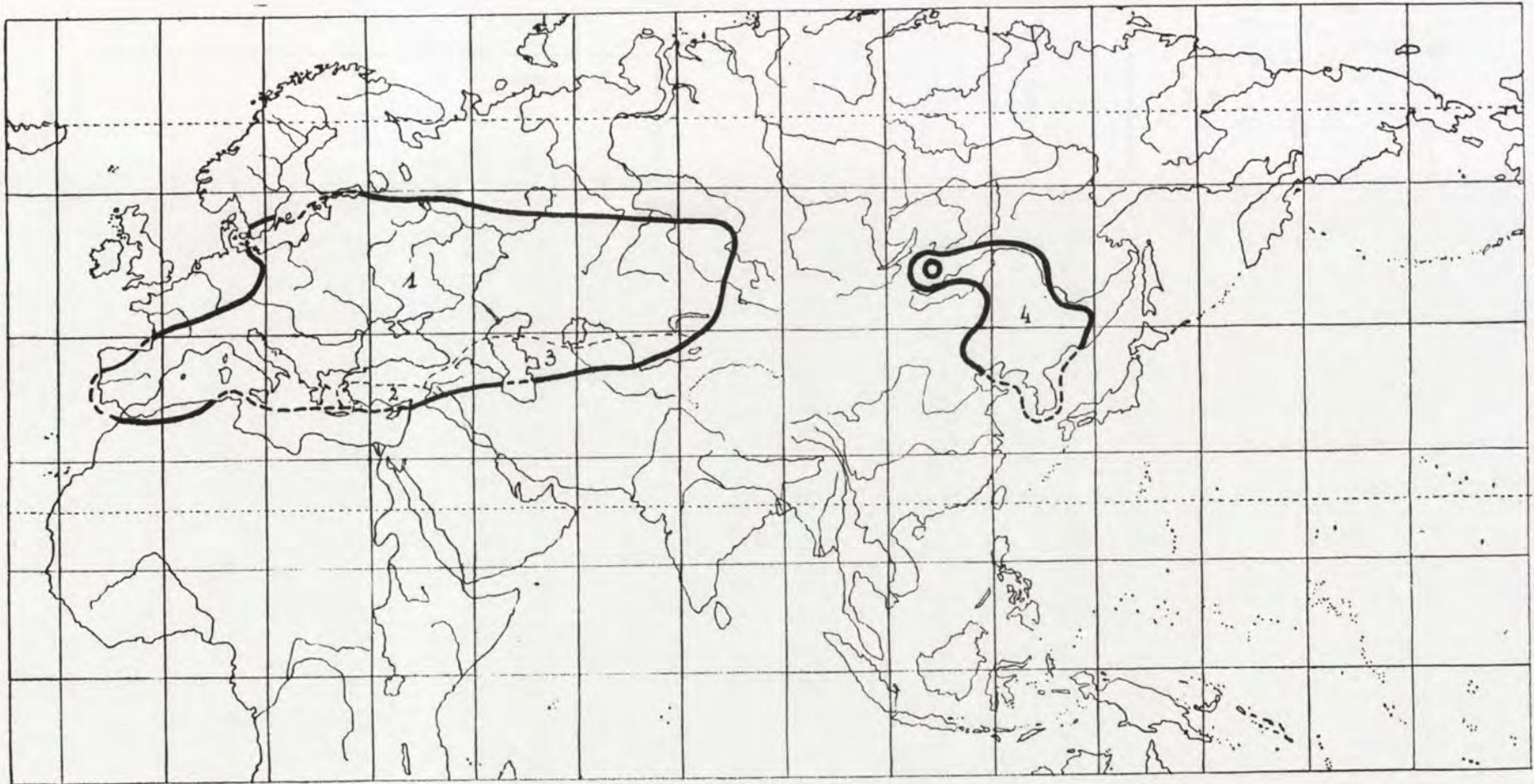




Map 19. Distribution of the genus *Dicerca* Esch.
--- ● *D. moesta* (F.)

