Revision of the tribe Caenocrypticini

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(Coleoptera: Tenebrionidae: Tentyriinae)

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INTRODUCTION

Status of the subfamily Tentyriinae

The tribe Caenocrypticini is here transferred to a group of tribes traditionally united in the subfamily Tentyriinae (Gebien, 1920, 1937; Doyen and Lawrence, 1979; Doyen and Tschinkel, 1982). In this group the aedeagus is invariably rotated by 180°, with the penis (median lobe) in a dorsal position above the parameres, and neither an exposed tegmen between the apical sternites nor defensive glands are present.

In recent years several changes to the higher classification of Tenebrionidae have been introduced. The suggested changes are largely based on rapidly accumulating knowledge about larval characters and adult internal structure. One of the changes involves the inclusion of Pimeliini in the subfamily Tentyriinae and consequently the name of the taxon should also be changed to Pimeliinae on grounds of priority (Doyen *et. al.,* 1989; Doyen 1993). In the newly constituted subfamily Pimeliinae the lack of defensive glands conforms with the other tribes, but the position of the aedeagus and the presence of an exposed tegmen between the apical sternites do not. Thus, the first key characters that can be used to identify tribes of the new subfamily are those characterizing the traditional subfamily Tentyriinae. For this reason Doyen and Lawrence (1979) suggested a polyphyletic origin for the subfamily Pimeliinae. However, Watt (1974, 1992) and later Doyen *et al.* (1989) and Doyen (1993) opted for a monophyletic origin, considering the appearance of the exposed tegmen between the sternites in Pimeliini a secondary development that arose independently of the usual state in the subfamily Tenebrioninae. The groupings therefore depend largely on inferences regarding homologies and convergences of character states.

The higher classification within the family Tenebrionidae is problematic, unlike the situation in most of the other coleopterous families, but it is currently being reassessed (references above). New discoveries, observations and evaluation techniques are resulting in new combinations with regard to the higher classification within the family. In the interim, I prefer to use the traditional subfamily name Tentyriinae for its original group of tribes rather than the broadened delimitation of the subfamily under the name Pimeliinae.

Systematics

When Gebien (1920) described the species *Caenocrypticus uncinatus* he placed the new genus in the tribe Crypticini, subfamily Tenebrioninae, mainly on gross morphological similarities. He considered the genus a primitive member of the Crypticini, hence the name *Caenocrypticus,* meaning an archaic *Crypticus.* Subsequently, Dr C. Koch (1952) described his first species and genera (*Lornamus* and *Cryptocarpes*) in the original tribe and subfamily of Crypticini. In 1958 he designated the new tribe Caenocrypticini for the relevant genera, retaining its position close to the Crypticini in the Tenebrioninae. The genera *Vernayella* Koch, 1958 (now a subgenus), and *Caenocrypticoides* Kaszab, 1969, were described in the tribe while it occupied this position. It is interesting to note that the two authors cited both the lack of an intersegmental tegmen between the sternites and the inverted position of the aedeagus as joint characters of the Caenocrypticini, and also noted that the opposite of these character states holds for the Crypticini. These two features jointly characterize all tribes of the Tentyriinae, although the lack of an intersegmental tegmen alone also occurs in tenebrionid tribes such as the Cossyphini. Nevertheless, neither Kaszab nor Koch considered the transfer of the Caenocrypticini to the Tentyriinae. The reason for this might have been the difficulty in finding an obvious sister group for the Caenocrypticini in the Tentyriinae, even though the situation was worse in the Tenebrioninae.

The present transfer of Caenocrypticini to Tentyriinae is based on both adult and larval characters. A description of larvae by Dr John Doyen is presented below. The missing intersegmental tegmen between the adult sternites is general in Caenocrypticini and in all tentyriine tribes, and is exceptional outside this subfamily. Its joint character, the inverted aedeagus, is predominant in this tribe. Nevertheless, in species with dorsoventrally arcuate aedeagi it is in a horizontal position, at least in dry specimens. Moreover, in some dry specimens, normally positioned (*i.e.,* not inverted) aedeagi were also observed. The horizontal position of the aedeagus is not typical for any of the species, but it was observed throughout the family. It is uncertain whether it occurs in live specimens or whether it is an artefact of preservation and desiccation.

Finally, a search for a sister or an outgroup for the Caenocrypticini, considering the total character complex, was unsuccessful within the subfamily Tenebrioninae. In the Tentyriinae, however, the tribe Stenosini was found as the only, sufficiently convincing sister group of the Caenocrypticini. As Doyen (1993) came to a similar conclusion through a detailed cladistic analysis of related tenebrionid tribes, the transfer of Caenocrypticini to Tentyriinae was indicated.

HISTORICAL BACKGROUND

The first specimens of the tribe Caenocrypticini were described as *Caenocrypticus uncinatus* by Gebien in 1920 and were collected in 1911 near Windhoek and Okahandja by J. W. Michaelsen. Thereafter, on the donkey-cart expedition of the South African Museum to Hereroland in 1925, a few specimens were collected at Sesfontein. The entomologist on the expedition was Dr A. J. Hesse, Head of the Entomology Department of that Museum. The systematic exploration of tenebrionids in the Namib was initiated by Dr C. Koch. After his first expedition to the Namib Desert in 1948, he visited the area several times. His main interest became the faunistic study of the dune desert and its immediate hinterland. In 1948, accompanied by Dr G. van Son, he travelled from Lüderitz into southern Angola and collected material of the first three species of Caenocrypticini to be described by himself in 1950. In 1951 he travelled to the northern Namib Desert and in 1954 participated in an expedition sponsored by Vernay and Lang. On this expedition he collected material of the first two species that he described in his new genus *Vernayella* in 1958. During a subsequent expedition to the central Namib, sponsored by Bernard Carp in 1958, Koch selected the site for a permanent research station at Gobabeb. The Namib Desert Research Station was inaugurated and started operating in 1963. This station was under the aegis of the Transvaal Museum and became the centre of Koch's activities until his death in 1970. In total he collected 13 species of Caenocrypticini, 12 of which were described by himself.

In 1970, Dr Mary-Louise Penrith started her scientific and field activities as Head of the Entomology Department of the State Museum, Windhoek, and between 1970 and 1982 led numerous expeditions throughout Namibia, accompanied at various times by her colleagues Dr S. Louw and Dr J. Irish. As her research interest during this period centred on the tenebrionid tribe Zophosini, an ecologically diverse group with a wide geographical distribution, she covered many areas previously not visited by coleopterists. She collected 13 species of Caenocrypticini, six of them described as new species in the present study. She was the sole collector of *C. (Vernayella) serratus* spec. nov.

I arrived in South Africa in 1973 and took charge of the Coleoptera Department at the Transvaal Museum, which housed the unique southern African collection of Tenebrionidae developed by Dr C. Koch. It was inevitable that I became involved in the study of this family. After an expedition along the coast north of Lüderitz in 1973, I was placed in temporary charge of the Namib Desert Research Station between October 1973 and February 1974. This period of initiation to the Namib Desert prompted me start an extended faunal survey of Coleoptera along the western coast of southern Africa. Between 1973 and 1989 the coast as well as the escarpments and their hinterlands were systematically surveyed, from the Kunene River to Cape Town. During these expeditions I was accompanied by Dr Lieselotte Prozesky-Schulze, Dr Mary-Louise Penrith, Mr A. Strydom, Mr M. Mathabathe, Mrs W. Breytenbach, Miss Ruth Müller and Mr J. Legwai, in teams and/or in succession. As a result of this 16-year survey, 19 species of Caenocrypticini (all but three of the currently known species) were collected and their preferred habitats and ecology recorded.

Another regular collector of Namib Desert tenebrionids was Prof. Eric Holm, a specialist on the family Buprestidae. He started his career as an assistant to Dr C. Koch at the Desert Research Station in the mid-1960s, and returned to the dune desert with his students several times between 1977 and 1981, collecting eight species of dune-dwelling Caenocrypticini and providing important distributional data for these species.

The Namib Desert Research Station at Gobabeb, later renamed the Namib Desert Ecological Station, continued its activities after the death of Dr Koch under the directorship of Dr Mary Seely. Under her guidance, detailed seasonal adult activity of four *C.* (*Vernayella*) species was recorded in the vicinity of Gobabeb.

Occasional records were also contributed by Mr Otlew Prozesky, Mr Wulf Haacke, Mr R. E. Schertz, Mr Eberlanz, Dr M. E. Irwin, Dr R. Wharton and Mr S. Braine.

The first South American specimen described by Dr Z. Kaszab (1969) in the genus *Caenocrypticoides* originated from the Deyrolle Collection, and must have been collected in Chile in the mid-1800s. About a century later, the Ross and Michelbacher expedition to the southern Peruvian coastal region in 1951 yielded many samples of this genus, and were identified by Dr Kaszab years after the description of the relevant species. The material that formed the basis of Kaszab's descriptions was collected by Dr L. Peña in southern Peru (*C. penai* Kaszab, 1969) in 1965, and in the same year by Dr I. Loksa (*C. loksai* Kaszab, 1969) in northern Chile during the Hungarian Soil-Zoological Expedition. The specimens of *C. peruanus* spec. nov. were collected by the Ross and Michelbacher expeditions during a faunal survey in Peru in 1950 and 1951, and by Dr L. Peña in 1965.

MATERIAL EXAMINED

The southern African material for this revision was provided by local institutions. Unidentified specimens were not received from foreign institutions. Specimens, mostly paratypes, were donated by or exchanged with several foreign institutions by Dr Koch. Such specimens were all labelled by him. As his identifications of Caenocrypticini were invariably correct, the specimens were not requested on loan, but their specific identity and paratype status (if labelled as such) are confirmed here.

Depositories of specimens

Southern African species (including *Fitzsimonsium*)
  Transvaal Museum, Pretoria (of these 997 via Gobabeb, 460 via the University of Pretoria), 3451.
  Namibia State Museum, Windhoek, 1323.
  Hungarian Natural History Museum, Budapest, 57.
  National Collection of Insects, Pretoria, 21.
  National Museum, Bloemfontein, 18.
  University of California, Berkeley, 10.
South American species
  California Academy of Sciences, San Francisco, 67.
  Field Museum of National History, Chicago, 16.
  Hungarian National History Museum, Budapest, 9.
  Transvaal Museum, Pretoria, 7.

BIOLOGY

Species of Caenocrypticini are generally cryptic. Surface activity of adults has only been observed in some of the ultrapsammophilous, dune-dwelling species. These species can be seen at night at the foot of barren dunes, feeding on windblown vegetation debris. Their larvae live in the thick pads of debris under the sand in the same position. Species inhabiting level sand were not seen on the surface but collected from sand among the roots of plants or from under stones.

Attempts at rearing Caenocrypticini species in the laboratory were generally unsuccessful. On five occasions up to 20 specimens were taken into our laboratory, but only one sample produced larvae. Eggs were produced within six weeks and larvae observed a month later. The last larvae died without pupating six months after the eggs were depositioned. The longest surviving adult lived for one year and seven months after being collected (January 1971 – 30 August 1972). One of the five preserved larvae was sent to Dr J. Doyen, who prepared the following description of the larva of *Caenocrypticus (Vernayella) noctivagus* Koch.

The larva of *Caenocrypticus (Vernayella) noctivagus* (Koch), Fig. 1 — by John Doyen

Late instar larva. Body subcylindrical, abdominal segments 8 and 9 tapering gradually to narrowly rounded apex; dorsum and venter lightly sclerotized, whitish; thoracic tergites and cranium slightly more sclerotized, slightly darker; tarsal claws and mandibles rigidly sclerotized, brown.

Head slightly flattened, prognathous, finely sculptured, whitish except for pale tan clypeofrontal suture. Epicranial suture extremely faint, length about one-third head width;

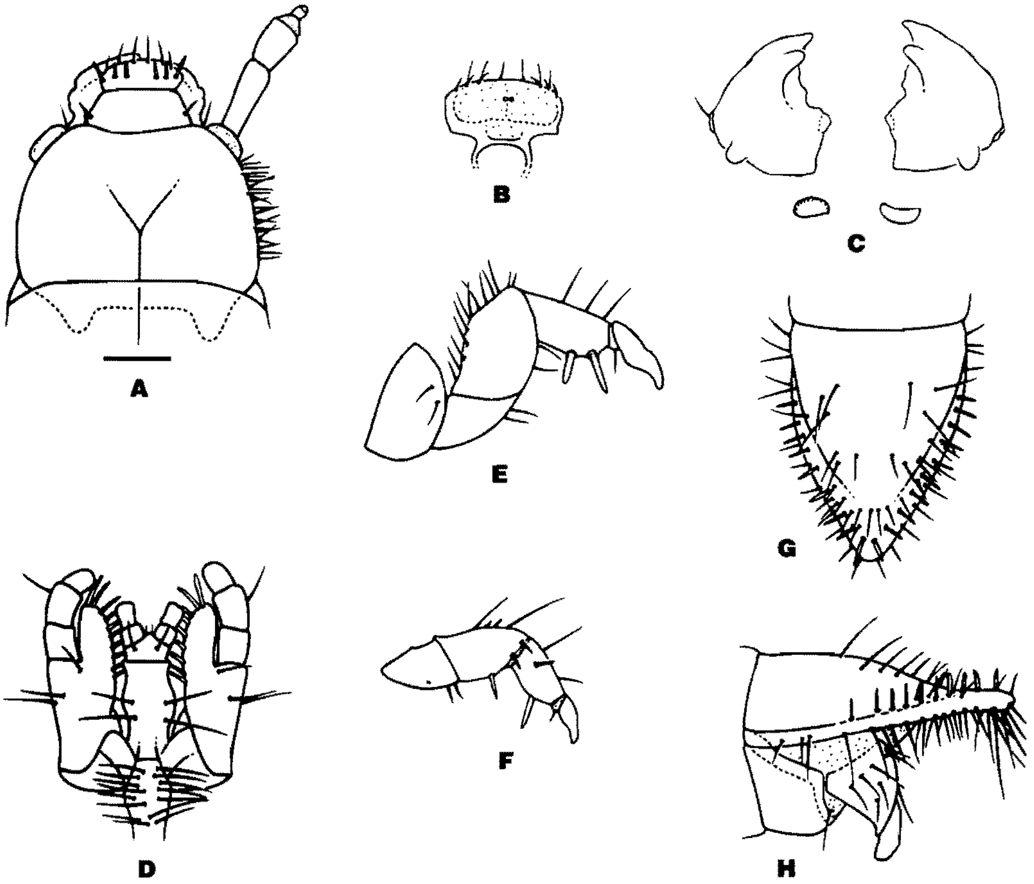

Fig. 1. Late instar larval characters of *Caenocrypticus (Vernayella) noctivagus* (Koch). **A**: head, dorsal view, left antenna removed; **B**: epipharynx; **C**: mandibles, ventral view (above), normal view of molar cups (below); **D**: maxillae and labium, ventral view; **E**: right foreleg, posterior view; **F**: right middle leg, posterior view; **G–H**: abdominal tergite 9, **G**: dorsal view, **H**: lateral view. Scale bar: A, E–H = 0,18 mm; B–D: 0,13 mm.

frontal arms nearly straight, short (Fig. 1A); endocarina absent. Ocelli and eye pigment absent. Cranial setae fine, arranged as band along gena (Fig. 1A) and ventral patch on gular and paragular areas; genal setae moderate in length, vertical setae about twice as long; clypeus bearing pair of slightly stouter setae basally near margins (Fig. 1A). Gular sutures nearly straight, diverging slightly, especially just before submentum. Antenna with second segment about 0,75 times length of first, sensorium indistinct in material at hand; apical segment papilliform; strip of head capsule absent between base of antenna and mandible. Labrum about twice as broad as long, fringed with six slender setae inserted dorsally along anterior margin and six stout, clavate arranged transversely along middle (Fig. 1A); epipharynx (Fig. 1B) with marginal row of six coarse setae, medially directed, along anterior margin; pair of faint annular sensilla centrally; masticatory processes absent; posterior margin of labrum sclerotized as in Fig. 1B, with faint transverse line between tormal bar on each side and also running longitudinally to vicinity of sensilla; tormal arms slender, medially arcuate. Mandibles (Fig. 1C) stout with apices bifid; retinacular ridge produced as one or two weak teeth; molas poorly defined, scarcely elevated; right mola a ridged cusp; left mola weakly crescentic, convex; mandibular bases with narrow, membranous patch near point of articulation with head capsule; membrane bearing several asperities (possibly setal sockets). Maxilla (Fig. 1D) with cardo distinctly divided by oblique suture; stipes with three projecting setae; mala with single row of about 10 stout, slightly spatulate setae along mesal margin. Labium with prementum about twice as wide as long, bearing two setae; ligula short, bearing two setae; mentum about 1,5 times as long as wide, poorly delimited from submentum, bearing two pairs of long setae; submentum slightly longer than broad, without setae; hypoharynx convex with tiny, dentate sclerome.

Thorax with pronotum about 1,25 times longer than mesonotum; distinct tergal or sternal sclerites not apparent; sternellum not enlarged. Forelegs (Fig. 1E) with coxae globular, with few slender setae; trochanter subtriangular in posterior aspect, with a pair of setae; femur thickened in middle, with ectal band of setae, two ental setae; tibia with few slender ectal setae, two very stout, blunt ental setae; claw slightly sinuous, spatulate, with base membranous, bearing single slender seta. Meso- and metathoracic legs similar to but about half size of prothoracic legs; femora with three spines along mesal face of distal margin; tibia with very large ental spine and smaller one on posterior face (Fig. 1F).

Abdominal segments 1–7 about 1,5 times as long as metathorax; tergites and sternites very indistinctly delimited;

essentially glabrous; segments about 0,75 times as broad as preceding segments, subequal in length; segment 7 subequal to 8 in width; tergite about 0,6 times as long, tapering to narrowly rounded apex (Fig. 1G); sparsely provided with long slender setae centrodorsally, with subperipheral fringe of 9–10 short, stout dorsally inclined spines on each side, interspersed with few longer, slender setae, and peripheral fringe of longer, slender, ventrally inclined setae, longest near apex (Fig. 1H); sternite about two-fifths length of tergite; pygopods with setose basal sclerite; sternite and pygopodial sclerite capable of refraction against underside of tergite. Spiracles minute, annular, apparently closed.

Material examined. Two late instar larvae, laboratory reared from adults collected at Gobabeb, Namibia (112 km SE Walvis Bay), viii.1967. Both specimens were pharate. Under the conditions of preservation the old cuticle was peeling off the new cuticle underneath, which was untanned, making observation difficult, especially of very small structures. Structures which were least clear were sensoria and sensilla on antennae and palpi; mandibular base structures, hypopharyngeal structure, spiracular structure, and setation of the trunk segments. Since the specimens were preserved in the last part of the instar, some setae may have been worn down or broken off. Whenever such aberrations might affect interpretations of relationship, they are mentioned below

Adult features (lack of defensive glands and external intersegmental abdominal membranes; inverted aedeagus) are consistent with the placement of Caenocrypticini in Pimeliinae (*sensu* Watt, 1974) (= Tentyriinae of authors). Within Pimeliinae, however, relationships of Caenocrypticini are obscure. Caenocrypticini have the maxillae somewhat exposed by the relatively small mentum. This character state is shared with, *e.g.*, Stenosini, Anepsiini, Eurychorini, Coniontini. By contrast, in Tentyriini, Asidini, Cryptoglossini, and many others, the mentum is relatively larger, concealing the maxillae. However, both groups of tribes are extremely diverse and very likely are not monophyletic clades. Adult characters are discussed at greater length below.

Larvae of Pimeliinae remain poorly known (Aalbu, 1985), partly because of difficulties in rearing many species under laboratory conditions (*e.g.*, persistent developmental diapause in Asidini; Brown, 1973). Furthermore, nearly all Pimeliinae inhabit soil or sand as larvae, almost always preventing direct association with adults. By contrast, many members of Tenebrioninae, Coelometopinae, Phrenapatinae, etc., occupy more specific substrates, often in aggregations including adults and larvae, so that direct association of life stages is often straightforward.

Larvae of the pimeliine tribes with small mentum are especially poorly known. Two genera each have been characterized for Coniontini (Doyen, 1976; Marcuzzi and Rampazzo, 1960: *Coelus, Coniontis*) and Stenosini (Keleinikova, 1976: *Stenosis, Dichillus*), and Schulze (1962) has constructed a key to larvae of most genera of Eurychorini. Most of the other tribes which might be pertinent here (Anepsiini, Lachnogiini, Cnemeplatiini, Cryptochilini, Calognathini, Ceratanisini) have never been characterized as larvae. Thus, only tentative conclusions are possible regarding relationship based on larval features.

Larvae of *C. (Vernayella)* show most of the important characteristics of Pimeliinae as summarized by Watt (1974).

1. The mandible has the external margin carinate, with a membranous patch near the base. However, only a single seta is visible on one mandible, none on the others. This condition may represent a traumatic loss occurring during the last instar. Owing to the general condition of the larvae at hand, it is difficult to determine whether or not additional setae were broken out of their sockets, but it is clear that no setal stubs are present.

Other Pimeliinae which have paucisetose mandibles include *Dichillus* (Stenosini) and *Idisia* (currently in Lachnogini). It is also worth mentioning that the membranous patch on the mandible of *C. (Vernayella)* is situated at the extreme basal outer margin, more proximad than in other larvae of Pimeliinae.

2. The forelegs are almost twice as large as the succeeding legs, with different setal arrangement on the tibia and femur. Such differentiation of the forelegs seems to be universal among larvae of Pimeliinae, but also occurs in soil-dwelling larvae of other subfamilies, as pointed out by Keleinikova (1963). In fact, even in some *Zophobas*, which inhabit decayed bat guano in nature, the forelegs are somewhat stouter and have slightly different setation than the posterior legs (personal observation).

The setal pattern of the foreleg of *C. (Vernayella)* is most similar to that of the two known Stenosini. In *C. (Vernayella)* and *Dichillus* the tibia bears only two stout spines on the mesal margin. In *Stenosis* there are two large spines and a third, much smaller one. By contrast, a comb of many spines (usually about 6) is present in most described pimeliine tribes. In several tribes (*e.g.*, Asidini, Pimeliini, Erodiini) the tibial setae are long and fine rather than spinose, or long, fine setae may be present in addition to spines. The femur of *C. (Vernayella)*, *Stenosis* and *Dichillus* is also paucispinose, in contrast to a more densely spinose member in, *e.g.*, Tentyriini, Triorophini (Aalbu, 1985) and Adesmiini, Eurychorini (Schulze, 1962).

In *C. (Vernayella)* the base of the claw is well differentiated from the more strongly sclerotized apex, as in other Pimeliinae, and bears a single seta. The claw base also bears a single seta in some Epitragini (Doyen, 1974), Elenophorini (Marcuzzi *et al.*, 1980), Stenosini, Triorophini, Akidini and Eurychorini. In Tentyriini, Zophosini, and Adesmiini two setae are present, and in Asidini, Coniotini, Pimeliini, Erodiini, the claw base bears many setae (Brown, 1973; Marcuzzi and Rampazzo, 1960; Keleinikova, 1962). The adaptive significance of variation in setal number is obscure, and such simple differences could easily be subject to convergence, but certainly warrant further examination as taxonomic characters.

The prosternellum in Coniontini, Asidini, Triorophini, Epitragini, Nyctoporini and probably in most other tribes of Pimeliinae is enlarged and almost quadrispherical for housing the muscles that remote the legs. However, in many treatments this feature is neither illustrated nor specifically described. It is worthy of note that in *C. (Vernayella)* the sternellum is not enlarged any more than in larvae of *Tenebrio*. The sternellum also appears small in the facies illustrations of *Stenosis* and *Dichillus* (Keleinikova, 1976), but no detailed illustration is presented and basal leg structure is not included in the description.

3. Abdominal tergite 9 is expanded posteriorly, producing a

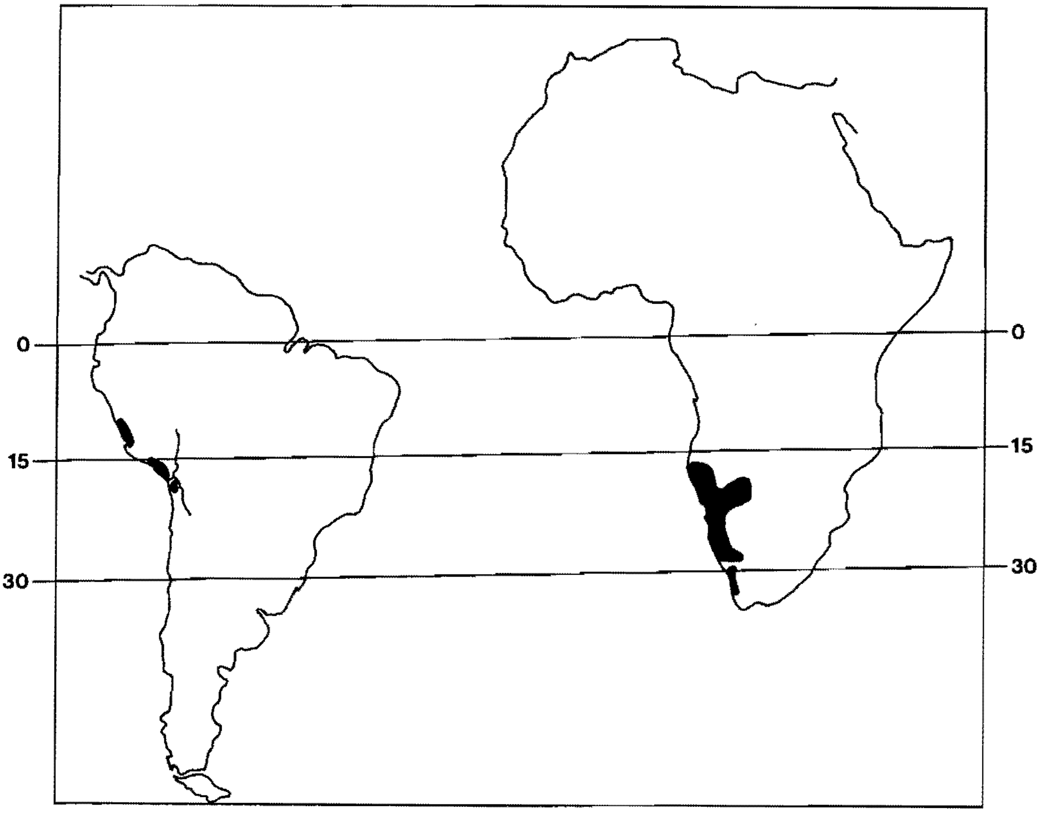

Fig. 2. World distribution of the tribe Caenocrypticini. *Caenocrypticus* in southwestern Africa, *Caenocrypticoides* in South America.

subacuminate shelf-like apex, with the true posterior margin (and anus) ventralized. Unrogomphi are absent, pseudopods well developed. This general configuration is widespread in Pimeliinae and also occurs in Opatrini, Eleodini, and other non-pimeliine tribes with soil-inhabiting larvae. The particular arrangement in *C. (Vernayella),* with a dorsal peripheral margin of stout, spinose setae and scattered, more slender setae both dorsally and ventrally occurs in Triorophini and Stenosini, and in slightly modified form in Epitragini and Tentyriini, where there are also a few stout spines over the disk of tergite 9. In Coniontini and Asidini the entire dorsum of tergite 9 is densely spinose.

A few other features of the *C. (Vernayella)* larva are noteworthy. First, the trunk is strongly orthosomatic and almost devoid of setae. Most other larvae of Pimeliini have distinct constrictions between the segments, often producing a submoniliform shape, as in Triorophini, Erodiini and Zophosiini. An orthosomatic trunk is more characteristic of, *e.g.,* Opatrini, Eleodini, Tenebrionini. Second, the spiracles of *C. (Vernayella)* are minute, indeed were invisible without staining. In fact, these spiracles appear to lack an opening into the tracheal system, but this is uncertain because of the general nature of the specimens and small size of the spiracles. The only other terrestrial beetle larvae known to have a closed tracheal system are those of *Stenosis* and *Dichillus* (Keleinikova, 1976; Crowson, 1981). Keleinikova (1976) speculates that the larvae of *Stenosis* and *Dichillus* might live in soil saturated with water, since closed tracheal systems in Coleoptera otherwise occur in aquatic forms. Saturated substrates appear unlikely for the *C. (Vernayella)* larvae, which originated from the extremely arid Namib Desert and were reared in laboratory containers in which dampness never reached the point of saturation. It seems more likely that such modifications represent mechanisms for reducing water loss.

The larval characters discussed above suggest that Caenocrypticini are more closely related to Stenosini than to any other pimeliine tribe. The general resemblance in mandibular, leg and trunk morphology involves simple characters which will be difficult to evaluate in the cladistic context, at least until many more larvae of Pimeliinae are characterized. The reduced spiracles, however, certainly represent a derived feature and can be considered a valid synapomorphy, but their condition needs to be confirmed in nonteneral material.

HISTORICAL BIOGEOGRAPHY AND ETHOECOLOGY

The tribe Caenocrypticini exists in two isolated areas in southern Africa and in South America (Fig. 2). They occur on both continents along their western oceanic coasts where the southern Antarctic cold currents originated and maintain arid coastal conditions and, in certain areas, barren dunelands. The present vicariant distribution suggests a period of dispersal at a time when the two continents had not yet separated. At that time the Atlantic basin was not open and the Benguela current could therefore not begin its desertifying effect along the emerging west coast of southern African where the southern African species of the tribe now occur (Fig. 3). Similarly,

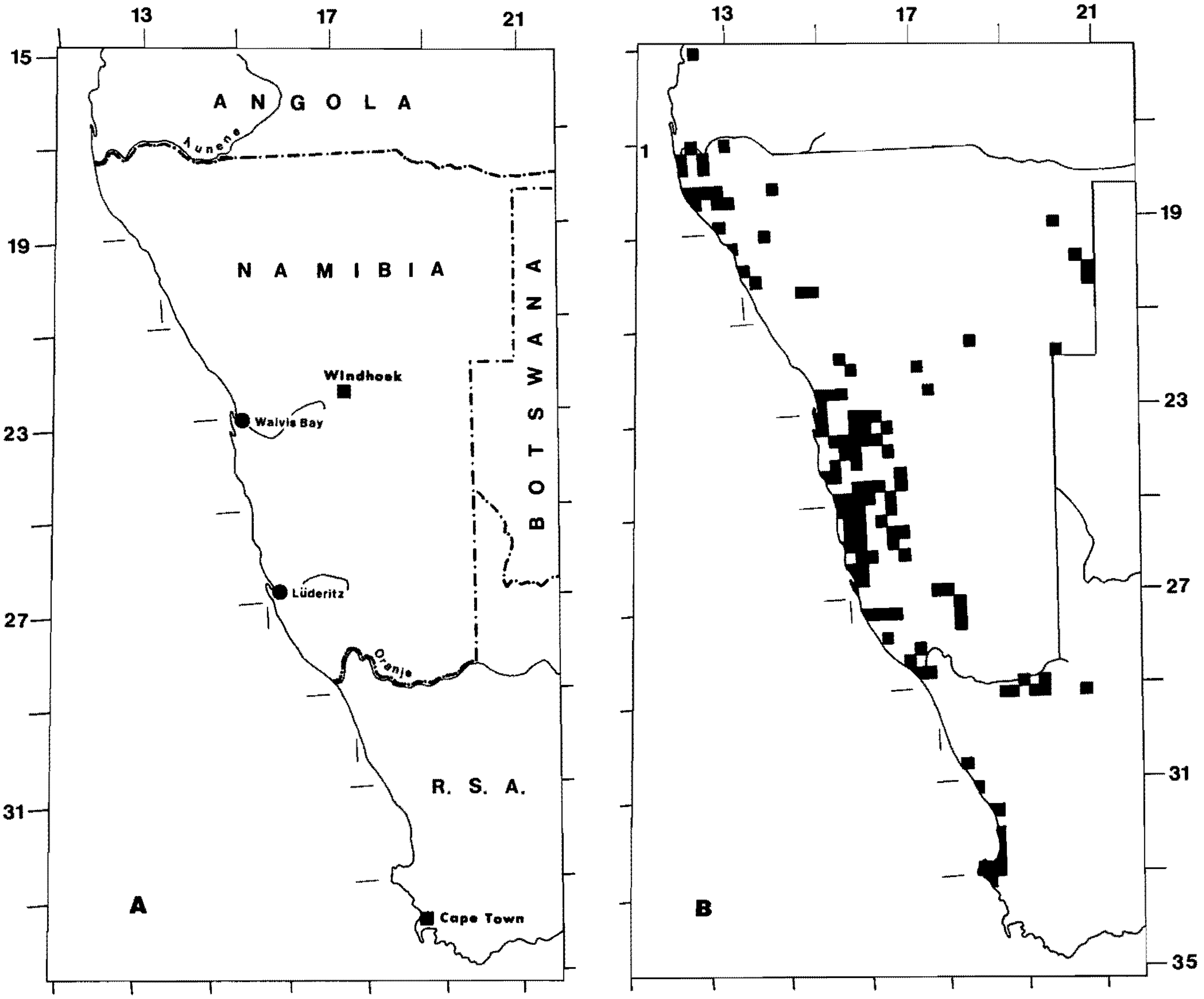

Fig. 3. Distribution of the *Caenocrypticus* species in southwestern Africa. **A**: geography; **B**: distribution.

in South America the Andes did not exist for a long time after the Gondwana break-up. Thus, the rainshadow effect that currently reinforces desertification on the Peru/northern Chile coastline was not operational either. Cladistic analysis of the tribe indicates that the primitive lineages are found in the southern African part of the vicariant world distribution. The origins of the tribe was, therefore, not coast-bound.

Questions relating to the centre of origin and native habitat of the emerging Caenocrypticini must consider the geographical distribution and habitat preferences of the extant primitive southern African species of the tribe. These species occur in five isolated areas, with only two of them overlapping in the upper Kuiseb area. Their distributions reach or approach the coast both in the south and in the north. A large area along the Namib coast lacks primitive species. This area is currently covered by barren dunes or was swept intermittently by northward-moving sand masses in the past (Endrödy-Younga: 1982*a*). It is evident that the ancestral species avoided barren dune conditions, but it is nevertheless likely that this is the area where the extant primitive lineages originated (Fig. 4). This may be the reason why *C. (Phyloradix) bushmanicus, C. (P.) soror* and in particular *C. (Caenocapicus) capensis* cannot be linked to each other or to the northern groups of primitive species. The present western coastal flats of southern Africa precede the continental break-up in age. The pre-desert (Namibia) environmental conditions on these flats can be deduced from the habitat preferences of the extant primitive species of Caenocrypticini.

During my 16-year (1973–1989) survey of the southern African west coast and its hinterland, from the Kunene River to Cape Agulhas at the southern tip of the continent and including the central Namib, the same broad set of standardized collecting methods (Endrödy-Younga, 1979, 1990) were applied to make sampling results comparable. The recorded geographic distributions and apparent gaps are therefore probably real, and are supported by earlier (Dr C. Koch) and concurrent fieldwork (particularly by Dr M.-L. Penrith and Prof. E. Holm). During my survey all but three

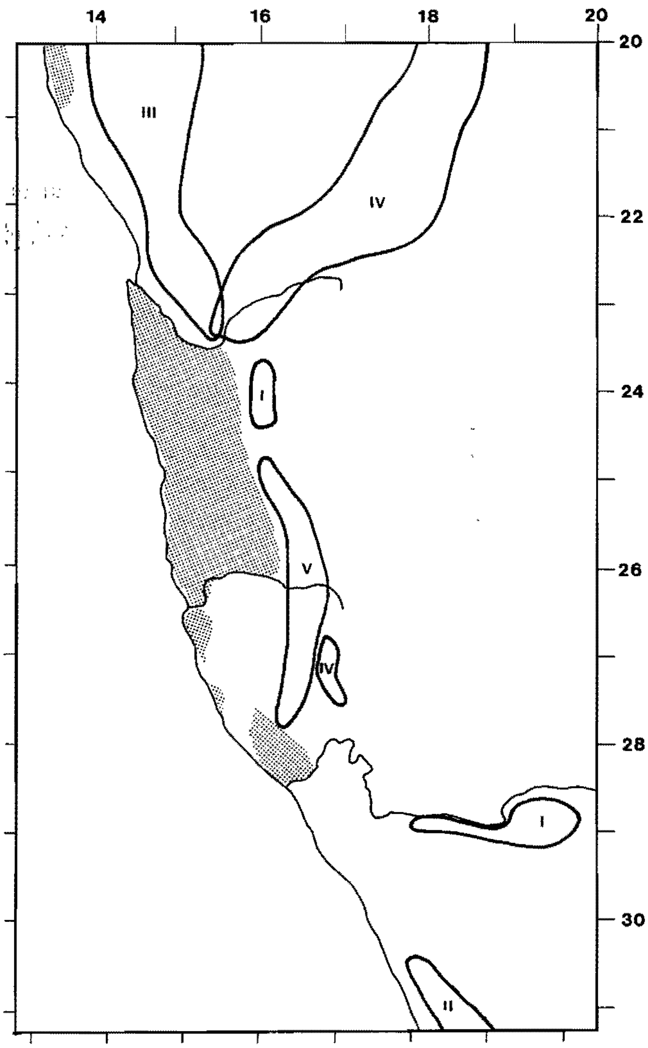

Fig. 4. Distribution of the *Caenocrypticus* subgenera around the Namib dune desert. **I**: *Phyloradix;* **II**: *Caenocapicus;* **III**: *Cryptocarpes;* **IV**: *Caenocrypticus;* **V**: *Psammotopulus.* The derived subgenus *Vernayella* is restricted to the central and northern dune desert that is void of the primitive subgenera.

Caenocrypticini species were collected and their environmental preferences recorded. This information forms the basis of the discussion below.

In all Caenocrypticini species, common environmental preferences are a sandy substrate and arid to semiarid climatological conditions. All primitive species avoid ultrapsammophilous barren dunes. They live on more or less compact and vegetated sandy flats or on sandblown rocky hillsides among the roots of plants or under stones. The area of origin can thus be assumed to have been somewhere in the western part of the present Namibia and to have extended, probably in a later phase, into parts of adjacent South America before it broke away. This assumed centre of origin, now in the western part of southern Africa, was within the landlocked central parts of Gondwanaland. The climate was presumably continental, as opposed to the humid coastal belt which is marked by the present and fossil *Nothofagus* forest belt along the margins of the megacontinent (Endrödy-Younga, 1995). Orogenic activity was limited, but sand-producing erosion must have occurred, resulting in sand accumulations along rivers and inland lakes, even before the rapid diversification of the order Coleoptera. Ample sandstone deposits from the Palaeozoic to barely solidified recent sandbanks testify to this.

Considering the origins of the Caenocrypticini, a discrepancy is apparent between the cladistic and geographical positions of the primitive species. The basal species of every clade within the primitive subgenera *Phyloradix, Caenocapicus* and *Cryptocarpes* are at present in distant geographical isolation (Fig. 4). Instead of forming a geographical cluster, these species are spread in an arch between the north-south limits of the total distribution of the genus (between 17° and 32° S latitude). Two of the extremes occur near the Atlantic coast, the three *Cryptocarpes* species in the north and the single *Caenocapicus* in the south, whereas the two other basal species occur inland and in between: *C. (Phyloradix) soror* in the hinterland of the Namib dune desert (Plate 12A,B) and *C. (P.) bushmanicus* in an inland section of the Orange River basin (Plate 13A). The common ancestors of these basal species are the metaphorical 'missing links' which must have existed in coastal areas of the Namib Desert since this area is central to all observable radiations. It is at present covered by the dune sea of the central Namib Desert, having in the past been periodically swept by northward-moving sand masses (Endrödy-Younga, 1982*a*). As mentioned above, the primitive species avoid barren dunes. The area in the southern Western Cape Province where *C. (Caenocapicus) capensis* occurs was presumably never covered by dunes and might be the original habitat type of the emerging tribe (Plate 13B). The area in the northern Namib where *Cryptocarpes* species occur is still not dune-covered. These species inhabit sandy flats (Plate 15A) but are cut off from the coast by emerging barren coastal dunes. The hypothesized geographic range of the ancestral stock, which had to give way to developing sand accumulation, shifting barren dunes and eventually to the continuous dune sea of the central Namib Desert, is indicated in Fig. 4. It is suggested that the sand-covered area temporarily became devoid of Caenocrypticini, subsequently to be inhabited by species of the subgenus *Vernayella* and some species of the subgenus *Psammotopulus.*

The species that could be close to the ancestral stock are *C. (C.) macintyrei* and *uncinatus.* These two species occupy the northeastern extreme of the tribe's distribution, from the Kalahari through southern Ovamboland to the Namibian high plateau north of Windhoek (Fig. 16). The habitat is semidesert to savanna, and the two species occur on consolidated red sand in the Kalahari in northeastern Namibia and softer, light-coloured sandy flats in Ovamboland (Plate 16B), sheltering among plant roots or under stones.

The lineage of the subgenus *Cryptocarpes* comprises three closely related species, *C. elongatus, C. damara* and *C. dividiopsis.* The cladistic displacement of the last species is discussed in the section on cladistics. This lineage occupies the northwestern section of the tribe's distribution (Fig. 13), avoiding the intruding coastal dunes. These species live on sandy flats among the roots of plants and in small hummocks (Plate 14A,B). They might represent a very early split from the ancestral stock, sharing an apomorphy, the increasingly divided eye according to species.

Adaptation to ultrapsammophilous conditions apparently started in the central Namib Desert on the inland margins of the accumulated sand masses and is characterized by dilated protibiae with a large apicolateral process (Fig. 18E), facilitating movement on and digging in the soft dune sand. This lineage comprises species of the subgenus *Psammotopulus.* Three species, *C. (P.) holmi, C. (P.) penrithae* and *C. (P.) klinghardtmontis,* occupy the inland margins of the dune desert on the sandblown slopes of the escarpment and the inselberg Klinghardt Mountains (Figs 4, 22). They live in soft sand, including vegetated marginal dunes, but do not penetrate into the dune sea (Plates 18B, 19B). The *Psammotopulus* lineage also includes species that inhabit dunes and shelter and feed in the sand-covered pads of vegetation debris at the foot of dunes. Penetration of the dune sea from the inland margins occurred at more than one point. *C. (P.) deserticus* occupies the southern coastal dunes (Plate 18A) between the Orange River and Lüderitz (Fig. 21), apparently not entering the central Namib, not even along the coastline. *C. (P.) peezi* is restricted to the central Namib dunes, only reaching the Swakopmund coastal dunes which were only very recently connected to the central Namib dunes (Endrödy-Younga, 1986). As dune-dwellers, they can disperse northwards on shifting barchans, or along continuous dune systems. It may thus be assumed that *C. (P.) deserticus* penetrated the Namib along the Orange River whereas *C. (P.) peezi* spread along one of the rivers in the central Namib (Fig. 21).

The earliest penetration of the *Psammotopulus* lineage must have occurred with the ultrapsammophilous adaptation of *C. (P.) phaleroides,* probably along a southern Namib route. This species is the only dune specialist in *Caenocrypticus* that occurs in all three parts of the dune Namib, *i.e.,* the southern, central and northern dune systems (Fig. 20). It bridged both duneless areas between the three sections of the Namib on shifting barchans during early periods of sand transportation (Endrödy-Younga, 1986). This type of early northward dispersal from the Orange to the Kunene Rivers is demonstrated also by the dune-specialist genus *Lepidochora* (Eurychorini). Ultrapsammophilous adaptation in *C. (P.) deserticus* and *C. (P.) peezi* occurred only after the northward transportation of sand masses ceased, and their distributions are therefore restricted to sections of the desert where they entered (Fig. 21). The distribution of *C. (P.) phaleroides* (Fig. 20) coincides with the distribution of the present dune systems, coastal in the south and in the north, and extends to the east in the central Namib area.