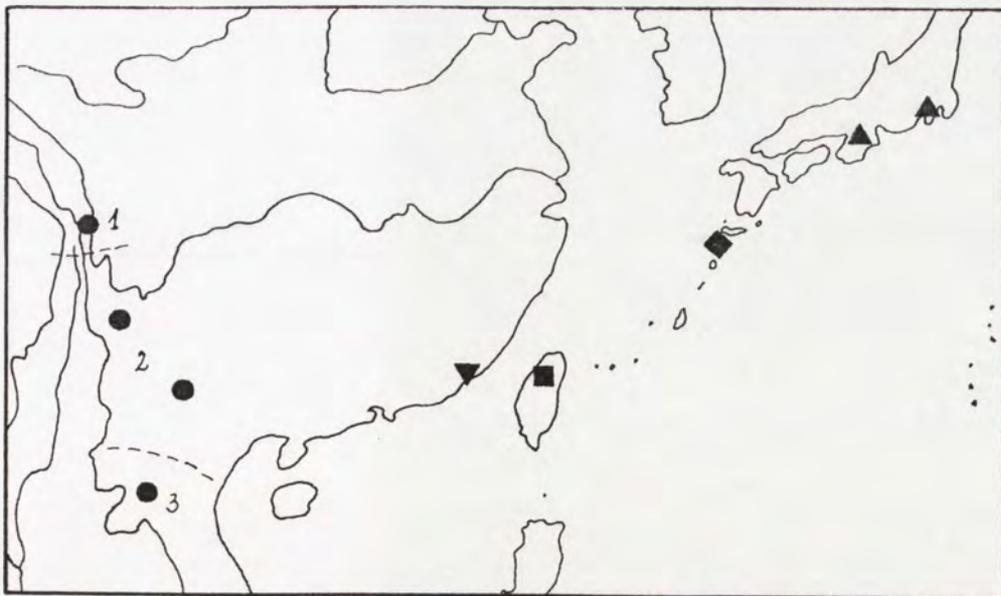


Map 20. Distribution of *Dicerca furcata* (THB.)



Map 21. Distribution of *Dicerca aenea* (L.)

1 - *ssp. aenea s.str.*; 2 - *ssp. bella AB.*; 3 - *ssp. validiuscula SEM.*; 4 - *ssp. chinensis OBB.*



Map 22. Distribution of:

● *Dicerca corrugata* FRM.

[1 - *ssp. thibetana* ssp.n.; 2 - *ssp. corrugata* s.str.; 3 - *ssp. vitalisi* D.V.];
 ▼ *D. latouchei* FRM.; ▲ *D. tibialis* LEW.; ■ *D. unokichii* HRI.; ◆ *D. nishidai* TMA.



Map 23

Distribution of *Archeopsila cordicollis* sp.n.



Map 24. Distribution of extralimital genera of the Psilopterina LAC.