The highest adaptations to ultrapsammophilous conditions (Plate 21A) are reached in the lineage comprising the subgenus *Vernayella,* with the four highest synapomorphies marking these species. The first speciation events leading to in *C. (V.) ephialtes* and *C. (V.) pauliani* seem to have been contemporaneous with that of *C. (Psammotopulus) phaleroides* since they show the similar distribution patterns in the central and northern Namib dune systems (Figs 25, 26). The *Vernayella* lineage apparently also adapted to the barren dune habitat in the central Namib Desert, as none of its species occur in the southern Namib dunes, in contrast to *C. (P.) peezi* which apparently entered the barren dunes in the Orange River area. A dispersal pattern similar to that of *Vernayella* is shown by species of the subgenus *Cardiosis* in the genus *Zophosis* (Endrödy-Younga, 1986). Two terminal species of the *Vernayella* lineage, namely *C. (V.) delabati* and *C. (V.) noctivagus,* are widespread in the central Namib (Figs 24, 27) but are probably younger than the occurrence of northward shifting sand masses, so that they could not reach the northern sand masses as did the two basal *Vernayella* species, *C. (V.) ephialtes* and *C. (V.) pauliani.* Two localized species, *C. (V.) kochi* in the central Namib (Fig. 27) and *C. (V.) serratus* in the north (Fig. 25), both seem to be derived from *C. (V.) ephialtes* and might represent the most recent speciation events in the lineage.

The lineage comprising the Atakama genus *Caenocrypticoides* provides a landmark date in the evolution of the tribe. Its species share an apomorphy with the southern African *Psammotopulus* species, namely dilated protibia with an anterolateral process, but not the sagittal elevation of the last abdominal sternite in females. It appears that the South American genus can be derived from the ancestry of the southern African *Psammotopulus* lineage and not from any of the more basal ones. It had to occur at least shortly before South America separated from the southern African coast. Because of a lack of geohistorical information, the history of the vicariance event between the Namib and Atakama remains unclear.

It appears that the more primitive species in South America, *C. peruanus* and *penai,* occur in the northern part of the Atakama distribution, along the coastline of southern Peru, whereas the derived species occur in the south in northern Chile (Fig. 29). A historical northern contact with the ancestral stock in southern Africa is therefore implied, prior to the elevation of the Andean mountains.

Habitat selection in the South American species is similar to that of the southern African species, namely coastal sand in the case of *C. peruanus* and *C. penai,* and off-coast riverine sand deposits in the case of *C. loksai,* the latter being comparable to the habitat of *Caenocrypticus (Phyloradix) bushmanicus* along the Orange River.

CLADISTICS AND PHYLOGENY

Comparative morphology of the Caenocrypticini species resulted in the identification of a large number of characters that are invariant within species. Some of the characters appear to be common to all species and thus define the tribe. Others appear in groups of species. Most of these characters were used by Koch (1950, 1952, 1958) in the descriptions of his four genus-level taxa, and by Kaszab (1969) in the description of his genus. A small number of characters appear to be unique to individual species. Cladistic methods were used to test the validity of these species groups (genera and subgenera) and to assess their phylogenetic relationships.

To identify the most likely outgroup for Caenocrypticini, all tenebrionid tribes were considered but the only supportable outgroup seems to be the Stenosini. Doyen (1993), in the first cladistic study of tribes of the subfamily Tentyriinae/Pimeliinae, also concluded that Caenocrypticini might be best derived from the stenosine clade. He supported this conclusion with numerous external and internal adult characters, and also with larval characters of Caenocrypticini that he describes in this Monograph for the first time (see pp. 2–5). Based on Doyen's (1993) cladograms, particularly the one rooted by a hypothetical outgroup (his fig. 209), the outgroup for the stenosine clade (including Caenocrypticini) should be the genus *Boromorphus* Wolloston that he transferred from the tribe Tenebrionini and suggested should be given tribal status.

Character	Plesiomorphic	Transitional	Apomorphic
0. Head	Not pedunculate		Pedunculate
1. Eye	Not divided	Partially divided	Completely divided
2. Gula	No stridulation		With stridulation
3. Prosternal apophysis 1	Narrow		Broad
4. Prosternal apophysis 2	Pointed		Truncate
5. Mesocoxa	Closer than metacoxa	Equal to metacoxa	More distant
6. Metacoxa	Strongly transverse		Moderately transverse
7. 3rd antennal segment	Longer than 2 or 4		Not longer
8. Anterior tibia 1	Slender	Moderately dilated	Strongly dilated
9. Anterior tibia 2	Straight		Curved
10. Anterior tibia 3	Apex truncate		Apex asymmetrical
11. Tibial spurs	Small		Large
12. Tarsal claws	Even		Uneven
13. Dimorphism 1	Not in male		Present in male
14. Dimorphism 2	Not in female		Present in female
15. Aedeagal apicale	Longer than basale	Equal	Shorter
16. Aedeagal paramere	Split		Fused
17 Paramere 1	Apex setose		Not setose
18. Penis 1	Apex split		Not split
19. Penis 2	Dorsoventrally compressed		Not compressed
20. Penis 3	Straight	Moderately arcuate	Strongly arcuate
21. Paramere 2	Not ark-shaped		Ark-shaped (baggy)
22. Epipleuron	Tapering evenly		Contracted anteriorly
23. Posterior claws	Less than ½ segment		Longer than ½ segment
24. Pronotum, lateral margin	Not setose		Setose
25. Mesotarsus	Short		Long
26. Antenna	Slender and clubbed		Moniliform
27. Protibia	Without apicolateral process		With apicolateral process

Fig. 5. Character polarization of the Caenocrypticini species.

Character evaluation of the Caenocrypticini species showed 28 external adult and male genital characters to be constant within species, with clearly defined transformation stages (Fig. 5). Six of the characters (0, 2, 16, 17, 18 and 26) are uniformly expressed in Caenocrypticini but are different in most of the outgroup taxa. These represent the tribal characters. In the transformation series, character states in the outgroup were considered plesiomorphic. The direction of transformation in two characters (nos 1 and 26) has been reversed. Both of these characters, namely framed eye and moniliform antennae, are dominant in but not exclusive to the outgroup and neither could be considered plesiomorphic in the subfamily. The character state matrix is given in Fig. 6.

The cladistic analysis was carried out with the Hennig86, version 1.5 (Farris, 1988) software program on an 486SX, IBM compatible PC. The implicit enumeration option (ie) was chosen, and used in conjunction with the successive weighting procedure (xs w). Consistency (ci) and retention (ri) indices were calculated. Six equally parsimonious cladograms of length 248, ci, 81, ri 95 were produced, one of which is presented in Fig. 7.

Four genera were taken to represent the outgroup Stenosini (*Oogaster* Falderman, 1837; *Hexagonocnemis* Solier, 1851; *Stenosis* Herbst, 1799, and *Platamodes* Menetries, 1849) along with the genus *Boromorphus.* The genus *Fitzsimonsium* Koch, here transferred from Caenocrypticini to Stenosini (see Appendix), was also included in the analysis. In a combined analysis with the Caenocrypticini species, all these taxa took a basal position, *Boromorphus* and *Fitzsimonsium* appearing as apical in the outgroup (Fig. 7). To support the validity of the outgroup selection, test runs of the program were made with *Boromorphus* as the sole outgroup without significant effects on the cladogram in Fig. 7.

The taxonomic treatment of Caenocrypticini is based on

			10..................		20.............	
	01234	**56789**	**1234**	**5678**	**1234**	**567**
Oogaster	02000	01000	00000	21000	00000	010
Hexagonochilus	02000	01000	10000	01000	00000	010
Stenosis	10000	01000	10000	01000	00000	010
Platamodes	02000	01000	10000	01000	00000	010
Fitzsimonsium	02100	10010	00000	10001	00000	010
Boromorphus	02000	01000	10000	01000	00000	010
CAENOCRYPTICUS	02000	00000	00000	10000	00000	010
(Phyloradix)						
soror	00100	00110	11000	21111	10000	100
bushmanicus	00100	00110	11000	21111	20000	100
(Caenocapicus)						
capensis	00100	00110	11010	21111	00000	100
(Cryptocarpes)						
elongatus	01100	00010	10000	01111	10000	100
damara	01100	00000	01000	21111	00000	100
dividiopsis	02100	10110	11000	11111	10000	100
(Caenocrypticus)						
uncinatus	00100	10121	11010	11111	20000	100
kaszabi	00100	10111	11010	11111	10000	100
wittmeri	00100	10111	11010	21111	10000	100
macintyrei	00100	00111	11010	21111	10000	100
(Psammotopulus)						
penrithae	00100	10120	11001	01111	21000	101
holmi	00100	10120	11001	21111	20000	101
klinghardtmontis	00100	00020	11001	21111	21000	101
deserticus	00100	10120	11001	21111	20000	101
peezi	00100	10120	11001	01111	20000	101
phaleroides	00100	10120	11001	01111	21010	101
CAENOCRYPTICOIDES						
peruanus	00100	01111	11000	21111	00100	001
penai	00100	01111	11000	21111	00100	001
loksai	00100	11120	11000	21111	00100	001
translucidus	00100	11121	11010	21111	00100	001
(Vernayella)						
noctivagus	00111	20110	11100	21111	00010	101
ephialtes	00111	20110	11100	21111	00011	101
kochi	00111	20110	11100	21111	00011	101
pauliana	00111	20110	11100	21111	00011	101
serratus	00111	20110	11100	21111	00011	101

Fig. 6. Character state matrix of the Caenocrypticini species and selected genera of the outgroup Stenosini.

morphological characters as well as on distributions while adhering to cladistic concepts. As a result, a single southern African genus, *Caenocrypticus,* and the South American genus *Caenocrypticoides* have been retained. The cladistic analysis confirmed that the species groups which Koch (1952, 1958) considered genera (*Cryptocarpes* and *Vernayella),* together with the new subgenera *Psammotopulus* and *Caenocrypticus,* indeed represent well-defined evolutionary lineages, but that the basal clades (subgenera *Phyloradix* and *Caenocapicus*) lack apomorphies. For this reason all genus-level taxa from southern African Caenocrypticini are considered subgenera of the single genus *Caenocrypticus* Gebien, 1920.

A dendrogram (Fig. 8) was also constructed, based on biogeographical information in addition to morphological characters but reversals were not allowed (see position of *C. dividiopsis* in the cladogram).

A feature of the cladogram, compared with the dendrogram, is that the resolution and presentation of phylogenetic events is not on the same level from the primitive to the derived clades. While the terminal clades (*Psammotopulus, Caenocrypticoides* and *Vernayella*) can be substantiated by synapomorphies and are consistent with their geographical distribution, it is not the case with regard to the primitive clades in the cladogram (*Phyloradix, Caenocapicus, Cryptocarpes* and *Caenocrypticus* (*s. str.*)). Thus, at the base of the cladogram it is more likely that misplacements (*C. dividiopsis*) might occur, and that the cladogram-sequencing of taxa (relationships) cannot be supported by synapomorphies and that it contradicts the species' distributions. For example, *C. (Caenocapicus) capensis* is placed at the base of the clade comprising the subgenus *Caenocrypticus* although it is confined to the southern extreme of the genus' distribution and is spatially separated by the derived clades from the rest of the primitive species (Fig. 4).

Discrepancies between the cladogram (Fig. 7) and the dendrogram (Fig. 8) appear in the basal clades and indicate

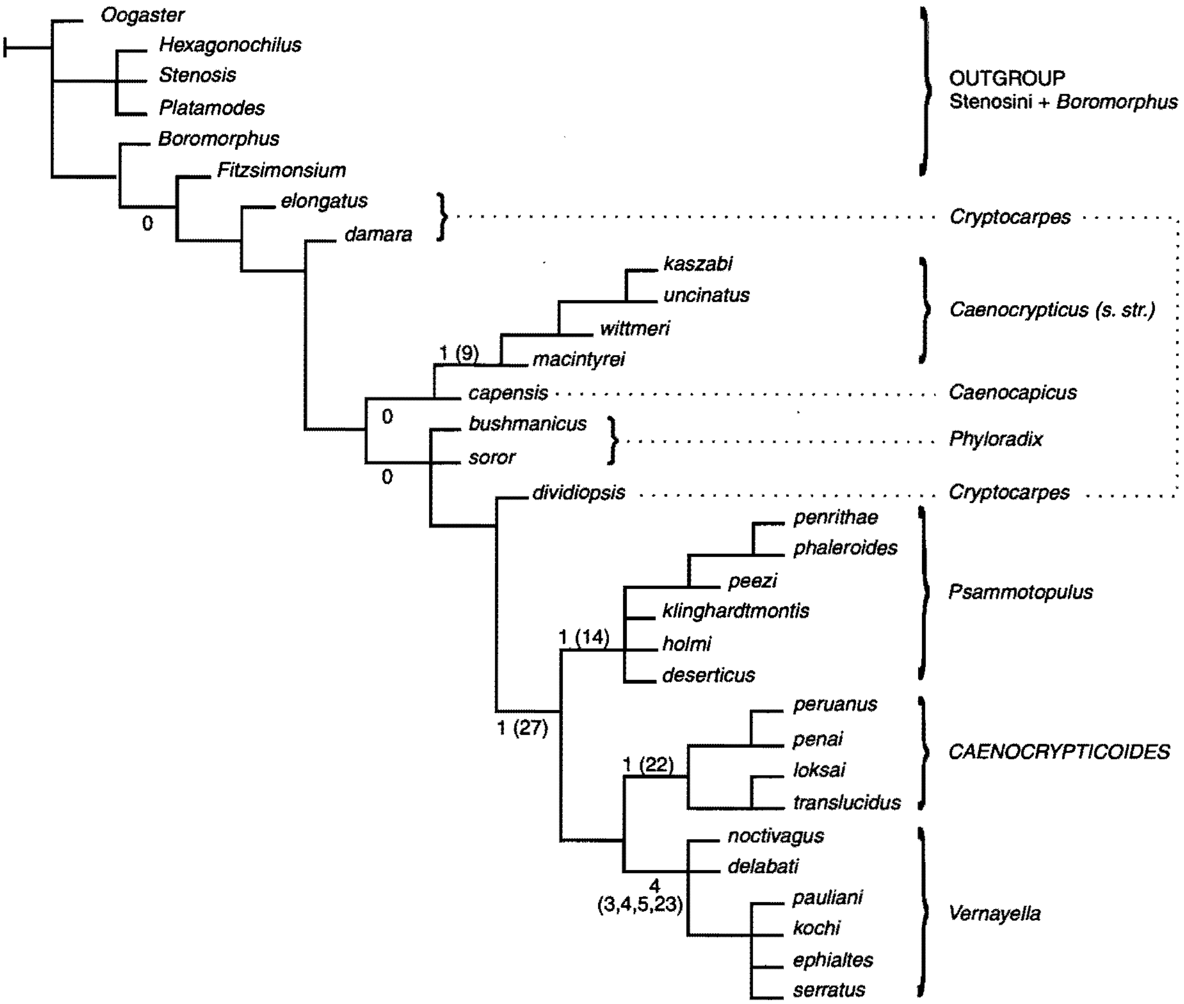

Fig. 7. Cladogram of the Caenocrypticini species.

that a computer-generated cladogram cannot necessarily be considered an endproduct elucidating the phylogeny of the group being studied (Nelson, 1994). Significantly, the incongruent display of primitive and derived characters appears among species in the basal clades, suggesting that increasing evolutionary age and its effects, such as possible extinctions, can adversely affect accuracy of resolution.

The evolutionary age of Caenocrypticini is likely to be 100 million years if we consider that one of the apical clades, *Caenocrypticoides,* has been isolated in South America since the separation of that continent. It is conceivable that the same environmental forces that triggered the evolution of the apical clades might have resulted in extinctions, particularly in the primitive, less adaptable species of the basal clades. Such extinctions remove the links between the primitive species and result in an incongruent character display between the extant species.

The distribution pattern of the primitive southern African species suggest a possible centre of extinction that could also have been the evolutionary centre of origin of the tribe (Fig. 4). The two most primitive species in the cladogram (*C. elongatus* and *C. damara*) occupy the northern extreme of the tribe's distribution, whereas the third (*C. capensis)* occupies the southern extreme. The other species of the primitive clades (subgenera *Caenocrypticus* and *Phyloradix*) are restricted to a crest inland of the present Namib dune desert, between the northern and southern extremes. The area devoid of primitive species is the intervening coastal section now occupied by the dune Namib (Fig. 4). In geological terms the recent massive sand movements and dune accumulation (Endrödy-Younga, 1982*a,b,* 1986) might have occurred in the area where the true ancestral species connecting the extant ones were lost to the accumulating sand masses. The dune Namib, which is devoid of primitive species, is at present only inhabited by the hyperpsammophilous species of the apical clades (all *Vernayella* and three *Psammotopulus* species) (Fig. 4).

Another aspect highlighted by the cladogram (Fig. 7) is that, for obvious reasons, apomorphies of any one taxon are evaluated in relation to all taxa compared, and not only within an evolutionary lineage. This might occasionally result in the placement of a taxon separate from its lineage on the cladogram. For example, *C. (Cryptocarpes) dividiopsis* is removed from the other two species of the subgenus, and indicated as the outgroup of the three apical clades.

A character shared by the three *Cryptocarpes* species is the partial to complete division of the eye by the genal margin (Plate 9). This character is considered homologous (monophyletic). According to the cladogram, however, this

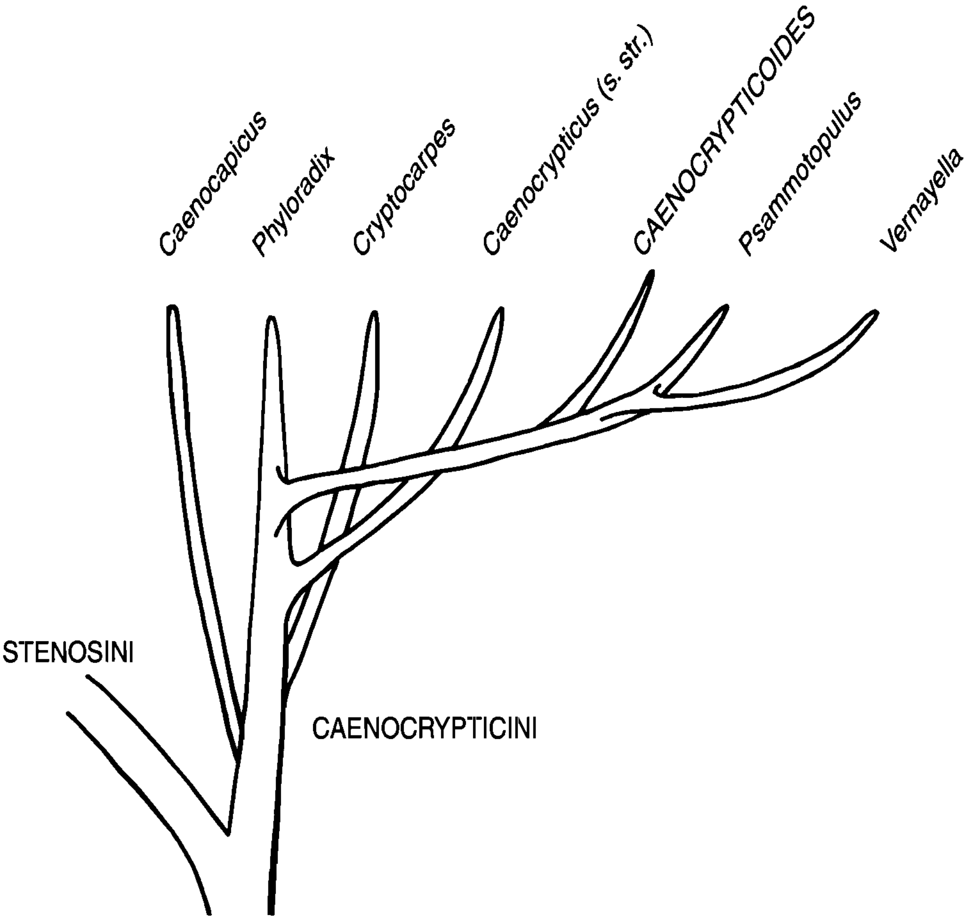

Fig. 8. Dendrogram of the genera and subgenera of the tribe Caenocrypticini .

character evolved twice and was lost twice, because *C. elongatus* and *C. damara* are at the base of the subgenus *Caenocrypticus* and *C. dividiopsis* is at the base of the apical lineages, all of which have completely free-standing eyes. Geographical distribution patterns supports the homology of this character, as all three species occupy the northwestern extreme of the genus' distribution, occasionally occurring sympatrically, but only in pairs (Fig. 13). The subgenus *Cryptocarpes* seems to represent an early split from the ancestral stock that acquired an increasingly framed eye. Within this lineage, two species exhibit the lowest number of apomorphies and are indicated at the base of the cladogram. The third species, *C. dividiopsis,* acquired three apomorphies (1, 5, 7) and thus became separated from the other two species.

An interesting and unusual feature of both diagrams (Figs 7, 8) is the derivation and positioning of the South American genus *Caenocrypticoides* between the two apical subgenera of the southern African *Caenocrypticus,* namely *Psammotopulus* and *Vernayella*. Both clades, *Caenocrypticoides* and *Vernayella,* can be derived from *Psammotopulus,* although with a considerable time lapse between the branching events. *Caenocrypticoides* evolved earlier and was isolated by the separation of the land masses. *Vernayella,* however, evolved much later, when hyperpsammophilous conditions developed in the coastal region, triggering the adaptations of species in the *Vernayella* clade.

TAXONOMY

Tribe CAENOCRYPTICINI

Koch, 1958: 39; 1962: 152. Kaszab, 1969: 322 (implicit). Doyen, 1993: 502.

Diagnosis. Base of maxillae exposed (Plate 4C). Procoxal cavity externally closed (Plate 5B–D). Prothorax and mesothorax articulate freely. Metepimeron interlocked with adjacent abdominal sternite. Metacoxal cavity closed by metepimeron (Plate 6A). Body wingless. Abdominal sternites without exposed intersegmental membranes (Plate 5). Aedeagus in inverted position, *i.e.,* penis in dorsal, paramere in ventral position. No defensive glands.

A group of small species in the family Tenebrionidae, between 1,7 and 5,0 mm. Colour in adults varies between pale yellow and black.

Redescription. Head retracted between more or less produced anterior angles of pronotum; much narrower than pronotum, exposed disc about as broad as long. Labrum much broader than long. Mentum about as long as broad, inverted trapezoid in shape, anteriorly truncate or slightly and evenly emarginate, basal articulation exposed (Plate 4C). Submentum with transverse impression. Median gular plate with distinct microscopic surface structure possibly facilitating stridulation (Plate 4C,D). Genal margin of head joins margin of eye at an acute or rounded angle, usually not reducing diameter of eye (Plate 10); occasionally (subgenus *Cryptocarpes*) drawn onto the eye's surface, reducing or completely separating eye into dorsal and ventral parts (Plate 9). Mandibles short and strong with inwardly curved apices and each with one preapical tooth at inner margin. Antenna 11-segmented, filiform with more or less distinct 3–4-segmented club. Labial palpi with cylindrical to moderately securiform apical segment.

Pronotum up to twice as broad as long, distinctly broader than head and occasionally narrower than elytra. Disc anteriorly slightly and evenly to deeply emarginate, anterior lateral angles correspondingly obtuse to strongly produced. Posterior margin usually truncate. Laterally and anteriorly marginate, latter occasionally interrupted in middle; posteriorly usually immarginate.

Elytra elongate to broadly ovate, broadest behind humeri (in *C. (Vernayella) noctivagus* broadest at humeri). Immarginate laterally in *Caenocrypticoides*, lateral margin sharp in *Caenocrypticus*. Epipleuron tapering evenly from humerus to apex in *Caenocrypticus* (Plate 5A), tapering abruptly at mesocoxa in *Caenocrypticoides* (Plate 5D).

Prosternum transversely convex, episternal septum faint to distinct. Coxal cavity rounded to slightly ovate, intercoxal process flat, not curved to venter, posterior face vertical or apex produced caudally. Mesosternum short, episternum sharply separated by a fossa, separation of epimeron indicated by a fine surface line. Episternum of metasternum broad and parallel, epimeron largely fused to episternum, line of fusion distinct in *Caenocrypticus* but not in *Caenocrypticoides;* external closure of metacoxal cavity in *Caenocrypticus* provided with inward-extending lobe of metepimeron, in latter genus with fused plate of metepisternum and metepimeron. Mesocoxal cavity round, metacoxal cavity transverse. Mesocoxal separation narrow in lapidophilous species (one-fourth to one-half of coxal cavity) (Plate 5A), but as broad as cavity in ultrapsammophilous species (subgenus *Vernayella*) (Plate 5C). Abdomen consisting of five visible sternites without exposed intersegmental membranes.

Legs rather short in lapidophilous, longer in psammophilous species. Important lineage and specific characters are the shape of the protibia, which may show secondary sexual dimorphism. Paired tibial spurs large. Tarsi shortest in front legs, longest in hind legs. Claws simple, slightly arcuate, equal in length except in subgenus *Vernayella*.

Aedeagus consists of simple basale and usually species-specific apicale. Relative length of the two structures differ between species. Apicale consists of penis (median lobe) and straight or sickle-shaped paramere. Usual position of aedeagus in body is inverted, with paramere in ventral and penis in dorsal position. In species with a strongly arcuate apicale its position is lateral, at least in dry specimens.

Distribution. Western coastal region of southern Africa (*Caenocrypticus*) and western coastal region of northern Chile and southern Peru (*Caenocrypticoides*) (Fig. 2).

Remarks. Two genera have been retained in the tribe on the basis of cladistic analysis. These genera each have at least one synapomorphy, and are vicariant on continental scale. The South American genus *Caenocrypticoides* comprises four closely related species, whereas the southern African genus *Caenocrypticus* comprises a number of lineages, all of them recognized as subgenera. Three new subgenera are described and some previously described genera have either been given subgeneric status or synonymized.

KEY TO THE GENERA OF CAENOCRYPTICINI

1(2) Epipleuron of elytra evenly tapering from humerus to apex (Plate 5A), dorsal margin of epipleuron usually forms sharp lateral crest of elytron, rarely curving below the lateral convexity. Metacoxal cavity more strongly transverse, approaching lateral margin of sternum at a rate of 3 to 1 (Plate 5A,C). First mesotarsal segment at least twice as long as second segment. Southern African species. . . *Caenocrypticus* Gebien

2(1) Epipleuron broad at humerus, short section of its margin visible from above, then curving abruptly ventrad, arcuately decreasing in breadth at mesocoxa (Plate 5D). Metacoxal cavity less transverse. First mesotarsal segment only slightly larger than second. South American species. . . . . *Caenocrypticoides* Kaszab

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Genus *CAENOCRYPTICUS* Gebien

Caenocrypticus Gebien, 1920: 139 (Crypticini); 1938: 508. Koch, 1950: 79; 1952: 188.

Caenocrypticus Gebien: Koch, 1958: 124 (Caenocrypticini).

Cryptocarpes Koch, 1952: 191 (gen. in Crypticini); 1958: 121 (gen. in Caenocrypticini). subgen. **stat. nov.**

Lomamus Koch, 1952: 191 (gen. in Crypticini); 1958: 121 (gen. in Caenocrypticini), syn. of subgen. *Cryptocarpes*. **syn. nov.**

Thorictophasis Koch, 1950: 80 (subgen. of *Caenocrypticus*); 1952: 188; 1958: 121. **syn. nov.**

Phyloradix **subgen. nov.**

Caenocapicus **subgen. nov.**

Psammotopulus **subgen. nov.**

Vernayella Koch, 1958, subgen. **stat nov.**

Type species: *Caenocrypticus uncinatus* Gebien (by original monotypy).

Diagnosis. Epipleuron of elytra tapering evenly from humerus to apex of elytra (Plate 5A). First mesotarsal segment twice as long as second segment or even longer (Plate 3A,B). Metacoxal cavity strongly transverse, more than twice as broad as episternum.

Redescription. Head small, pronotum 1,5 times to more than twice as broad and recessed in collar emargination of pronotum. Clypeus narrow, truncate or slightly emarginate. Gena ends in an angle in front of the more or less recessed eye, or extends onto eye from front, or divides it into a dorsal and a ventral part. Tempora simple or laterally extended, supporting eye from behind. Eye positioned deeper than ocular margin of vertex, latter more or less crested. — Pronotum up to twice as broad as long, lateral margins evenly arcuate between lateral angles, or bell-shaped or contracted before broadening towards posterior angle. Anterior lateral angles angular or lobiform.

Anterior and lateral edges marginate, posterior margin smooth, rarely finely marginate. — Elytra almost parallel behind humeri or arcuate to evenly ovate, transversely markedly convex when epipleural margin is concealed by convexity, or moderately convex with broadly exposed lateral margins when epipleuron is not in same curvature as disc. Epipleuron tapering evenly from humerus to apex. — Mesocoxae at the same distance to each other or closer than metacoxae. Metasternal process usually much narrower than mesocoxal cavity, only broader in *C. phaleroides,* but meso- and metacoxae remain equidistant. — Antenna with 11 segments, three club segments slightly to moderately enlarged. — Protibia differs considerably between species or lineages. Straight or curved inwards and moderately to strongly dilated towards apex. Apex truncate or inner or lateral angle produced into a process. Aedeagi distinct and characteristic of all species except in the subgenus *Vernayella.*

Several species exhibit distinct secondary sexual dimorphism, mainly in the protibia or in the structure of the anal sternite.

Length: 1,7–5,0 mm.

Distribution. Desert to semiarid areas in the Atlantic coastal region of southern Africa, extending into the Kalahari in the north.

Remarks. Of the genus-level taxa named by Koch, *Cryptocarpes* and *Vernayella* have been retained, but at subgeneric level. *Lornamus* appears to represent the terminal state of transformation from a partly to completely divided eye by the genal margin, beginning with the two species of the subgenus *Cryptocarpes.* Consequently, *Lornamus* is considered an objective synonym of *Cryptocarpes.*

Koch (1950) described *Thorictophasis* as a subgenus of *Caenocrypticus,* with *deserticus* as type species. He considered the primary character of this subgenus to be the absence of a transverse impression on the metacoxa as opposed to the nominate subgenus, with *C. uncinatus* as the type (and only) species. In a subsequent paper, Koch (1952) omitted the coxal character from his diagnosis, as all species of the genus have a transverse impression. Therefore, *Thorictophasis* cannot be retained or synonymized with any of the present subgenera.

The monotypic genus *Fitzsimonsium* Koch is here transferred from Caenocrypticini to Stenosini. A redescription of the genus and the reasons for its transferral is provided in the Appendix.

KEY TO THE SUBGENERA AND SPECIES OF *CAENOCRYPTICUS*

1(32) Tarsal claws equal in length. Elytral margin smooth. Protarsal segments 2–4 as long as broad or shorter. Mesocoxae more closely set (usually much more closely) than metacoxae.

2(7) Eye partially or completely divided into dorsal and ventral parts by genal margin (Plate 9) .... subgenus *Cryptocarpes* Koch

3(6) Only anterior portion of eye framed by the extension of genal margin, a narrow unframed bridge connecting dorsal and ventral parts of eye (Plate 9A,B).

4(5) Protibia narrow, only moderately dilated towards apex, length:breadth ratio 26:8; its external apical angle rectangular and not produced (Fig. 14B). Posterolateral angle of pronotum sharp, almost rectangular (Plate 6C). Aedeagus simple and straight, dorsoventrally flattened, apicale much shorter than basale, penis straight (Fig. 15C,D). Length: 2,2–3,1 mm. Damaraland. ..... *C. damara* (Koch)

5(4) Protibia distinctly dilated, length:breadth ratio 27:11, external apical angle acute and produced (Fig. 14A). Posterolateral angle of pronotum obtuse and rounded (Plate 6B). Apicale of aedeagus much longer than basale, penis arcuate, paramere sharply pointed (Fig. 15A,B). Length: 2,55–3,25 mm. Kaokoveld. .... *C. elongatus* (Koch)

6(3) Eye completely divided into dorsal and ventral parts by extended genal margin (Plate 9B,C). Protibia and pronotum as in *C. elongatus.* Aedeagus arcuate, apicale only slightly longer than basale, apicale rather broad and cylindrical, penis cylindrical and comparatively thick (Fig. 15E,F). Length 2,0–3,5 mm. Southwestern Angola to northwestern Namibia. .... *C. dividiopsis* (Koch)

7(2) Lateral margin of eye free along entire length, dorsal and ventral portions connected (Plate 10A).

8(21) Apex of tibia truncate or inner angle lobed (Fig. 9).

9(16) Apical one-third of protibia curved inwards in male. External margin of tibia almost straight in female, but inner margin slightly curved inwards, resulting in apical dilation of tibia (Fig. 18C,D) .... subgenus *Caenocrypticus*

10(15) Protibial spurs subequal in length, even in male not extending beyond third protarsal segment.

11(12) Margin of postgenal lobe along posterior margin of eye visible from above. Protibia strongly dilated at apex in male, forming a distinct inner apical lobe (Fig. 14D,E). Aedeagus sharply arcuate (Fig. 17A,B). Length: 2,15–3,00 mm. Central Namibia. .... *C. uncinatus* Gebien

12(11) Margin of postgenal lobe not visible from above. Protibia also less dilated, not forming an inner apical lobe. Aedeagus slightly arcuate.

13(14) More elongate, elytra more parallel and narrower, length:breadth ratio 1,84:1,36 mm or 74 %. Prosternal apophysis narrower than procoxa, its apex more narrowly rounded. Protibia less curved inwards in male, outer margin almost straight (Fig. 18A). Apicale of aedeagus longer than basale (Fig. 17C,D). Length 2,25–3,30 mm. Inland margin and hills of central Namib Desert. .... *C. kaszabi* spec. nov.

14(13) Broader and less parallel, length:breadth ratio of elytra 1,84:1,20 mm or 65 %. Prosternal apophysis as broad as procoxae with broadly rounded apex. Protibia more strongly curved inwards in male, outer margin distinctly arcuate (Fig. 18B). Apicale of aedeagus shorter than basale (Fig. 17E,F). Length: 1,68–2,05 mm. Hinterland of southern Namib. . *C. wittmeri* spec. nov.

15(10) Protibial spurs very long and unequal in length. Inner lateral spur of male almost as long as protarsus and nearly twice as long as second spur (Fig. 18C). Longer spur extends to claw segment in female (Fig. 18D). Aedeagus moderately arcuate, apicale shorter than basale (Fig. 17G,H). Length: 2,40–2,75 mm. North-eastern Namibia. . . . . *C. macintyrei* Koch

16(9) Protibia not curved inwards, outer margin straight, inner margin straight or curved in a concave arc into transversely extended inner apical lobe.

17(18) Punctation of pronotum extremely dense, punctures elongate, almost touching, intervals convex (Plate 8A,B)). Inner apical lobe of protibia transverse, particularly in male, thus inner margin more (male) or less (female) concavely arcuate (Fig. 9D,E). Body only twice as long as broad. Aedeagal shape unique in the genus, apicale extremely short relative to basale (1:2,8) (Fig. 10E,F). Length: 1,9–2,6 mm. Coastal belt of southern Western Cape Province.
. . . . *Caenocapicus* subgen. nov.
. . . . *C. capensis* spec. nov.

18(17) Punctation of pronotum well spaced, punctures round or slightly ovate, intervals broad and flat (Plate 1A). Protibia evenly and moderately dilated from base to apex, inner apical lobe not extended transversely inwards. Apicale and basale of aedeagus of closer proportions
. . . . *Phyloradix* subgen. nov.

19(20) Outline of head in dorsal view angularly contracted between apex of gena and front margin of eye, eye not protuberant laterally (Plate 10B). Prosternal apophysis more broadly ovate. Anterior lateral angle of protibia somewhat acutely angled and produced (Fig. 9C). Apicale of aedeagus moderately shorter than basale, arcuate apicale notched at base (Fig. 10C,D). Length: 2,05–3,10 mm. South Africa: Bushmanland. . . . . *C. bushmanicus* Koch

20(19) Outline of head not contracted at front margin of eye, eye protuberant (Plate 10A). Prosternal apophysis narrower and more elongate. Lateral angle of protibia sharply rectangular and not produced (Fig. 9A,B). Apicale of aedeagus distinctly shorter than basale, apicale not notched at base (Fig. 10A,B). Length: 2,3–3,1 mm. Inland margin of Namib Desert to central southern Namibia, two subspecies.
. . . . *C. soror* spec. nov.

21(8) Protibia deplanate, anterolateral angle strongly produced, usually in form of a process, inner angle not lobed (Fig. 18E). Anal sternite in lateral view flat in males, more or less arcuate in females . . . . *Psammotopulus* subgen. nov.

22(27) Posterolateral angle of pronotum broadly and evenly rounded or indistinctly rounded and obtusely angled, lateral margin more arcuate into rounded angle. Dorsal outline distinctly contracted at common base of pronotum and elytra.

23(24) Body broadly ovate, elytra almost as broad as long (Plate 2C). Elytra moderately convex transversely, lateral portion (not only sharp margin) clearly visible from above. Intercoxal section of mesosternum slightly broader than mesocoxa (Plate 5B). Paramere of aedeagus ark-shaped in lateral view (Fig. 19A,B). Length: 2,2–3,6 mm. Coastal Namib Desert.
. . . . *C. phaleroides* Koch

24(23) Body more elongate-ovate, elytra much longer than broad. Elytra markedly convex transversely, lateral portions almost vertical, only sharp lateral margins visible from above. Intercoxal section of mesosternum much narrower than mesocoxa. Paramere follows the sickle-shaped penis, narrow in lateral view.

25(26) Sutural profile of elytra evenly arcuate without a steep and distinct apical declivity. Elytra broader, transversely more evenly convex. Aedeagus sickle-shaped with narrow paramere (Fig. 19C,D). Length: 2,5–3,1. Southern Namib Desert and northern margin of Richtersveld. . . . . *C. deserticus* Koch

26(25) Sutural profile of elytra with steep apical declivity. Elytra more elongate, transverse convexity slightly deplanate in middle. Paramere of aedeagus shallow ark-shaped, apex of penis retrovert (Fig. 19E,F,G). Length: 2,15–2,90 mm. Southern Namib Desert, Klinghardt Mountains.
. . . . *C. klinghardtmontis* spec. nov.

27(22) Posterior lateral angle of pronotum distinctly angular or narrowly rounded, not nearly continuously arcuate into posterior margin; lateral margins of pronotum straight or almost straight preapically, but not necessarily parallel. Dorsal outline of body not or hardly contracted at common base of pronotum and elytra. The only secure characters of the following three species are those of aedeagi.

28(29) Posterior half of pronotal margins parallel or very nearly so, arcuately contracting in front of middle. Dorsum of elytra flattened in cranial view. Paramere of aedeagus wedge-shaped in dorsal view, tapering evenly from broad base to pointed apex; in lateral view narrow, finely emarginate preapically. Penis evenly broad, more strongly arcuate (Fig. 23A,B). Length: 2,4–3,5 mm. Central Namib Desert. . . *C. peezi* Koch

29(28) Pronotum broadest near base, from there tapering arcuately towards anterior angles.

30(31) Dorsum of elytra (as in *C. peezi*) flattened in cranial or caudal view. Apical declivity of elytra more slanting, sutural profile reaching apex at angle of 60°. Paramere of aedeagus deeply ark-shaped, its apical process broadly triangular; penis evenly arcuate, not narrowed at base (Fig. 23C,D). Length: 2,5–3,5 mm. Inland margin of central Namib dune desert. . . *C. penrithae* spec. nov.

31(30) Dorsum of elytra more evenly convex in cranial view. Apical declivity of elytra slightly steeper, sutural profile reaching apex at angle of 70°. Aedeagus in dorsal view bilaterally compressed, blade-like behind broad base. Paramere in lateral view sickle-shaped, tapering to sharply pointed apex. Evenly arcuate penis narrow at base (Fig. 23E,F). Length: 2,5–3,4 mm. Hinterland of central and northern Namib Desert. .... *C. holmi* spec. nov.

32(1) Tarsal claws unequal in length (Fig. 18F). Elytral margin finely or distinctly denticulate posteriorly (Plate 11A,B). Protarsal segments 2–4 longer than broad. Mesocoxae more widely apart than metacoxae (Plate 5C). Aedeagi of all species simple and uniform (Fig. 23G,H) .... subgenus *Vernayella* Koch

33(34) Evenly ovate, body broadest at common base of pronotum and elytra, where dorsal outline is not contracted (Plate 2D). Body more convex. Anterior emargination of pronotum shallow, disc behind 3,5 times longer. Anterolateral angle of pronotum narrowly rounded, triangular. Length: 3,6–5,0 mm, largest species in genus. Northern half of central dune Namib. .... *C. noctivagus* (Koch)

34(33) Dorsal outline of body contracted at common base of pronotum and elytra, broadest in a section behind humeri (Plate 3B,C). Anterior emargination of pronotum deeper, disc behind only 2–3 times longer. Anterolateral angle of pronotum lobiform, more or less broadly rounded (*cf.* Plate 6D). Body less convex.

35(36) Disc of prosternum with long setae emerging from each puncture (visible also on card-mounted specimens). Punctures on entire dorsum with microscopic setae. Clypeus evenly emarginate. Length: 3,45–4,25 mm. Small section of central Namib coast. .... *C. kochi* spec. nov.

36(35) Disc of pronotum and at least disc of elytra bare. Clypeus truncate.

37(38) Elytral margins from behind middle prominently and densely denticulate, resembling a string of pearls, nearing apex without a gap between denticles (Plate 11A). Marginal setation of pronotum dense and rather long (*cf.* Plate 11C). Length: 3,60–4,25 mm. Namib Desert, northern Skeleton Coast. ... *C.serratus* spec. nov.

38(37) Marginal serration of elytra evanescent or denticles well spaced with straight sections between them, denticles might be more densely set in apical one-tenth of elytral length (Plate 11B). Marginal setation of pronotum absent or different.

39(40) Pronotum distinctly bell-shaped, lateral margins in different rates per section, but diverging evenly from anterior to posterior lateral angles (Plate 3A). Marginal setation of pronotum long and well spaced, setae almost as long as those of antennae (Plate 11C). Discal granulation of elytra coarse near apex, granules emerge from uneven surface, each bearing a microscopic seta. Length: 2,7–4,6 mm. In two isolated areas in northern and central dune Namib. .... *C. pauliani* (Koch)

40(39) Pronotum semiparallel behind middle, margins usually slightly emarginate in front of posterolateral angles. Marginal setation of pronotum absent or very dense and short. Discal granulation of elytra near apex very fine on uniform background and without setae.

41(42) Marginal setation of pronotum dense and very short, length of setae only a fraction of those of antennae; marginal setation of elytra 2–3 times longer. Integument of dorsum shiny with fine shagreen, punctation fine but distinct (*cf.* Plate 7C). Length: 2,8–4,8 mm. Two isolated areas: Kuiseb basin and northern Namib coast. .... *C. ephialtes* (Koch)

42(41) Margins of pronotum and elytra bare. Marginal serration of elytra evanescent. Integument of dorsum matt owing to fine but sharp shagreen; punctation, particularly of pronotum, indistinct (Plate 7D). Length 2,9–4,1 mm. Central Namib dunes at Kuiseb River mouth. .. *C. delabati* (Koch)

Subgenus *PHYLORADIX* subgen. nov.

Type species: *Caenocrypticus (Phyloradix) soror* spec. nov.

Description. Eye undivided, posterior angle of genal margin ending in front of eye (Plate 10A). Pronotum moderately emarginate anteriorly, anterolateral angles about rectangular, not lobiform. Elytra convex transversely, smooth lateral margins concealed in mid-section in dorsal view. Mesocoxa close to each other, intercoxal process of mesosternum narrowly triangular. Protibia slender to moderately dilated, apical third not curved inwards. Anterior margin straight or undulate-truncate, without an external or inner apicolateral lobe. Protarsal segments 1–4 as broad as or broader than long. Tarsal claws short and equal in length. Apicale of aedeagus cylindrical and moderately sickle-shaped.

Distribution. The two species in the genus occur in isolation on the escarpment of the northern central Namib (*C. soror*) and in Bushmanland on the Orange River (*C. bushmanicus*) (Fig. 11).

Etymology. Abbreviation of phylogeny and Latin noun *radix, -icis,* feminine = root, meaning root of phylogeny.

Remarks. This subgenus includes the two most primitive species in the genus. These species do not share any of the synapomorphies defining the other subgenera (lineages) and have no apomorphies in common either.

Caenocrypticus (Phyloradix) soror spec. nov., Figs 9A,B, 11, Plates 1A, 7A, 10A, 12A

Diagnosis. Closely related to *C. bushmanicus,* very similar in habitus. Lateral outline of head not contracted in dorsal view between genal angle and eye; eye extends beyond gena

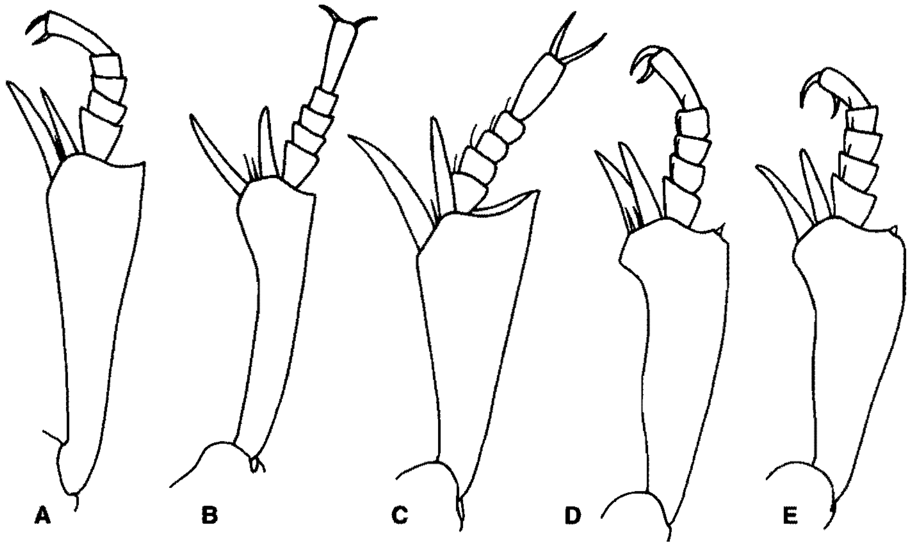

Fig. 9. Protibiae of *Caenocrypticus* species. **A**: nominate subspecies of *C. (Phyloradix) soror* spec. nov., male; **B**: *C. (P.) soror nauwkluftensis* subspec. nov., male; **C**: *C. (P.) bushmanicus* Koch, male; **D**: *C. (Caenocapicus) capensis* spec. nov., male; **E**: same species, female.

laterally (Plate 10A). Protibia straight or very slightly arcuate but not curved inwards (Fig. 9A,B), somewhat narrower than in *C. bushmanicus* (Fig. 9C); apex obliquely truncate, but inner apical lobe extends slightly beyond outer angle. Prosternal apophysis more elongate. Basale of aedeagus longer than apicale; narrow paramere parallel in lateral view, tapering abruptly to pointed apex (Fig. 10A,B). Dark brown to almost black. Characters not referred to below are similar to those of *C. bushmanicus.*

Description. Head broadest at convex eyes, slightly narrower at apex of genae. Apex of genae not curving inwards before reaching anterior margin of eye, thus not contracted between genae and eyes. — Pronotum often more parallel in a posterior section, outline less contracted between pronotum and elytra. Convexity of pronotum differs between subspecies. Punctation well spaced, punctures with fine, rather long microscopic hairs (Plate 7A) hardly visible under a light-microscope. — Prosternal apophysis distinctly more elongate, measured from basal contraction length:breadth ratio is 12:7. — Protibia distinctly narrower than in *C. bushmanicus* and differ slightly between subspecies. — Aedeagus comparable in proportions to *C. bushmanicus,* slightly smaller: basale 0,42 mm, apicale 0,32 mm long. Apicale more filiform, inner margin emarginate preapically, forming sharply pointed apex. Penis more thinly filiform (Fig. 10A,B).

Female. Similar to male.

Etymology. *Soror -is,* feminine, Latin noun for sister, signifying the close relationship between this species and *C. bushmanicus.*

Remarks.The species comprises the following two subspecies.

Caenocrypticus (Phyloradix) soror soror, Figs 9A, 11, Plates 1A, 7A, 10A, 12A

Diagnosis. On average somewhat smaller, more convex. Pronotum broadest in middle or semiparallel in its basal half. Protibia straight (Fig. 9A).

Description. Pronotum more convex transversely, both lateral margins visible in dorsal view from mid-length to posterior angle. Pronotum broadest at about mid-length, contracting slightly towards posterior angle, or semiparallel in posterior half of length (Plate 1A). Punctation well spaced, punctures with fine, rather long microscopic hairs (Plate 7A) hardly visible under a light-microscope. — Elytra slightly more convex in middle of disc, in a cranial view more evenly arcuate towards lateral margins; apical declivity evenly arcuate, straight in preapical section or there slightly impressed. — Protibia straight in both sexes, inner or outer margins not arcuate; anterior margin slightly more deeply emarginate, outer apical angle more distinct (Fig. 9A).

Length: 2,3–2,9 mm; breadth: 1,12–1,35 mm.

Distribution. Central part of southern Namibia in Maltahöhe District (Fig. 11).

Material examined. Nineteen ♂ (8 dissected), 25♀ and 39 additional specimens. In Transvaal Museum, Pretoria.

Holotype ♂, allotype ♀ and 33 paratypes: S. W. Afr. (Namibia). Maltahöhe Dist., Farm Hoheacht, 24° 40′ S, 16° 23′ E, 13.3.1975, baited ground-traps, 178 days, leg. Endrödy-Younga & Breytenbach, E-Y:741. Additional paratypes: 2 *idem,* but 22.10.1974, traps 137 days E-Y:433; 10 *idem,* but 7.9.1975, traps 178 days, E-Y:867; 36 *idem,* but E-Y:868.

Ethoecology. At Hoheacht, traps were set at two sites: on a level plateau on a *c.* 50 m limestone hill with steep rocky sides, compacted substrate, rocky limestone rubble and scattered low vegetation (E-Y:433, 741, 867). The second site was on a flat, sandy and gravelly limestone plain below the hill (E-Y:868) (Plate 12A). The two sites yielded comparable numbers of specimens, *i.e.,* 47 and 36 respectively. It is unclear why no specimens were obtained from the limestone-plain traps in

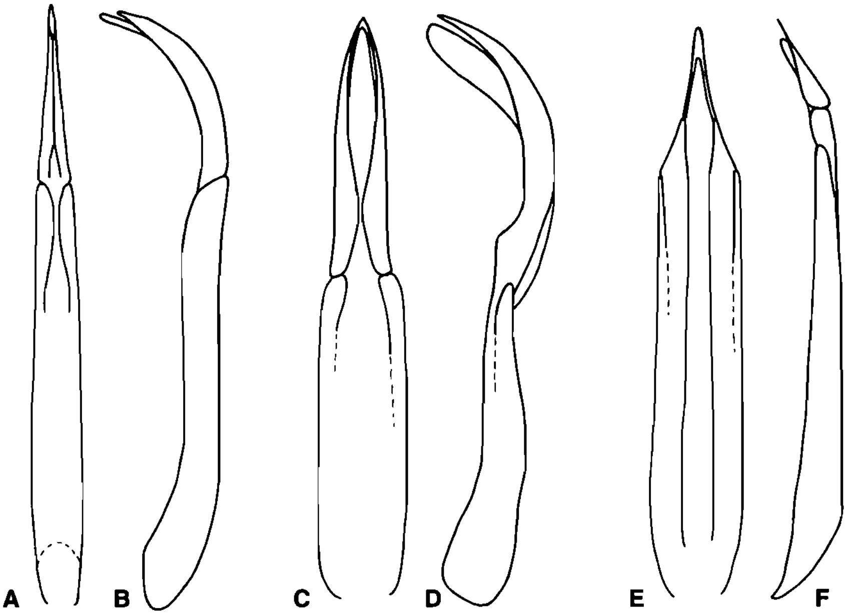

Fig. 10. Aedeagi of *Caenocrypticus* species, alternately in dorsal and lateral views. **A–B**: nominate subspecies of *C. (Phyloradix) soror* spec. nov.; **C–D**: *C. (P.) bushmanicus* Koch; **E–F**: *C. (Caenocapicus) capensis* spec. nov.

1974/75 (E-Y:434 and 742). All specimens were collected in baited ground-traps.

Months recorded. March, September and October.

Caenocrypticus (Phyloradix) soror nauwkluftensis subspec. nov., Figs 9B, 11, Plate 12B

Diagnosis. On average somewhat larger, less convex. Pronotum broadest near posterior angles, lateral margins tapering evenly and arcuately towards anterior angles. Protibiae very slightly arcuate inwards (Fig. 9B).

Description. Pronotum less convex transversely, both lateral margins visible in dorsal view from just behind anterior angle. Pronotum broadest near posterior lateral angles, from where lateral margins taper arcuately towards anterior angles. — Elytra in cranial view slightly flattened in middle of disc, lateral declivity narrowly rounded towards lateral margin. — Protibia evenly and moderately dilated, both the inner and outer margins slightly arcuate inwards, apical portion not curved inwards. Outer apical angle not or hardly produced, anterior margin almost straight towards reduced inner apical lobe (Fig. 9B).

Length: 2,56–3,10 mm; breadth: 1,12–1,34 mm.

Distribution. Nauwkluft Mountain/Park on the eastern edge of the central Namib Desert (Fig. 11).

Material examined. Three ♂ (all dissected) and 10♀. In Transvaal Museum, Pretoria.

Holotype ♂, allotype ♀ and 7 paratypes: S. W. Afr., (Namibia), Nauwkluft Park, 24° 16′ S, 16° 15′ E, 12.3.1975, baited ground-traps, 178 days (6 banana, 3 meat bait), leg. Endrödy-Younga & Breytenbach, E-Y:735. Additional paratypes: 1 *idem*, but 21.1.1975, ground-traps, 49 days, meat bait, leg. Endrödy-Younga, E-Y:565; 3 *idem*, but 6.9.1975, ground-traps, 178 days, meat bait, leg. Endrödy-Younga, E-Y:866.

Ethoecology. Two of five sites (in riverine bush and on a vegetated gravel plain) in the Nauwkluft Park did not yield material of this subspecies. Two of the successful sites were on stony hillsides with good grass cover (Plate 12B), and the third on level sandy ground, near a windmill, with traps under low bushes. During the first three months (26 October 1974 – 22 January 1975) no specimens were captured.

Months recorded. January, March and September.

Caenocrypticus (Phyloradix) bushmanicus Koch, Figs 9C, 10C,D, 11, Plates 1B, 7B, 10B, 13A

Caenocrypticus bushmanicus Koch, 1950: 81; 1952: 190.

Diagnosis. Medium-sized, convex, contracted between pronotum and elytra. Pronotum broadest around middle where slightly narrower than elytra, lateral margins arcuate (Plate 1B). Outline of head angularly contracted between tip of gena and eye. Protibia evenly and rather strongly dilated, but apical portion not curved inwards; apical margin truncate, emarginate between small inner lobe and hardly more produced outer angle (Fig. 9C). Basale of aedeagus longer than apicale, paramere narrow in lateral view, tapering evenly to sharply pointed apex; penis with broadly rounded apex (Fig. 10C,D). Yellow to dark chestnut-brown.

Redescription. Genal margin straight between truncate clypeus and posterior angle; posterior angle rounded and curving inwards before reaching anterior margin of eye, producing a triangular gap to the convexity of eye; gena, where broadest, and eye on same lateral level (Plate 10B). Puncta-

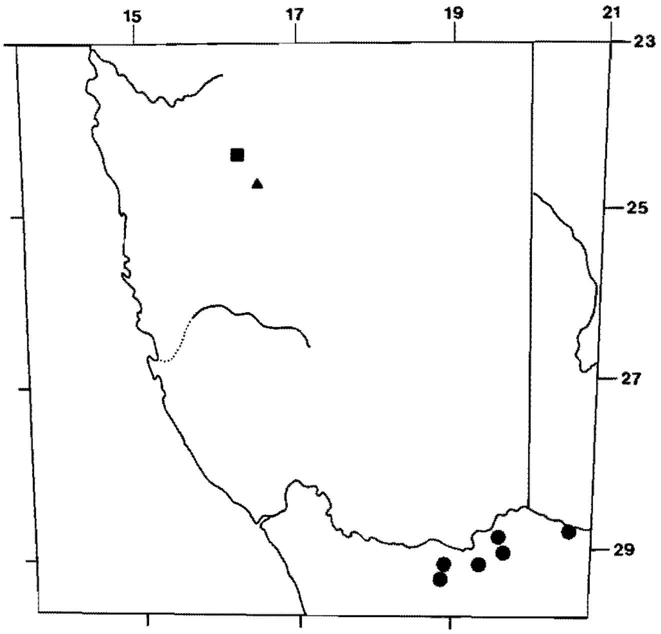

Fig. 11. Distribution of the *Caenocrypticus (Phyloradix)* species. ■ = nominate subspecies of *C. (P.) soror* spec. nov.; ▲ = *C. (P.) soror nauwkluftensis* subspec. nov.; ● = *C. (P.) bushmanicus* Koch.

tion fine and dense, very dense on clypeus, shagreen dense and crisp. — Pronotum moderately transverse, about one-quarter broader than long (59:44); broadest about in middle, margins arcuate, dorsal outline contracted between pronotum and elytra. Disc convex, both lateral margins visible only behind mid-length. Punctation coarser than on head, densely and uniformly set, shagreen fine and distinct. Punctation denser than in *C. soror*, microscopic hairs extremely short (Plate 7B). — Elytra one-quarter longer than combined breadth (83:63). Lateral margins evenly arcuate, broadest in anterior third of length (Plate 1B). Sutural profile arcuate, rather flat from base to apical declivity, highest behind anterior third of length. Apical declivity evenly arcuate towards apex, not forming a caudal protuberance. — Prosternal apophysis very broad, measured from basal contraction barely longer than broad (11:9). — Protibia evenly dilated, straight, anterior margin slightly obliquely truncate, acute outer angle slightly produced in front of flat inner lateral lobe, emarginate in between (Fig. 9C). — Aedeagus 0,78 mm long; basale longer (0,44 mm), apicale shorter (0,34 mm). Apicale moderately arcuate in lateral view, paramere narrow, tapering evenly to long, sharply pointed apical portion; penis in resting position as long as paramere, evenly thick with broadly rounded apex. Apicale not compressed bilaterally (Fig. 10C,D).

Female. Similar to male.

Length: 2,05–3,10 mm; breadth: 0,96–1,44 mm, holotype: 2,70×1,26 mm.

Distribution. South Africa, Bushmanland (Fig. 11).

Type material. Holotype ♂, allotype ♀ and 13 paratypes: Aggeneys, Bushmanland, 16.XII.1948, Koch & Van Son; additional paratypes: 4 Kakamas, Bushmld. 7.XII.1949, Koch; 3 Nabeis (between Kakamas and Pofadder, 18.XII.1948, Koch & Van Son). 1 Pofadder (17.XII.1948, Koch & Van Son, ex descr.). Holotype, allotype and 18 paratypes in Transvaal Museum, Pretoria; 1 paratype in South African Museum, Cape Town; 1 paratype in Musée Royal de l'Afrique Centrale, Tervuren.

Material examined. Twelve ♂ (all dissected), 15♀ and 3 additional specimens, including type series. In Transvaal Museum, Pretoria.

Additional localities: all South Africa, Bushmanland and leg. Endrödy-Younga: 1 betw. Onseepkans and Kakamas, 28° 52′ S, 19° 37′ E, 9.9.1976, ground-traps with meat bait 24 days, E-Y:1244; 3 Pofadder, 30 km E, 29° 00′ S, 19° 41′ E, 23.8.1977, ground-traps, banana bait, 64 days, E-Y:1326; 1 Pofadder, 80 km W, 29° 15′ S, 18° 48′ E, 25.8.1977, ground-traps, banana bait, 62 days, E-Y:1329. 1 Pofadder, XI.1948, Koch & Van Son.

Ethoecology. Koch (1950) collected the type series in wind-blown sand under plants, and on sandy soil under stones. The specimens collected later were all found in baited ground-traps (E-Y:1244), on a loose gravelly plain (E-Y:1326, 1329) on soft, red Kalahari-type sand (Plate 13A), between August and December. Activity is dependent on rain.

Months recorded. August, September and December.

Remarks. The type series, including the holotype and allotype, originally consisted of 33 specimens from Aggeneys; 12 specimens are housed in the Transvaal Museum. The holotype, allotype and a male paratype agree in all respects with the paratypes from Kakamas, Pofadder and Nabeis as well as with the reported additional specimens. Most of the Aggeneys paratypes are slightly different in that they occupy the lower range of size variation (2,05–2,65 mm) in the species and the lateral margins of the pronotum are less arcuate. The aedeagus also appears to be different. All ten specimens are, however, yellow to light brown. Two males with feebly sclerotized aedeagus are probably immature. The status of this form is uncertain and awaits new material of adult specimens.

Subgenus *CAENOCAPICUS* subgen. nov.

Type species: *Caenocrypticus (Caenocapicus) capensis* spec. nov.

Description. Eye not divided, posterior angle of genal margin reaching anterior margin of eye. Anterior emargination of pronotum moderately deep, anterolateral angles produced, slightly acutely angled, not lobiform. Punctation of dorsum unique in genus, particularly dense on pronotum, punctures sharp and elongate with microscopic hairs on elytra (Plate 8A,B). Smooth lateral margin of elytra concealed by elytral convexity in mid-section in dorsal view. Mesocoxa close to each other, intercoxal process of mesosternum sharply triangular. Protibia sexually dimorphic: inner margin inwardly arcuate in males and inner apical angle more distinctly lobiform. Protarsus short, segments 2–4 times as broad as long, segment 1 twice as long as broad. Tarsal claws short and equal in length (Fig. 9D,E). Aedeagus unique in genus, particularly in the length ratio of basale and apicale: apicale only one-fifth of total length (Fig. 10E,F).

Distribution. Geographically isolated from rest of genus; Namaqualand and the southwestern coastal regions of the Western Cape Province (Fig. 12).

Etymology. Compound name from the first part of the genus name and its distribution range in the Western Cape.

Remarks. This subgenus includes a single species that belongs to a group of primitive species within genus (see position in the cladogram, Fig. 7). Its unique characters are either autapomorphies or of uncertain direction (aedeagus). Its geographic isolation at the southern extreme of the geographic range of the genus together with the possession of both primitive and derived characters, suggest that it is an extant representative of an early cleavage.

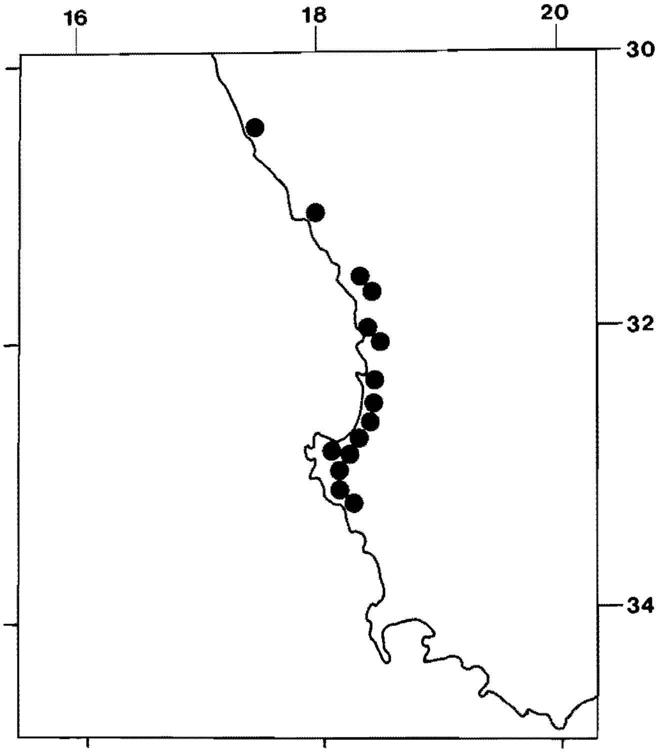

Fig. 12. Distribution of *Caenocrypticus (Caenocapicus) capensis* spec. nov.

Caenocrypticus (Caenocapicus) capensis spec. nov., Figs 9D,E, 10E,F, 12, Plates 1C, 8A–C, 13B

Diagnosis. Small to medium-sized, dark chestnut-brown, shiny. Pronotum with characteristic dense and coarse elongate punctation (Plate 8A,B). Pronotum slightly broader than or as broad as elytra; dorsal outline barely contracted between pronotum and elytra. Posterior lateral angle of pronotum narrowly rounded, obtuse (Plate 1C). Protibia broadening towards apex, there curved slightly inwards, with inner dilation; inner angle of apical margin broadly produced (Fig. 9D,E). Aedeagus narrow, parallel with very short, pointed apicale (Fig. 10E,F).

Description. Head small, pronotum more than twice as broad (5,4:2,3), slightly broader than long (2,3:2,0). Eye not protuberant, composed of few, large convex corneal facets. — Pronotum broader than long (5,30:4,25), broadest in front of posterior angles, tapering evenly to anterior angles, lateral margins almost straight, slightly curved only towards lateral angles; anterior angles narrow, collar emargination shallow in relation to dorsal length: 0,3:3,8. Disc transversely convex, both sharp lateral margins hardly discernible in dorsal view. Punctation coarse, in middle of disc consisting of elongate punctures with narrow and convex intervals, in posterolateral area punctures joined to form crisp longitudinal reticulation (Plate 8A,B). — Elytra much longer than broad (7,3:5,0), broadest behind humeri, thereafter straight in a slightly contracting section before curving into rounded apex. Convex transversely, both lateral margins visible only in a short humeral and apical section. Sutural profile slightly and evenly arcuate before curving into apical declivity. Punctation of disc more widely spaced, punctures only slightly elongate, flat intervals broader than punctures, each bearing a short reclinate bristle. Integument densely and finely shagreened (Plate 8C). — Prosternum convex transversely, episternal fossa indistinct. Prosternal apophysis narrow, elongate-ovate, extending far beyond coxae. Punctation coarse but well spaced, forming few longitudinal furrows on inner anterior portion of episternum. Mesocoxae close to each other, apex of narrow triangular apophysis briefly truncate. Metacoxae slightly further apart. — Protibia short and broad, dilated towards apex, inner margin with distinct median dilation in males (Fig. 9D). Inner apical angle roundly produced. — Aedeagus long, narrow, parallel, dorsoventrally compressed, slightly and evenly arcuate ventrad. Small apicale only one-fifth of total length, weakly separated from long basale; apex of apicale sharply pointed. Simple penis concealed in tegmen of paramere, only its short apex exposed below apex of apicale (Fig. 10E,F). Length 0,58 mm, of which apicale constitutes 0,16 mm.

Secondary sexual dimorphism. Inner margin of protibia with median dilation and inner apical angle slightly more extended inwards in male (Figs 9D,E).

Length: 1,9–2,6 mm; breadth: 0,94–1,30 mm.

Distribution. Coastal belt of southern Western Cape Province between latitudes 29° 57′ and 33° 12′ S (Langebaanweg and Gelbeck Farm) (Fig. 12).

Material examined. Fifty ♂ (3 dissected) and 77♀. Holotype, allotype and all paratypes in Transvaal Museum, Pretoria.

Holotype ♂, allotype ♀ and 21 paratypes: S. Afr., S. W. Cape, Bookram farm, 32° 39′ S, 18° 17′ E, 30.8.1981, ground-traps, 59 days, with bait: meat (holotype, allotype and 14 paratypes), faeces (5); ferm. banana (2), leg. Endrödy-Younga, E-Y:1868. Additional paratypes: 2 Gemsbok vlakte frm., 30° 30′ S, 17° 29′ E, 1.9.1977, ground-traps, 56 days, bait: faeces (1), banana (1), leg. Endrödy-Younga, E-Y:1366; 1 Hoekbaai, 2 km ENE, 31° 11′ S, 17° 47′ E, 27.8.1979, ground-traps, 62 days, faeces bait, leg. Endrödy-Younga, E-Y:1610; 1 Seweputs coast, 31° 39′ S, 18° 17′ E, 23.8.1981, ground-traps, 64 days, meat bait, leg. Endrödy-Younga, E-Y:1836; 2 Seweputs farm, 31° 39′ S, 18° 22′ E, 23.8.1981, ground-traps, 64 days, faeces bait, leg. Endrödy-Younga, E-Y:1835; 6 Nortier farm, 32° 03′ S, 18° 19′ E, 25.8.1981, ground-traps, 62 days, bait: meat (3), faeces (2), banana (1), E-Y:1845; 1 Lamberts Bay E (dunes), 32° 05′ S, 18° 24′ E, 25.8.1981, ground-traps, 60 days, faeces bait, leg. Endrödy-Younga, E-Y:1849; 1 *idem* but 28.8.1989, litter under bushes, leg. Endrödy-Younga & Klimaszewski, E-Y:2672; 17 Kliphoutkop, 32° 17′ S, 18° 24′ E, 28.8.1981, ground-traps, 60 days, bait: meat (10), faeces (6), banana (1), leg. Endrödy-Younga, E-Y:1852; 1 Elands Bay forestry (dune forestation), 32° 18′ S, 18° 21′ E, 28.8.1981, ground-traps, 60 days, meat bait, leg. Endrödy-Younga, E-Y:1853; 6 St Helenafontein, 32° 36′ S, 18° 20′ E, 30.8.1981, ground-traps, 60 days, bait: meat (2), faeces (2), banana (2), leg. Endrödy-Younga, E-Y:1867; 28 Duiker Island (on the continent), 32° 43′ S, 17° 56′ E, 22.8.1983, ground-traps, 73 days, bait: meat (12), faeces (11), banana (5), leg. Endrödy-Younga & Penrith, E-Y:1962; 11 Veldrif, 3 km E, 32° 46′ S, 18° 14′ E, 31.8.1981, ground-traps, 59 days, bait: meat (8), faeces (2), banana (1), leg. Endrödy-Younga, E-Y:1870; 7 Cape Columbine, 32° 49′ S, 17° 51′ E, 22.8.1983, ground-traps, 73 days, bait: meat (3), faeces (2), banana (2), leg. Endrödy-Younga & Penrith, E-Y:1964; 1 *idem*, but 32° 48′ S, 18° 08′ E, 22.8.1983, ground-traps, 73 days, (1 meat bait), leg. Endrödy-Younga, E-Y:1961; 12 Brackfontein farm, 32° 56′ S, 18° 15′ E, 23.8.1983, ground-traps, 72 days, bait: meat (6), faeces (2), banana (2), leg. Endrödy-Younga & Penrith, E-Y:1967; 3 Langebaanweg, 32° 57′ S, 18° 08′ E, 24.8.1983, ground-traps, 71 days, bait: meat (1), faeces (1), banana (1), leg. Endrödy-Younga, Penrith, E-Y:1970; 1 Geelbek farm, 33° 12′ S, 18° 07′ E, 25.8.1983, ground-traps, 70 days, faeces bait, leg. Endrödy-Younga & Penrith, E-Y:1975. 3 Abrahamskraal, 33° 14′ S, 18° 09′ E, 25.8.1983, ground-traps, 70 days, bait: meat (1) and banana (2), leg. Endrödy-Younga & Penrith, E-Y:1976.

Ethoecology. The preferred habitat of the species is rather densely vegetated (herbaceous and bush) white coastal flats and dunes (Plate 13B). With one exception, it was collected only in baited ground-traps. Thorough collecting at and in the vicinity of all trap sites suggests that it is an exceptionally cryptic species. Bait preferences suggest that it prefers decaying material of animal (66 specimens collected with decaying meat and 40 on faeces) rather than of plant origin, as only 20 specimens were attracted to fermenting banana.

Months recorded. August and September.

Subgenus *CRYPTOCARPES* Koch

Cryptocarpes Koch, 1952: 191, genus in Crypticini; 1958: 121, genus in Caenocrypticini. **stat. nov.**

Lornamus Koch, 1952: 191, genus in Crypticini; 1958: 121, genus in Caenocrypticini. **syn. nov.**

Type species: *Cryptocarpes elongatus* Koch (by original monotypy)

Redescription. Genal margin drawn onto surface of eye from front, reducing connection between dorsal and ventral parts to one-third, or separating it completely (Plate 9A–C) in *C. dividiopsis*. Anterior emargination of pronotum moderate, even or slightly angular bilaterally. Anterolateral angle moderately produced, about rectangular, not lobiform. Elytra convex transversely, smooth lateral margin hardly concealed by convexity in median section in dorsal view. Mesocoxa close to each other, intercoxal process of mesosternum sharply triangular. Protibia straight, slightly to moderately dilated towards apex, anterolateral angle moderately produced, rectangular or sharply angled, not lobiform. Protarsus short, only basal segment longer than broad. Tarsal claws short and equal in length. Aedeagus simple, more or less arcuate, not sickle-shaped.

Distribution. Northern extreme of the genus' distribution (Fig. 13).

Remarks. The subgenus comprises three species of a monophyletic lineage, with the highest number of apomorphies in *C. dividiopsis* (see position in cladogram (Fig. 7) and remark on p. 11). The early cleavage and northward dispersal of the lineage seems to have coincided with a tendency of genal extension onto the eye during the first speciation event that gave rise to this lineage.

Concerning the synonymies, the monotypic genus *Lornamus (dividiopsis)* Koch was based on the completely divided eye compared to the partial division exhibited in *Cryptocarpes*. Since the expression of these characters represent stages in the same evolutionary process, the two genera are synonymized, with *Cryptocarpes* as senior synonym because it appeared first in print, albeit on the same page as *Lornamus*. The reduction of *Cryptocarpes* to subgeneric status is based on cladistic principles.

Caenocrypticus (Cryptocarpes) elongatus (Koch) comb. nov., Figs 13, 14A, 15A,B, Plates 1D, 6B, 9A, 14A

Cryptocarpes elongatus Koch, 1952: 191.

Diagnosis. Dark reddish brown, almost black, elongate, pronotum as broad as or almost as broad as elytra. Lateral margins of pronotum evenly arcuate although anterior angles are more closely set than basal angles. Ventral side of eye supported by a rounded temporal lobe; edge of latter clearly visible in dorsal view along margin of protuberant eyes. Short genal process reduces eye from front. Protibia dilated, straight and similar in both sexes (Fig. 14A). Base of pronotum finely margined. Aedeagus simple, parameres straight, sharply pointed, penis parallel, moderately arcuate (Fig. 15A,B).

Redescription. Head with eyes as broad as frontal emargination of pronotum. Clypeus slightly emarginate in width of labrum. Gena curved in an obtuse angle towards eye, forming a short, deflected process that reduces eye slightly from front. Inner margin of eye simple, disc elevated, but without supraorbital canthus. Disc with slight impressions, punctation dense and coarse, integument shagreened. Eye protuberant laterally beyond outline of head, covered ventrally by rounded temporal lobe. Eye extends a few ocular facets onto ventral surface of head between genal process and temporal lobe (Plate 9A). — Lateral margins of pronotum evenly arcuate; contracted towards anterior and basal angles. Laterally sharply, basally finely, anteriorly hardly discernibly margined. Posterior lateral angle more rounded (Plate 6B) than in *C. damara* (Plate 6C). Punctation of disc similar to that of head, integument less distinctly shagreened. — Elytra about 1,5 times longer than combined breadth (9,5:6,0), semiparallel, broadest in front of middle (Plate 1D), but margins only slightly arcuate, semiparallel, slightly contracted behind sharp humeral angles. Dorsal profile almost straight, apical declivity steep, apex protruding slightly. Disc of elytra transversely convex. Lateral margin only sharp and visible from above in the first fifth of elytral length, then curving slightly ventrad, flattening onto surface of roundly retrovert lateral portion of elytron. Epipleuron broader and flattened post-humerally, tapering into an evenly narrow strip level with metacoxa; from there on it falls into the plane of lateral portion of elytron. Epipleuron evenly very narrow and parallel with inner margin of elytron. Base of elytra finely marginate, which together with scutellum is only exposed if pronotum is bent slightly ventrad. Punctation and shagreen similar to those of pronotum. — Ventral side of head with sharp, transverse pregular fossa. Gular stridulatory file broad, its transverse reticulation rather smooth. Episternal suture of prosternum distinct. Prosternal apophysis pointedly ovate. Punctation of prosternum coarse with round punctures, confluent in longitudinal impressions on its episternum. Meso- and metacoxae rather closely set, intercoxal portions of sterna narrowly triangular. Punctation and shagreen of ventral surface comparable to shagreen of elytra. — Protibia straight, evenly dilated from base to apex, inner apical lobe small, obliquely truncate; external apical angle moderately produced; spurs of protibia large and subequal, as long as first three tarsal segments together (Fig. 14A). — Aedeagus 0,6 mm long, of which apicale constitutes 0,36 mm. Width of fused parameres 0,1 mm (Fig. 15A,B).

Female. Similar to the male.

Length: 2,50–3,25 mm; breadth of pronotum: 0,90–0,98 mm; elytra: 0,92–1,02 mm.

Distribution. Kaokoveld in Namibia (Fig. 13).

Type material. Holotype ♂, allotype ♀ and 8 paratypes: S. W. Afr., Kaokov., Oropembe, VI.1951, Koch. Additional paratypes: 6 S. W. Afr., Kaokov., Sanitatas, VI.1951, Koch; 3 Zesfontein, S.W.A., Feb. 1925. Holotype, allotype and 16 paratypes in Transvaal Museum, Pretoria, 1 paratype in South African Museum, Cape Town.

Material examined. Two ♂, 2♀, 17 additional specimens (types) and one additional ♂ in Transvaal Museum, Pretoria: Ohopoho, Kaokoveld, VIII.1956, Koch.

Ethoecology. The species occurs in sand pockets around the base of bushes or tussocks in generally flat, gravelly areas (Plate 14A).

Months recorded. February, June and August.

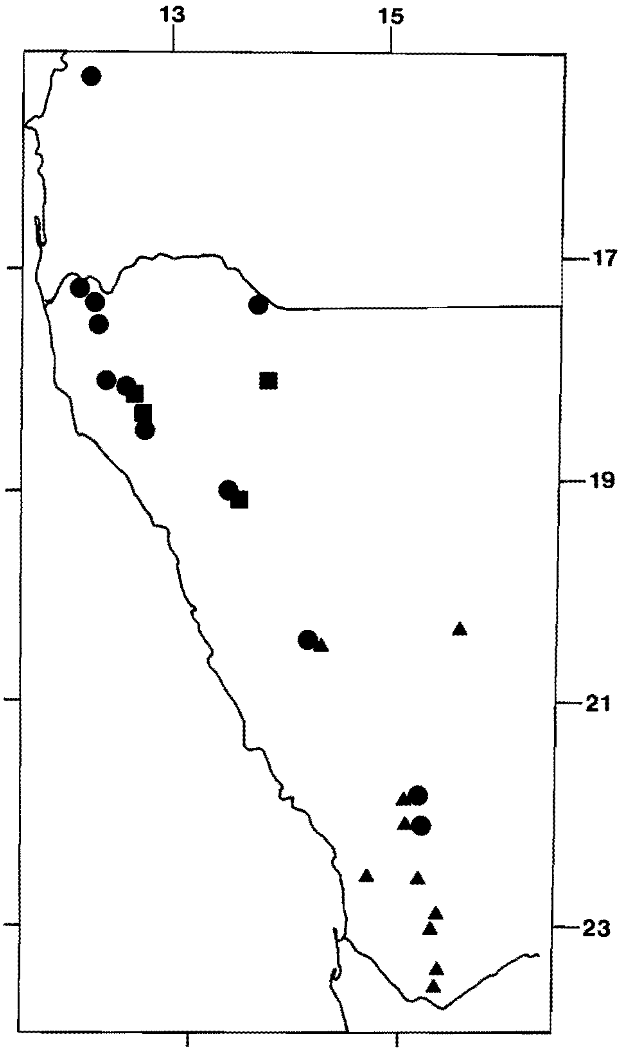

Fig. 13. Distribution of the *Caenocrypticus (Cryptocarpes)* species. ■ = *C. (C.) elongatus* (Koch); ● = *C. (C.) dividiopsis* (Koch); ▲ = *C. (C.) damara* (Koch).

Caenocrypticus (Cryptocarpes) damara (Koch) comb. nov., Figs 13, 14B, 15C,D, Plates 2A, 6C, 9B, 14B

Lornamus damara Koch, 1958: 128.

Diagnosis. Elongate, body transversely convex, epipleuron with same vertical curvature as rest of elytron from middle of elytral length. Eye strongly reduced but not completely divided by genal process. Vertex without a sharp supraorbital canthus. Margins of pronotum straight towards posterior angle (Plate 6C). Protibia narrow, straight, external angle sharp but not projecting in front of anterior margin (Fig. 14B). Prosternal apophysis broadly rounded at apex. Apicale of aedeagus much shorter than basale (Fig. 15C,D). Dark reddish brown to black with lighter appendages; integument finely shagreened and shiny.

Redescription. Head narrower than in *C. dividiopsis*, clypeus truncate, almost straight. Disc without transverse impression (present in *C. elongatus*) and without supraorbital canthus. Punctation sharp and moderately dense, integument finely shagreened and shiny. Eye supported from below by a temporal lobe visible from above. Genal canthus forming long, narrow process, reducing eye from front but leaving posterior margin of eye free by width of a single facet, thus eye not entirely divided into dorsal and ventral parts (Plate 9B). — Pronotum parallel-sided in posterior half or broadest in middle, very

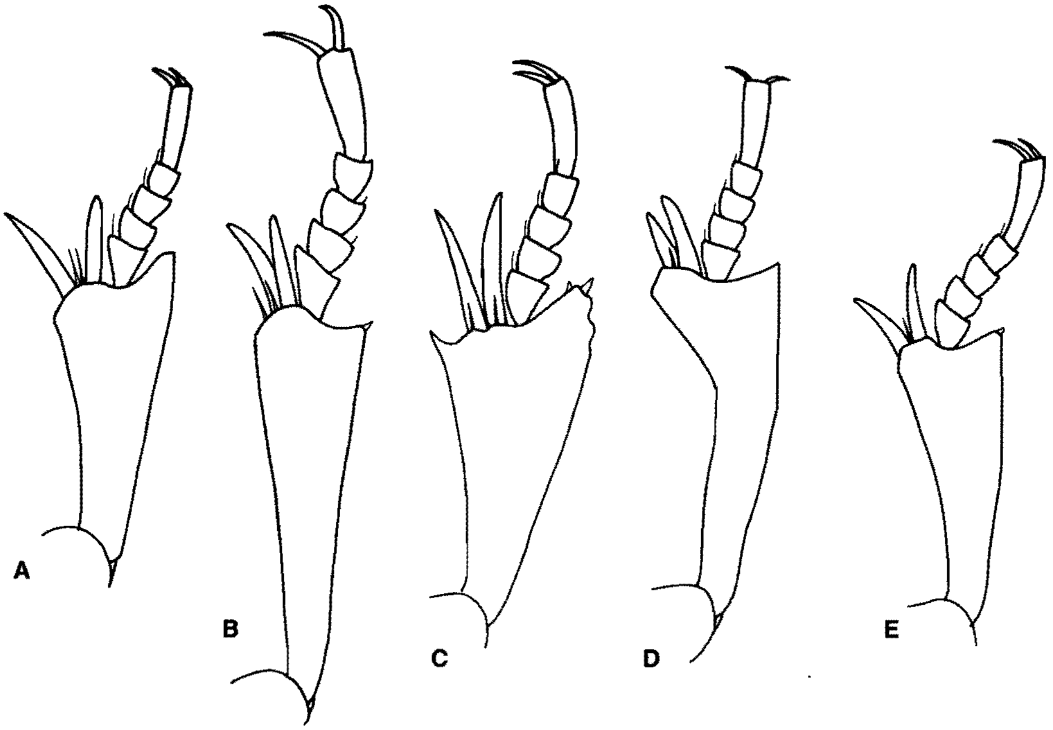

Fig. 14. Protibiae of *Caenocrypticus* species. **A**: *C. (Cryptocarpes) elongatus* (Koch), male; **B**: *C. (C.) damara* (Koch), male; **C**: *C. (C.) dividiopsis* (Koch), male; **D**: *C. (Caenocrypticus) uncinatus* Gebien, male; **E**: same species, female.

slightly contracting to basal angles; lateral margin in posterior section straight. Lateral margins finely but sharply, anterior and posterior margins very finely margined (Plate 6C). Punctation of surface sharp, punctures elongate, larger and more widely spaced than in *C. dividiopsis*, integument finely shagreened and more shiny than in *C. dividiopsis*, but less shiny than in *C. elongatus*. — Elytra almost 1,5 times longer than broad (8,5:6.0), convex transversely, sutural profile flatly arcuate to apical declivity that reaches apex at angle of about 60°. In dorsal view elongate-ovate, broadest in front of mid-length, contracting distinctly to sharp humeral angle (Plate 2A). Lateral margin sharply crested and visible from above only in anterior half, thereafter gradually finer and concealed by retracted convexity of elytra. Base of elytra margined with sharp humeral angle (Plate 6C). Punctation similarly dense or somewhat more widely spaced than on pronotum, punctures finely asperate in apical declivity. — Gula with apparent functional stridulatory file. Prosternum often with a fine impunctate transverse median line, seen only in males. Prosternal apophysis broadly rounded at apex. Mesosternal apophysis as in *C. elongatus*, more broadly triangular (about 55°) than in *C. dividiopsis* (45°). — Third segment of antenna about 1,5 times longer than fourth. Protibia straight and moderately dilated from base to apex; inner apical angle slightly lobiform and extending beyond pointed external lateral angle. Spurs subequal in length, about as long as three basal tarsomeres (Fig. 14B). —Aedeagus poorly sclerotized, 0,6 mm long, of which apicale constitutes only 0,2 mm; breadth of apicale 0,06 mm. Sheath of parameres flat, open from base (positioned dorsally in body) exposing only slightly arcuate penis (Fig. 15C,D).

Female. Similar to male.

Length: 2,2–3,1 mm; breadth: 0,95–1,28 mm.

Distribution. Damaraland in Namibia (Fig. 13).

Type material. Lectotype (here designated) and 24 paralectotypes: Ebony, S.W.A., VII.1954, Vernay - Tvl. Mus. Expedition (leg. C. Koch); 5 paratypes: Roessing Mount., 25 (miles) E Swakopmund, VIII.1954, Vernay - Tvl. Mus. Exp. (leg. C. Koch). All type specimens in Transvaal Museum, Pretoria.

Material examined. Thirteen ♂ (12 dissected), 5♀ and 45 additional specimens; 61 in Transvaal Museum, Pretoria, 2 at University of California, Berkeley.