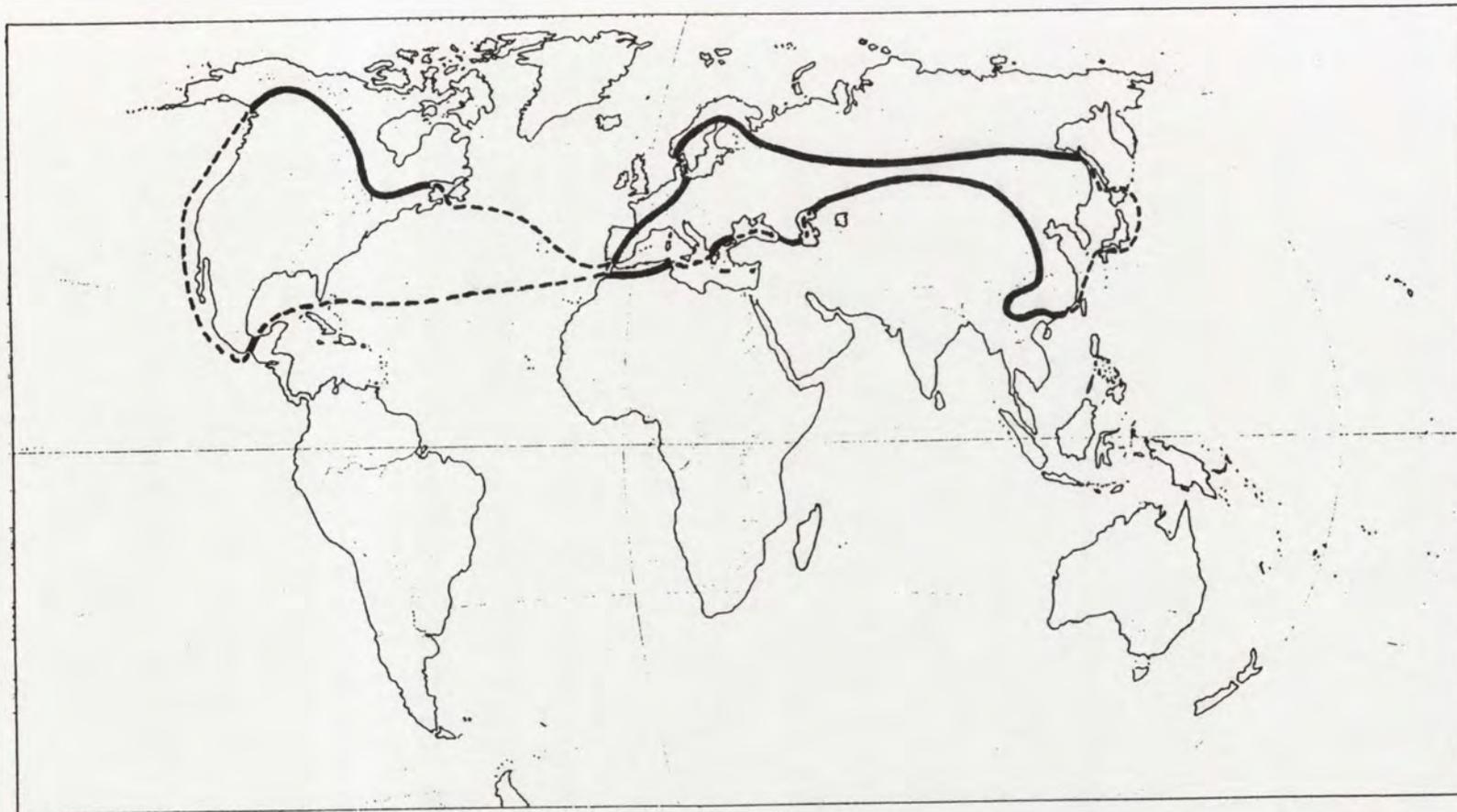
..... *Hilarotes* THS.; — *Ectinogonia* SPIN. [incl. *Kheiliella* OBB.];

-.-.- *Chalcopoecila* THS. [incl. *Achardella* OBB.];