Additional material: 16 S. W. Afr., Damara., Farm Bethanis 20° 25′ S, 14° 24′ E, 19.2.1975, from under stones, leg. Endrödy-Younga, E-Y:677; 1 *idem,* but 18.2.1975, singled at night, E-Y:676; 2 Khan River, S.W.A., SW of Trekkopje, VII.1954, Vernay - Tvl. Museum Exp. (leg. C. Koch); 3 *idem,* but X.1957, C. Koch; 2 S. W. Afr., Kl.(-ein) Spitzkoppe, 15.5.1972, L. & O. Prozesky; 3 *idem,* but 2 m(-iles) N., 19.XI.1971, L. Prozesky; 1 S. W. Afr., c. Namib, Gobabeb, 52 km NE, 23° 23′ S, 15° 28′ E, 7.7.1978, from under stones, leg. Endrödy-Younga, E-Y:1463. 1 S. W. Afr., Namib, Ganab-Hotsas, 23° 00′ S, 15° 25′ E, 18.11.1974, ground-trap with cheese bait, leg. Endrödy-Younga, E-Y:482; 1 S. W. Afr., c. Namib, Bloedkopee, 22° 50′ S, 15° 23′ E, 7.7.1978, ground-traps 2 years, leg. Endrödy-Younga, E-Y:1471; 2 South West Africa, Gorob Mine, 27.2.1979, leg. Wharton; 1, 50 m(iles) W of Welwitschia, XI.1961.

Ethoecology. The species occurs in stony areas in the arid Namib, east of the dune Namib (Plate 14B). Almost all specimens were collected from under stones, and only two individuals from numerous pitfall traps set in the area.

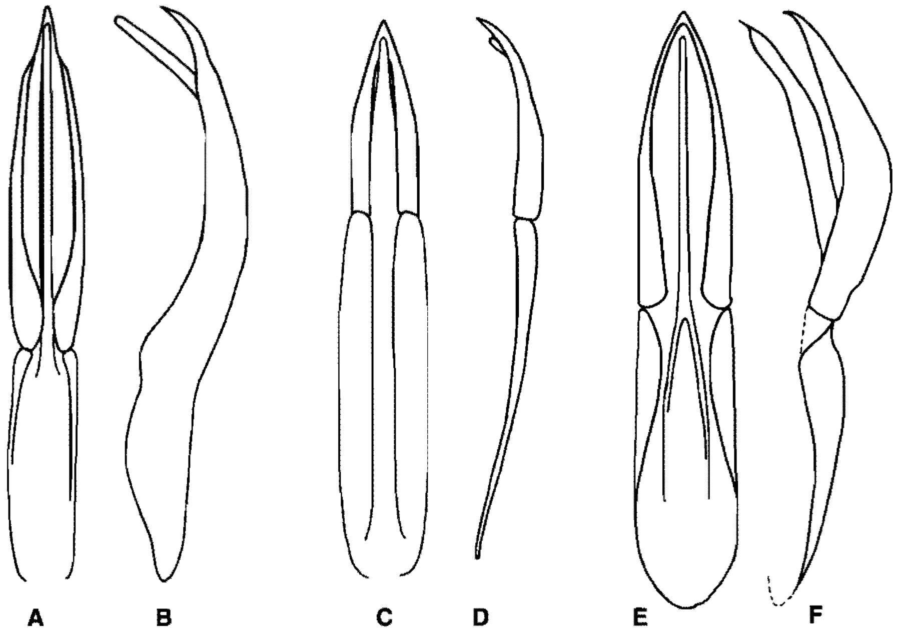

Fig. 15. Aedeagi of *Caenocrypticus* species, alternately in dorsal and lateral views. **A–B**: *C. (Cryptocarpes) elongatus* (Koch); **C–D**: *C. (C.) damara* (Koch); **E–F**: *C. (C.) dividiopsis* (Koch).

Months recorded. February, May, July, August, October and November.

Caenocrypticus (Cryptocarpes) dividiopsis **(Koch) comb. nov., Figs 13, 14C, 15E,F, Plates 2B, 5A, 6A, 9C,D, 14B, 15A**

Lornamus dividiopsis Koch, 1952: 191; 1958: 128.

Diagnosis. Elongate-ovate, elytra evenly arcuately reducing from behind humeri to apex. Eye completely divided into dorsal and ventral portions by extended genal margin (Plate 9C,D). Vertex with sharp-edged supraorbital canthus. Lateral margins of pronotum evenly arcuate. Protibia straight, strongly dilated towards apex, external angle slightly produced (Fig. 14C). Prosternal apophysis broadly ovate but with angular apex. Apicale of aedeagus longer than basale, arcuate and not flattened dorsoventrally (Fig. 15E,F). Chestnut-brown to black, appendages hardly paler. Punctation fine and dense, shagreen of integument strong, imparting a greasy sheen to surface.

Redescription. Head somewhat broader and clypeal emargination deeper than in *C. damara*. Inner margin of eyes bordered by a sharply crested supraorbital elevation. Surface evenly, densely and finely punctate, shagreen of integument sharply incised. Genal canthus fused to temporal lobe below eye, completely dividing it into dorsal and ventral parts; ventral part vertical and directed forwards, not visible in ventral view (Plate 9C,D). — Lateral margins of pronotum evenly arcuate, not straight in posterior section. Lateral margin sharp, anterior margination fine but complete, posterior margination interrupted in middle. Punctation and shagreen similar to head. — Elytra 1,5 times longer than broad, broadest in anterior quarter of length, moderately contracting to small humeral angle and evenly and flatly arcuate towards apex (Plate 2B). Lateral margin visible from above for most of length, epipleuron only flattened in anterior quarter. Punctation of disc slightly more widely spaced than on pronotum, shagreen slightly finer and integument accordingly less dull. — Gula with apparent functional stridulatory file. Prosternum without transverse shiny line. Prosternal apophysis broadly ovate with angular apex; sharp margination of procoxal cavity continues onto margins of apophysis. Mesosternal apophysis narrowly triangular, about 40° (Plate 5A). — Length of antennal segments evenly reduced from second to fourth segments. Protibia strongly dilated from base to apex; apex obliquely truncate with a dorsal lobe at inner angle falling slightly short of sharply pointed external angle; spurs equal in length, as long as three basal tarsomeres (Fig. 14C). — Aedeagus 0,58 mm long, of which apicale constitutes 0,31 mm; measurements the same in a 2,5 mm and a 3,0 mm specimen. Apicale arcuate, open from fused base dorsally (concave side), penis rather thick, not filiform as in *C. damara* (Fig. 15E,F).

Female. Similar to male.

Length: 2,0–3,5 mm; breadth: 0,88–1,45 mm.

Distribution. In Namibia from the Kaokoveld into Ovamboland and apparently geographically isolated in southern Damaraland as well as in the Angolan Namib (Fig. 13).

Type material. Holotype ♂, allotype (designated by Koch but sex not confirmed) and 1 paratype: S. W. Afr., Kaokoveld, Oropembe, VI.1951, Koch. Additional paratypes: 7 S. W. Afr., Kaokoveld, Sanitatas, VII.1951, Koch; 1 15 m of Moçamedes (Angola).

Material examined. Nineteen ♂ (10 dissected), 12♀ and 29 additional specimens. Specimens and type specimens in Transvaal Museum, Pretoria. One specimen via Department of Zoology and Entomology, University of Pretoria.

Additional material: 2 S. W. Afr., Kaokoveld, Kunene Riv. W of Hartmansberg, 17° 12′ S, 12° 10′ E, 13.2.1984, ground-traps, faeces bait, 54 days, leg. Penrith & Müller, E-Y:2070; 2 *idem,* but dunes and hummocks, day, E-Y:2066; 3 *idem,* Kunene, 27 km S, 17° 26′ S, 12° 18′ E, 16.2.1984, ground and stones, leg. Penrith & Müller, E-Y:2073; 5 *idem,* Kunene Riv., 44 km S, 17° 34′ S, 12° 17′ E, 16.2.1984, ground and vegetation, leg. Penrith & Müller, E-Y:2074; 11 *idem,* 17.2.1984, ground-traps, 54 days, bait: meat (7), faeces (2), fermented banana (2); 17 *idem,* 9.4.1984, on sandy gravel (flats), leg. Endrödy-Younga, E-Y:2103; 1 Swartbooisdrift, VII.1951, leg. C. Koch; 1 between Engo and Munitum Rivers, 18° 03′ S, 12° 19′ E, 10.4.1984, leg. Endrödy-Younga, E-Y:2111; 3 *idem,* Sesfontein basin, 19° 08′ S, 13° 36′ E, 3.2.1975, ground-traps, 14 days, faeces bait, leg. Endrödy-Younga, E-Y:613; 3 N Namib, inland dunes, Farm Bethanis, Outjo Distr., VIII.1962, C. Koch; 1 S. W. A. Ebony, VII.1954, Vernay - Tvl. Mus. Expedition (leg. C. Koch); 1 Klein Spitzkoppe, SE 21.15Cc, 19.1.1980, leg. E. Holm; 1 without locality.

Ethoecology. The main part of the geographic range of *C. dividiopsis* covers the northeastern Kaokoveld, inland from the coastal dunes. Environmental conditions in the area range from arid to desert, consisting mostly of sandy plains with occasional rocky hills. Most specimens collected south of the Kunene River in 1984 were found at the foot of a range of rocky hills, under stones on sand, or attracted to baited ground-traps in the same area (Plates 14B, 15A).

Months recorded. January, February, April, June to August.

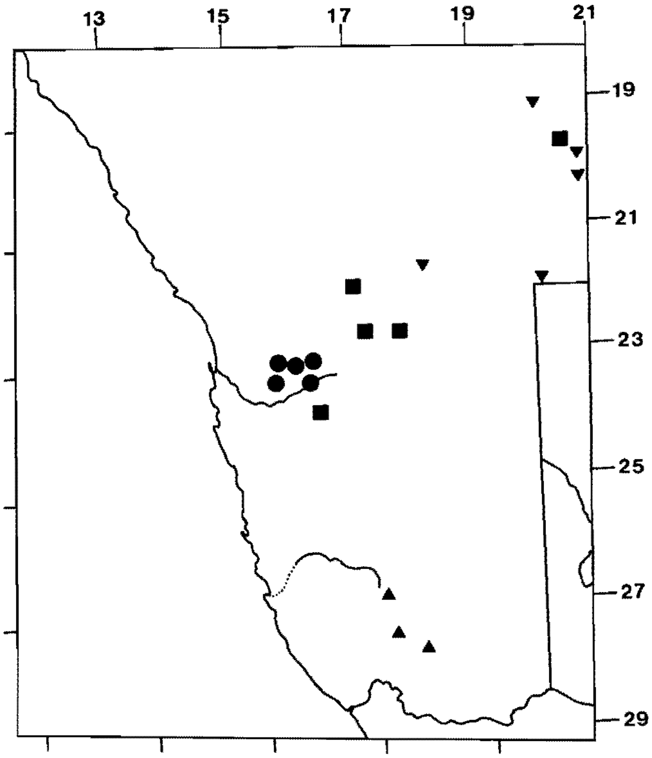

Fig. 16. Distribution of the *Caenocrypticus (Caenocrypticus)* species. ▼ = *C. (C.) macintyrei* Koch; ■ = *C. (C.) uncinatus* Gebien; ● = *C. (C.) kaszabi* spec. nov.; ▲ = *C. (C.) wittmeri* spec. nov.

Subgenus *CAENOCRYPTICUS*

Caenocrypticus Gebien, 1920: 139; 1938: 508 (Crypticini).
Caenocrypticus Koch: 1952: 188.
Type species: *Caenocrypticus uncinatus* Gebien.

Redescription. Small, elongate-ovate, transversely convex, lateral margins of elytra concealed by convexity in mid-section. Eye free, not reduced or divided by genal margin. Intercoxal process of mesosternum much narrower than coxa, triangular with narrowly truncate apex. Protibia slightly dilated towards apex, only in *C. uncinatus* apex broad owing to an inner apical lobe. Apical third of protibia strongly curved inwards in males, less so in females. Protarsal segments short, only first longer than broad. Tarsal claws short and equal in length. Apicale of aedeagus narrow, slightly arcuate, only in *C. uncinatus* almost sickle-shaped.

Distribution. Mostly in the northeastern area of the genus' distribution, from the Namib hinterland to the Kalahari. One species, *C. wittmeri*, occurs further south where it is geographically isolated on escarpments of the southern Namib Desert (Fig. 16).

Remarks. The four species of this subgenus appear as a clade together with *C. capensis* in the cladogram (Fig. 7). The last species is apparently more primitive, and is not considered a member of this lineage (subgenus).

Caenocrypticus (Caenocrypticus) uncinatus Gebien, Figs 14D,E, 16, 17A,B

Caenocrypticus uncinatus Gebien, 1920: 140; 1938: 508; Koch, 1950: 80; 1952: 189.

Diagnosis. Elongate-ovate, elytra transversely convex; sharp lateral margins partially concealed by retracted convexity of lateral portion of elytra. Apical declivity of elytra evenly and flatly arcuate, reaching apex at angle of 50°. Genal canthus curving ventrad at anterior margin of undivided eye. Temporal lobe beneath eye well developed, edge extending beyond convexity of eye in dorsal view. Apical quarter of protibia, particularly in males, abruptly dilated and curved inwards (Fig. 14D,E). Dark chestnut-brown to almost black, ventral side and appendages slightly lighter.

Redescription. Head narrow, evenly arcuate between genal angles, clypeus truncate. Genal angle not produced laterally beyond anterior angle of eye. Temporal lobe beneath eye well developed, edge extending beyond curvature of eye laterally and discernible in dorsal view. Posterior portion of genal canthus curves ventrad along anterior margin of eye, not reducing it anteriorly. Eye complete, lateral in position, dorsal part broadest, reducing to a triangle ventrally. Punctation dense anteriorly, here punctures broader than intervals, more widely spaced on vertex; integument densely shagreened, imparting a greasy sheen. — Pronotum considerably broader

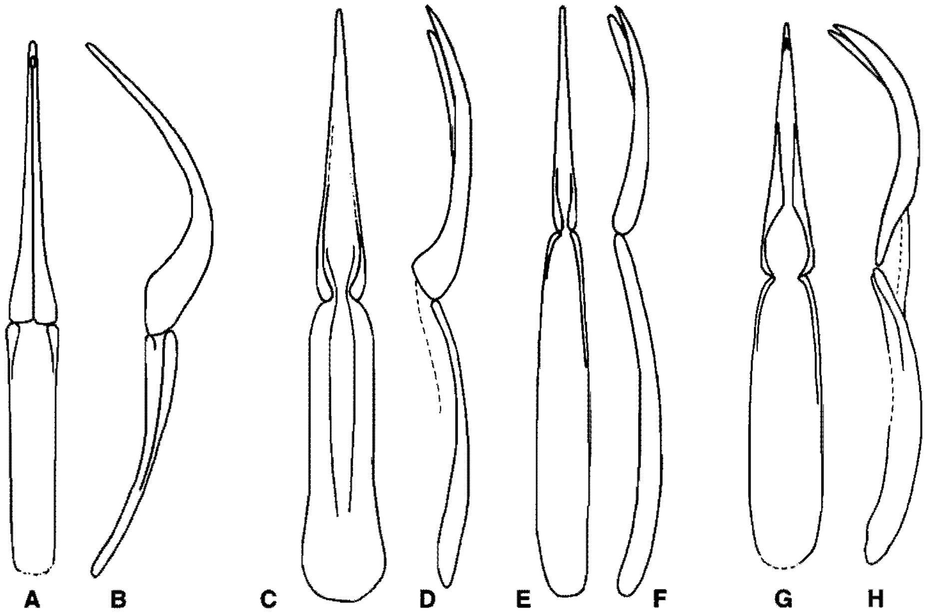

Fig. 17. Aedeagi of *Caenocrypticus (Caenocrypticus)* species, alternately in dorsal and in lateral views. **A–B**: *C. (C.) uncinatus* Gebien; **C–D**: *C. (C.) kaszabi* spec. nov.; **E–F**: *C. (C.) wittmeri* spec. nov.; **G–H**: *C. (C.) macintyrei* Koch.

than long (64:50). Lateral margins more or less straight in posterior half of length, there semiparallel or slightly contracting to base. Lateral margin reaching posterior angle in a straight line; angle narrowly rounded, slightly obtuse (about 100°). Lateral margins sharply marginate, anterior and posterior margins only briefly marginate in lateral sections. Punctures slightly bigger and more widely spaced than on vertex, integument also slightly more shiny. — Elytra elongate, broadest behind humeri, slightly arcuate and contracting to level of apical declivity, evenly arcuate to apex behind. Sutural profile flat anteriorly and evenly curved towards apex in apical declivity, joining apex at angle of 60–65°. Humeral angle sharp, but obtuse, not produced. Lateral crest sharp and continuous between humerus and apex, concealed in a large median section by convexity of elytra. Epipleuron well demarcated and on a different level than lateral portion of elytron over entire length. Punctation shallower and more widely spaced than on pronotum, integument slightly more shiny. — Gula with apparently functional stridulatory file. Mesosternal apophysis narrowly triangular with pointed or narrowly rounded apex. — Protibia narrow at base, abruptly dilating in apical quarter, outer margin curved slightly inwards. Inner apical angle large, lobiform, strongly produced beyond sharp rectangular external angle. Spurs of protibia large, subequal, inner one being somewhat longer, outer one only as long as two basal tarsomeres (Fig. 14D,E). — Aedeagus 0,65 mm long, of which apicale constitutes 0,34 mm; breadth of apicale at base 0,06 mm. Aedeagus simple, apicale well sclerotized, thin, spike-like with a characteristic sharp dorsal curvature (towards open tegmen). Penis filiform, concealed within partly closed tegmen of apicale (Fig. 17A,B).

Length. 2,14–3,00 mm; breadth: 1,05–1,22 mm.

Secondary sexual dimorphism. Protibia curved inwards and with inner apical lobe in male (Fig. 14D); straight and without produced inner apical lobe in female (Fig. 14E).

Distribution. Central Namibia: Windhoek to Kungveld (Fig. 16).

Type material. Holotype ♂: Damaraland, Osona, near Okahandja, VI.1911, Prof. J. W. Michaelsen; 1 paratype ♂: Farm Voigtsland, 38 km E Windhoek, 16–19.V.1911, J. W. Michaelsen. Both specimens seen by Koch (1952: 189) were not available for the present study.

Material examined. Five ♂ (dissected), 3♀ and 10 additional specimens. Sixteen in Transvaal Museum, Pretoria; 2 in Namibia State Museum, Windhoek.

Additional material: 14 Windhoek, VII.1951, Koch & Scherz; 3 Guisis 180 (farm), Windhoek, 23° 50' S, 16° 15' E, 5–7 May 1980, S. Louw & M.-L. Penrith, H-42232; 1 Gautscha Pan, Kaukau-Kungveld, IX.1951, C. Koch.

Months recorded. May, July and September.

Caenocrypticus (Caenocrypticus) kaszabi spec. nov., Figs 16, 17C,D, 18A, Plates 4C,D, 16A

Diagnosis. Very similar to *C. uncinatus* but reduced temporal lobe not visible from above. Elytra semiparallel and narrow, length:breadth ratio 65 %. Sutural profile of elytra forming a slightly sharper curve at apical declivity towards apex. Protibia in males moderately curved inwards, outer margin only slightly arcuate (Fig. 18A). Aedeagus simple, spike-like, paramere only gently arcuate. Apicale longer than basale (Fig. 17C,D). Black to reddish brown.

Description. Head slightly broader than in *C. uncinatus*, outline more angular, gena flattened between eye and more broadly truncate clypeus. Ocular angles of genae parallel, as reaching anterior margin of eyes but not reaching convexity of eye laterally. Temporal lobe reduced, leaving eye free below.

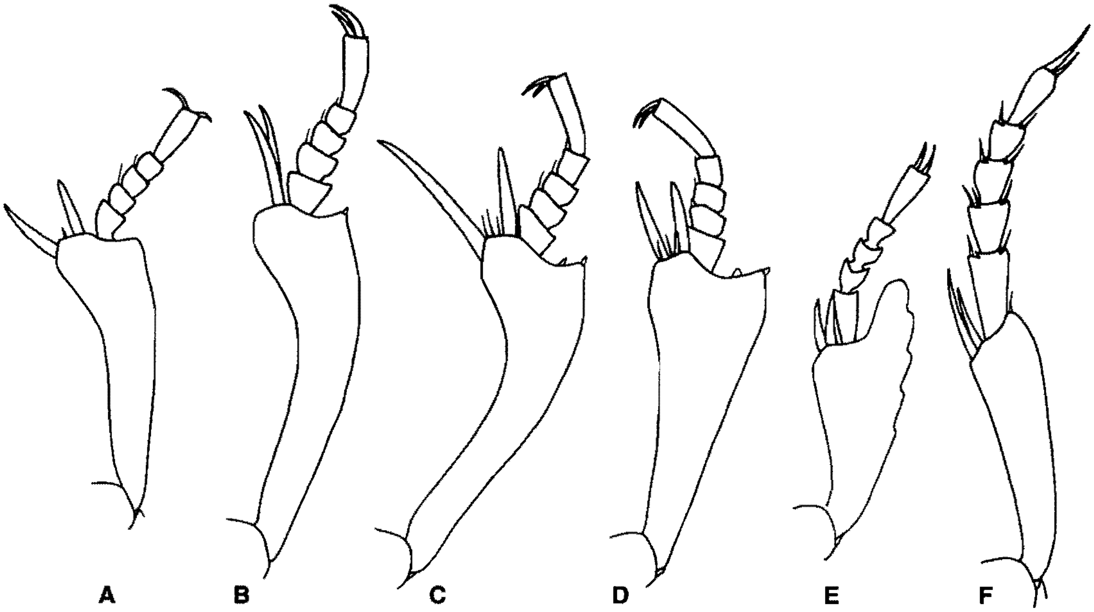

Fig. 18. Protibiae of *Caenocrypticus* species. **A**: *C. (Caenocrypticus) kaszabi* spec. nov., male; **B**: *C. (Caenocrypticus) wittmeri* spec. nov., male; **C**: *C. (Caenocrypticus) macintyrei* Koch, male; **D**: same species, female; **E**: *C. (Psammotopulus) phaleroides* Koch, male; **F**: *C. (Vernayella) pauliani* (Koch), male.

Gula with apparently functional stridulatory file (Plate 4C,D). — Elytra narrow, length:breath ratio 1,84:1,2 mm or 65 %. Lateral margins nearly parallel to each other in median section. Sutural profile gently arcuate from scutellum to apical declivity, there curving more sharply towards apex, reaching apex at angle of about 70°. — Protibia moderately curved inwards, apical portion considerably narrower than in *C. uncinatus* (Fig. 18A). — Aedeagus 0,6 mm long, of which apicale constitutes 0,32 mm, apicale thus longer than basale. Apicale 0,05 mm broad at base, spike-like, evenly and only gently arcuate, concealed penis filiform (Fig. 17C,D).

Secondary sexual dimorphism. Protibia slightly more curved inwards at apex in males than in females. Anal sternite slightly more convex longitudinally in females than in males.

Length: 2,25–3,30 mm; breath: 0,9–1,3 mm. The series from 60 km NE Gobabeb consists of generally larger specimens although the range of variation is also wide, 2,4–3,3 mm.

Distribution. Western slopes of Khomas-Hochland and the adjoining edge of the gravel plains in the central Namib. All specimens originated from the lower parts of the Us Pass and adjoining plains (Fig. 16).

Material examined. One hundred and two ♂ (13 dissected), 50♀ and 17 additional specimens. All specimens, including holotype and allotype, in Transvaal Museum, Pretoria.

Holotype ♂, allotype ♀ and 20 paratypes: S. W. Afr., Namib, Gobabeb, 60 km NE, 23° 20′ S, 15° 32′ E, 28.2.1975, baited ground-traps, 97 days, leg. Endrödy-Younga, E-Y:704. Additional paratypes: 10 same data as holotype, but 5.6.1975, traps, 94 days, E-Y:844; 3 *idem*, 28.8.1975, traps, 88 days, E-Y:882; 1 Namib, Us Pass/Park Gate, 23° 04′ S, 15° 35′ E, 5.6.1975, baited ground-traps, 88 days, leg. Endrödy-Younga, E-Y:851; 2 S. W. Afr., Namib Us Pass, 20 km fr. Park [gate], 23° 03′ S, 15° 44′ E, 15.11.1974, baited ground-traps, 70 days, leg. Endrödy-Younga, E-Y:470; 45 *idem*, 1.9.1975, traps, 75 days, E-Y:901; 1 S. W. Afr., Komashochl. (hochland), Us Pass, 42 km Park, 23° 04′ S, 15° 55′ E, 2.3.1975, baited ground-traps, 90 days, leg Endrödy-Younga, E-Y:717; 51 *idem*, traps, 75 days, 1.9.1975, E-Y:903; 2 S. W. Afr., Komahshochl., Us Pass, 44 km Park, 23° 04′ S, 15° 56′ E, 1.9.1975, baited ground-traps, 75 days, leg. Endrödy-Younga, E-Y:904; 15 S. W. Afr., Komashochl., Us Pass, 46 km Park, 23° 03′ S, 15° 58′ E, 5.6.1975, baited ground-traps, 88 days, leg. Endrödy-Younga, E-Y:857; 5 *idem*, but 1.9.1975, traps, 75 days, E-Y:905; 9 *idem*, 7.7.1978, traps (collected after) 3 years, E-Y:1474; 1 S. W. Afr., Komashochl., Farm Chausib, 23° 20′ S, 16° 05′ E, 7.11.1974, baited ground-traps, 27 days, leg. Endrödy-Younga, E-Y:450; 3 S. W. Afr., Komashochl., Farm Chanquas, 23° 04′ S, 15° 55′ E, 7.7.1978, baited ground-traps (collected after) 3 years, leg. Endrödy-Younga, E-Y:1473.

Ethoecology. All specimens were collected in pitfall traps set with different bait. All sites were on sandy soil with scattered stones that varied in abundance (Plate 16A). Trap sites on pure sand did not yield this species. Their activity seems to be triggered by rains.

Etymology. This species is named after Dr Zoltán Kaszab, late Director of the Natural History Museum, Budapest. As an outstanding specialist of Tenebrionidae he described the South American genus *Caenocrypticoides* and first drew attention to the biogeographical significance of that discovery.

Caenocrypticus (Caenocrypticus) wittmeri spec. nov., Figs 16, 17E,F, 18B

Diagnosis. Black or dark chestnut-brown, shiny with dense and uniform punctation. Elytra semiparallel and broad, length:breadth ratio 74 %. Genal angles not reaching level of eye's convexity. Protibia strongly curved inwards in males, inner spur moderately enlarged (Fig. 18B). Apicale of aedeagus shorter than basale (0,34:0,48 mm) (Fig. 17E,F). Most closely related to *C. kaszabi* and characters not repeated below are similar in both species.

Description. Head similar. — Elytra distinctly broader with a length: breadth ratio of 1,89:1,36 mm or 74 %. Lateral margins of elytra slightly more arcuate, sutural profile evenly arcuate from apical declivity to apex. — Protibia distinctly more strongly curved inwards, imaginary line between outer apical angle and outer basal angle runs in a section along longitudinal median line of tibia (Fig. 18B). — Aedeagus 0,82 mm long, of which apicale constitutes only 0,34 mm, apicale thus much shorter than basale (0,48 mm). Apicale very similar in shape (Fig. 17E,F).

Secondary sexual dimorphism. Protibia strongly curved inwards in males, only slightly arcuate in females. Anal sternite similar in both sexes.

Length: 1,68–2,05 mm; breadth: 0,72–0,95 mm.

Distribution. Central part of southern Namibia: Karasburg and vicinity of Bethanien (Fig. 16).

Material examined. Twenty-eight ♂ (3 dissected), 27♀ and 1 additional specimen. Holotype, allotype and 21 paratypes in Transvaal Museum, Pretoria; 33 paratypes in Namibia State Museum, Windhoek.

Holotype ♂, allotype ♀ and 9 paratypes: S. W. Africa: South inland, Goageb, S. Bethanien, 26° 46′ S, 17° 13′ E, 18.9.1987, dry grasses and *Galenia,* leg. Endrödy-Younga, E-Y:2506. Additional paratypes: 43 Churutabis 108 (farm), Bethanien, SE 2717 Ad, 4–12 October 1974, H-21095; 2 Galaus 6 (farm), Karasburg, SE 2717 Da, 13–17 October 1974, H-21314.

Ethoecology. This species was collected in a limited area in September and October. The series containing the holotype was collected under small stones and in sand blown into clumps of vegetation.

Etymology. The new species is named after Dr Walter Wittmer, Basel, who was my companion on the trip through Bethanien, and on many other expeditions over the past 12 years.

Caenocrypticus (Caenocrypticus) macintyrei Koch, Figs 16, 17G,H, 18C,D, Plate 16B

Caenocrypticus macintyrei Koch, 1952: 190.

Diagnosis. Protibia sexually dimorphic: strongly curved inwards in males, external margin straight in females; apex of protibia forms a large inner lobe in both sexes and with unusually large inner claws in males (Fig. 18C,D). Genal margin forms a rounded angle before reaching front margin of eye. Eye free beneath. Elytra distinctly broadened behind small humeral angles. Basale of aedeagus only slightly longer than apicale (20:17). Aedeagus filiform, apicale gently arcuate (Fig. 17G,H). Often smaller and paler in colour than *C. wittmeri.*

Redescription. Head small, less than half of thoracical breadth (45 %). Clypeus truncate and slightly emarginate. Genal margin straight or slightly emarginate in middle, curving inwards before reaching eye, resulting in a triangular gap in outline between gena and eye; posterior angle of gena reaching lateral level of eye's convexity. Eye entirely free below and not reduced anteriorly by gena. Surface densely punctate and shagreened. — Pronotum broadest in front of base, gently contracting towards basal angle; angle narrowly rounded, obtusely angular. Punctation coarser and more widely spaced than on head, shagreen fine but sharp, honeycomb-like, imparting a greasy sheen. — Elytra slightly ovate, broadest at anterior one-fifth of length, from here distinctly contracting to small humeral angles, margins almost straight in a median section. Apical declivity in lateral view evenly and flatly arcuate. Punctation shallower and more widely spaced than on pronotum, shagreen similar but somewhat less sharp, surface slightly more shiny. — Gula with apparently functional stridulatory file. Apex of ovate prosternal apophysis slightly angular. — Protibia parallel from base over two-thirds of length, from there expanding and curving inwards, inner margin more strongly arcuate than outer margin. Apical margin perpendicular in outer half, forming a sharp outer angle and drawn into a large lobe at inner half, concealing insertion of tarsus and spurs. Inner spur strongly enlarged, thicker and almost twice as long as outer spur, in fresh specimens almost as long as tarsus (Fig. 18C). — Aedeagus simple and filiform, basale moderately longer than apicale (20:17), apicale 0,34 mm long, basale 0,4 mm. Aedeagus filiform in dorsal view, tapering evenly from basale to apex; breadth at base of apicale 0,07 mm (Fig. 17G,H).

Secondary sexual dimorphism. In females, protibia evenly dilated from basal one-third of length, outer margin only slightly arcuate, almost straight, evenly arcuate inwards at inner margin. Inner apical lobe smaller; outer spur only moderately longer than inner spur (Fig. 18D). Anal sternite similar in both sexes.

Length: 2,40–2,75 mm; breadth: 1,17–1,35 mm.

Distribution. Kungveld and Hereroland in northeastern Namibia (Fig. 16).

Type material. Holotype ♂, allotype ♀; 10♂ and 6♀ paratypes: Samengeigei, NW Kalahari August 51, Koch. In Transvaal Museum, Pretoria.

Material examined. Twenty-one ♂ (11 dissected) and 17♀, including type specimens. Eighteen type specimens and 11 additional specimens in Transvaal Museum, Pretoria; 10 specimens in Namibia State Museum, Windhoek.

Additional localities: northeastern Namibia, Kungveld: 15 Botswana border at 20° 17′ S, 21° 00′ E, 29 June – 2 July 1978, pitfall traps, leg. S. Louw & M.-L. Penrith, H-36860; 1 *idem,* but at 20° 07′ S, 21° 00′ E, 1.7.1978, from grass roots, leg. Endrödy-Younga, E-Y:1456; Hereroland East: 2 Farm 855, 21° 59′ S, 20° 02′ E, 27.6.1978, ground-traps, 7 days, bait: faeces (1), banana (1), leg. Endrödy-Younga, E-Y:1446. Hereroland: 1 farm Okarukondovi, 21° 35′ S, 18° 10′ E, 4.7.1978, ground-traps, 1 night, banana bait, leg. Endrödy-Younga, E-Y:1459.

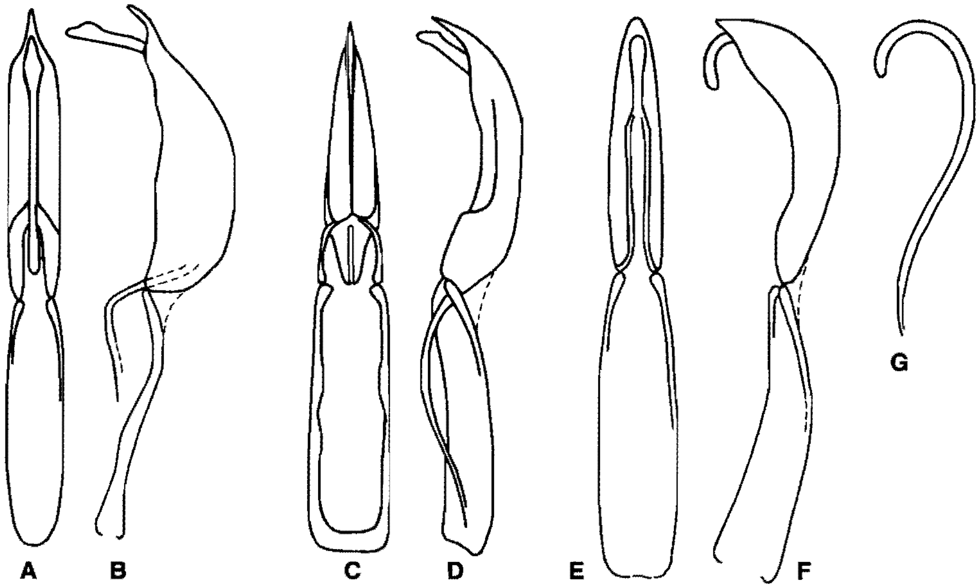

Fig. 19. Aedeagi of *Caenocrypticus (Psammotopulus)* species, alternately in dorsal and ventral views. **A–B**: *C. (P.) phaleroides* Koch; **C–D**: *C. (P.) deserticus* Koch; **E–G**: *C. (P.) klinghardtmontis* spec. nov.; **G**: retrovert penis removed from tegmen of the apicale.

Ethoecology. This species is found on red and consolidated Kalahari-type sand at the base of herbaceous plants (Plate 16B).

Subgenus *PSAMMOTOPULUS* subgen. nov.

Type species: *Caenocrypticus (Psammotopulus) penrithae* spec. nov.

Description. Eye not divided or reduced by genal margin. Anterior margin of pronotum rather deeply emarginate, anterolateral angles produced. Elytra moderately convex transversely, smooth, lateral margins clearly discernible over entire length from above (except in *C. klinghardtmontis*). Intercoxal process of mesosternum broad with truncate apex; width of process varies between species, from considerably narrower (10:15 in *C. penrithae*) to as broad as coxal cavity (*C. phaleroides*). Protibia straight, strongly dilated towards apex, apicolateral process strongly produced (Fig. 18E). Protibia rather uniform between species. Protarsus short with segments slightly longer than broad. Tarsal claws short and equal in length. Apicale of aedeagi species-specific, sickle-shaped, paramere in two species dorsoventrally deep (baggy). Anal sternite of male flat in lateral view (usual condition in genus) but distinctly convex in female (female dimorphism).

Distribution. Three species are restricted to the inland marginal dunes of the Namib Desert. The other three species inhabit barren dunes in different sections of the dune Namib, from the Skeleton Coast to the southern banks of the Orange River (Figs 20, 21, 22).

Etymology. A latinized compound noun derived from two Greek nouns, *psammos* = sand and *topos* = place (habitat) with the Latin diminutive suffix: *-ulus,* meaning 'the small inhabitant of sand'. Gender masculine.

Remarks. The gradual ultrapsammophilous adaptation in the genus, signified by the broad, digging protibia in all species with a broad anterolateral process, began with species of the subgenus *Psammotopulus.* This adaptation culminated in *C. phaleroides* that has a broadly ovate and comparatively flat body shape and mesocoxae far removed from each other, resulting in the intercoxal section being as broad as a coxal cavity. Among other characters, similar adaptations occur in the *C. (Vernayella)* species, though independently, not through *C. phaleroides* spec. nov.

Caenocrypticus (Psammotopulus) phaleroides Koch, Figs 18E, 19A,B, 20, Plates 2C, 5B, 17A,B

Caenocrypticus phaleroides Koch, 1950: 84; 1952: 191.

Diagnosis. Body, particularly elytra, unusually broad for the subgenus, length:breadth ratio 82:76 or 92 %. Pronotum broadest behind basal quarter of length, arcuately contracted anteriorly and curving into broad basal angle posteriorly. Prosternal apophysis broad, mesosternum beneath impressed; mesosternal apophysis unusually broad (Plate 5B). Apical sternite convex in lateral view in females. Protibia with long, produced, outer apical angle (Fig. 18E). Paramere of aedeagus ark-shaped with small and narrow, arcuate apical process. Yellow, dorsum with very dense and fine punctation, integument densely and sharply shagreened.

Redescription. Head deeply recessed between anterior angles of pronotum. Clypeus broadly truncate, emarginate in middle, clypeal angles broadly rounded. Head broadest at posterior genal angles, length:breadth ratio measured between here and clypeus 1:3,4. Genal angles narrowly and roundly rectangular, contracting to meet anterior margin of eye. Eye not protuberant, only flatly convex. Punctation rather

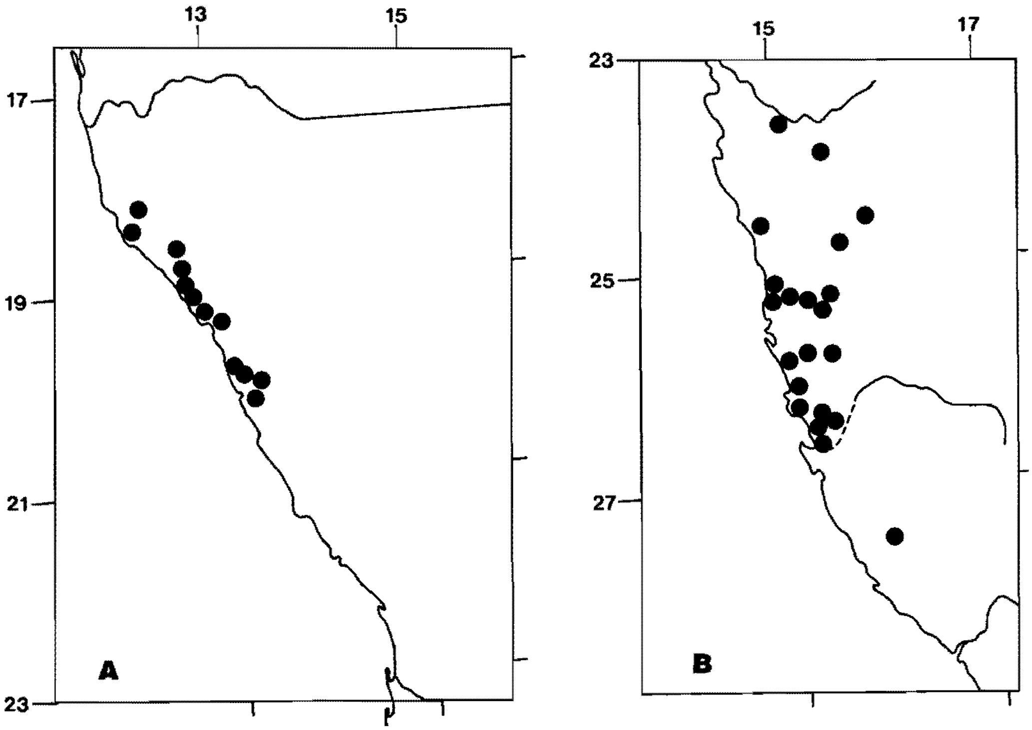

Fig. 20. Distribution of *Caenocrypticus (Psammotopulus) phaleroides* Koch in the Namib dune desert.

fine but regularly dense, punctures occasionally touching, regularly round and sharp-edged. Integument densely and sharply shagreened, providing surface with a greasy sheen. — Pronotum broad, about one-third broader than long, broadest at posterior third of length or behind, lateral margins arcuately contracted towards anterior angles, and evenly curved into broadly arcuate posterior angles. Disc moderately convex, both lateral margins clearly discernible over entire length in dorsal view. Posterior margin flatly and broadly emarginate in middle. Punctation fine and dense, punctures about as broad as intervals on middle of disc, touching or confluent in lateral third. Shagreen dense and clear, imparting an oily sheen. — Elytra very broad but variable in breadth, 89–94 % of length. Humeral angle not produced, but very finely denticulate. Broadest between anterior quarter and third of length, margins evenly arcuate. Sutural profile flatly and evenly arcuate, meeting apical margin at angle of 45°, profile occasionally slightly impressed preapically. Disc moderately convex transversely, both lateral margins clearly discernible over entire length in dorsal view. Punctation and shagreen as on pronotum. Integument transparent, revealing cellular structure of elytra beneath (even at ×63 magnification). — Gula as usual in genus with functional stridulatory file. Broad apex of prosternal apophysis drawn bilaterally into triangular processes that join the skeletal structure at an angle, enclosing procoxal cavity posteriorly; mesosternum impressed in middle, forming anteriorly sharply bordered pit. Latter structure concealed by prosternal apophysis when pronotum is bent ventrad; apophysis lacks matching structure that might act as a lock with the edge of the pit. The significance or use of this structure is unknown. Mesosternal margin between mesocoxae as broad as round mesocoxal cavities and almost as broad as in *C. (Vernayella)* spp. (Plate 5B). Intercoxal section of metasternum somewhat narrower between metacoxae. Anal sternite even, not convex in lateral view in males. — Protibia short and very broad, length:breadth ratio 0,44:0,22 (mm). Outer apical angle drawn into a large triangular process, inner angle simply rounded, anterior margin curving evenly into margin of outer process. External margin of protibia with four or five short, stout bristles originating from indentations on tibial edge (Fig. 18E). — Apicale of aedeagus much longer (0,64 mm) than basale (0,4 mm). Penis strongly arcuate dorsoventrally, sickle-shaped, apex broadly rounded. Paramere developed as a bilaterally compressed ark-shaped tegmen concealing entire penis except apex. Apex of paramere reduced to narrow apical process (Fig. 19A,B).

Secondary sexual dimorphism. Anal sternite in males flat longitudinally, strongly convex towards apex in females with a slight sagittal elevation providing a flat roof shape to apical half of that plate.

Length: 2,2–3,6 mm; breadth: 1,25–2,10 mm. Extent of size variation is unusual in the genus, with a continuous range of intermediates.

Distribution. In Namibia from the northern Namib coast, through the central dune Namib to Lüderitz, with a single locality on dunes southeast of the Klinghardt Mountain (Fig. 20).

Type material. Holotype ♂, allotype ♀ and 1 paratype: 10 m N of Lüderitz, S. Namib, 4.XII.1948, Koch & Van Son. All three specimens in Transvaal Museum, Pretoria. A fourth specimen with an identical photographic label in the Transvaal Museum was most likely overlooked by Koch and not indicated as a paratype.

Material examined. Twenty-nine ♂ (22 dissected), 27♀ and 515 additional specimens; 284 in Transvaal Museum, Pretoria (137 via Department of Zoology and Entomology, University of Pretoria), and 287 in Namibia State Museum, Windhoek.

Localities: Namibia. Northern Namib Desert, coastal belt: 326:1 Munitum Riv. at 18° 10′ S, 12° 13′ E, 10.4.1984, sand-blown hill, leg. Endrödy-Younga, E-Y:2114; 1 Cape Fria, 40 km E, 10.1965, leg. W. D. Haacke; 6 Okau, 18° 19′ S, 12° 06′ E, 17.10.1978, leg. Louw & Penrith, H-37125; 2 Rocky Point, 18° 59′ S, 12° 30′ E, 6.1951, leg. C. Koch; 1 Khumib Riv., 15 km from mouth, 18.12 Dc, 21.1.1981, leg. E. Holm; 1 Hoarusib Riv., 19.12 Ba4, 21.1.1981, leg. E. Holm; 62 Mövebaai, 19.12 Bc/d, 11–15.8.1973, H-1342; 36 Hoanib Riv., 6 km inland, 19.12 Bd, 12.8.1973, H-13447; 38 Hoanib water hole, 19.12 Bd, 27.10.1978, leg. Louw & Penrith; 80 Kharu-Gaiseb Riv., 19° 53′ S, 13° 10′ E, 4–5.8.1982, leg. Penrith & Braine, H-54235; 4 Terrace Bay, 19° 58′ S, 13° 02′ E, 7–8.4.1979, leg. Louw & Penrith, H-39055; 1 Samanab Riv., 20° 02′ S, 13° 19′ E, 26.8.1982, dunes & hummocks, leg. Endrödy-Younga, E-Y:1927; 32 *idem,* but 20° 02′ S, 13° 18′ E, 2–5.8.1982, leg. Penrith & Braine, H-54211; 9 Unjab Riv., 20° 08′ S, 13° 18′ E, 3–4.4.1979, leg. Penrith & Wharton, H-38951; 3 *idem,* but 16–27 February 1985, E. Griffin; 39 Unjab Riv., dunes, 20° 10′ S, 13° 16′ E, 5–6.8.1982, Penrith & Braine, H-54256; 13 *idem,* but 10.1965, leg. W. D. Haacke. Central Namib Desert: 285:15 Gobabeb, 8.1965, leg. C. Koch; 28 *idem,* but 9.1965; 11 *idem,* but 10.1957; 1 *idem,* but 10 km S, 3.1968, leg. E. Holm; 13 Tsondab vlei, 23° 59′ S, 15° 26′ E, 13.1.1975, dunes, leg. Endrödy-Younga, E-Y:540; 15 *idem,* but 12.1.1975, E-Y:537; 1 Meobbaai, 10 km S, 24.14 Da1, 1.1977, leg. E. Holm; 3 Sossus vlei, 20 km W, 24.15 Cc1, 1.1977, leg. E. Holm; 6 Sossus vlei, 24.15 Da4, 14.7.1975, leg. E. Holm; 13 St Francis Bay, 25.14 Bb1, 8.7.1976, leg. E. Holm; 9 *idem,* but 25.14 Dd3; 2 Diamond Area 2 at 25° 14′ S, 14° 54′ E, 22.6.1982, leg. Irish, H-53932; 2 *idem,* but 25° 20′ S, 15° 28′ E, H-53928; 50 Uri-Hauchab Mt., 10 km W, 25.15 Ac1, 1.1977, leg. Holm; 5 *idem,* but 25.15 Ac2, 6.7.1976; 1 Guinasibberg W, 25.15 Ad2, 6.7.1976, leg. E. Holm; 7 Spencer Bay, 40 km ESE, 25.15 Cc2, 1.1977, leg. E. Holm; 13 *idem,* but 70 km ESE, 25.15 Cd2; 9 Anigab dunes, 26° 18′ S, 15° 02′ E, 19.1.1974, from hummocks, leg. Endrödy-Younga, E-Y:298; 5 *idem,* but 5.10.1979, leg. E. Holm; 6 Hottentots Bay, 50 km E, 26.15 Ab4, 1.1977, leg. E. Holm; 8 *idem,* but 60 km ESE, 26.15 Ad4; 11 Coichab Pan E, 26.15 Ad3, 7.1978, leg. E. Holm; 4 Lüderitz, 24 km N, 4.12.1948, leg. C. Koch; 5 Lüderitz, 5.1963, leg. C. Koch; 6 Agatstrand, 26.15 Cc2, 12.1978, leg. E. Holm. Southern Namib Desert, inland: 1: Klinghardt Mt E, 27.15 Db2, 7.1982, leg. E. Holm.

Ethoecology. This species occurs exclusively on sand dunes in the Namib Desert, Namibia. It inhabits the soft dune sand around plants, but is not reported from barren parts on nearby dunes as, *e.g., C. (Vernayella)* spp. (Plate 17A,B). The gaps in distribution in the southern duneless part of the northern Namib and near the Klinghardt Mountain were discussed above in the section on biogeography.

Months recorded. Like most of the dune specialists of the Namib Desert, they are active virtually throughout the year. For *C. phaleroides* there are no records in February and November.

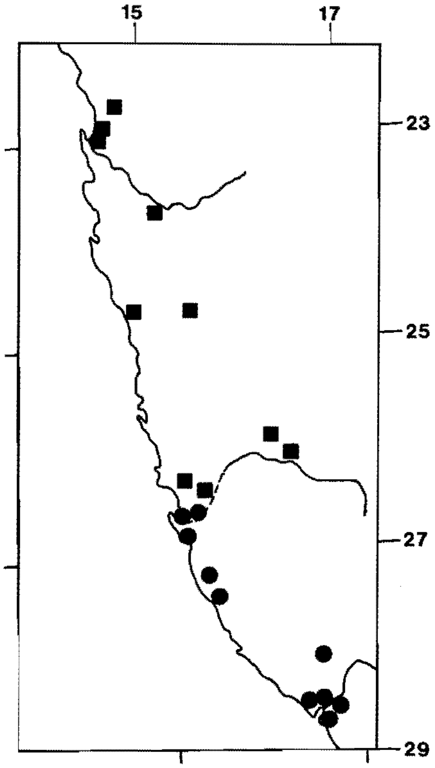

Fig. 21. Distribution of the *Caenocrypticus (Psammotopulus)* species inhabiting portions of the Namib dune desert. ■ = *C. (P.) peezi* Koch; ● = *C. (P.) deserticus* Koch.

Caenocrypticus (Psammotopulus) deserticus Koch, Figs 19C,D, 21, Plate 18A

Caenocrypticus deserticus Koch, 1950: 82; 1952: 190.

Diagnosis. Reddish brown to almost black. Protibia with large outer apical process. Body moderately broad. Intercoxal process of mesosternum in apical breadth only about half width of mesocoxal cavity (8:14), intercoxal section of metasternum somewhat broader. Prosternal apophysis elongate-ovate, apex in lateral view extended to about middle of mesosternum. Lateral margins of pronotum and elytra arcuate, dorsal outline distinctly contracting at their common base. Posterior angle of pronotum broadly rounded, posterior section of lateral margin arcuate towards it. Apical declivity of sutural profile evenly arcuate and slanting. Basale of aedeagus only slightly longer than apicale; shallowly arcuate paramere tapering into pointed apex, narrowing evenly from broad base in dorsal view; penis with short and slightly curved apex (Fig. 19C,D).

Redescription. Head narrow, clypeus emarginate, clypeal angle broader or narrowly rounded, genal margin straight, usually minutely emarginate; transverse face of genal process falling steeply to level of eye. Convexity of eyes usually not reaching breadth of genal angles laterally, rarely, however, on same lateral level. Supraorbital margin falls sharply and vertically to level of eye, but not crested. Punctation fine and dense, punctures occasionally touching but not confluent. Shagreen dense, fine and clear. — Pronotum about 1,5 times broader than long (*c.* 70:45), distinctly narrower than elytra, lateral margin of both body parts curving to their common base where the outline is distinctly contracted. Pronotum broadest at about posterior third of length, posterior part of lateral margin evenly curved into broadly rounded posterior angle (angle varies). Both sharp lateral margins discernible in dorsal view over almost entire length. Shagreen and punctation similar to that of head, but punctures slightly elongate, in some specimens longitudinally confluent on lateral portions. — Elytra broadest around anterior fifth of length, evenly arcuate to unarmed humeri and to apex. Sutural profile evenly and flatly arcuate up to apical declivity and reaching apex at angle of 50–55°. Punctation even, more widely spaced, punctures rounder than on pronotum and never touching, occasionally distinctly finer, and always so towards margins. Shagreen similar or occasionally less distinct than on pronotum. — Prosternal apophysis elongate-ovate, apical portion produced over mesosternum to about middle of latter. — Aedeagus 1,1 mm long, apicale somewhat shorter (0,5 mm) than basale (0,6 mm). Flatly arcuate paramere beaked at apex. Tip of penis slightly but evenly curved dorsad (Fig. 19C,D).

Secondary sexual dimorphism. Anal sternite in females slightly more convex longitudinally than in males.

Length: 2,5–3,1 mm; breadth: 1,22–1,70 mm.

Distribution. Southern Namib Desert in Namibia and extreme northern Richtersveld in South Africa (Fig. 21).

Type material. Holotype ♂, allotype ♀ and 12 paratypes: Bogenfels, S. Namib, 1.XII.1948, Koch/Son. Additional paratypes: 18 Lüderitz, 27.XI.1949, Koch & Eberlanz; 1 Lüderitz, S. Namib, 4.XII.1948, Koch & Van Son; 12 Grootderm, Richtersveld, 18.XI.1949, Koch; 20 Grootderm, E of Alexander Bay, C.P., 11.XII.1948, Koch/Son; 5 18 m S of Alexander Bay NW C.P., 12.XII.1948, Koch/Son. Holotype, allotype and 61 paratypes in Transvaal Museum, Pretoria. Additional paratypes: 4 in Musée Royal de l'Afrique Centrale, Tervuren; 2 in Zoologische Staatssammlung, München; 1 in South African Museum, Cape Town.

Material examined. Fifty-two ♂ (34 dissected), 46♀ and 286 additional specimens (excluding type material); 138 in Transvaal Museum, Pretoria (5 via Department of Zoology and Entomology, University of Pretoria); 232 in National Museum of Namibia, Windhoek; 18 in National Museum, Bloemfontein; 2 at University of California, Berkeley.

Additional localities: Namibia, central Namib Desert: 7 Lüderitz, 7 km E, 26° 40′ S, 15° 13′ E, 23.7.1981, sandy ground, leg. Endrödy-Younga, E-Y:1793; 30 *idem,* but leg. Penrith, H-43459; 4 Lüderitz, Agat Beach, 26.15 Cc, 6.10.1979, leg. Holm; 1, Garasplatz, 26° 41′ S, 15° 17′ E, 8.9.1985, from (under) *Stipagrostis,* leg. Endrödy-Younga, E-Y:2231. Southern Namib Desert: 2 Elisabeth Bay, 26.15 Cc, 1–2.3.1972, H-7111; 14 Pomona, 27° 13′ S, 15° 28′ E, 1–2.9.1980, leg. Louw & Penrith, H-42435; 10 *idem,* but 6.12.1948, leg. Koch & Van Son; 8 Bogenfels, 10 km E, 27° 27′ S, 15° 24′ E, 20.8.1989, shifting dunes, leg. Endrödy-Younga & Klimaszewski, E-Y:2656; 35 Bogenfels, 27.15 Ad, 28–29.2.1972, H-7096; 26 *idem,* but leg. Penrith & Louw, H-35488; 3 Obib dunes, 28° 02′ S, 16° 37′ E, 20.9.1973, grass tussocks, leg. Endrödy-Younga, E-Y:126; 10 *idem,* but H-14432; 4 *idem,* but 28–30.10.1977, leg. Penrith & Louw, H-35146; 1 Oranjemund, 10 km N, 28.16 Ad, 7.1978, leg. Holm; 1 Oranjemund, 28° 33′ S, 16° 27′ E, 9–11.9.1980, leg. Louw & Penrith, H-42594; 1 Orange Riv. N. bank, 6 km from mouth, 19.11.1980, leg. J. Irish. South Africa, Richtersveld: 21 Brandkaross, 3 km S, 28° 30′ S, 16° 39′ E, 30.9.1991, leg. Endrödy-Younga & Klimaszewski, E-Y:2814; 12 *idem,* but 5.1953, leg. Koch; 2 *idem,* but 9.9.1950, leg. Koch & Van Son; 30 Grootderm, 28° 31′ S, 16° 38′ E, 3.9.1976, leg. Endrödy-Younga, E-Y:1211; 1 *idem,* but 4–6.9.1982, leg. Irish, H-54285; 7 Beauvallon farm, 28° 33′ S, 16° 36′ E, 24.11.1975, H-32131; 52 Jakkalsputs, 28° 38′ S, 16° 54′ E, 19–21.11.1975, H-32023; 72 *idem,* but 9–11.9.1982, leg. Penrith, H-54397; 6 *idem,* but leg. Louw, NMBH-8514; 16 *idem,* but 15.9.1985, leg. Louw & Van Rensburg, NMBH-15289.

Ethoecology. *Caenocrypticus deserticus* occurs in the coastal margin of the southern Namib Desert and northern Richtersveld to the Holgat River mouth. It only enters marginal inland dunes along the Orange River. The typical habitats of the species are hummocks, around plants, and under stones on sandy soil (Plate 18A).

Months recorded. Throughout the year except January, April and June. Its absence in January is certainly accidental.

Remarks. Koch (1950) remarked that specimens from the Richtersveld (south of the Orange River) are more slender with narrower intercoxal structures and that the elytra have a more abrupt apical declivity. This variant recorded by Koch can be confirmed, but only in part. It has still not been found in the north, and is not general in the south either. There are numerous typical specimens from the south too.

Caenocrypticus (Psammotopulus) klinghardtmontis spec. nov., Figs 19E,F,G, 22, Plate 18B

Diagnosis. Externally similar to *C. deserticus.* Only the apical declivity of the elytra and characteristics of the aedeagus are different. In all other characters, *C. deserticus* is comparable to *C. klinghardtmontis.*

Description. Sutural profile flatly arcuate up to apical declivity where it curves steeply ventrad, reaching apex at angle of 70°. First metatarsomere much shorter than following segments together excluding claws (13:17). — Aedeagus 0,9 mm long, apicale and basale subequal in length (0,44:0,46 mm). Paramere of apicale baggy, edges closed but not fused on dorsal side, enclosing most of penis. Penis in lateral view hook-shaped with apical portion evenly curved retrovert by 180°. When enclosed in paramere, only retrovert apex exposed (Fig. 19E,F,G). All specimens light reddish brown.

Secondary sexual dimorphism. Anal sternite slightly more convex longitudinally in females.

Length: 2,15–2,90 mm; breadth: 1,1–1,5 mm.

Distribution. Klinghardt Mountains in hinterland of the southern Namib Desert in Namibia (Fig. 22).

Material examined. Forty-two ♂ (29 dissected), 19♀ and 75 additional specimens. Holotype, allotype and 80 paratypes in

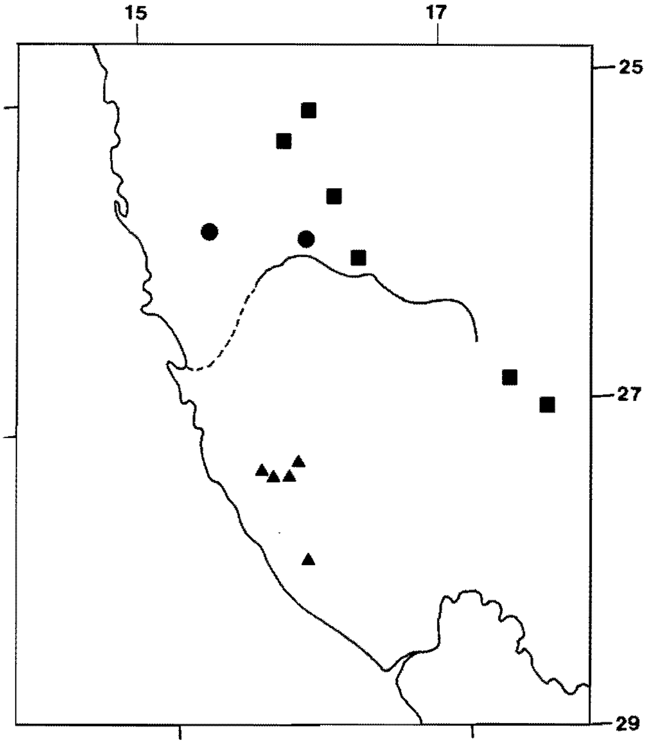

Fig. 22. Distribution of the *Caenocrypticus (Psammotopulus)* species inhabiting marginal dunes of the Namib Desert. ■ = *C. (P.) holmi* spec. nov.; ● = *C. (P.) penrithae* spec. nov.; ▲ = *C. (P.) klinghardtmontis* spec. nov.

Transvaal Museum, Pretoria (13 via Department of Zoology and Entomology, University of Pretoria); 54 paratypes in Namibia State Museum, Windhoek.

Holotype ♂, allotype ♀ and 9 paratypes: S. W. Afr., Klinghardt Mt., 27° 18′ S, 15° 42′ E, 24.7.1981, dunes & humm. (-ocks), day, leg. Endrödy-Younga, E-Y:1796. Additional paratypes: 24 as holotype, but 22.8.1989, hummocks and stones, E-Y:2661; 12 *idem,* but Se 27.15 Bd, 7.1978, leg. E. Holm; 14 *idem,* but 27° 20′ S, 15° 45′ E, 3–6 September 1980, S. Louw & M.-L. Penrith, H-42468; 1 Klinghardt Mt NE, Se 27.15 Bb2, 1.1983, leg. E. Holm; 8 Sargdeckel, Klinghardt Mts., SE 27.15 Bc, Diamond Area 1, 3–6 September 1980, S. Louw & M.-L. Penrith, H-42468; 51 Heioab, SE 27.16 Ac, Diamond Area 1, 22–25 October 1977, leg. M.-L. Penrith & S. Louw, H-35028; 14 paratypes with small label marked 'B' in this series was later erroneously labelled as: Pomona, S. Namib, 6.XII.1948, Koch & Van Son; 1 Boegoeberg, 27° 54′ S, 15° 56′ E; Diamond area 1, 20–21 August 1983, Irish & Griffin, H-56781.

Ethoecology. All specimens with site information were collected in valleys of the Klinghardt Mountains at medium altitudes. They live in soft, windblown sand around the stems of plants (Plate 18B).

Months recorded. July to October.

Remarks. There can be no doubt that the 'Pomona' labels of the 'B' specimens represent an error. The same label appears on a series of *C. deserticus,* the only species collected repeatedly at Pomona. Those specimens of the series that received the additional Pomona label have also been labelled by Koch as *C. deserticus.*

Etymology. Named after the Klinghardt Mountains on the inland margins of the southern Namib Desert, the only area where the new species occurs.

Caenocrypticus (Psammotopulus) peezi Koch, Figs 21, 23A,B, Plate 19A,B

Caenocrypticus peezi Koch, 1958: 128.

Diagnosis. Consistently light reddish brown to reddish yellow. Posterior angle of pronotum narrowly rounded. Lateral margin of pronotum straight and parallel in posterior half or two-fifths. Dorsal outline only slightly contracted between pronotum and elytra. Apical declivity of elytra steep. Paramere of aedeagus narrow, sickle-shaped, with slight apical emargination; wedge-shaped in dorsal view. Penis evenly broad with broadly rounded apex (Fig. 23A,B). Characters not repeated below are similar to those of *C. deserticus.*

Redescription. Posterior lateral angle of pronotum distinctly angular with narrowly rounded apex, lateral margin in semilateral view straight, not curving towards posterior angle. Margins in dorsal view straight and parallel in posterior half or two-fifths, occasionally slightly broader in middle and contracting in a straight line to base. Punctation slightly coarser and more widely spaced. — Elytra in cranial or caudal view flattened in middle with more arcuate lateral portions. Shape in dorsal view markedly variable (*cf. C. deserticus*), but always somewhat narrower with less arcuate lateral margins. Nevertheless, proportions and shape are only diagnostic between extreme specimens of both species. Dorsal outline of body only slightly contracted between pronotum and elytra. Sutural profile not quite evenly arcuate at apical declivity, making a slight but distinct curve preapically, becoming steep and reaching apex at angle of 60°. — First metatarsomere short compared to metatibia (12,5:28), or to combined length of rest of segments (12,5:17,5). — Aedeagus 1,1 mm long, proportions of apicale and basale as in *C. deserticus* (0,6:0,5 mm). Paramere sickle-shaped, only very finely emarginate preapically; in dorsal view wedge-shaped, tapering evenly from broad base to pointed apex. Penis evenly arcuate and evenly broad in lateral view, apex broadly rounded without an apical nick (Fig. 23A,B).

Secondary sexual dimorphism. Anal sternite in males flat in lateral view, in females also slightly convex, margins not curving dorsad at apex.

Length: 2,4–3,5 mm; breadth: 1,15–1,60 mm.

Distribution. Central Namib Desert, from the Swakopmund dunes southwards but not reaching Lüderitz (Fig. 21).

Type material. Lectotype ♂ (here designated) and 43 paralectotypes (labelled as paratypes): Walvisbaai, VII.1954, Vernay - Tvl. Mus. Expedition (leg. C. Koch).

Material examined. Thirty-three ♂ (23 dissected) 35♀ and 197 additional specimens (including type series). Lectotype, 43

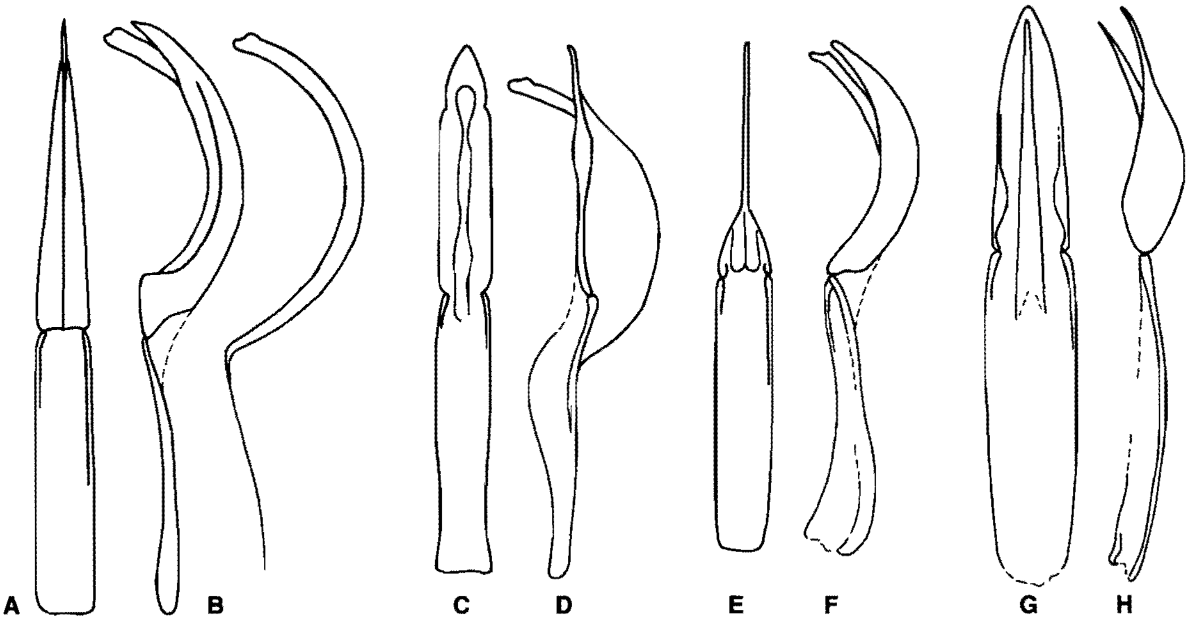

Fig. 23. Aedeagi of *Caenocrypticus* species, alternately in dorsal and lateral views. **A–B**: *C. (Psammotopulus) peezi* Koch; **C–D**: *C. (P.) penrithae* spec. nov.; **E–F**: *C. (P.) holmi* spec. nov.; **G–H**: *C. (Vernayella) pauliani* (Koch).

paralectotypes and 172 specimens in Transvaal Museum, Pretoria (16 via Department of Zoology and Entomology, University of Pretoria); 49 specimens in Namibia State Museum, Windhoek; 2 at University of California, Berkeley.

Additional localities: 4 Swakopmund, 22° 40′ S, 14° 31′ E, 29.4–2.5.1980, leg. S. Louw & M.-L. Penrith, H-41997; 44 Walvisbaai (type series); 4 Kuiseb delta, SE 23.14 Ba, 9–16.8.1976, leg. S. Louw & M.-L. Penrith, H-33231; 1 *idem*, but 29.3–1.4.1977, H-34223; 56 Gobabeb, leg. C. Koch; 1 *idem*, but 15.6–20.7.1979, leg. Wharton, H-40598; 81 Sossus vlei, 24° 40′ S, 15° 24′ E, 14.8.1989, dunes, day, leg. Endrödy-Younga & Klimaszewski, E-Y:2650; 10 *idem*, but 10.1957, leg. C. Koch; 10 *idem*, but SE 24.15 Cb3, 4.1979, leg. E. Holm; 15 *idem*, but 4–5.7.1979 leg. S. Louw & M.-L. Penrith, H-39240; 1 Witteberg SE 24.15 Cd1, 22.6.1979, leg. E. Holm; 1 Koichab Pan E, SE 26.15 Ad3, 7.1978, leg. E. Holm; 2 Uri-Hauchab Mt, SE 25.15Ac, 10.7.1980, leg. E. Holm; 2 *idem*, but 1.1977, leg. E. Holm & C. Scholtz; 3 Kanaän 104 (farm), SE 25.16 Cc, 22–27.1.1976, leg. S. Louw & M.-L. Penrith, H-33056 (only *C. peezi*); 13 *idem*, but 25.4–2.5.1977, H-34794 (together with *C. penrithae*); 2 *idem*, but 22–27.6.1976, H-33055 (together with *C. penrithae*); 13 Excelsior 59 (farm), SE 26.16 Ab, 1–4.7.1979, leg. S. Louw & M. L. Penrith, H-39196.

Ethoecology. *Caenocrypticus peezi* is a true dune dweller where it is found at the base of plants. Surface activity of adults is nocturnal. Most of the known localities are on the northern and eastern margins of the central dune Namib, also penetrating the interior (Sossusvlei, Koichab Pan, Uri-Hauchab) where some vegetation is always present (Plate 19A,B).

Months recorded. As is characteristic for the Namib dune biome, adults can be found in variable densities virtually throughout the year. The absence of records for *C. peezi* in February, March, September, November and December is probably coincidental.

Caenocrypticus (Psammotopulus) penrithae spec. nov., Figs 22, 23C,D, Plate 19B

Diagnosis. Outer apical process of protibia produced to form a large forward-pointing process. Pronotum broadest in front of posterior angle; latter more or less narrowly rounded, not sharply angled. Sutural section of elytra in cranial view slightly convex, not deplanate. Apical declivity of elytra even and less steep than in *C. holmi*. Paramere of aedeagus deeply ark-shaped in lateral view (Fig. 23C,D). Externally very similar to *C. holmi* and characters not repeated below are similar in both species.

Description. Apical declivity of elytra less steep and reaching apex at angle of about 60°. Dorsum of elytra in cranial view slightly arcuate, not flatly deplanate. — Aedeagus 1,00–1,05 mm long, apicale much longer than basale (3:2). Penis evenly and strongly arcuate, tapering evenly from base to apex; apex evenly rounded or with a tiny dilation. Paramere as in *C. phaleroides*, deeply ark-shaped tegmen concealing penis except apical portion. Apex of paramere less sharply pointed than in *C. phaleroides* (Fig. 23C,D).

Secondary sexual dimorphism. Anal sternite in males almost completely flat in lateral view, distinctly convex with dorsad-curving margins, particularly apically in females. In *C. peezi*, which also occurs at Kanaän, this dimorphism is less pronounced.

Length: 2,5–3,5 mm; breadth: 1,25–1,74 mm.

Distribution. Eastern margin of the central Namib dune desert, where it is known only from the farm Kanaän (Fig. 22).

Material examined. Sixty ♂ (19 dissected), 134♀ and two additional specimens. Holotype ♂, allotype ♀ and 73 paratypes in Transvaal Museum, Pretoria; 101 paratypes in Namibia

State Museum, Windhoek.

Holotype ♂, allotype ♀ and 11 paratypes: S. W. Afr., Namib des., Namtib dunes (on farm Kanaän), 25° 58′ S, 16° 02′ E, 8.8.1989, red dunes, night, leg. Endrödy-Younga & Klimaszewski, E-Y:2641. Additional paratypes: 31 as holotype but 7.8.1989, E-Y:2636; 3 Kanaän 104 (farm), SE 2516 Cc, Lüderitz (district), 22–27 June 1976, S. Louw & M.-L. Penrith H-33055; 43 Kanaän, dunes at 25° 58′ S, 16° 02.5′ E, Lüderitz, 21 October 1976, H-33322; 56 Dunes SW of Kanaän, SE 2516 Cc, Lüderitz, 2 May 1977, M.-L. Penrith & S. Louw, H-34731; 21 Kanaän 104, SE 2516 Cc, 25 April – 2 May 1977, M.-L. Penrith & S. Louw, H-34794; 20 Dunes SW Kanaän, 25° 58′ S, 16° 02,5′ E, Diamond Area 2, 19 June 1977, M.-L. Penrith & S. Louw, H-35340; 9 *idem*, but 6 Aug. 1977, M. J. & M.-L. Penrith & J. U. M. Jarvis, H-35393.

Ethoecology. This species occurs on a small group of red dunes on the eastern margin of the Namib dune desert. The dunes are moderately high, occasionally with patchy vegetation. The beetles were collected around plants and were active on the surface at night (Plate 19B).

Months recorded. April, May, June, August and October. Adults are presumably present throughout the year.

Remarks. On the dunes at Kanaän, *C. peezi* and *C. penrithae* occur together, and were even found in the same samples (Penrith H-33055 and H-34794). However, while *C. peezi* occurs widely in the central Namib dune systems, *C. penrithae* is apparently endemic to the Kanaän dunes. External separation of these two partly sympatric species is difficult. A third externally similar species, *C. holmi*, does not occur on the main dune systems but is restricted to soft sandy areas in the hinterland.

Etymology. The species is named in honour of my former colleague and frequent companion on field trips, the renowned specialist on Tenebrionidae, Dr Mary-Louise Penrith.

Caenocrypticus (Psammotopulus) holmi spec. nov., Figs 22, 23E,F

Diagnosis. Very similar to *C. deserticus*. It differs in the angular posterior lateral angle of pronotum, less contracted outline at the common base of pronotum and elytra, and steeper apical declivity of the latter. From both *C. penrithae* and *C. peezi* it can only be positively separated by the shape of the aedeagus. Characters not mentioned below are similar to those of *C. deserticus.*

Description. Pronotum broadest near posterior angles slightly contracting forward, lateral margin straight or almost straight in posterior section. Posterolateral angle forming a distinctly obtuse angle with narrowly rounded apex. — Elytra not much broader than pronotum, dorsal outline less distinctly contracted at its common base with pronotum. Apical declivity steeper, reaching apex at angle of 70°. Dorsum of elytra distinctly deplanate in cranial view. — Aedeagus 1,0 mm long, apicale slightly longer than basale (27:25). Paramere flat, compressed bilaterally in dorsal view, blade-like from behind its broad base; in lateral view rather broad, tapering evenly to sharply pointed apex, without a preapical emargination on inner edge. Penis evenly and moderately arcuate, very narrow at base in lateral view, then dilated to slight and even preapical constriction (Fig. 23E,F).

Secondary sexual dimorphism. Anal sternite in males only slightly convex transversely, in females more convex, particularly at base of plate, margin not curving dorsad apically as in *C. penrithae;* in lateral view straight from middle towards apical margin.

Length: 2,5–3,4 mm; breadth: 1,4–1,7 mm.

Distribution. In Namibia on the escarpments and highlands east of the central and southern Namib Desert (Fig. 22).

Material examined. Sixty ♂ (32 dissected) 49♀ and 171 additional specimens. Holotype, allotype and 78 paratypes in Transvaal Museum, Pretoria; 202 paratypes in Namibia State Museum, Windhoek.

Holotype ♂, allotype ♀ and 7 paratypes: S. W. Afr., c. Namib des., Wissenborn farm (hills E from farmstead), 26° 03′ S, 16° 24′ E, 9.8.1989, general collecting, leg. Endrödy-Younga & Klimaszewski, E-Y:2643. Additional paratypes: 48 Suiderkruis on Nubib 42 (farm), Maltahöhe (district), SE 25.16 Aa, 4 July 1979, S. Louw & M.-L. Penrith, H-39212; 51 Gorrasis 99, Lüderitz, SE 25.15 Bd, 25–31 Jan. 1974, H-17127; 13 *idem*, but 12–15 Feb. 1973, H-1165; 25 Spes Bona 62, Lüderitz, SE 25.16 Ca/b, 31 October 1977, red sand dunes, leg. S. Louw & M.-L. Penrith, H-35508; 69 Sandverhaar 80, Bethanien, SE 26.17 Cd, 21–22 October 1976, S. Louw & M.-L. Penrith, H-33477; 39 *idem*, but 3 May 1977, H-34571; 28 Vogelstrausskluft 87, Bethanien, SE 2717 Ba, 24–29 Sept. 1974, H-20660.

Ethoecology. The species occurs on plains or dune sand accumulations on the escarpments and highlands bordering the dune Namib, but it has not been collected on the Namib plains or inselbergs.

Months recorded. January, February, May and July to October.

Etymology. This species is named in honour of my friend and colleague Prof. Eric Holm, who is one of the enthusiastic researchers of the Namib coleopterous fauna.

Subgenus *VERNAYELLA* Koch stat. nov.

Vernayella Koch, 1958: 129; 1962: 153.

Type species: *Vernayella noctivaga* Koch (by original designation)

Redescription. Medium-sized to large species for tribe. Pale yellow to dark reddish brown. Eyes immarginate laterally. Elytra moderately convex transversely, sharp lateral margins readily discernible over entire length in dorsal view; at least apical portion of margin serrate or denticulate (Plate 11A,B). Mesosternal process broader than coxal cavity, broadly truncate behind (Plate 5C). Mesocoxae further apart than metacoxae. Antennae elongate, extending beyond posterior angle of pronotum; funicular segments twice as long as broad, or longer. Three or four apical segments distinctly broadened.

Protibia straight, similar in all species, evenly dilated from base to apex, apicolateral angle produced, apical margin transversely truncate. Protarsus elongate, all segments longer than broad. Claws of all tarsi long and thin, unequal in length, moderately arcuate (Fig. 18F). Aedeagi simple and similar in all species (Fig. 23G,H). No secondary sexual dimorphism.

Distribution. Sand dune areas of the central and northern Namib Desert, absent from southern Namib (Figs 24–27).

Remarks. All species are ultrapsammophilous, inhabiting unvegetated dunes. The derivation of the lineage from the ancestral stock of *Psammotopulus* is indicated by a synapomorphy, the produced apicolateral process of the protibia.

Caenocrypticus (Vernayella) noctivagus (Koch) comb. nov., Fig. 24, Plates 2D, 20A

Vernayella noctivaga Koch, 1958: 130; 1962: 156.

Diagnosis. Largest species in genus. Dark reddish brown, convex and shiny. Body broadest where pronotum and base of elytra meet, these structures equal in breadth, outline of body not contracted here. Lateral margins of pronotum evenly arcuate towards narrowly rounded anterior angle. Collar emargination of pronotum shallow, disc about 3,5 times longer behind. Metasternum coarsely punctate.

Redescription. Head relatively small, about 2,5 times narrower than pronotum. Clypeus straight, truncate, finely edged. Genal angle obtuse and rounded. Vertex coarsely punctate with narrow intervals, becoming sharply crested towards clypeus; clypeus not granulate. — Pronotum large and long compared to elytral length (7:12). Lateral margins evenly and arcuately contracted towards anterior angles, not contracted in front of base (not bell-shaped). Anterior angle triangular, collar emargination shallow, disc behind 3,5 times longer. Disc, except narrow posterior margin, coarsely punctate, punctures deep and round. Anterior and lateral margins finely edged. Lateral margins not setose. Pronotum exactly as broad at its base as elytra between humeri, lateral outline not contracted but broadest at that point. — Elytra about one-tenth longer than broad, markedly convex transversely in posthumeral section, sharp but fine lateral margins both just discernible in dorsal view. Elytra broadest at humeri, lateral margins first contracting in a straight line, evenly arcuate to obtusely angled apex from behind mid-length (Plate 2D). Sutural profile highest behind scutellum, then rather flatly arcuate to apex; arc usually slightly flattened in middle, but in some specimens evenly arcuate. Sutural profile reaching apex at angle of about 60°. Lateral margins in fresh specimens provided with short and stiff setae that are shorter than distance between them; in most specimens these setae are worn off. Punctation at basal half similar to that on pronotal disc, but punctures more widely spaced. Punctures becoming gradually smaller from middle of length, gradually transforming into file-punctures, then into small, sharp granules at apex. Integument densely shagreened, giving surface a distinct greasy sheen. Slightly elevated and smoother basal margin complete and largely concealed by margin of pronotum. — Scutellum marked only by indistinct sutures, narrowly triangular, broadening in concave lines to baseline of elytra, occasionally completely concealed under margin of pronotum. — Prosternum convex, mid-section with prosternal apophysis more elevated than in all other species of genus. Prosternal apophysis broadens evenly between coxae, posterior lateral corners rounded, apex flatly arcuate. Episternal suture distinct and incised, particularly at both ends. Punctation coarse and dense, continuing over and beyond episternal suture. Punctures large and flat with sharp edges, occasionally touching, laterally coalescent. Punctures microscopically setose. Intercoxal process of first sternite broadest among *C. (Vernayella)* spp., 70 % of mesocoxal distance. Punctation of meso- and metasternum similar to that of prosternum, punctures gradually smaller and denser from first sternite. Microscopic setae emerge from anterior inner margin of punctures, as short as diameter of punctures. Shagreen of integument more sharply incised than on dorsum.

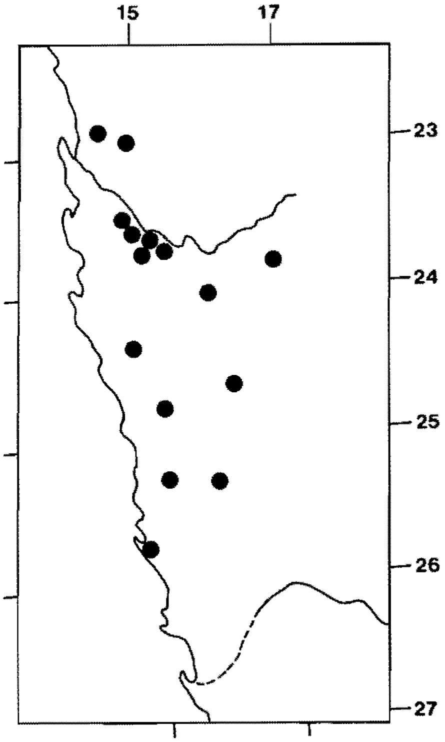

Fig. 24. Distribution of *Caenocrypticus (Vernayella) noctivagus* (Koch) in the central Namib dune desert.

Length: 3,6–5,0 mm; breadth: 2,15–3,15 mm.

Distribution. Northern half of the central dune Namib, between the Walvis Bay/Swakopmund dunes and Sossusvlei (Fig. 24).

Type material. Holotype ♂, allotype ♀ (female sex not verified): Bayo Tigres, S. W. Ang(ola), VI.1954, Vernay - Tvl. Mus. Expedition. Both in Transvaal Museum, Pretoria.

Material examined. Nineteen ♂ (10 dissected), 19♀ and 468 additional specimens; 440 specimens including the two types in Transvaal Museum, Pretoria (238 via Namib Desert Research Station; 33 via Department of Zoology and Entomology, University of Pretoria); 6 in National Collection of Insects, Pretoria; 3 in Namibia State Museum, Windhoek.

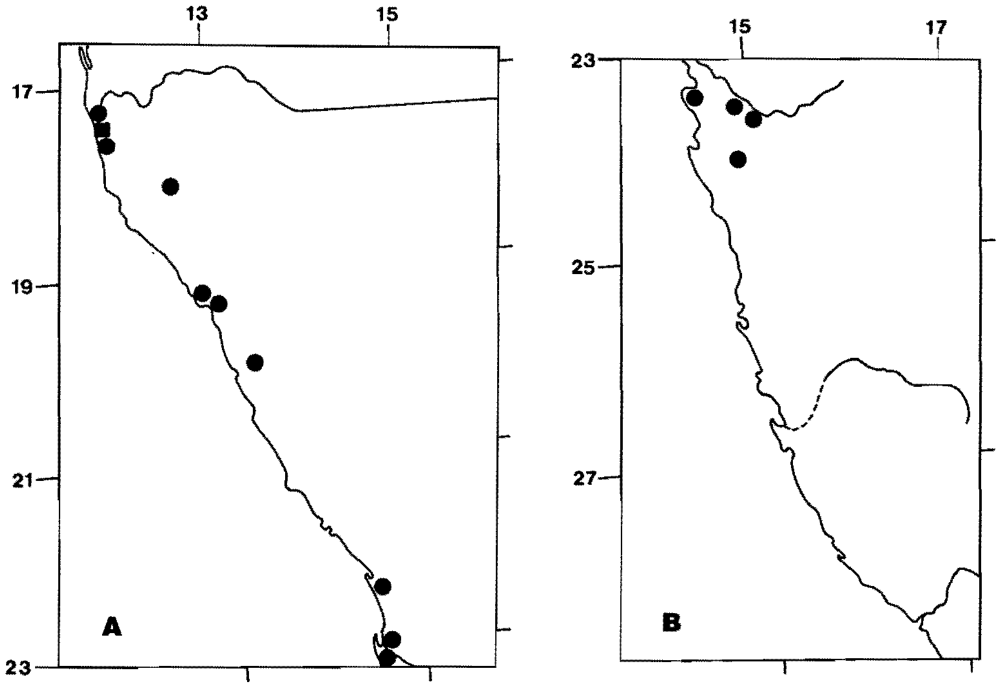

Fig. 25. Distribution of *Caenocrypticus (Vernayella)* species in the central and northern Namib dune desert. ● = *C. (V.) ephialtes* (Koch); ■ = *C. (V.) serratus* spec. nov.

The locality of the type specimens is almost certainly erroneous. This species has not been collected in the past forty years, neither in southern Angola nor anywhere in the northern Namib. Dr C. Koch collected these specimens on the same expedition when he collected *C (V.) ephialtes* on the Gobabeb dunes, where both species are sympatric. It is suspected that the locality of the sample with *C. (V.) noctivagus* might have been erroneously noted.