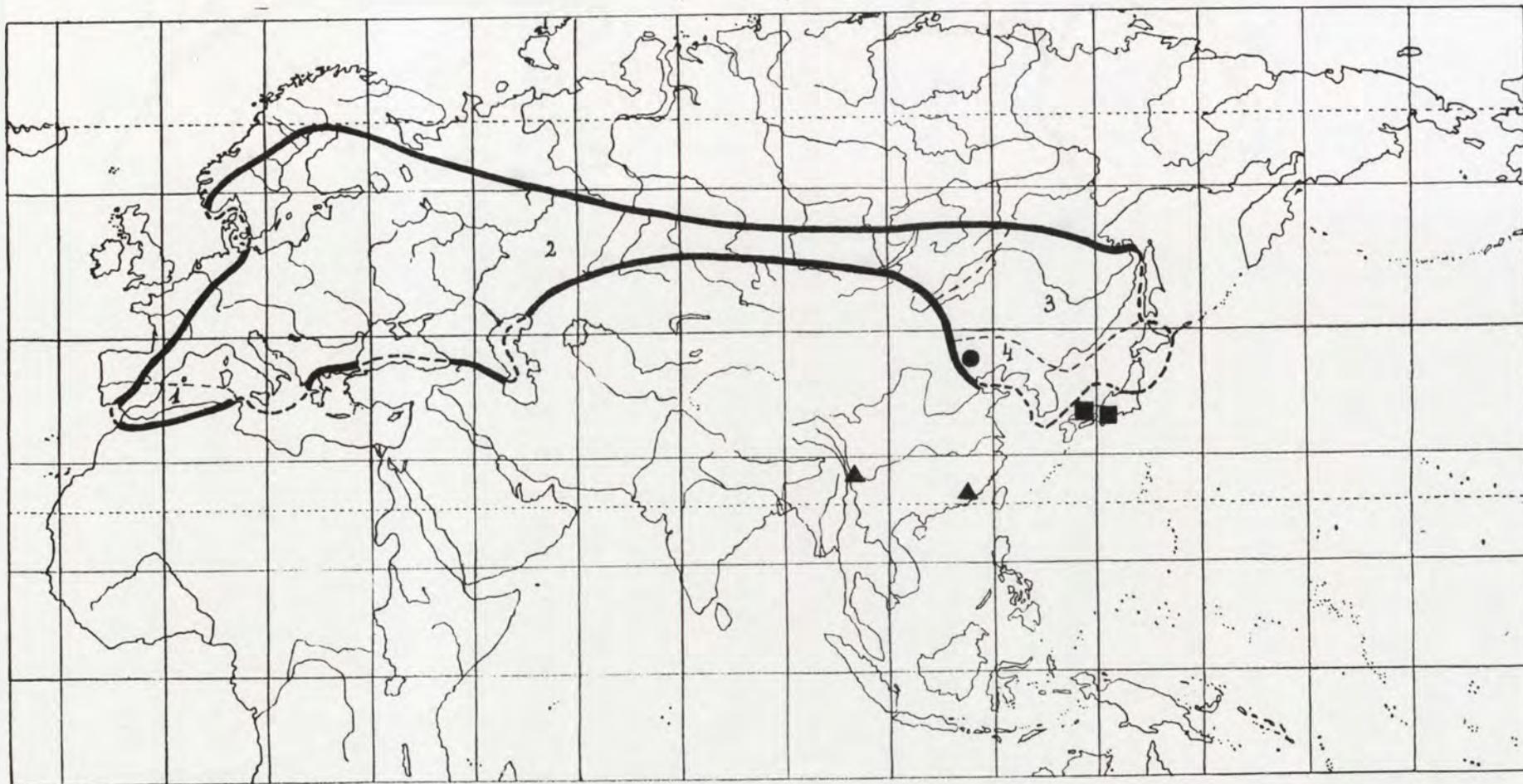
- - - *Oedisterna* LAC. [incl. *Monosacra* THS.];

● [Madagascar] *Sororcula* HOL.; ● [Mediterraneum] *Latipalpis* SOL.;