Additional localities: 9 Swakopmund, horizontal marginal dunes (between Swakopmund and Walvis Bay), January 1971. O. & L. Prozesky; 1 *idem*, but December 1950, E. R. Scherz; 20 Walvis Bay (dunes), X.1957, C. Koch; 2 *idem*, but Dune 7 (further inland), 17.IV.1979, E. Holm; 21 Gobabeb dunes, 23° 34′ S, 15° 03′ E, 2.11.1974, ground-traps, leg. Endrödy-Younga, E-Y:444; 160, *idem* but trapped on 18 occasions between 29 July and 1 October 1965 (Koch & Holm); 166 *idem*, but dunes nos. 1 to 5 at: 23° 37′ S, 15° 01′ E; 23° 35′ S, 14° 49′ E; 23° 35′ S, 14° 48′ E; 23° 35′ S, 14° 47′ E and 23° 35′ S, 14° 46′ E respectively, trapped on five occasions between 7 June and 21 October 1978, leg. M. Seely; 5 *idem*, but 22.8.1982, leg. Endrödy-Younga, E-Y:1919; 2 *idem*, but 26–28.VI.1975, M.-L. Penrith, H-31713; 11 Gobabeb, 18 km S, III.1968, E. Holm; 1 Homeb, 13.II.1974, leg. Irwin, H-18542; 54 Natab, dunes nos. 1 to 5, at: 23° 38′ S, 15° 02′ E; 23° 38′ S, 15° 04′ E; 23° 38′ S, 15° 05′ E; 23° 38′ S, 15° 05′ E and 23° 38′ S, 15° 06′ E respectively, trapped on 5 occasions between 5 August and 10 October 1978, leg. M. Seely; 9 Ururas, 50 km SSE, SE 23.15 Db, 15.X.1979, leg. Holm & Scholtz; 11 *idem*, but 90 km SSE, SE 24.14 Bd, 14.X.1979, leg. Holm & Scholtz; 1 Tsondab vlei, on dunes, 23° 59′ S, 15° 26′ E, 12.1.1975; leg. Endrödy-Younga, E-Y:537; 5 Sossus vlei, at SE 24.15 Da3, 14.VII.1975; 4 *idem*, but at 24.15 Cc1, January 1977, leg. Holm & Scholtz; 2 Guinasibberg, at 25.15 Ac1, January 1977; 5 *idem*, but at 25.15 Ad2, 6.7.1976; 1 Spencer Bay Water, 25° 47′ S, 14° 54′ E, on dunes, 14.1.1974, leg. Endrödy-Younga, E-Y:286.

Ethoecology. The species is nocturnal and lives in the main dune systems of the central Namib Desert. It inhabits both inland and coastal dunes, but not coastal hummocks. The larvae develop in pads of accumulated vegetation debris at the foot of dunes (Plate 20A).

Months recorded. Specimens were collected throughout the year.

Caenocrypticus (Vernayella) ephialtes (Koch) comb. nov., Fig. 25, Plates 15B, 17A, 20B

Vernayella ephialtes Koch 1958: 132; 1962: 156.

Diagnosis. Small to medium-sized in genus. Yellow or pale brown, base of elytra with large triangular hyaline area. Moderately convex, outline of body contracted between pronotum and elytra, broadest at anterior quarter of elytra. Pronotum semiparallel behind middle, anterior angle lobiform and broadly rounded, setation of lateral margins very short. Episternal suture of prosternum oblique. Denticulation of lateral margin of elytra very fine, well spaced, denser only before apex. Prosternal apophysis broadens towards apex, posterior corners angular, posterior margin emarginate.

Redescription. Clypeus of head truncate or slightly emarginate, edge smooth. — Pronotum moderately convex transversely, anterior emargination deep, disc behind only about twice as long. Lateral margins diverging only slightly behind mid-length, margins even or contracting slightly in front of posterior angle; margins moderately arcuate from middle to anterior angle. Anterior angles lobiform and broadly rounded. A broad submarginal area usually bilaterally deplanate or slightly depressed, only occasionally evenly curved. Punctation of disc distinct, well spaced, intervals 2–4 times as broad as diameter of punctures, laterally moderately denser. Setation of lateral margins dense and very short. Integument finely shagreened. — Elytra considerably less convex transversely than in *C. (V.) pauliani*, more broadly ovate, broadest at anterior quarter of length. Punctation denser anteriorly than on pronotum, becoming very fine and well-spaced tubercles at about posterior third. Punctures and tubercles without microscopic setae. Integument finely shagreened. Lateral margin smooth up to or behind posterior third where small and spaced denticulation appears, becoming denser at apex. Lateral setation much longer than on pronotum. Triangular basal hyaline area always present but often not contrasting in colour. — Prosternum moderately convex, episternal suture very fine. Prosternal apophysis broadens towards apex, apicolateral corners angular, apical margin truncate or slightly emarginate. Punctation rather deep but well spaced, only a few indistinct punctures on episternum; shagreen as on dorsum. Punctures without setae. Intercoxal process of first stemite narrow, as in *C. (V.) pauliani*.

Length: 2,8–4,8 mm; breadth: 1,45–2,80 mm.

Distribution. In two isolated areas in Namibia: in the Kuiseb basin and in the northern Namib coastal dunes (Fig. 25).

Type material. Holotype, unsexed: Walvis Bay, VII.1954, Vernay - Tvl. Mus. Expedition (leg. C. Koch) in Transvaal Museum, Pretoria.

Material examined. Thirteen ♂ (all dissected), 23♀ and 190 additional specimens; 96 in Transvaal Museum, Pretoria; 123 in Namibia State Museum, Windhoek; 5 in National Collection of Insects, Pretoria; 2 at University of California, Berkeley.

Additional localities: 9 Bosluisbaai, 3 km E, 17° 23′ S, 11° 47′ E, 2.2.1982, Irish, H-50884; 1 Kunene River, 45 km S, 17° 40′ S, 11° 45′ E, 18.10.1978, Louw & Penrith, H-37130; 48 Hoarusib River, 18° 03′ S, 12° 36′ E, 13.4.1987, barchan dunes, night, Endrödy-Younga, E-Y:2120; 45 Mövebaai, 19° 22′ S, 12° 42′ E, 28.10.1978, Louw & Penrith, H-37188; 6 Hoanib River, 19° 27′ S, 12° 52° E, 5.4.1979, Louw & Wharton, H-39012; 1 Samanab River, 20° 02′ S, 13° 18′ E, 3.8.1982, Penrith & Braine, H-54212; 8 Swakopmund, 22° 20′ S, 14° 31′ E, 27.5.1972, H-8572; 12 *idem* but 2.5.1980, Louw & Penrith, H-41995; 6 Kuiseb delta, 23° 07′ S, 14° 24′ E, Louw and Penrith, H-33233; 31 Rooibank, 23° 09′ S, 14° 39′ E, May 1959, Koch; 5 *idem* but 9.7.1975, Holm; 8 Sandwich Harbour, 23° 19′ S, 14° 30′ E, 16.8.1976, Louw & Penrith, H-33296; 4 *idem* but May 1959, Koch; 8 Gobabeb, 23° 34′ S, 15° 03′ E, trapped on six occasions between June and 19 September 1965, Koch & Holm; 1 *idem* but 22.8.1982, leg. Endrödy-Younga, E-Y:1919; 2 *idem* but November 1968, Schulze; 3 *idem*, but dune no. 2, 23° 35′ S, 14° 49′ E, 7.6.1978, Seely; 5 Ururas, 90 km S, 24° 03′ S, 14° 50′ E, 14.10.1979, Holm & Scholtz.

Ethoecology. This species predominantly inhabits coastal dunes, but is occasionally found on inland dunes (Gobabeb) in small numbers. It is nocturnal and lives at the foot of unvegetated dunes (Plates 15B, 17A,B, 20B).

Months recorded. Active throughout the year but has not been recorded in December, January and March.

Caenocrypticus (Vernayella) kochi spec. nov., Fig. 27, Plate 21A

Diagnosis. Yellow or light brown, usually with a triangular hyaline area at base of elytra. Transversely more convex and dorsum less glossy than in *C. (V.) pauliani*. Clypeus emarginate. Pronotum less bell-shaped, lateral margin finely and densely setose. Prosternum and prosternal apophysis with long and erect setae (unique character in genus). Ventral punctures with microscopic setae. Characters not repeated below are similar to those of *C. (V.) pauliani*.

Description. Clypeus of head distinctly and broadly emarginate in middle, edge not granular. — Pronotum slightly more convex transversely. Anterior (collar) emargination shallower, disc behind three times longer; anterolateral angles more narrowly rounded. Lateral setation much shorter and denser. Punctation of disc considerably denser but not coarser. Integument more strongly shagreened, sheen distinctly greasy in appearance. — Punctation and granulation of elytra denser, punctures of basal portion carry a fine papilla at anterior margin of each puncture and a microscopic bristle; bristles also emerge from granules on posterior part of elytra. Serration of lateral margins in density matching the punctation/granulation of disc. Marginal setation in anterior half longer than that of pronotum. Shagreen and sheen of integument similar to that of pronotum. Base of elytra with large triangular hyaline area. — Prosternum moderately convex, episternal suture deepened only in a short anterior section. Posterior margin of prosternal apophysis arcuate (convex). Punctation restricted to between episternal sutures, bearing long and erect setae that are much longer than those of antennae or clypeus. Shallow punctures of meso- and metasternum and sternites with inclined microscopic setae. Shagreen of ventral integument indistinct.

Length: 3,45–4,25 mm; breadth: 1,73–2,45 mm.

Distribution. A small section of the Namib coast, 80–120 km north of Lüderitz (Fig. 27).

Material examined. Three ♂ (2 dissected), 3♀ and 2 additional specimens. All specimens, including holotype, in Transvaal Museum, Pretoria; 1 via University of Pretoria.

Holotype ♂, allotype ♀ and 5 paratypes: S. W. A., Saddle Hill, 24° 54′ S, 14° 55′ E, 17.1.1974, on dunes, day, leg. Endrödy-Younga, E-Y:296; 1 paratype: Namib Expedition at SE 25.15 Ac1, January 1977, leg. Holm, Kirsten & Scholtz.

Ethoecology. The Saddle Hill series was collected in the depression of a high, near-coastal dune around the base of *Stipagrostis* grass. The single specimen was collected further inland (Plate 21A).

Month recorded. January.

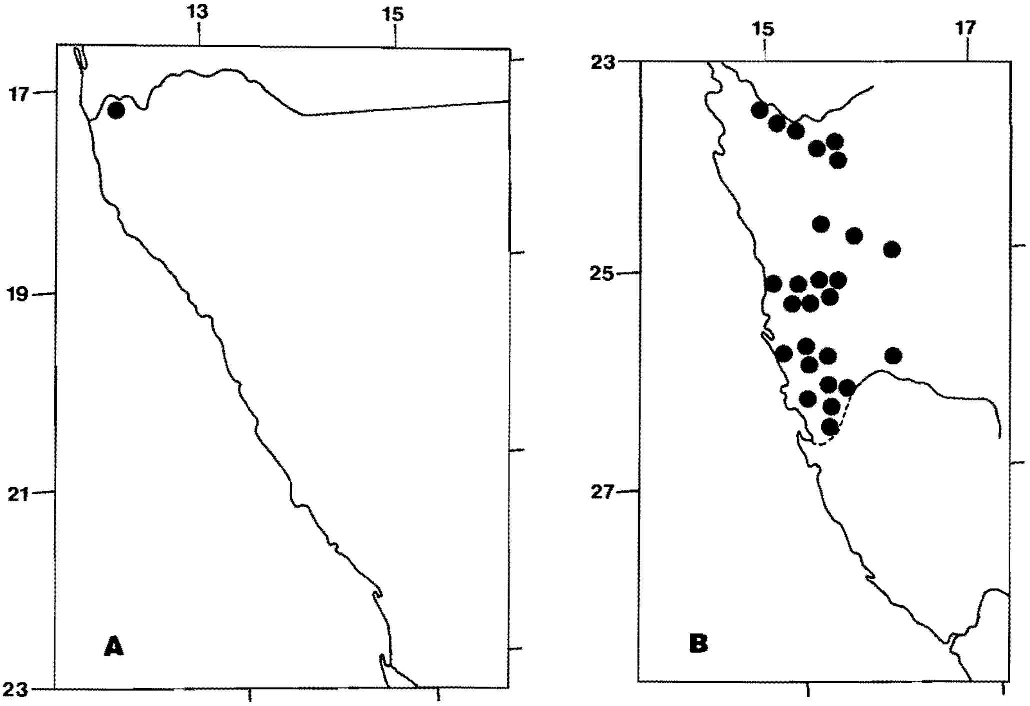

Fig. 26. Distribution of *Caenocrypticus (Vernayella) pauliani* (Koch) in the central and northern Namib dune desert.

Etymology. The new species is named after Dr Carlo Koch, former head of the Coleoptera Department, Transvaal Museum, founder of the Namib Desert Research Station and an outstanding student of southern African Tenebrionidae.

Caenocrypticus (Vernayella) pauliani (Koch) comb. nov., Figs 18F, 23G,H, 26, Plates 3A, 5C, 7C, 11B,C, 21B

Vernayella pauliani Koch, 1962: 155.

Diagnosis. Greatest size variation in subgenus. Specimens from the vicinity of Gobabeb as large as specimens of *C. (V.) noctivagus.* Light to dark reddish brown. Moderately convex, integument shiny with fine dorsal punctation. Ventral punctation coarse but shallow, punctures not sharp-edged. Body broadest behind humeri, outline slightly contracted between pronotum and humeri. Pronotum bell-shaped, lateral margin usually slightly contracted preapically. Anterior emargination of pronotum deep. Lateral setation of pronotum long, setae well spaced. Disc of prosternum bare. Posterior margin of prosternal apophysis convex. Preapical denticulation of elytral margin spaced as tubercles of disc near apex. Habitus: Plate 3A.

Redescription. Head small, about 2,8 times narrower than pronotum. Clypeus truncate or slightly convex, edge with few granules. Vertex densely punctate, behind clypeus finely granulate. Integument with a slight greasy sheen owing to indistinct shagreen. — Pronotum moderately convex, collar emargination deep, disc behind 2,8 times as long; anterior angles lobiform with rounded apices. Disc bell-shaped, lateral margins from behind middle diverging gradually up to posterior lateral angles, margins straight or indistinctly contracting preapically. Lateral setation long, setae almost as long as those of funicular segments of antennae in specimens from the central Namib, somewhat shorter in the north (Plate 11C). Long setation a unique character of this species. Integument shiny with indistinct shagreen, punctation sparser and punctures smaller than in *C. (V.) noctivagus* (Plate 7C). — Elytra more elongate (9,5:11,5) and less convex transversely than in *C. (V.) noctivagus,* sharp lateral margins clearly discernible in dorsal view. Apically pointed-ovate, broadest behind humeri, lateral margins evenly arcuate. Sutural profile highest behind scutellum, evenly and flatly arcuate towards apex. Integument shiny with indistinct shagreen. Anterior one-third punctate, gradually transforming into a file-punctation, and in apical third into a fine granulation. Granulation of lateral margin matching surface granulation in density (Plate 11B). Setation of lateral margin slightly longer than on pronotum. Scutellum equilaterally triangular, lateral margins only slightly concave in front of apex, almost entirely concealed by pronotal margin. — Prosternum moderately convex, mid-section less elevated than in *C. (V.) noctivagus.* Prosternal apophysis broadens to rounded posterolateral angles, apex flatly arcuate-truncate. Episternal suture sharply incised. Prosternum coarsely punctate, punctures well spaced, shallow and not sharp-edged, punctation of episternum indistinct. Disc of prosternum bare. Intercoxal process of first sternite hardly broader than half mesocoxal distance (Plate 5C). Punctation of mesosternum similar to prosternum, from there to anal sternite gradually denser and punctures smaller. Shagreen of integument varying from indistinct to fine but sharply incised (no geographic association). Punctures apparently without microscopic setae. Protibia as in Fig. 18F. Aedeagus as in Fig. 23G,H.

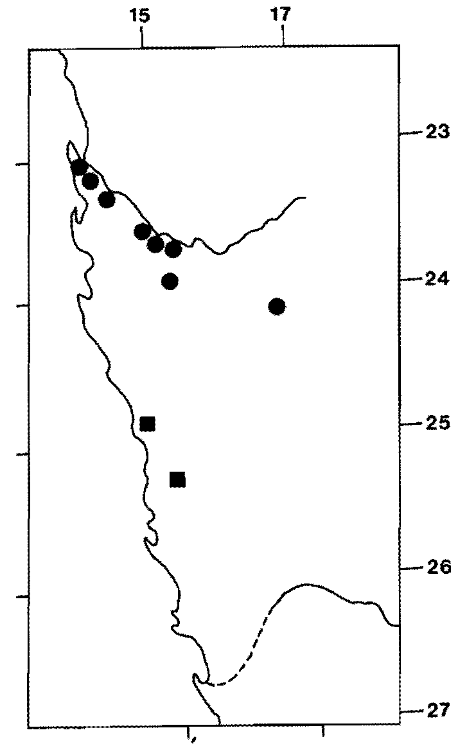

Fig. 27. Distribution of *Caenocrypticus (Vernayella)* species in the central Namib dune desert. ● = *C. (V.) delabati* (Koch); ■ = *C. (V.) kochi* spec. nov.

Length: 2,7–4,6 mm; breadth: 1,35–2,74 mm; both extremes from near Gobabeb.

Distribution. Central and northern Namib Desert from the Kunene River to Lüderitz, and from the coast to the inner margins of the dune desert. The Kunene population is isolated by more than 600 km from the Walvis Bay dunes. It could occur in between but has not been recorded on the dune system between the Unjab and Kunene Rivers (a distance of 350 km). Its absence is predictable between Walvis Bay and the Unjab River (a distance of 300 km) where no suitable dunes are present (Fig. 26).

Type material. Lectotype ♂ (here designated) and 17 paralectotypes: Gobabeb, Kuiseb Riv., Centr. Namib, X.1957, C. Koch; 9 additional paralectotypes: Tsauchab Riv. (dunes 30 mi W. Sesriem), X.1957, C. Koch.

Material examined. Thirty-two ♂ (all dissected), 14♀ and 1120 additional specimens. Lectotype ♂, 26 paralectotypes and 1039 specimens in Transvaal Museum, Pretoria; (281 via Namib Desert Research Station, and 254 via Department of Zoology and Entomology, University of Pretoria); 76 specimens in Namibia State Museum, Windhoek and 5 in National Collection of Insects, Pretoria.

Additional localities: 52 Kaokoveld, Kunene R., W Hartmannberge, 17° 12′ S, 12° 10′ E, 6.4.1984, dunes night, leg. Endrödy-Younga, E-Y:2093; 39 *idem* but dunes and hummocks, day, 13.2.1984, leg. Penrith & Müller, E-Y:2066; 1 Walvis Bay, dune 7, 22° 59′ S, 14° 30′ E, 14.4.1979, leg. Holm; 6 Gobabeb dunes, night, 23° 33′ S, 15° 02′ E, 27.2.1975, leg. Endrödy-Younga, E-Y:694; 4 *idem* but 23° 34′ S, 15° 03′ E, 21.10.1974, leg. Endrödy-Younga, E-Y:412; 323 *idem* but leg. Koch & Holm, trapped on 21 occasions between 27 July and 1 October 1965; 41 *idem* but leg. Seely, trapped on 11 occasions on dunes nos. 1 to 5 (for coordinates see *C. (V.) noctivagus*) between 7 June and 18 September 1978; 4 Gobabeb, Elephant valley, 23° 40′ S, 15° 15′ E, 24.8.1982, dunes and hummocks, night, leg. Endrödy-Younga, E-Y:1923; 1 Gobabeb, 10 mi S, III.1968, leg. Holm. 242 Natab dunes nos. 1 to 5 (for coordinates see *C. (V.) noctivagus*), trapped on 11 occasions between 5 August and 10 October 1978, leg. M. Seely; 17 Tsondab vlei, dunes, 23° 59′ S, 15° 26′ E, 13.1.1975, leg. Endrödy-Younga, E-Y:541; 1 *idem* but X.1957, leg. Koch; 32 *idem* but at 23° 50′ S, 15° 20′ E, 23° 50′ S, 15° 35′ E, 24° 05′ S, 15° 35′ E, 24° 40′ S, 15° 35′ E, March and July 1975, leg. Holm; 3 Vreemdelingspoort farm, 24° 47′ S, 15° 46′ E, 22.1.1980, leg. Holm; 7 Nubib, 24° 59′ S, 16° 09′ E, January 1980, leg. Holm; 7 St Francis Bay, 25° 06′ S, 14° 52′ E, 8.7.1976, leg. Holm. 30 Hauchab N, 25° 10′ S, 15° 10′ E, January 1977, Holm & Scholtz; 2 Guinasibberg north, 25° 10′ S, 15° 25′ E, January 1977, Holm & Scholtz; 2 *idem* but southwest, 25° 12′ S, 15° 35′ E, 5.7.1976; 13 *idem* but at 25° 18′ S, 15° 26′ E, January 1977; 25 Uri-Hauchab, 25° 22′ S, 15° 05′ E, January 1977, Holm & Scholtz; 1 *idem* but at 25° 22′ S, 15° 10′ E; 17 *idem* but at 25° 27′ S, 15° 12′ E; 24 central dune desert at 25° 50′ S, 15° 12′ E, January 1977, Holm & Scholtz; 42 *idem* but at 25° 50′ S, 15° 25′ E; 1 *idem* but at 25° 57′ S, 15° 12′ E, 15.7.1976, leg. Holm; 1 Saddle Hill, 25° 54′ S, 14° 55′ E, 17.1.1974, dunes, day, leg. Endrödy-Younga, E-Y:296; 50 Namtib dunes, 25° 58′ S, 16° 02′ E, 7.8.1989, dunes, night, leg. Endrödy-Younga, E-Y:2636; 11 *idem* but E-Y:2641; 15 Kanaän, farm 104, SE 25.16 Ca, 22–27.6.1976, Penrith & Louw, H-33054; 30 *idem* but at 25° 53′ S, 16° 07′ E, 15–21.10.1976, H-33373; 21 *idem* but 26–31.1.1977, H-33893; 6 *idem* but 2.5.1977, H-34732; 1 *idem* but at 25° 58′ S, 16° 02′ E, 1.8.1981, H-43594; 18 Koichab Pan, 26° 12′ S, 15° 25′ E, January 1977, leg. Holm & Scholtz; 17 *idem* but at 26° 14′ S, 15° 32′ E, July 1978; 8 *idem* but at 26° 25′ S, 15° 18′ E; 3 Lüderitz, 30 km N, 26° 20′ S, 15° 05′ E, 5.7.1979, Holm & Scholtz; 1 Haalenberg NW, 26° 34′ S, 15° 26′ E, January 1977, Holm & Scholtz. 1 Haris, 3 km E, 26° 34′ S, 15° 25′ E, 6–7 October 1982, Penrith & Irish, H-55070.

Ethoecology. *Caenocrypticus (Vernayella) pauliani* also inhabits the main dune areas but shows a definite preference for clumps of plants on or at the foot of dunes. It was occasionally collected in the same pitfall traps at Gobabeb and Natab dunes together with *C. (V.) noctivagus*, and at Saddle Hill with *C. (V.) kochi* (Plate 21B).

Months recorded. Active throughout the year but has not been recorded in November and December.

Caenocrypticus (Vernayella) serratus spec. nov., Fig. 25, Plates 3B, 11A, 15B

Diagnosis. Apparently a daughter species of *C. (V.) ephialtes*. Large to medium-sized for genus with little size variation. Light reddish yellow with triangular hyaline area at base of elytra.

Elytral margin densely denticulate from in front of middle to apex (Plate 11A). Setation of pronotal margin distinctly longer, punctation of pronotum, elytra and ventrum denser and coarser than in *C. (V.) ephialtes*. Characters not repeated below are similar to those of *C. (V.) ephialtes*. Habitus: Plate 3B.

Description. Anterior emargination of pronotum shallower, disc behind about 2,2 times as long. Punctation of disc coarser and denser, intervals in middle of disc hardly broader, laterally narrower than diameter of punctures. Submarginal lateral depression of disc absent or hardly indicated. Setation of lateral margins long, setae only slightly shorter than on elytral margin. — Elytra similar in shape, punctation of disc denser and coarser, intervals not, or not much, broader than diameter of punctures. Apicodistal granulation as fine as and hardly denser than in *C. (V.) ephialtes*. Disc without microscopic setation. Tuberculations of lateral margin dense from behind humerus but concealed by sharp lateral crest almost to middle of length where they appear as closely-set sharp tubercles. In posterior third they become increasingly rounded and resemble a matched string of pearls (Plate 11A). Lateral setation longer, and more densely set. — Sternal structure similar, apex of prosternal apophysis truncate or slightly convex. Punctation of venter slightly denser and considerably coarser.

Length: 3,60–4,25 mm; breadth: 1,85–2,25 mm.

Distribution. Northern Skeleton Coast of the Namib Desert (Fig. 25).

Material examined. Five ♂, 5♀ and 108 additional specimens. Holotype, allotype and 80 paratypes in Namibia State Museum, Windhoek; 36 paratypes in Transvaal Museum, Pretoria.

Holotype, allotype and all 116 paratypes: 45 km S. Kunene R. M. (river mouth), SE 1711 Db, 18–22 Oct. 1978, S. Louw & M.-L. Penrith, H-37130.

Ethoecology. On high dunes facing the coast (Plate 15B).

Remarks. As pointed out in the section on historical biogeography, it is suggested that the subgenus *C. (Vernayella)* evolved on coastal riverine sand accumulations of the Koichab River before the advent of massive sand accumulation in the central Namib area. The *C. (Vernayella)* populations in the northern Namib area must have been transported northwards during periods of sand transportation. *C. (V.) serratus* is here considered a daughter species of *C. (V.) ephialtes*. The ancestral populations of *V. serratus* might have arrived earlier, already having had speciated by the time of the subsequent arrival of *C. (V.) ephialtes*. One specimen of *C. (V.) ephialtes* was collected together with the long series of *C. (V.) serratus* (same locality label, but H-37188) and was collected on two other occasions in the close vicinity without producing phenotypic intermediates.

Caenocrypticus (Vernayella) delabati (Koch) comb. nov., Fig. 27, Plates 3C, 6D, 7D, 20A

Vernayella delabati Koch, 1962: 154.

Diagnosis. Small to medium-sized in the genus. Matt, pale yellow, hyaline area of elytra not prominent. Body least convex in genus. Pronotum narrower than elytra, parallel behind middle, slightly contracted before apex (Plate 6D); anterior emargination deep, anterior angles lobiform, moderately broadly rounded. Punctation of dorsum fine, shagreen very dense, reducing the sheen of integument. Margins and surface not setose. Marginal serration and apical tuberculation of elytra hardly discernible.

Redescription. Clypeus slightly emarginate, disc behind edge finely and densely tuberculate. Punctation of vertex clear but fine. — Pronotum narrower than elytra, margins parallel behind middle, finely contracting before posterolateral angles (Plate 3C). Anterior emargination very deep, disc behind only 2,15 times as long. Anterolateral angles lobiform. Disc somewhat finer and more sparsely punctate than head, shagreen very dense, integument almost matt (Plate 7D). Lateral margins without setation. — Elytra elongate-ovate, body outline contracting between pronotum and elytra. Sutural profile very flatly arcuate. Punctation and shagreen as on pronotum, apical tuberculation indistinct, like marginal serration, lateral margin not setose. — Episternal suture of prosternum complete and fine. Apex of prosternal apophysis truncate. Punctation and shagreen as on dorsum.

Length: 2,9–4,1 mm; breadth: 1,52–2,25 mm, the maximum dimensions are exceptional.

Distribution. Occurs almost exclusively among dunes along the Kuiseb River, with only three specimens having been found approximately 40 km further the south (Fig. 27).

Type material. Holotype ♂ and 20 paratypes: Rooibank, nr. Walvis Bay, V.1959, C. Koch. All in Transvaal Museum, Pretoria.

Material examined. Eight ♂ (dissected), 3♀ and 259 additional specimens; 178 in Transvaal Museum, Pretoria (18 via Namib Desert Research Station); 69 in Namibia State Museum, Windhoek; 5 in National Collection of Insects, Pretoria; 2 at University of California, Berkeley.

Additional localities: 137 Gobabeb, trapped by C. Koch and E. Holm on 16 occasions between 1 August and 1 October 1965; 2 *idem* but XI.1968, L. Schulze; 7 *idem* but at 23° 34′ S, 15° 03′ E, dunes at night, 21.10.1974, Endrödy-Younga, E-Y:412; 11 *idem* but ground-traps with meat bait, 3.11.1974, Endrödy-Younga, E-Y:448; 18 *idem* but dunes 2, 3, 4 and 5 (coordinates under *C. (V.) noctivagus*), trapped between 7 June and 21 October 1978, Seely; 3 Natab, dunes 2 and 4 (coordinates under *C. (V.) noctivagus*), trapped on 10 October 1978, Seely; 3 Kuiseb River at 23° 20′ S, 14° 42′ E, 4.7.1975, Holm; 66 Kuiseb Delta, 23° 05′ S, 14° 24′ E, 9–16 September 1976, Louw & Penrith, H-33232; 2 *idem* but 29.3.1977, H-34224; 1 Witberg, 24° 07′ S, 15° 52′ E, 14.9.1971, H-5656; 2 Tsondab plains at 23° 54′ S, 15° 04′ E, 15.7.1976, Holm.

Ethoecology. Found in the main dunefield of the central Namib Desert between the Kuiseb (268 specimens) and Tsondab Rivers (3 specimens). The species occurs mainly at the foot of dunes with or without vegetation. *C. (V.) delabati* was collected at the same site and occasionally in the same pitfall trap as *C. (V.) noctivagus*, *C. (V.) pauliani* and *C. (V.) ephialtes* (Plate 20A).

Months recorded. Likely to be active throughout the year, but has not been collected from December to February or in April.

Genus *CAENOCRYPTICOIDES* Kaszab

Caenocrypticoides Kaszab, 1969: 322.

Type species: *Caenocrypticoides loksai* Kaszab (by original designation).

Diagnosis. Epipleuron abruptly contracting behind humerus, evenly tapering posterior section not reaching apex of elytra (Plate 5D). Metacoxa ovate, moderately transverse. Breadth: length ratio 20:13 (Plate 5D).

Redescription. Head comparatively broad, consistently broader than half breadth of pronotum. Clypeus broadly truncate, almost straight or deeply and broadly emarginate. Eye free-standing laterally, ventrally free or covered by lateral portion of postgena. — Pronotum subquadrate, moderately broader than long, anterior emargination broad, not particularly deep, anterior lateral angle sharply acute, posterior angle sharply rectangular or slightly obtuse. — Elytra transversely convex without a sharp lateral margin. Epipleuron covers humerus, tapering rapidly and arcuately along metasternum, after a semiparallel narrow median section reaching only base of anal sternite. — Prosternal apophysis elongate with pointed or rounded apex. Mesocoxae closer to each other than metacoxae. Metacoxae moderately transverse, less than double their length. Antennae slender with distinct 3-segmented club. Protibia with produced anterolateral angle or lobe. — Aedeagus simple, straight with lanceolate apicale that is much shorter than basale; very similar in the three known species, see description of *C. peruanus* (Fig. 28B,C).

No secondary sexual dimorphism was observed.

Cladistic evaluation within the tribe:

Apomorphies: arcuately tapering epipleuron and comparatively narrow metacoxa.

Plesiomorphy: first mesotarsal segment moderately longer than second.

Distribution. Coastal regions of southern Peru and northern Chile (Fig. 29).

KEY TO THE SPECIES OF *CAENOCRYPTICOIDES*

1(4) Pronotum broadest at anterior third of length, or semiparallel behind this point. A large area of eye exposed ventrally, only supported by postgenal margin from behind (Plate 10D). Species from Peru.

2(3) Lateral profile of eye less convex in dorsal view, not contracted behind. Postgenal margin blends smoothly into convexity of eye without forming an angle (Plate 10D). Prosternal apophysis almost rectangular in lateral view, hardly produced posteriorly (Fig. 28D). Length 2,4–3,3 mm. Central Peru coast. . . *C. penai* Kaszab

3(2) Lateral profile of eye more convex in dorsal view, slightly contracted towards base. Postgenal margin forms a small, laterally exposed protuberance where meeting lateral margin of eye (Plate 10C). Prosternal apophysis acutely angled in lateral view, sharply produced posteriorly (Fig. 28E). Length 2,8–3,2. Southern Peru coast . . . . *C. peruanus* spec. nov.

4(1) Pronotum broadest in middle, slightly arcuate over entire length or semiparallel behind middle. Ventral portion of eye almost entirely covered by postgena, leaving only a narrow lateral margin exposed. Species from Chile.

5(6) Humeral angle of elytra evenly and smoothly rounded. Punctation of dorsal surfaces inconspicuous; shagreen fine, integument more glossy. Lateral deflection of elytra narrowly rounded in caudal view. Length 2,0 mm . . . . *C. loksai* Kaszab

6(5) Humeral angle callous. Punctation very distinct, coarse on elytra; shagreen fine but sharply incised, integument with greasy sheen. Lateral deflection broadly rounded. Length 2,5–3,0 mm . . . . *C. translucidus* Kaszab

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Caenocrypticoides peruanus spec. nov., Figs 28E, 29, Plates 4A, 10C, 11D

Diagnosis. Black, appendages, occasionally clypeus and anterior angles of pronotum reddish brown. Punctation of dorsal and ventral surfaces usually finer than in *C. penai.* Lateral profile of eye more convex, contracted towards base, where postgenal margin forms a small protuberance (Plate 10C). Prosternal apophysis acutely angled in lateral view (Fig. 28E). Habitus: Plate 4A.

Description. Head broad, more than half of pronotal breadth, clypeus broadly and evenly emarginate. Genal margins flatly contracting towards eye but not forming an angle with eye. Head broadest at eyes. Lateral profile of eye distinctly convex in dorsal view, contracting slightly to basal margin. Postgenal margin forming a small and sharp protuberance at base of eye (Plate 10C). Punctation of entire dorsal surface fine, intervals broader than diameter of punctures. Shagreen of integument very fine and sharp. — Pronotum about one-third broader than long, anterior emargination broad and moderately deep; anterolateral angles acute and narrowly rounded, posterior angles rectangular and narrowly rounded. Disc broadest at anterior third of length, semiparallel behind or slightly bell-shaped. Lateral and anterior margination fine but sharp, continuous, basal margin immarginate. Punctation of disc similar, but sparser than on head, shagreen similar. Prosternal apophysis produced posteriorly, forming acute angle in lateral view (Fig. 28E). Episternum of prosternum, as well as reflected lateral portion of elytra with long silky hairs. — Elytra only slightly longer than combined breadth (10:9), convex transversely, lateral margin only visible at humerus from above before curving ventrad. Punctures of disc slightly larger than on pronotum, each puncture with a short, microscopic, reclining hair. Episternum of prosternum with few very fine and short silky hairs, often not visible, apparently absent from reflected portion of elytra. — Aedeagus simple, apicale moderately arcuate, sharply pointed-lanceolate, length 0,25 mm. Penis straight filiform, feebly sclerotized. Basale

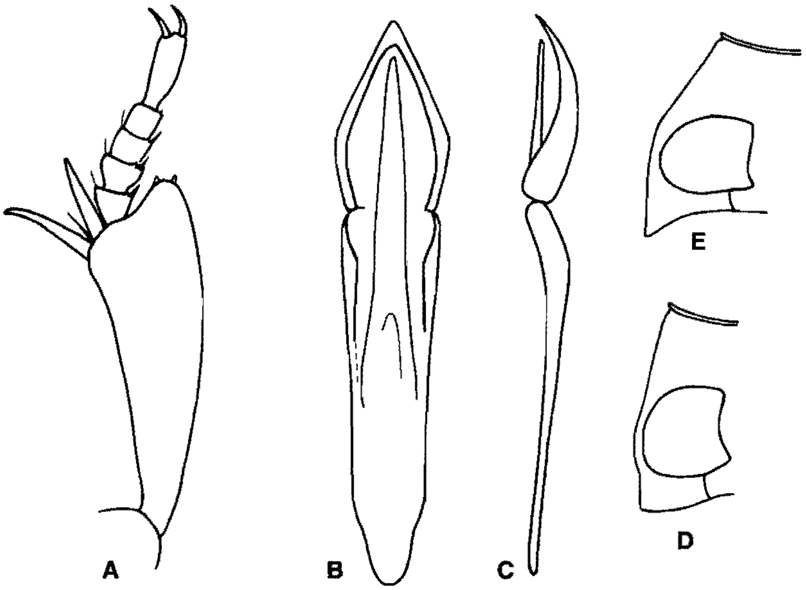

Fig. 28. *Caenocrypticoides penai* Kaszab (**A–D**) and *C. peruanus* spec. nov (**E**). **A**: male protibia; **B–C**: aedeagus in dorsal and in lateral views; **D–E**: prosterna in lateral views.

0,45 mm long. Shape apparently subject to the effects of preservation and shows slight variation.

Length: 2,8–3,2 mm; breadth: 1,5–1,9 mm.

Distribution. Southern coastal region of Peru (Fig. 29).

Material examined. Twenty-six ♂ (7 dissected), 8♀ and 21 additional specimens. Holotype, allotype and 29 paratypes in California Academy of Sciences, San Francisco. Additional paratypes: 15 in Transvaal Museum, Pretoria; 6 in Field Museum, Chicago; 3 in Natural History Museum, Budapest.

Holotype ♂, allotype ♀ and 39 paratypes: 22 mi. S of Mollendoo, PERU, XI.19.1950, Loma zone; Ross and Michelbacher collectors. Additional paratypes: 16, Peru, 16 km S Rio Tambo, 9.II.1965, (leg. or collection) Peña (on different labels); 1, 12 mi SE Camana, SW Peru, iv.3.51, E. S. Ross, stones, coastal loma.

Caenocrypticoides penai Kaszab, Figs 28A–D, 29, Plates 4B, 5D, 10D

Caenocrypticoides penai Kaszab, 1969: 325.

Diagnosis. Black, appendages reddish brown. Punctation of dorsal and ventral surfaces usually coarser than in *C. peruanus*. Lateral profile of eye less convex, not contracting towards base where postgenal margin blends smoothly into surface of eye (Plate 10D). Prosternal apophysis almost rectangular in lateral view (Fig. 28D). Habitus: Plate 4B. Closely related and very similar to *C. peruanus*. Characters not repeated below are similar to those of *C. peruanus*.

Redescription. Eyes not protuberant laterally, lateral profile less convex and not contracted towards base (Plate 10D). Prosternal apophysis hardly produced backwards over mesosternum; posterior angle almost rectangular in lateral view (Fig. 28D). Punctation of entire dorsal and ventral surfaces coarser, usually more distinct on elytra, where intervals of larger punctures are also slightly convex. Microscopic pubescence of elytral dorsum similar, silky hairs of episternum of prosternum and reflected portion of elytra longer and distinct (Plate 5D). Protibia as in Fig. 28A. Aedeagus as in Fig. 28B,C.

Length: 2,4–3,3 mm; breadth: 1,19–1,73 mm.

Distribution. Coastal area of central Peru (Fig. 29).

Type material. According to the original description the entire type series originated from the same samples: S Huarmey, Peru, 13.II.1965, Coll. L. E. Peña. From those seen: holotype ♂ and 1 paratype in Natural History Museum, Budapest; 1 paratype in Field Museum, Chicago; 1 paratype in Transvaal Museum, Pretoria.

Additional specimens: 18 in California Academy of Sciences, San Francisco; 10 in Transvaal Museum, Pretoria; 4 in Field Museum, Chicago; 2 in Hungarian Natural History Museum, Budapest.

Material examined. Eleven ♂ (5 dissected), 9♀ and 18 additional specimens.

Additional localities: 3 as holotype (not paratypes); 6 Peru, 220 km N Lima, 10.VII.1965, Coll. L. E. Peña; 23, 22 mi S Huacho, Peru, iii-15-51, Ross & Michelbacher collectors; 2, 18 mi S Huacho, Peru, iii-15-51, Ross & Michelbacher collectors.

Caenocrypticoides loksai Kaszab, Fig. 29

Caenocrypticoides loksai Kaszab, 1969: 323.

Diagnosis. Smallest species in genus. Body semiparallel between middle of pronotum and middle of elytra, only very slightly contracted in between. Moderately convex, sutural profile almost straight up to apical declivity. Genal margins straight towards distinct clypeal angles, clypeus broadly and distinctly emarginate. Punctation of dorsum and ventrum very

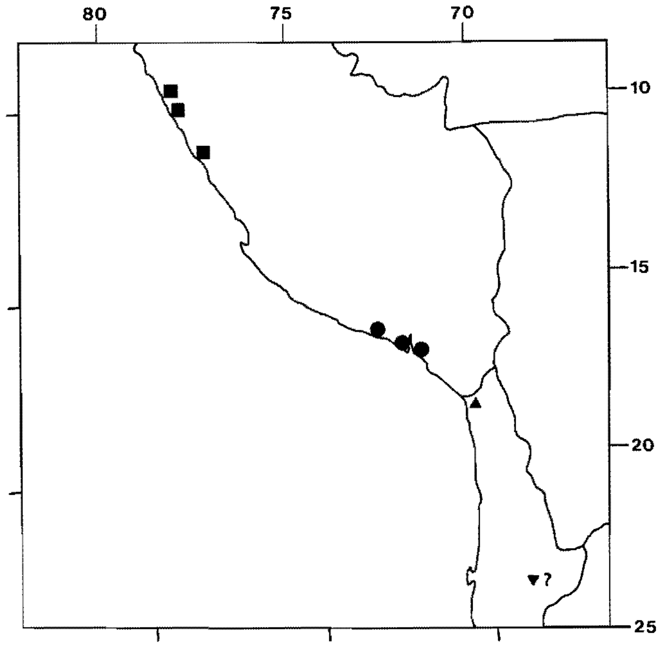

Fig. 29. Distribution of *Caenocrypticoides* species in Peru and Chile. ■ = *C. peruanus* spec. nov.; ● = *C. penai* Kaszab; ▲ = *C. loksai* Kaszab; ▼ = *C. translucidus* Kaszab.

fine, not conspicuous, fine hairs of both surfaces hardly discernible, with few long and fine setae on pronotal margin and humeri. Protibia short and broadly dilated towards apex. Antenna short with segments 4–12 moderately longer than broad. Both existing specimens light reddish brown.

Redescription. Head only slightly broader than long, only very slightly convex. Genal margins almost straight between ocular and clypeal angles. Clypeal angles distinct and relatively narrowly rounded. Clypeus broadly and distinctly emarginate. Eye small, evenly convex, postgenal margin just discernible at posterior margin of eye. Integument with greasy sheen owing to sharp, honeycomb-like microshagreen, punctation very fine, not conspicuous. — Pronotum broader than long at middle (60:44), moderately convex transversely, sharp lateral margins clearly discernible from above. Lateral margins semiparallel between middle and posterior angle, converging slightly towards angles. Apicolateral angles relatively broad with arcuate lateral margins. Anterior emargination not forming an even curve, median section straight. Posterior margin straight-truncate. Shagreen of integument similar to, but less sharp than that of head, punctation similar on disc, punctures hardly bigger than facets of shagreen, gradually coarser towards lateral portions. Microscopic discal hairs emerging from punctures, hardly discernible but more distinct along lateral margins, where a few fine, long silky hairs also emerge from below lateral carina. — Elytra longer than combined breadth (38:31). Lateral margins semiparallel in anterior half, here hardly arcuate, across humeral angles a fraction broader than base of pronotum; from middle evenly arcuate towards broad and almost commonly rounded apex. Transverse convexity moderate on disc, arc slightly flattened in middle, lateral portions, however, roundly reflected, concealing epipleural margin, which is only visible from above at humeri. Shagreen of integument more diffuse than on pronotum, punctures somewhat larger but still fine. — Venter finely punctate, punctures only slightly larger than on elytra; microscopic shagreen inconspicuous. Prosternal apophysis ovate with rounded apex, mesosternum evenly and flatly curved under apex of prosternal apophysis. Sterna longitudinally flat. — Antenna relatively short. Segment 1 broad, twice as long as broad, segment 2 slightly shorter (6:5) and narrower, segment 3 again shorter (5:4) and is the narrowest segment. Segments 4–8 shortened and more ovate, slightly longer than broad. First two club segments as broad as long, cup-shaped; apical segment elongate-ovate. Protibia short, strongly dilated towards apex, length:breadth ratio 25:10; apicolateral process strongly produced, reaching base of fourth tarsal segment. The two existing specimens have not been dissected.

Length: 2,0 mm; breadth: 0,97 mm (middle of elytra).

Distribution. Northern Chile (Fig. 29).

Material examined. Two specimens, unsexed.

Holotype and one paratype: Hungarian Soil-Zool. Exp., CHILE: Prov. Tarapaca, Azapa, on riverside of Rio Lauca, 18.XI.1965, Nr. P-B 128-2, leg. Loksa. Both in Hungarian Natural History Museum, Budapest.

Ethoecology. The specimens were collected near Azapa, about 25 km east of Aruca (also in original description). The site was on the Atakama flats near the foothills of the Andes, and the habitat apparently consisted of sand accumulations of the river (Kaszab, personal communication).

Remarks. It is not certain whether the pale colour is a specific character, or is due to the specimens' immaturity. *C. loksai* can be readily recognized by its small size and very fine punctation.

Caenocrypticoides translucidus Kaszab, Fig. 29

Caenocrypticoides translucidus Kaszab, 1969: 324.

Diagnosis. Of average size in the genus. Dark brown, appendages somewhat paler. Body elongate-ovate, dorsal outline more contracted between pronotum and elytra, lateral margins of both structures more arcuate. Elytra more convex transversely than in *C. loksai.* Genal margin evenly and broadly arcuate without a distinct lateral angle, clypeal emargination narrower than in other species. Punctation of dorsum distinct, coarser and denser on elytra, apparently bare. Characters not repeated below are similar to those of *C. loksai.*

Redescription. Genal margins of head more convergent, broadly arcuate into middle of clypeal margin, not forming a distinct clypeolateral angle to head. Shagreen of integument similar but slightly less sharp, punctation denser, punctures larger. — Pronotum broadest in middle, lateral margins evenly arcuate, contracting more towards base and less curved towards more pointed anterior angle. Shagreen similar and sharp, punctation much denser, punctures as large as 4–6 facets of shagreen together, punctation moderately coarser laterally. — Elytra longer than broad (58:44); broadest in front of middle, evenly and gently arcuate from humeri to more pointed apex, thus dorsal outline more contracted between pronotum and elytra. Humerus callous. Transverse convexity less depressed in middle. Shagreen of integument less sharp, punctation dense, large punctures almost as large as intervals between them. Surface apparently bare. — Punctation of venter comparable to that of elytra, gradually finer on sterna towards anal segment. — Funicular segments of antenna slightly more elongate; segments 9–10 (first two club segments) broader than long, the ninth regularly triangular. Protibia similar, only produced apicolateral process slightly shorter. Aedeagus as in other species.

Length: 2,5–3,0 mm; breadth: 1,2–1,5 mm.

Distribution. Northern Chile (Fig. 29).

Type material. Holotype (not sexed): Chile, coll. R. Oberthür, ex coll. Deyrolle, with a collection name *Crypticus translucidus*. Deyrolle (*in litt.*) on green label. In the Hungarian Natural History Museum, Budapest. The holotype is light brown, apparently immature, as all other specimens known are dark brown.

Material examined. Holotype, 1♂ and 3 additional specimens. One in Natural History Museum, Budapest; 2 in Transvaal Museum, Pretoria; 1 in Field Museum, Chicago.

Localities: all four additional specimens originate from the same sample, labels with different handwriting: Tumbre, Cord. Antofagasta, 4000 m, 8.XII.1965, L. E. Peña.

Remarks. All additional specimens are dark brown, not brownish yellow like the apparently immature holotype. The locality of those specimens (Tumbre) could not be traced. The label data refer to the high Andes at 4000 m, thus far removed from the coastal area. This is unusual in the tribe and the record requires confirmation.

APPENDIX

The monotypic genus *Fitzsimonsium* Koch, described by its author under Caenocrypticini, was also examined during the present revision. As a result, the genus is transferred to the tribe Stenosini. The main characters leading to the transfer are: moniliform antenna; apically split paramere of aedeagus carrying fine hairs; very broad scutellum (here three times broader than long); simply truncate apex of protibia.

Tribe STENOSINI

Genus *FITZSIMONSIUM* Koch

Fitzsimonsia Koch, 1955: 415 (Crypticini);
Fitzsimonsium Koch, 1962: 152 (Caenocrypticini), nom. nov.
Type species: *Fitzsimonsia cymbium* Koch, by monotypy.

Redescription. Body flat, elongate-ovate, elytra evenly attenuate from behind humeri to rounded apex. Head much narrower than pronotum and recessed up to eye in anterior emargination of pronotum. Eye divided by gena that joins a broad lateroventral temporal lobe. Dorsal portion of eye consists of about ten convex corneal facets, ventral portion (not mentioned by Koch), facing forward, consisting of only five facets (Plate 8D). Mentum transverse with rounded lateral margins and emarginate apex. Postgena deeply excavate at base of antenna to accommodate its basal segments in a retrovert position; lateral edges of furrow sharp. Submentum produced. Transverse impression of postgena not deep or sharp. — Pronotum broad, moderately convex, broadest between posterior angles. Anterior margin emarginate, anterior angles sharply rectangular. — Elytra much longer than combined breadth, broadest behind humeri, margins flatly arcuate to commonly rounded apex. Epipleura tapering evenly from humeri to apex. — Prosternum convex, anteriorly shorter than procoxal cavity, prosternal apophysis elongate-ovate, its long projecting apical portion fitting into excavate intercoxal portion of mesosternum; episternum of prosternum deeply concave. Mesosternum short and convex. Margins of excavate apophysis sharply raised. Mesocoxal cavity large and round. Metasternum also convex, episternum oblong, rather broad, epimeron well marked although apparently fused to episternum. Metacoxal cavity transverse but much narrower than in *Caenocrypticus,* its breadth ratio to episternum 14:7, moderately slanting in a mediocaudal direction. Metacoxal cavity laterally closed by episternum. Sternites gradually less convex towards anal sternite; no intersegmental membrane. — Antennae short, moniliform, shorter than breadth of head, segments subcylindrical, gradually accrescent to penultimate segment without forming a club; all segments with straight margins and all tightly fitting

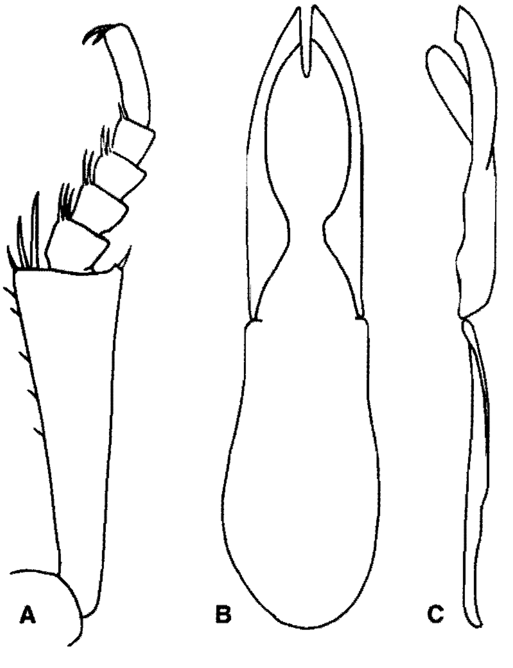

Fig. 30. *Fitzsimonsium cymbium* Koch. **A**: male protibia; **B–C**: aedeagus in dorsal and in lateral views.

each other. Posterior margin of femora longitudinally excavate, protecting folded tibiae. Protibia straight, moderately dilated towards simply truncate apex, all tarsomeres except distal one short, claws very small and equal in length (Fig. 30A). Mesotarsomeres only slightly more elongate, but metatarsomere 1 longer than 2 and 3 together or than claw segment. — Aedeagus inverted, paramere in ventral position. Parameres not completely fused, incised apically with fine setae in apical portion; penis shorter, less sclerotized (Fig. 30B,C).

Secondary sexual dimorphism. Small tubercle in middle of anterior margin of prosternum with few microscopic hairs in male.

Distribution. From the central Namib Desert to north of Cape Town (Fig. 31).

Remarks. The generic name *Fitzsimonsia* was preoccupied in Reptilia (Scincidae) by De Witte (1943), and the replacement name *Fitzsimonsium* was proposed by Koch (1962).

Fitzsimonsium cymbium **Koch, Figs 30A–C, 31, Plates 3D, 8D**

Fitzsimonsia cymbium Koch, 1955: 415.
Fitzsimonsium cymbium Koch, 1962: 152.

Redescription. Dark chestnut-brown with greasy sheen. Head small, pronotum about twice as broad. Pronotum broad, only slightly narrower than elytra behind humeri, outline of body almost completely continuous between pronotum and elytra. Body moderately and evenly convex, lateral margins of pronotum and elytra sharply crested (Plate 3D). Dorsum apparently bare, ventrum, particularly sternites, with long, inclined pilosity corresponding in density with punctation. Integument densely shagreened and punctate, punctation fine to coarse. Considerable variation in shape of lateral crest of pronotum, in coarseness of punctation and shagreen. These characters apparently vary independently, both within samples and geographically. Adaptations in shape, antennae, postgena and legs seem to support field observations regarding myrmecophily.

Clypeus broadly truncate, slightly emarginate, anterior and lateral angles smoothly rounded. Punctation even, from very fine to distinct, well spaced, surface without granulation. Integument very finely but sharply shagreened without marked variation. — A pair of faint prebasal impressions on disc of pronotum usually present; occasionally a second pair present in a median and more lateral position. Lateral margin produced by a shallow submarginal depression. Elevated margin either evenly narrow or dilated towards anterior angle of pronotum, its vertical or semivertical face occasionally double-edged and smooth or punctate. Series from single localities are uniform. Margin narrow in the north (23° 20′ S to 30° 00′ S), broadest in the south (32° 00′ S to 33° 30′ S) but with intermediate specimens and misplaced forms in between. Punctation uniformly fine in the Gobabeb specimen and in all specimens south of 32° S, but laterally coarse in the range in between. Shagreen of integument fine and sharp to indistinct, with a similarly disjunct pattern. — Scutellum concealed by posterior margin of pronotum, poorly marked, very broadly obtusely angled, more than three times as broad as long, as is usual in Stenosini. — Lateral margin of elytra sharp. Elytra with a fine submarginal depression, broader towards apex; punctation fine to laterally coarse, not corresponding with distribution or other characters. — Ventral structure as described for genus. Protibia and tarsomeres Fig. 30A. — Antennae cylindrical, moniliform, only apical segments slightly compressed, slightly accrescent from base without demarcated club. Segment 3 longer than broad, about as long as segments 10 or 11, funicular segments 4–9 broader than long. — Aedeagus 0,55 mm long, basale and apicale subequal in length. Microscopic preapical bristles of parameres occasionally not discernible. No significant variation in aedeagi (Fig. 30B,C).

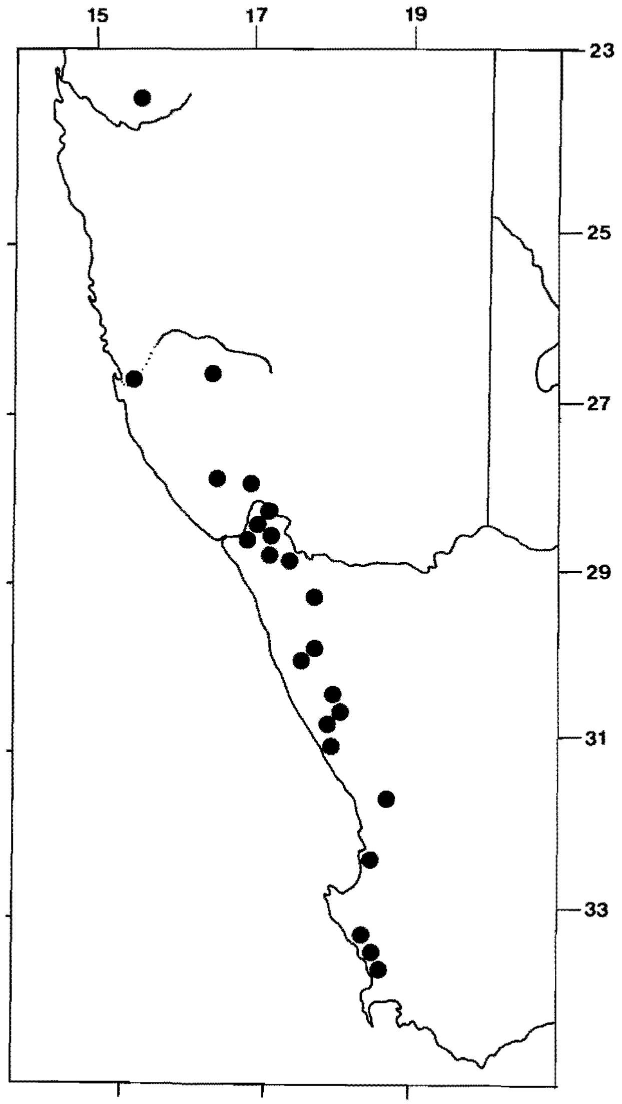

Fig. 31. Distribution of *Fitzsimonsium cymbium* Koch (Stenosini)

Length: 2,10–3,25 mm; breadth: 1,25–1,65 mm.

Distribution. Subcoastal Atlantic belt of southern Africa from north of the Kuiseb River in the Namib Desert to close to Cape Town (Fig. 31).

Type material. Holotype ♀: Steinkopf, Namaqualand, 13.XII.1948, Koch & Van Son. Paratypes: 1 Steinkopf, Na, 16.XI.1949, C. Koch; 1 Grasplatz, S. W. A., X.1950, C. Koch; 1 15 m after Garies (15 miles northwest of Garies, December 1948, ex descr.); 1 same data as holotype. All type and additional specimens in Transvaal Museum, Pretoria, except 1 in Namibia State Museum, Windhoek.

Material examined. Ten ♂ (8 dissected), 7♀ and 66 additional specimens. In Transvaal Museum, Pretoria.

Additional localities: Namibia: 1 60 km NE Gobabeb, 23° 20′ S, 15° 32′ E, 28.2.1975, ground-traps, 97 days, leg. Endrödy-Younga, E-Y:704; 1 between Aus and Kubub, V.1953, leg. Koch; 3 Aus, 20–30 km E, *c.* 26° 37′ S, 16° 28′ E, 18.9.1987, ground and stones, leg. Endrödy-Younga, E-Y:2504; 1 Rosh-Pinah, 27° 53′ S, 16° 50′ E, 14.9.1973, from under stones, leg. Endrödy-Younga, E-Y:104; 1 *idem* but 21.9.1973, E-Y:130; 3 *idem*, but E-Y:132; 1 Aurus Mt S., Diamond Area 1, 27° 50′ S, 16° 20′ E, 26.10.1977, leg. Louw & Penrith, H-35098. South Africa, Richtersveld: 1 Rooiberg valley, 28° 12′ S, 17° 07′ E, 4.9.1976, ground-traps, meat bait, 30 days, leg. Endrödy-Younga, E-Y:1217; 1 De Hope, 10 km SW, 28° 13′ S, 17° 06′ E, 3.8.1989, from under stones, leg. Endrödy-Younga & Klimaszewski E-Y:2627; 3 Helskloof Neck, 28° 20′ S, 16° 59′ E, 3.9.1976, from under stones, leg. Endrödy-Younga, E-Y:1214; 1 between Dornkloof and Kuboos, II.1953, leg. Koch; 2 Orange valley flats, 28° 28′ S, 16° 51′ E, 3.9.1978, ground-traps, meat bait, 37 days, leg. Endrödy-Younga, E-Y:1213; 7 Gelykswerf, X.1955, leg. Koch; 4 Doornpoort, X.1955, leg. Koch; 5 Upper Holgat, 28° 43′ S, 17° 07′ E, 7.9.1976, ground-traps, bait: banana (3), meat (1), faeces (1), 33 days, leg. Endrödy-Younga; 5 Eksteenfontein, 13 km SW, 28° 53′ S, 17° 10′ E, 9.9.1987, ground (from under stones), leg. Endrödy-Younga, E-Y:2485. Namaqualand: 2 Buffels River, 29° 55′ S, 17° 40′ E, 28.8.1977, ground-traps, millipede bait, 59 days, leg. Endrödy-Younga, E-Y:1349; 1 Wildepaarde Hoek, 29° 57′ S, 17° 33′ E, 28.8.1977, ground-traps, meat bait, 60 days, leg. Endrödy-Younga, E-Y:1351; 1 Dikdoorn farm, 30° 43′ S, 18° 00′ E, 4.9.1977, coarse sandy hill, leg. Endrödy-Younga, E-Y:1382; 1 Perdekraal 3 km W, 30° 46′ S, 17° 53′ E, 24.8.1979, ground-traps, 62 days, leg. Endrödy-Younga, E-Y:1585; 4 Rooivlei farm, 31° 05′ S, 17° 52′ E, 28.10.1979, from under stones, leg. Endrödy-Younga, E-Y:1663. Western Cape Province: 27 Wiedouw farm, 31° 43′ S, 18° 43′ E, 19.8.1983, ground-traps, bait: meat (1), faeces (15), banana (11), 77 days, leg. Endrödy-Younga & Penrith, E-Y:1944; 1 Verlorevlei farm, 32° 19′ S, 18° 22′ E, 28.8.1981, ground-trap, meat bait, 80 days, leg. Endrödy-Younga, E-Y:1856; 2 Grootdrif farm, 32° 24′ S, 18° 27′ E, 29.8.1981, ground-trap, banana bait, 81 days, leg. Endrödy-Younga, E-Y:1861; 2 Yzerfontein, 8 km N, 33° 15′ S, 18° 11′ E, 25.8.1983, ground-traps, bait: meat (1), faeces (1), 70 days, leg. Endrödy-Younga & Penrith, E-Y:1978; 2 Cape Town, 63 km N, 33° 24′ S, 18° 16′ E, 30.8.1983, ground-traps, meat bait, 63 days, E-Y:2001, leg. Endrödy-Younga & Penrith; 2 Cape Town, 38 km N, 33° 34′ S, 18° 27′ E, 30.8.1983, ground-traps, meat bait, 63 days, leg. Endrödy-Younga & Penrith, E-Y:2002.

Ethoecology. All individually collected specimens were found under stones in association with ants. One of the ants was identified by Dr H. Robertson (South African Museum) as *Tetramorium solidum* Emery. It seems to be nocturnally surface-active, as most specimens were caught in baited ground-traps. As *F. cymbium* is attracted to bait it is likely that it does not prey on any developmental stages of ants, which would be unusual in the detrivorous Tenebrionidae. The association seems to be spatial (under stones) or foraging on the organic matter collected by ants. If its morphological peculiarities are correctly interpreted as adaptive characters to a myrmecophilous life style, *Fitzsimonsium* is the most highly adapted species of southern African tenebrionids. The species seems to be little affected by differences between ecological zones. It occurs from the summer rainfall desert area of the Namib (Gobabeb) to the moderately mesic winter rainfall area north of Cape Town. The best inhabited area is nevertheless the arid semidesert areas of the Richtersveld and Namaqualand. This degree of environmental tolerance is exceptional and might be linked to a strong association with ants. It occurs in habitats similar to those depicted in Plates 13A,B..

Months recorded. February, May, August to October, apparently reflecting the seasonality of fieldwork.

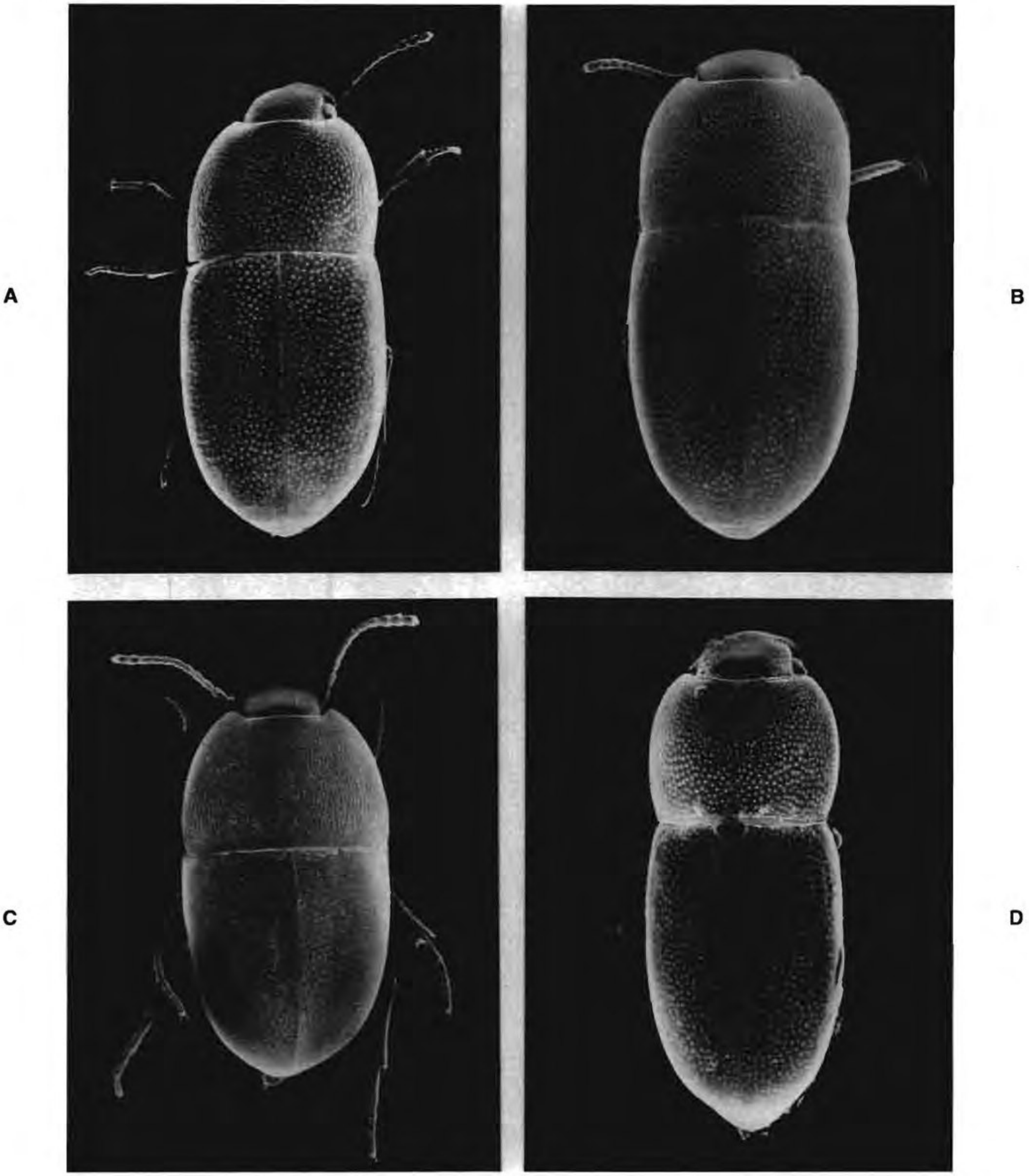

Plate 1

Scanning electron micrographs of *Caenocrypticus* species. **A**: nominate subspecies of *C. (Phyloradix) soror* spec. nov. (×22); **B**: *C. (P.) bushmanicus* Koch (×30); **C**: *C. (Caenocapicus) capensis* (×20); **D**: *C. (Cryptocarpes) elongatus* (Koch) (×27).

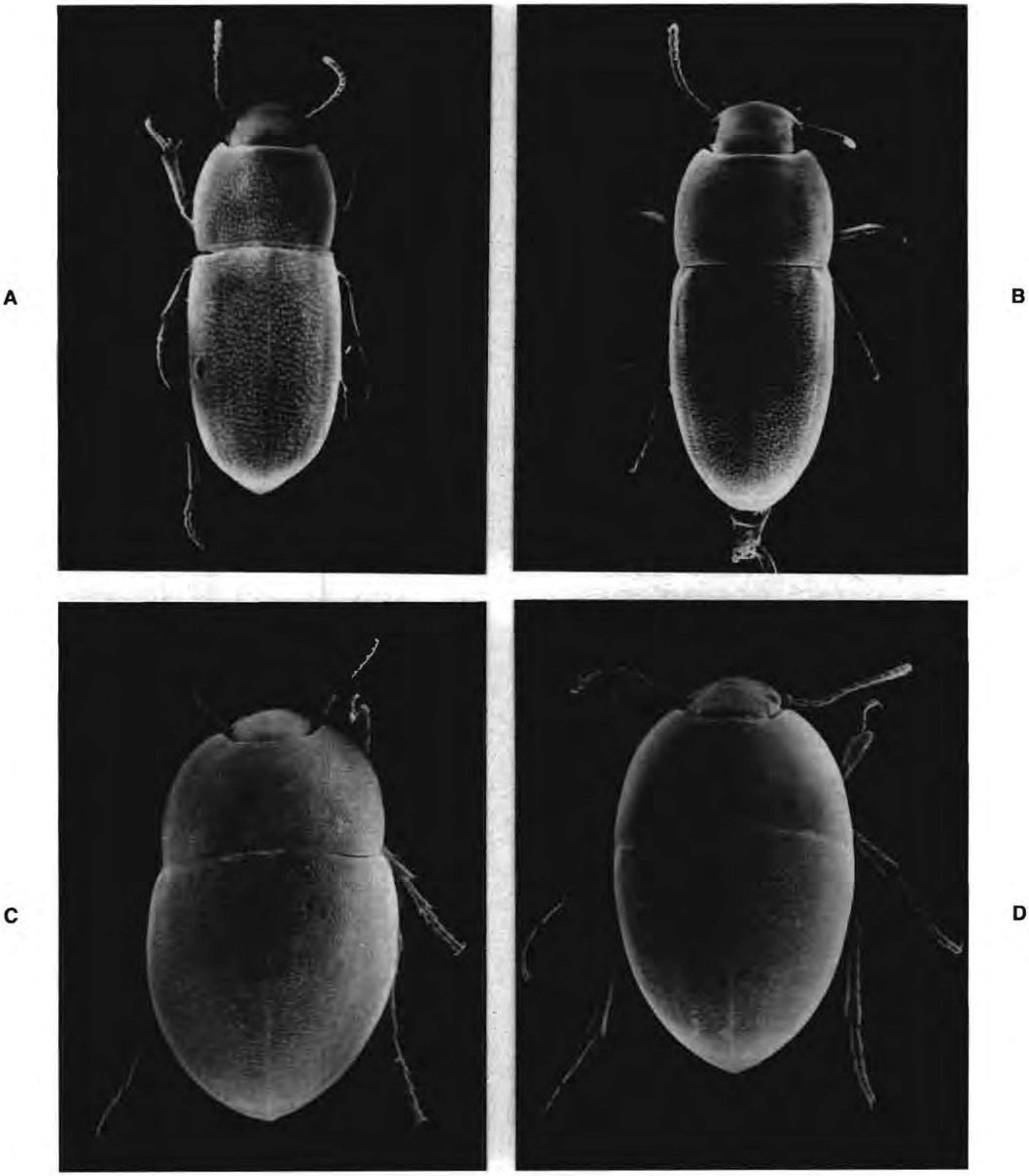

Plate 2

Scanning electron micrographs of *Caenocrypticus* species. **A**: *C. (Cryptocarpes) damara* (Koch) (×18); **B**: *C. (C.) dividiopsis* (Koch) (×20); **C**: *C. (Psammotopulus) phaleroides* (Koch) (×16); **D**: *C. (Vernayella) noctivagus* (Koch) (×11).

Plate 3

Scanning electron micrographs. **A–C**: *Caenocrypticus (Vernayella)* species. **A**: *C. (V.) pauliani* (Koch) (×13); **B**: *C. (V.) serratus* spec. nov. (×13); **C**: *C. (V.) delabati* (Koch) (×13); **D**: *Fitzsimonsium cymbium* (Koch) (Stenosini) (×22).

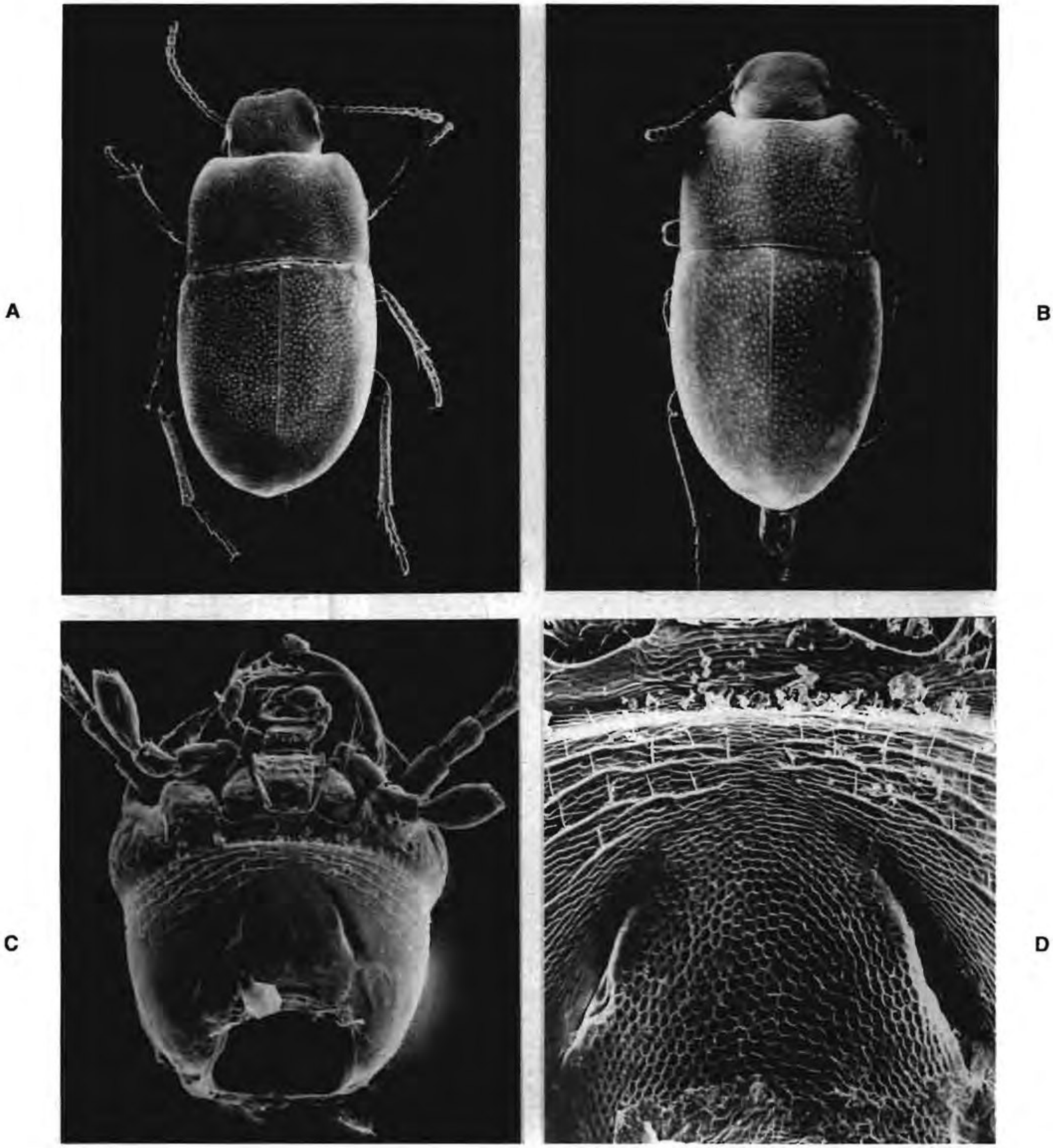

Plate 4

Scanning electron micrographs of *Caenocrypticoides* species. **A**: *C. peruanus* spec. nov. (×15); **B**: *C. penai* Kaszab (×18). *Caenocrypticus* (*s. str.*): **C**: *C. kaszabi* spec. nov, ventral aspect of head (×100); **D**: same species, gular surface (×33).

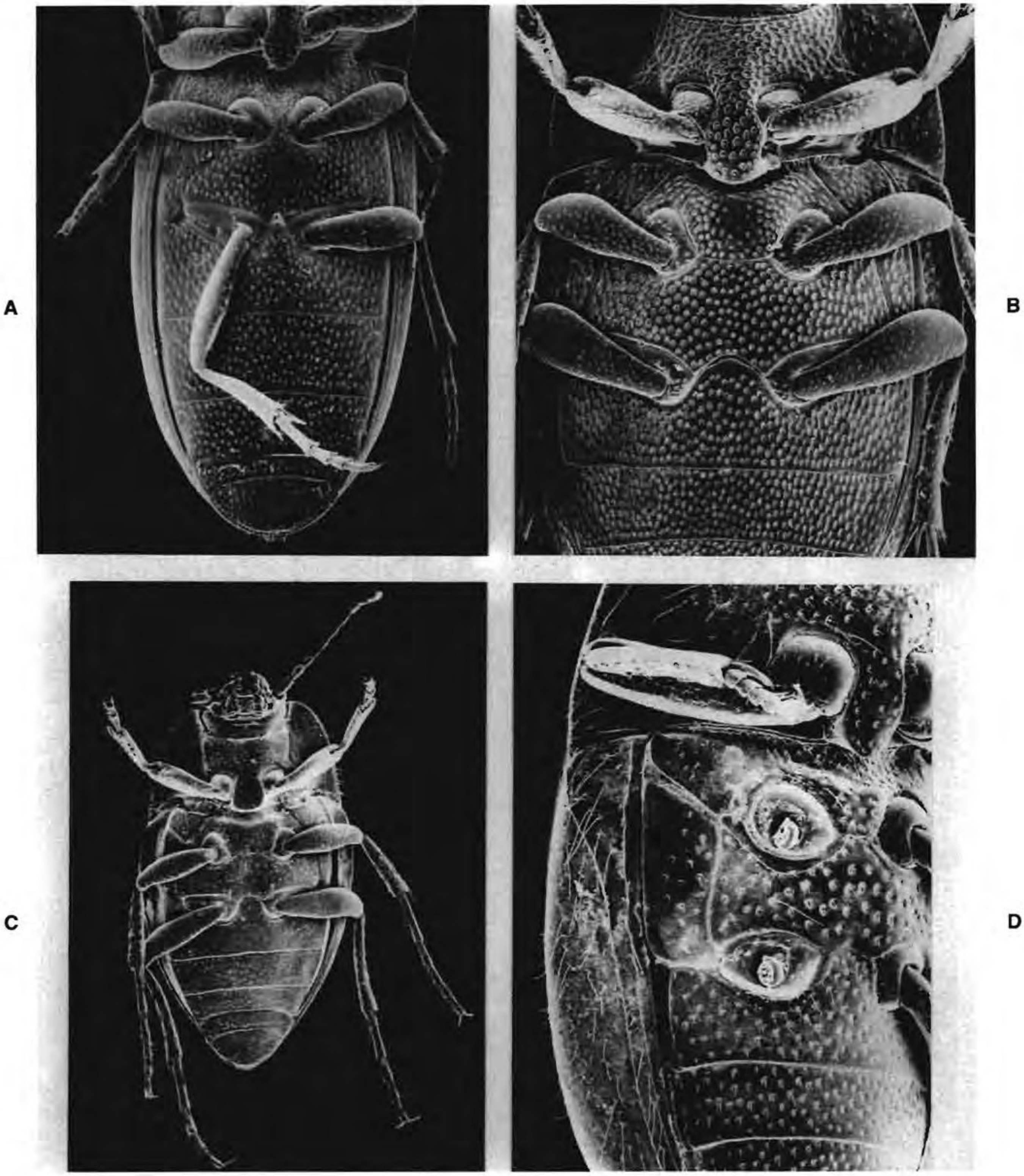

Plate 5

Scanning electron micrographs of ventral structures. **A**: *Caenocrypticus (Cryptocarpes) dividiopsis* (Koch) (×39); **B**: *C. (Psammotopulus) phaleroides* Koch (×39); **C**: *C. (Vernayella) pauliani* (Koch) (×13); **D**: *Caenocrypticoides penai* Kaszab (×50).

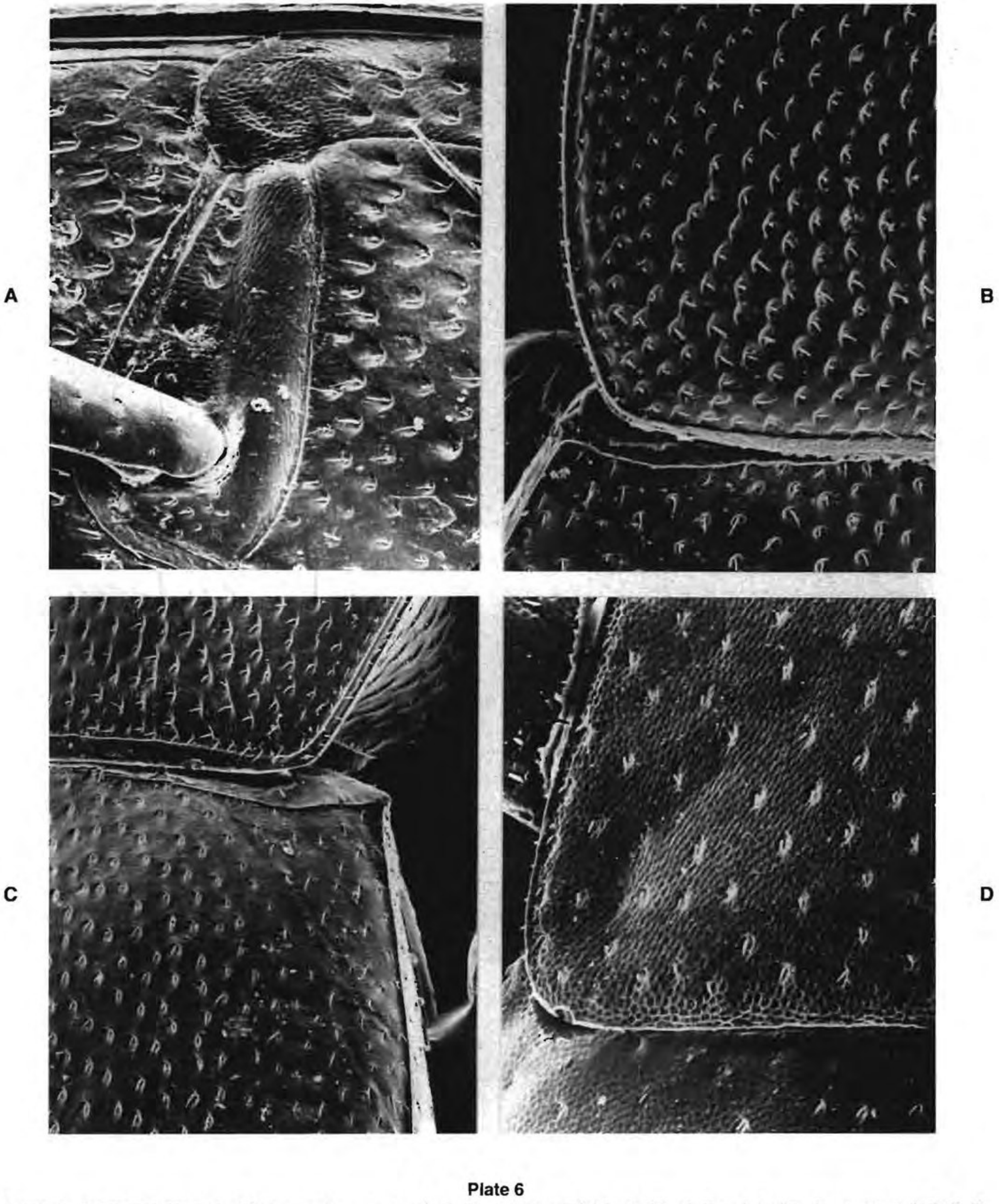

Plate 6

Scanning electron micrographs of *Caenocrypticus* species. **A**: *C. (Cryptocarpes) dividiopsis* (Koch), lateral closing of metacoxa (×200); **B–D**: posterolateral angle of pronotum and humerus in **B**: *C. (Cryptocarpes) elongatus* (Koch) (×150); **C**: *C. (C.) damara* (Koch) (×130); **D**: *C. (Vernayella) delabati* (Koch) (×200).

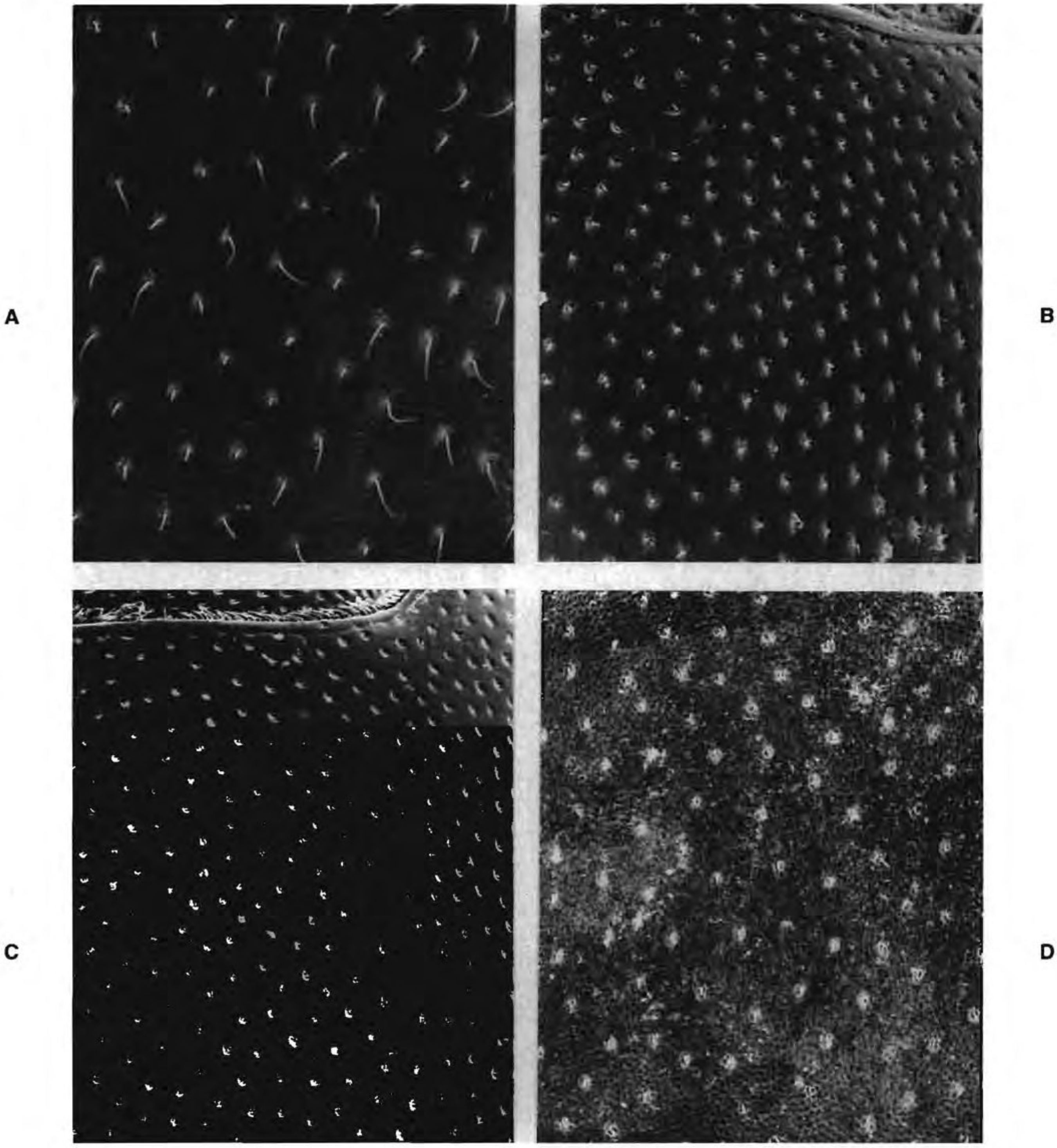

Plate 7

Scanning electron micrographs of pronotal surface in *Caenocrypticus* species. **A**: nominate subspecies of *C. (Phyloradix) soror* spec. nov. (×200); **B**: *C. (P.) bushmanicus* Koch (×200); **C**: *C. (Vernayella) pauliani* (Koch) (×100); **D**: *C. (V.) delabati* (Koch) (×300).