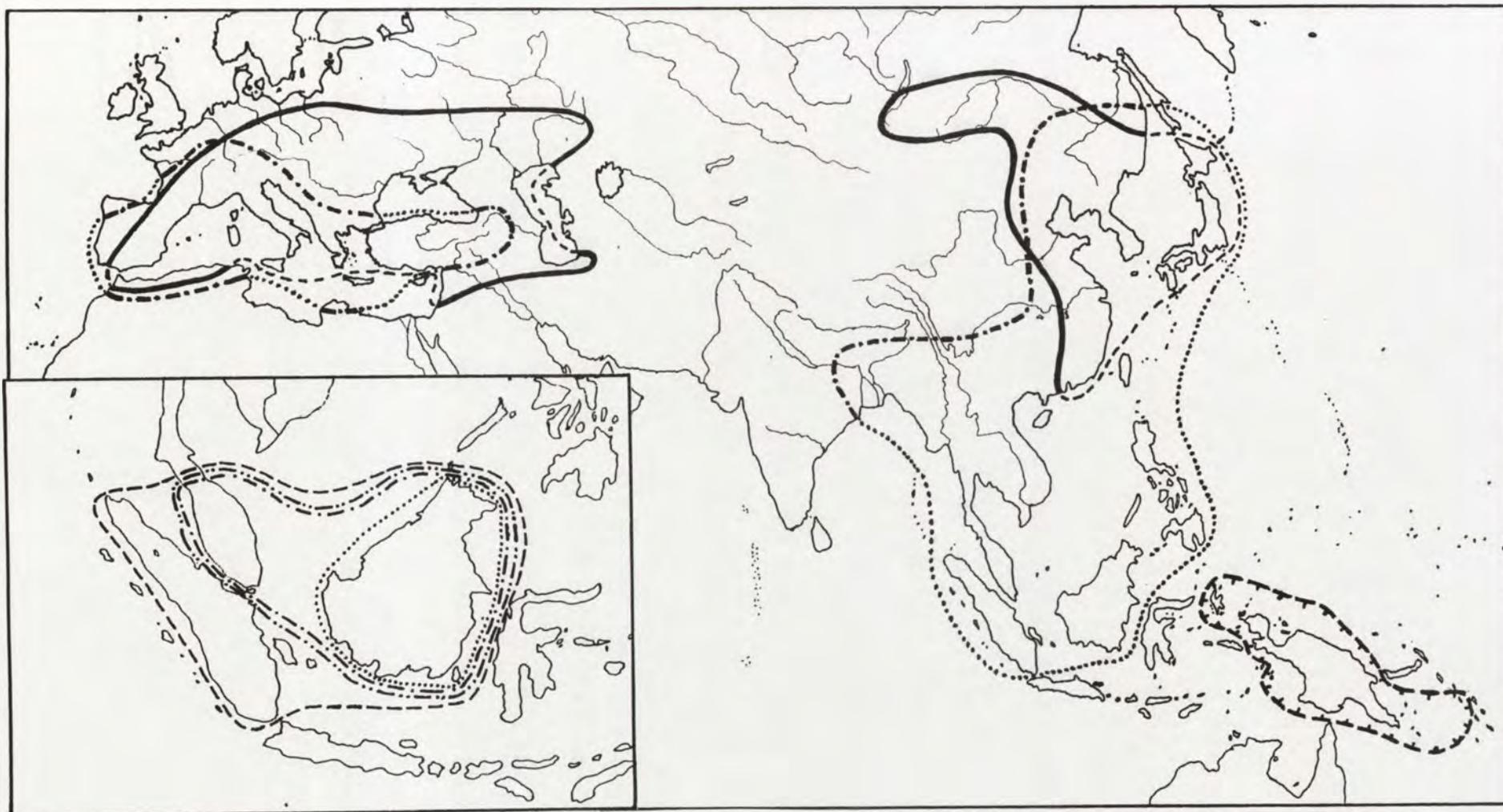
● *Perotis* DEJ.



Map 25. Distribution of the genus *Poecilonota* Esch.

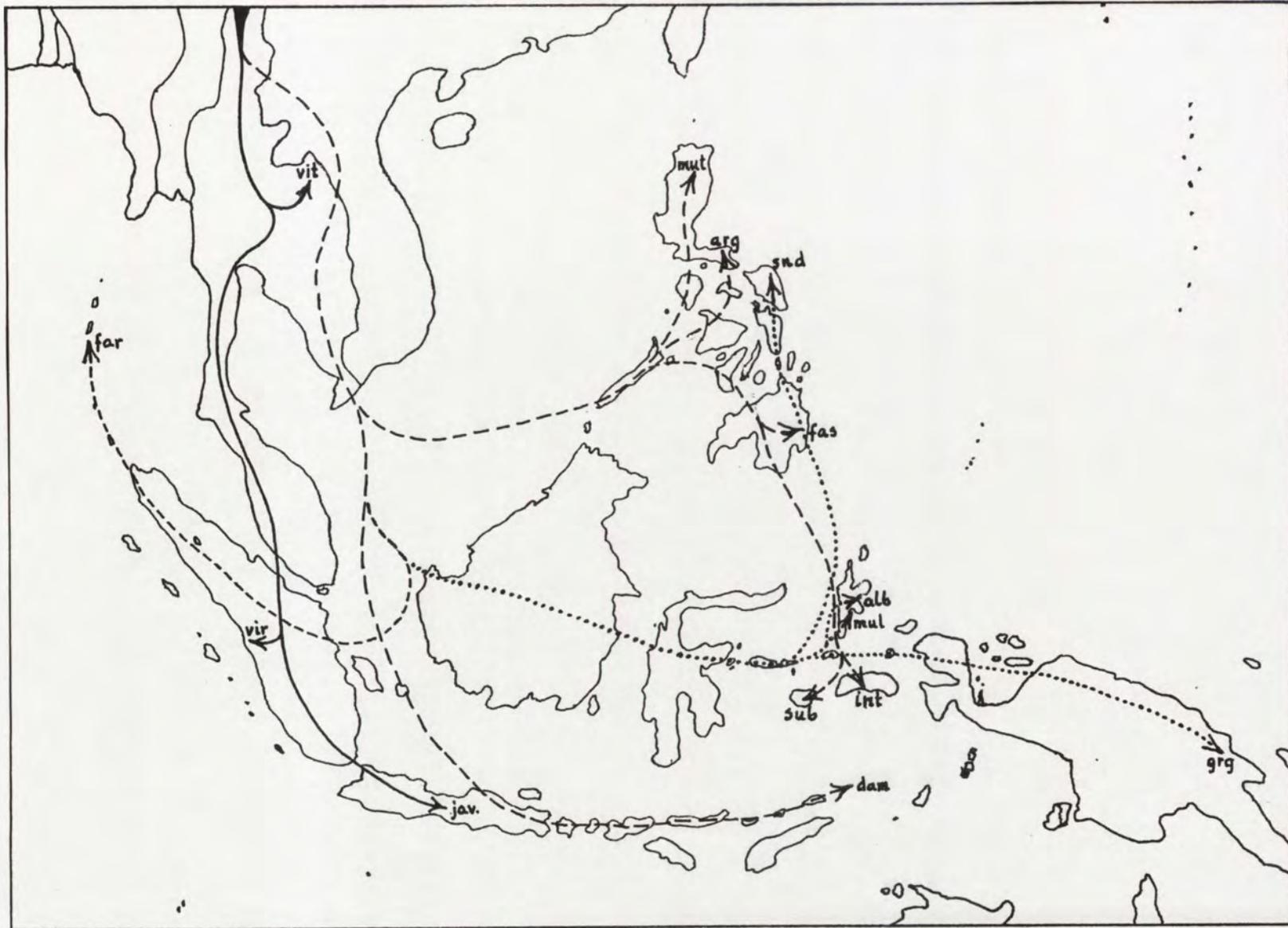


Map 26. Distribution of:
 ● *Poecilonota variolosa* (Pk.) [1 - *ssp. populiabae* RICH.; 2 - *ssp. variolosa* s.str.; 3 - *ssp. dicercoides* RTT.;
 4 - *ssp. chinensis* THY.]; ▲ *P. semenovi* OBB.; ■ *P. yanoi* KUR.



Map 27. Distribution of the genus *Ovalisia* KERR. s.l.:

[main map]: — — — *sg. Scintillatrix* OBB.; - . - *sg. Palmar* SCHAEF.; - + - + *sg. Ovalisia s.str.*
 [insert]: - - - *Poecilisia* *sg.n.*; *Maboisia* *sg.n.*; - - - *sg. Cinyristia* *sg.n.*; - - - *Erialata* ZYK.



Map 28. Hypothetical routes of dispersal of the genus *Dicercomorpha* DEYR.
 alb - *D. albosparsa* (C.G.); arg - *D. argenteoguttata* THS.; dam - *D. dammarana* sp.n.;
 far - *D. farinosa* THS.; fas - *D. fasciata* WATH.; grg - *D. m. grosseguttata* THS.;
 int - *D. interrupta* DEYR.; jav - *D. javanica* (C.G.); mul - *D. m. multiguttata* s.str.;
 mut - *D. mutabilis* SND.; snd - *D. m. saundersi* KERR.; sub - *D. subcincta* DEYR.;
 vit - *D. viridisparsa* THY.; vit - *D. vitalisi* BRG.

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