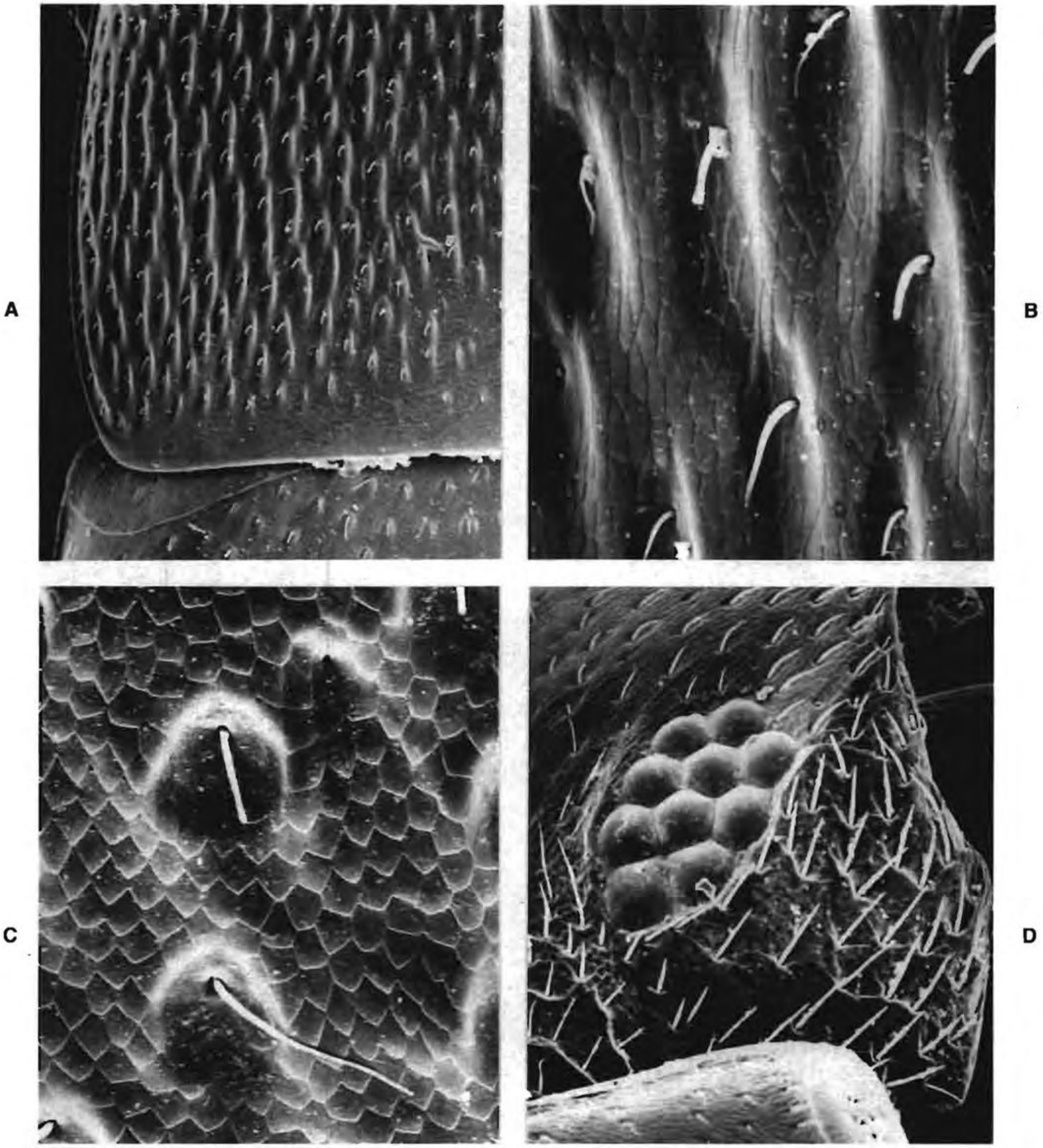

Plate 8

Scanning electron micrographs. **A–C**: *Caenocrypticus (Caenocapicus) capensis* spec. nov. **A**: pronotum (×200); **B**: surface structure of pronotum (×2000); **C**: surface structure of elytron (×2000); **D**: *Fitzsimonsium cimbium* (Koch), dorsal half of eye (×390).

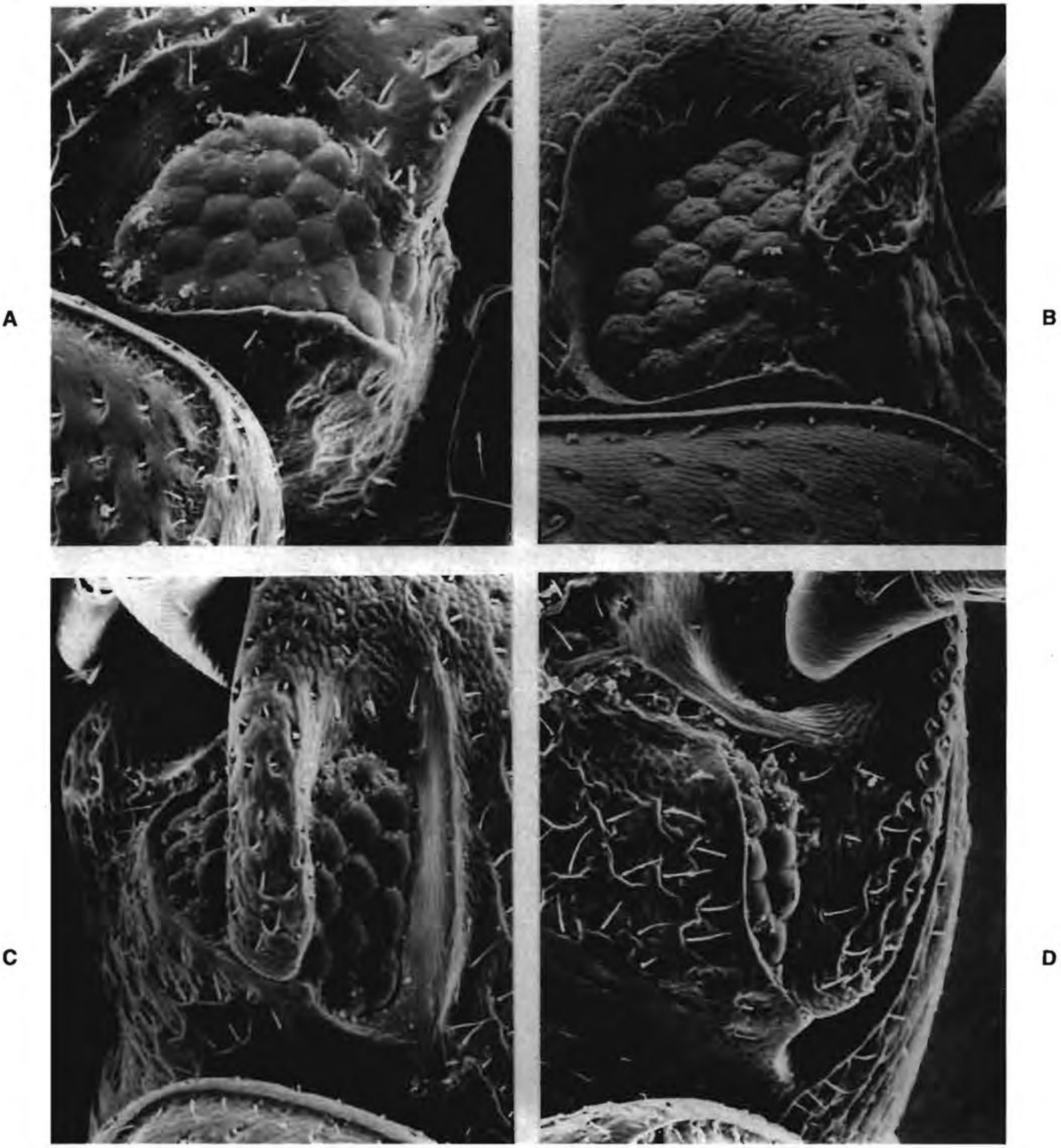

Plate 9

Scanning electron micrographs of eye in *Caenocrypticus (Cryptocarpes)* species. **A**: *C. (C.) elongatus* (Koch) (×390); **B**: *C. (C.) damara* (Koch) (×470); **C**: *C. (C.) dividiopsis* (Koch), lateral view (×390); **D**: same species, ventrolateral view (×360).

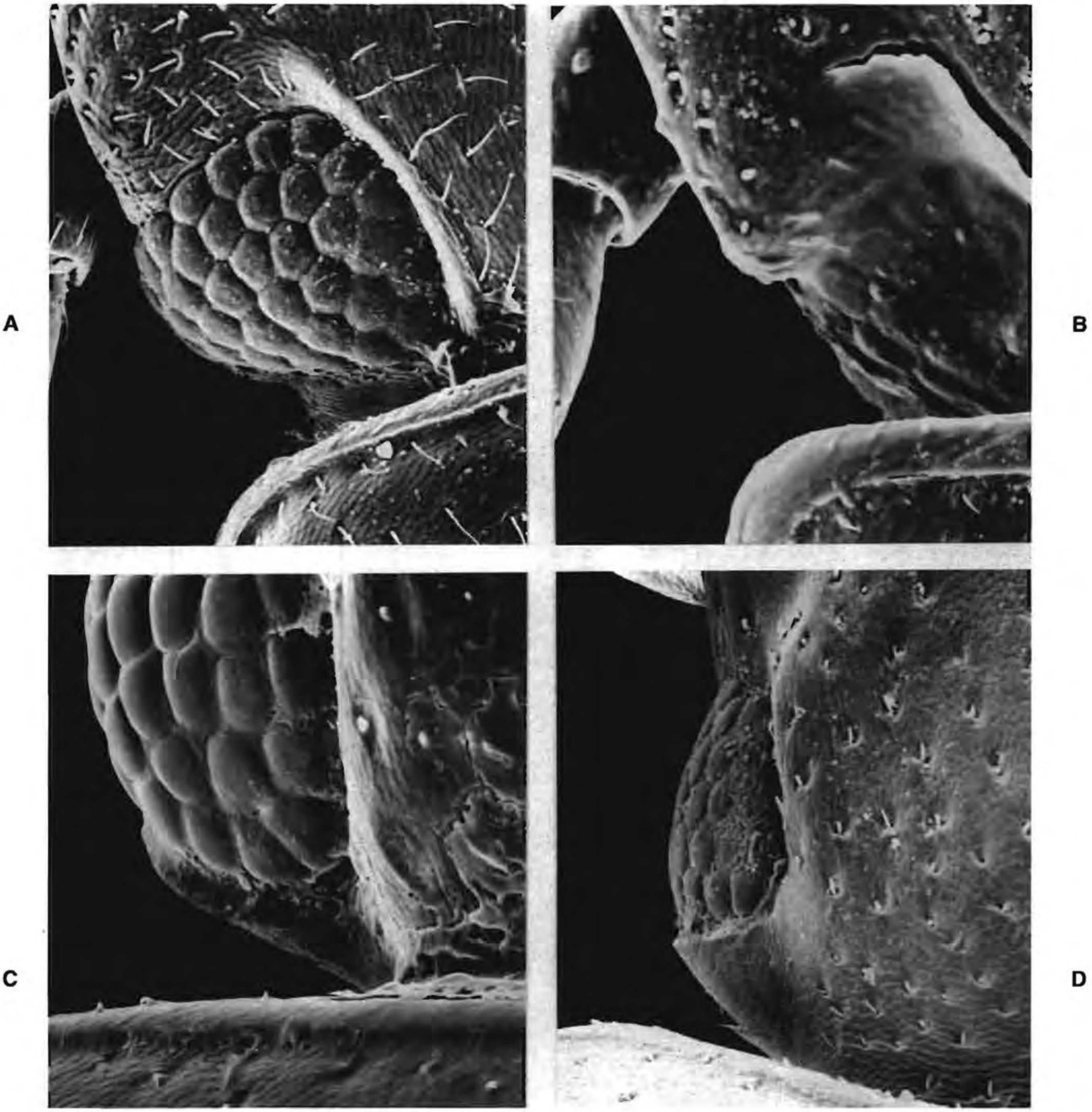

Plate 10

Scanning electron micrographs of eye. **A–B**: *Caenocrypticus (Phyloradix)* species. **A**: nominate subspecies of *C. (P.) soror* spec. nov. (×360); **B**: *C. (P.) bushmanicus* Koch (×600). **C–D**: *Caenocrypticoides* species. **C**: *C. peruanus* spec. nov. (×550); **D**: *C. penai* Kaszab (×200).

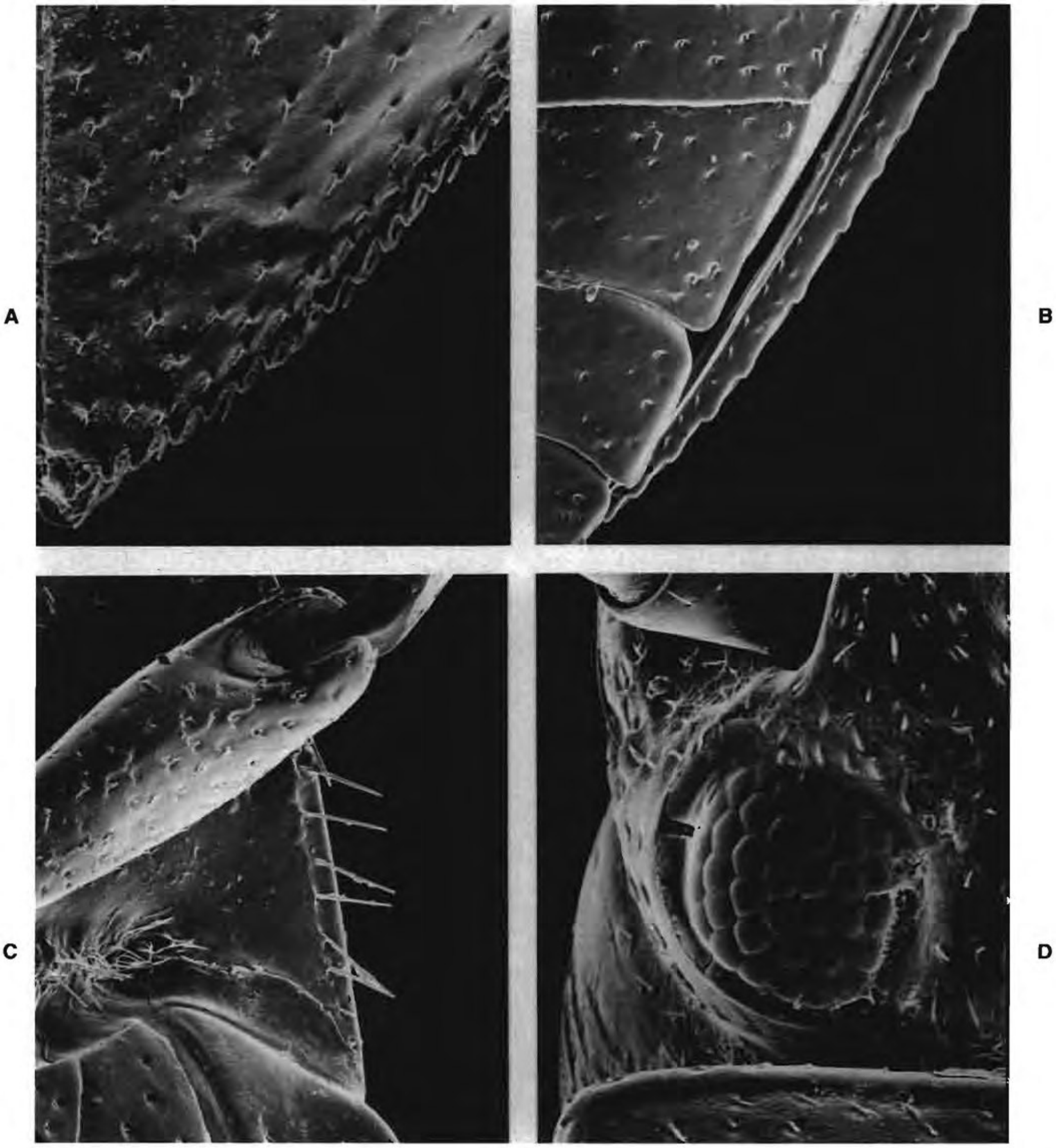

Plate 11

Scanning electron micrographs. **A–B**: lateral serration in **A**: *Caenocrypticus (Vernayella) serratus* spec. nov., dorsal view (×200); **B**: *C. (V.) pauliani* (Koch), ventral view (×120); **C**: *C. (V.) pauliani* (Koch), lateral pilosity of pronotum (×130); **D**: *C. caenocrypticoides peruanus* spec. nov., eye in dorsolateral view (×270).

A

B

Plate 12

A: Namibia: farm Hoheacht. Sparse grass and short bushy vegetation on sandy ground between stones and boulders. Trap site of nominate subspecies of *Caenocrypticus (Phyloradix) soror* spec. nov. Traps both on hilltop (E-Y:741, 433) and on the flats below (E-Y:868).

B: Namibia: Nauwkluft Nature Reserve. Sparse vegetation on coarse sand between rocks. Trap site of *Caenocrypticus (Phyloradix) soror nauwkluftensis* subspec. nov. (E-Y:565).

A

B

Plate 13

A: South Africa: Bushmanland, Pofadder. Rocky ground with Kalahari-type sand ripples. Habitat of *Caenocrypticus (Phyloradix) bushmanicus* Koch.

B: South Africa: Western Cape Province, farm Nortier. Vegetated sand flats near coast. Trap site of *Caenocrypticus (Caenocapicus) capensis* spec. nov. (E-Y:1845).

A

B

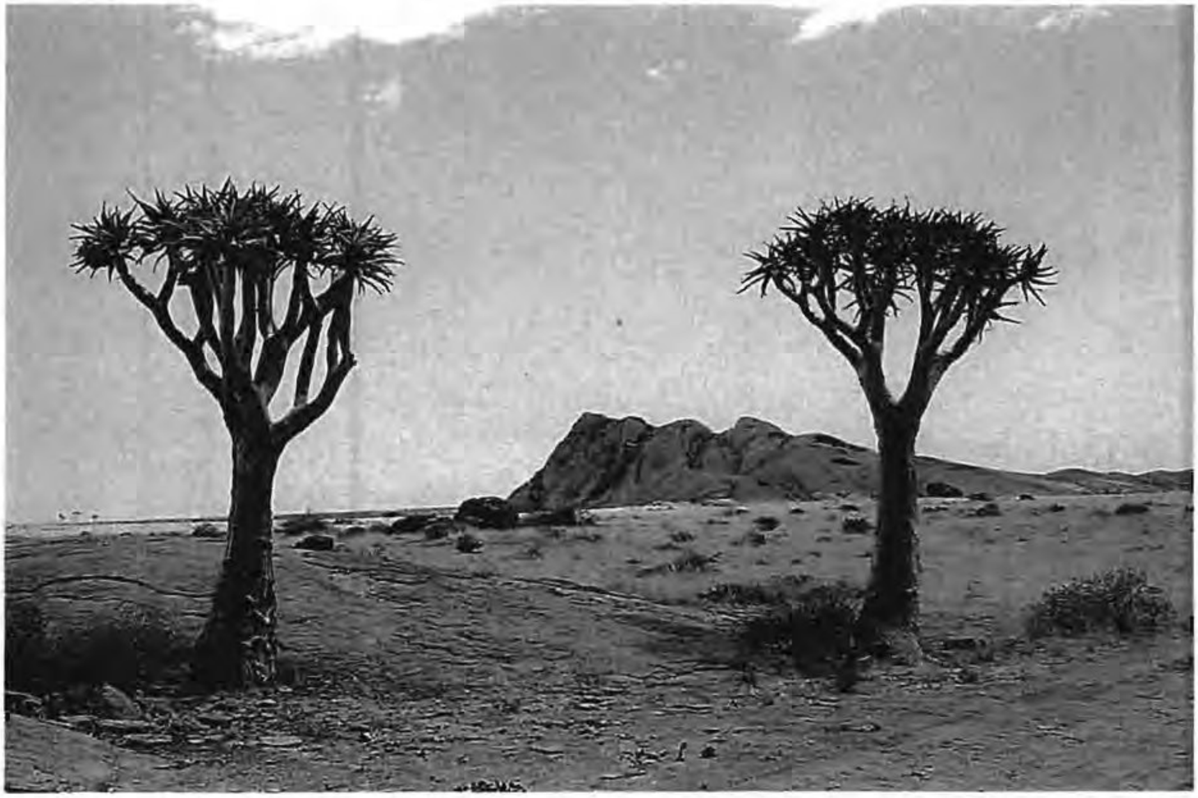

Plate 14

A: Namibia: Sesfontein Basin. Sand-filled gravel flat with sand accumulation around bushes. Locality of *Caenocrypticus (Cryptocarpes) elongatus* (Koch).

B: Namibia: central Namib Desert, Bloedkopee. Sand-filled gravel flats with rocky outcrops. Trap site of *Caenocrypticus (Cryptocarpes) damara* (Koch) and *C. (C.) dividiopsis* (Koch) (E-Y:613).

A

B

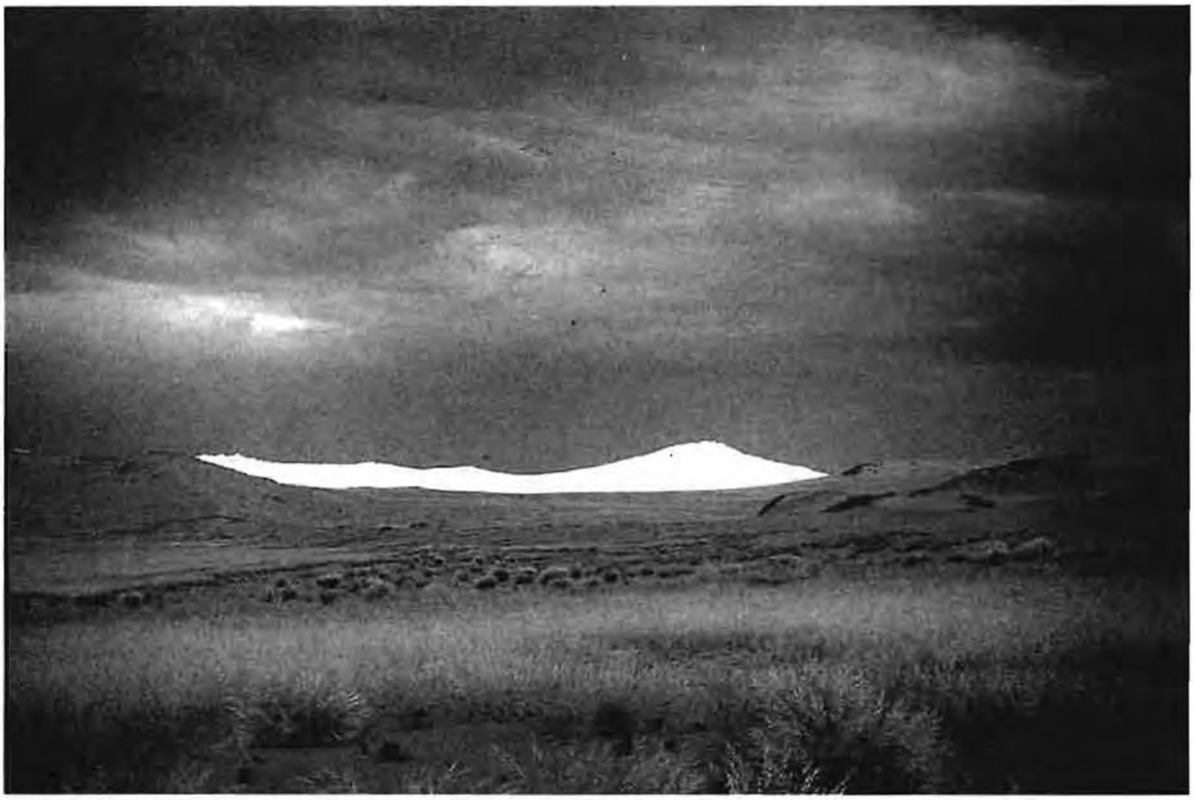

Plate 15

A: Namibia: northern Kaokoveld, south bank of Kunene River. Red sand hummocks on gravelly sandflats. Trap and collecting sites of *Caenocrypticus (Cryptocarpes) dividiopsis* (Koch) (E-Y:2070).

B: Same site as 15A, with white coastal dunes in background (west). Locality of *Caenocrypticus (Vernayella) serratus* spec. nov. and *C. (V.) ephialtes* (Koch).

A

B

Plate 16

A: Namibia: escarpment on the eastern flank of the central Namib Desert, Us Pass. Rocky mountain-side with hummocks and small sand pockets. Trap site of *Caenocrypticus (Caenocrypticus) kaszabi* spec. nov. (E-Y:857).

B: Northeastern Namibia: Kungveld-Botswana border. Dense and short vegetation on compact, red, coarse sand. Collecting site of *Caenocrypticus (Caenocrypticus) macintyrei* Koch at roots of grass (E-Y:1456).

A

B

Plate 17

A: Namibia: Skeleton Coast, Huarusib River, north bank. Sand dunes between rocky outcrops. Bottom of dune slipfaces. Locality of *Caenocrypticus (Psammotopulus) phaleroides* Koch and *C. (Vernayella) ephialtes* (Koch) (E-Y:2120).

B: Namibia: central Namib dune desert, Tsondab Vlei. Locality of *Caenocrypticus (Psammotopulus) phaleroides* Koch at the slipfaces, in the south of the geographic range of species (E-Y:540).

A

B

Plate 18

A: Namibia: southern Namib Desert, Bogenfels dunes. Shifting sand dunes 10 km inland from coast. Collecting site of *Caenocrypticus (Psammotopulus) deserticus* Koch, (E-Y:2656).

B: Namibia: Klinghardt Mountain, inland inselberg in the southern Namib Desert. Sandblown western slope of the mountain. Collecting site of *Caenocrypticus (Psammotopulus) klinghardtmontis* spec. nov. in hummocks and around plants (E-Y:1796).

A

B

Plate 19

A: Namibia: central Namib dune desert, Sossusvlei. At the foot of slipfaces and at different levels on large dunes, collecting site of *Caenocrypticus (Psammotopulus) peezi* Koch, (E-Y:2650).

B: Namibia: Namtib or Kanaän dunes on the inland margin of central Namib dune desert. Trap and collecting site of *Caenocrypticus (Psammotopulus) penrithae* spec. nov. and *C. (P.) peezi* Koch along partly vegetated dunes (E-Y:2641, 2636).

A

B

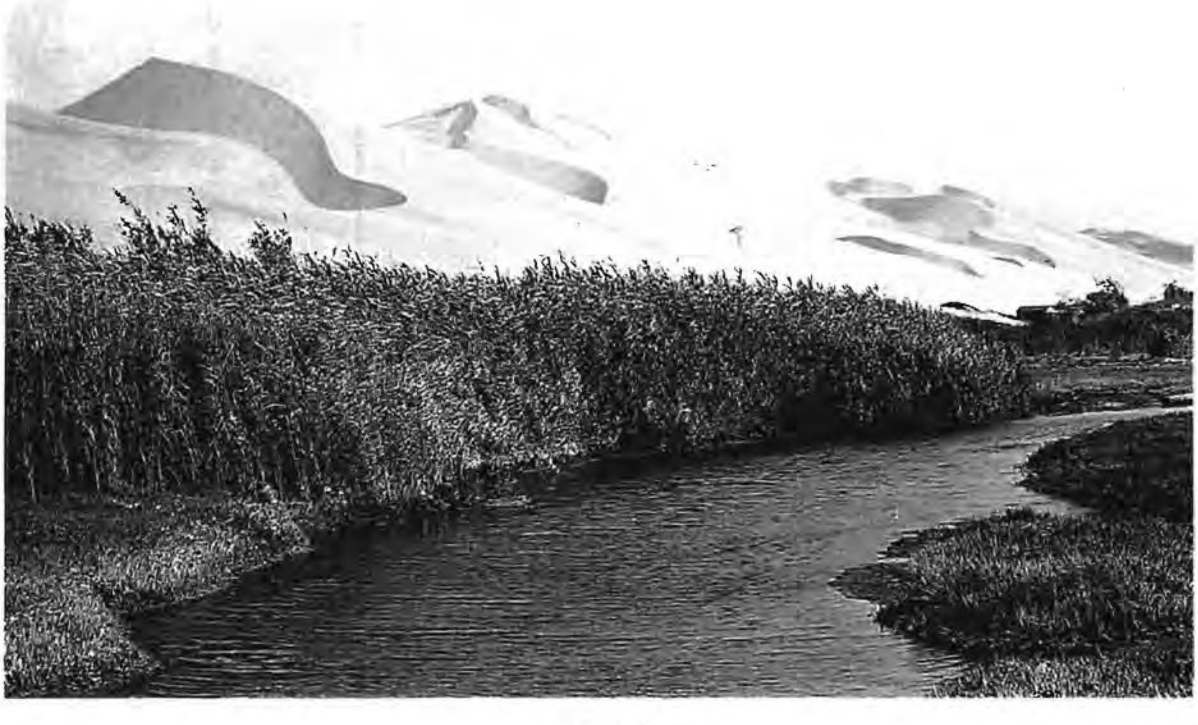

Plate 20

A: Namibia: central Namib dune desert, barren dunes and grass-covered dune-streets on south bank of the Kuiseb River at Gobabeb. Trap site of *Caenocrypticus (Vernayella) noctivagus* (Koch) (E-Y:444) and collecting site of *C. (V.) delabati* (Koch) (E-Y:412) at the foot of the dunes.

B: Namibia: central Namib coast, Sandwich Harbour. High dunes along the coast. Bottom of slipfaces at different levels. Habitat of *Caenocrypticus (Vernayella) ephialtes* (Koch).

Catalogue of the Caenocrypticini

Tribe CAENOCRYPTICINI

Koch, 1958: 39; Kaszab, 1969: 322; Doyen, 1993: 502; Endrödy-Younga, 1996: 12.

Type genus: *Caenocrypticus* Gebien, 1920.

Genus *CAENOCRYPTICUS* Gebien, 1920

Gebien, 1920: 139 (Crypticini); 1938: 508 (Crypticini); Koch, 1950: 79 (Crypticini); 1952: 188 (Caenocrypticini); Endrödy-Younga, 1996: 13.

Type species: *Caenocrypticus uncinatus* Gebien, 1920.

> *Thorictophasis* Koch, 1950: 80; 1952: 188; 1958: 121 (as subgenus of *Caenocrypticus*); Endrödy-Younga, 1996: 14 (syn.).

Subgenus *Phyloradix* Endrödy-Younga, 1996

Type species: *Caenocrypticus* (*Phyloradix*) *soror* Endrödy-Younga, 1996: 16.

soror Endrödy-Younga, 1996: 16.
  subspecies *soror* Endrödy-Younga, 1996: 17.
  subspecies *nauwkluftensis,* Endrödy-Younga, 1996: 18.
bushmanicus Koch, 1950: 81; 1952: 190; Endrödy-Younga, 1996: 18.

Subgenus *Caenocapicus* Endrödy-Younga, 1996

Type species: *Caenocrypticus* (*Caenocapicus*) *capensis* Endrödy-Younga, 1996: 19.

capensis Endrödy-Younga, 1996: 20.

Subgenus *Cryptocarpes* Koch, 1952

Koch, 1952: 191 (as genus in Crypticini); 1958: 121 (as genus in Caenocrypticini); Endrödy-Younga, 1996: 21 (subgenus).

Type species: *Cryptocarpes elongatus* Koch, 1952.

> *Lornamus* Koch, 1952: 191 (as genus in Crypticini); 1958: 121 (as in Caenocrypticini); Endrödy-Younga, 1996: 21 (synonym)

elongatus (Koch), 1952: 191; Endrödy-Younga, 1996: 21.
damara (Koch), 1958: 128; Endrödy-Younga, 1996: 22.
dividiopsis (Koch), 1952: 191 (*Lornamus*); 1958: 128; Endrödy-Younga, 1996: 24.

Subgenus *Caenocrypticus* (*s. str.*) Gebien

Type species: *Caenocrypticus uncinatus* Gebien, 1920.

uncinatus Gebien, 1920: 140; 1938: 508; Koch, 1950: 80; 1952: 189; Endrödy-Younga, 1996: 25.
kaszabi Endrödy-Younga, 1996: 26.
wittmeri Endrödy-Younga, 1996: 27.
macintyrei Koch, 1952: 190; Endrödy-Younga, 1996: 28.

Subgenus *Psammotopulus* Endrödy-Younga, 1996

Type species: *Caenocrypticus* (*Psammotopulus*) *penrithae* Endrödy-Younga, 1996: 29.

phaleroides Koch, 1950: 84; 1952: 191; Endrödy-Younga, 1996: 29.
deserticus Koch, 1950: 82; 1952: 190; Endrödy-Younga, 1996: 31.
klinghardtmontis Endrödy-Younga, 1996: 32.
peezi Koch, 1958: 128; Endrödy-Younga, 1996: 33.
penrithae Endrödy-Younga, 1996: 34.
holmi Endrödy-Younga, 1996: 35.

Subgenus *Vernayella* Koch, 1958

Koch, 1958: 129 (as genus in Caenocrypticini); Endrödy-Younga, 1996: 35 (subgenus).

Type species: *Vernayella noctivaga* Koch, 1958.

noctivagus (Koch), 1958: 130; 1962: 156; Endrödy-Younga, 1996: 36.
ephialtes (Koch), 1958: 132; 1962: 156; Endrödy-Younga, 1996: 37.
kochi Endrödy-Younga, 1996: 38.
pauliani (Koch), 1962: 155; Endrödy-Younga, 1996: 39.
serratus Endrödy-Younga, 1996: 40.
delabati (Koch), 1962: 154; Endrödy-Younga, 1996: 41.

Genus *CAENOCRYPTICOIDES* Kaszab, 1969

Kaszab, 1969: 322; Endrödy-Younga, 1996: 42.

Type species: *Caenocrypticoides loksai* Kaszab, 1969.

peruanus Endrödy-Younga, 1996: 42.
penai Kaszab, 1969: 325; Endrödy-Younga, 1996: 43.
loksai Kaszab, 1969: 323; Endrödy-Younga, 1996: 43.
translucidus Kaszab, 1969: 324; Endrödy-Younga, 1996: 44.

Gazetteer

A

Abrahamskraal (South Africa)	33.14S - 18.09E
Agatstrand	26.36S - 15.10E
Aggeneys (South Africa)	29.12S - 18.51E
Alexander Bay (South Africa)	28.40S - 16.30E
Anigab Dunes	26.18S - 15.02E
Aurus Mt (South Africa)	27.50S - 16.20E
Aus (South Africa)	26.41S - 16.16E
Azapa (Chile)	18.30S - 70.15W

B

Bayo Tigres (Angola)	16.36S - 11.43E
Beauvallon Farm (South Africa)	28.33S - 16.36E
Bethanien	26.46S - 17.13E
Bethanis Farm	20.25S - 14.24E
Bloedkopee	22.50S - 15.23E
Boegoeberg	27.54S - 15.56E
Bogenfels Dunes	27.27S - 15.24E
Bosluisbaai	17.23S - 11.46E
Bookram Farm (South Africa)	32.39S - 18.17E
Brakfontein Farm (South Africa)	32.56S - 18.15E
Brandkaross	28.28S - 16.40E
Buffels River (South Africa)	29.55S - 17.40E

C

Camana (Peru)	16.38S - 72.29W
Cape Columbine (South Africa)	32.48S - 17.51E
Cape Fria	18.14S - 12.01E
Cape Town (South Africa)	33.56S - 18.28E
Chanquas Farm	23.04S - 15.55E
Chausib Farm	23.20S - 16.05E
Churutabis 108 Farm	27.25S - 17.27E

D

De Hope (South Africa)	28.12S - 17.12E
Dikdoorn Farm (South Africa)	30.43S - 18.00E
Doornpoort (South Africa)	not traced
Doornkloof (South Africa)	not traced
Duiker Island (on continent) (South Africa)	32.43S - 17.56E
Dune 7, E Walvisbaai	22.56S - 14.34E

E

Ebony	22.04S - 15.16E
Eksteenfontein (South Africa)	28.50S - 17.16E
Elands Bay, N Dunes (South Africa)	32.18S - 18.21E
Elephant Valley	23.40S - 15.15E
Elisabeth Bay	26.54S - 15.12E
Engo River Crossing	17.50S - 12.10E
Excelsior 59 Farm	26.10S - 16.29E

G

Galaus 6 Farm	27.40S - 17.44E
Ganab Hotsas	23.00S - 15.25E
Garies (South Africa)	30.30S - 18.00E
Gautscha Pan	19.48S - 20.35E
Geelbek Farm (South Africa)	33.12S - 18.07E
Gelykswerf Mt (South Africa)	28.22S - 17.07E
Gemsbokvlakte (South Africa)	30.30S - 17.29E
Goageb	26.46S - 17.13E
Gobabeb Dunes	23.34S - 15.03E
Gorob Mine	23.33S - 15.25E
Gorrasis 99 Farm	25.19S - 15.56E
Grasplatz	26.44S - 15.17E
Grootderm Farm (South Africa)	28.31S - 16.38E
Grootdrif Farm (South Africa)	32.24S - 18.27E
Guinasibberg	25.17S - 15.16E
Guisis 180 Farm	23.50S - 16.15E

H

Haalenberg	26.38S - 15.29E
Haris	26.34S - 15.25E
Hartmansberg	17.12S - 12.10E
Hauchab River at:	25.10S - 15.10E
Heioab Farm	27.25S - 15.59E
Helskloof Neck (South Africa)	28.20S - 16.59E
Hereroland E, Farm 855	21.59S - 20.02E
Hoanib River Mouth	18.53S - 12.25E
Hoanib Water	19.27S - 15.47E
Hoarusib River at:	18.03S - 12.36E
Hoekbaai (South Africa)	31.11S - 17.47E
Hoheacht Farm	24.40S - 16.23E
Homeb	23.39S - 15.10E
Hottentots Bay	26.08S - 15.02E
Huacho (Peru)	11.05S - 77.36W
Huarmey (Peru)	10.03S - 70.08W

J

Jakkalsputs Farm (South Africa)	28.38S - 16.54E

K

Kakamas (South Africa)	28.45S - 20.33E
Kanaän 104 Farm	25.58S - 16.02E
Kharu-Gaiseb River at	19.53S - 13.10E
Khorixas	20.21S - 14.57E
Khumib River Mouth	18.53S - 12.25E
Klein Spitzkoppe	21.50S - 15.09E
Klinghardt Mt, E Dunes	27.33S - 15.50E
Klinghardt Mt	27.18S - 15.42E
Kliphoutkop (South Africa)	32.17S - 18.24E
Koichab Pan	26.18S - 15.36E
Kuboos (South Africa)	28.27S - 16.59E
Kubub (South Africa)	26.47S - 16.59E
Kuiseb Delta	23.03S - 14.27E
Kunene River Mouth	17.16S - 11.48E

L

Lamberts Bay, inland dunes (South Africa)	32.05S - 18.24E
Langebaanweg (South Africa)	32.57S - 18.08E
Lima, 220 km N (Peru)	*c.* 10.58S - 77.35W
Lüderitz	26.35S - 15.10E

M

Meobbaai	24.30S - 14.37E
Moçamedes (Angola)	15.10S - 12.16E
Mollendo (Peru)	17.00S - 72.00W
Mövebaai	19.22S - 12.42E
Munitum River at :	18.10S - 12.13E

N

Nabeis (South Africa)	28.51S - 20.09E
Namtib Dunes *See* Kanaän	

Natab	23.38S - 15.04E
Nauwkluft	24.16S - 16.15E
Nortier Farm (South Africa)	32.03S - 18.19E
Nubib 42 Farm	25.05S - 16.13E
Nubib Farm	*24.59*S - 16.09E

O

Obib Dunes	28.02S - 16.37E
Ohopoho	18.03S - 13.50E
Okarukondovi Farm	21.35S - 18.10E
Okau	18.19S - 12.06E
Oranjemund	28.33S - 16.27E
Orange River Flats (South Africa)	28.28S - 16.51E
Oropembe	18.10S - 12.33E
Osona (Okahandja)	22.00S - 16.55E

P

Perdekraal Farm (South Africa)	30.46S - 17.53E
Pofadder (South Africa)	29.09S - 19.25E
Pomona	27.13S - 15.28E

R

Rio Lauca at Azapa (Chile)	*c.* 18.30S - 70.15W
Rio Tambo (mouth) (Peru)	17.11S - 71.50W
Rocky Point	18.59S - 12.30E
Rössing Mt	22.31S - 14.45E
Rooibank	23.09S - 14.39E
Rooiberg (South Africa)	28.12S - 17.07E
Rooivlei Farm (South Africa)	31.05S - 17.52E
Rosh-Pinah (South Africa)	27.53S - 16.50E

S

Saddle Hill	24.54S - 14.55E
Samanab River	20.02S - 13.19E
Samengeigei	19.06S - 20.12E
Sandverhaar 80 Farm	26.52S - 17.22E
Sandwich Harbour	23.19S - 14.30E
Sanitatas	18.18S - 12.41E
Sargdeckel	27.24S - 15.40E
Sesfontein	19.08E - 13.36E
Seweputs (coast) (South Africa)	31.39S - 18.17E
Seweputs Farm (South Africa)	31.39S - 18.22E
Sossusvlei	24.40S - 15.24E
Spencer Bay	25.43S - 14.50E
Spencer Bay Water	25.47S - 14.54E
Spes Bona 62 Farm	25.33S - 16.17E
Steinkopf (South Africa)	29.15S - 17.44E
St Francis Bay	25.06S - 14.52E
St Helenafontein (South Africa)	32.36S - 18.20E
Suiderkruis Farm	25.05S - 16.13E
Swakopmund	22.40S - 14.31E
Swartbooisdrift	17.20S - 13.50E

T

Terrace Bay	19.58S - 13.02E
Trekkopje	22.32S - 15.01E
Tsauchab River Dunes	24.40S - 15.30E
Tsondab Vlei	23.59S - 15.26E
Tumbre (Chile)	not traced

U

Unjab River	20.08S - 13.18E
Unjab River Dunes	20.10S - 13.16E
Upper Holgat River (South Africa)	28.43S - 17.07E
Uri-Hauchab Mt	25.22S - 15.10E
Ururas	23.14S - 14.44E
Us Pass Centre	22.42S - 16.02E
Us Pass - Namib Park Gate	23.03S - 15.44E

V

Veldrif (South Africa)	32.46S - 18.14E
Verlorevlei Farm (South Africa)	32.19S - 18.22E
Vogelstrausskluft 87 Farm	27.01S -17.34E
Voigtsland Farm	22.33S - 17.11E
Vreemdelingspoort Farm	24.47S - 15.46E

W

Walvisbaai	22.58S - 14.30E
Welwitschia *See* Khorixas	
Wiedouw Farm (South Africa)	31.43S - 18.43E
Wildepaarde Hoek (South Africa)	29.57S - 17.33E
Windhoek	22.34S - 17.06E
Wissenborn Farm	26.03S - 16.24E
Witberg	24.07S - 15.52E
Witteberg	24.50S - 15.17E

Y

Yzerfontein Farm (South Africa)	33.20S - 18.12E

Z

Zesfontein *See* Sesfontein

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