RESTRUCTURING OF THE TRIBE CRYPTOCHILINII
(COLEOPTERA: TENEBRIONIDAE: TENTYRIINAE)

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The higher classification of taxa related to the traditional tribe Cryptochilini is revised. As a result two monotypic tribes are incorporated as the subtribes Calognathina and Vansoniina in the tribe Cryptochilini. An additional subtribe, Homebiina, is proposed for a recently discovered apomorphic Namib desert species, Homebius kaszabi gen. et spec. nov. A new subspecies, Calognathus chevrolati lucanoides, is also described.

In a recently discovered small group of species, a unique form of sexual dimorphism was found. The males fit conveniently into a known genus of Cryptochilini, but the females do not resemble anything within or outside the tribe. This lineage of species is described under the names Cerasoma irrea/e, C. cerasus and C. kochi gen. et spp. nov. within the Cryptochilini. The notion that the lineage originated from a sympatrically occurring Cryptochile species by saltatorial change warrants investigation.

Keywords: Southern Africa, Systematics, Phylogenetics, Coleoptera, Tenebrionidae, Tentyriinae.

INTRODUCTION

This study originated in an effort to find a logical affiliation for two markedly different tenebrionids discovered almost simultaneously on the sandy west coast of Southern Africa. One of the enigmatic forms (described as Cerasoma gen. nov. below) with highly anomalous females, was deduced by a process of exclusion to belong to the tribe Cryptochilini. At that stage of the investigation, however, there was no clear indication whether the other form (described as Homebius gen. nov. below) belonged to the subfamily Tentyriinae at all.

A characteristic feature of Cerasoma females is their small head, which is unusual among the Cryptochilini. A wealth of material of Cryptochilini, then largely unidentified, was screened for small heads. As a result, two sets of seemingly cryptochile species were found that exhibited this character, but otherwise they were highly dissimilar. At first it seemed only peculiar that the dissimilar sets with small head came, without exception, from the same samples. Among these sets of specimens, all the bulbous, cherry-like specimens were females, and all the Cryptochile-like ones males. The matching of sexes became clear when the populations of both localities could be separated at species level, differing from each other in the same characters in both sexes.

During the detailed description of these species, the few knobs on the vertex (the position of the stridulatory organ in the Cryptochilini) seemed to be hardly suitable as a pars stridens to produce the sound heard when handling specimens. Eventually, the pars stridens was found in the inner anterior margin of the pronotum, whereas the knobs of the vertex proved to be a characteristic type of plectrum. This type of vertico-pronotal stridulation is unparalleled in the Tenebrionidae, but is the common characteristic of all Cryptochilini.

When the same vertico-pronotal stridulatory organ was found in Homebius kaszabi, its position in the Cryptochilini was established. Furthermore, the same organ was found in Vansonium bushmanicum, resulting in its inclusion in the same tribe. Calognathus chevrolati, now also included, is the only species of the restructured tribe that lacks a specialized stridulatory organ. Its diagnostic characters are, however, insufficient to separate it from Vansonium at tribal level, and it is thus considered to be an apomorphic offshoot of the alter by the loss of the key character of the tribe, the vertico-pronotal stridulatory organ.

Thus the systematic problem of the tenebrionid tribe Cryptochilini, and with it the position of the enigmatic monotypic tribes Calognathini and Vansoniin, seems to be solved.

The monophyletic origin of the tribe is indicated by the unique vertico-pronotal stridulatory organ, but the extraordinary diversity reached within the tribe is worthy of consideration. The subtribe Cryptochilina is composed of more than 120 species, which, with the exception of Cerasoma females, are reasonably similar. The three other subtribes are strikingly different and are all monotypic. The monotypic subtribes and the overwhelming majority of Cryptochilini inhabit the same southwestern zoogeographic zone.
(Endrödy-Younga, 1978: 819). It is hypothesized that this diversity may have come about by an unusual high rate of speciation in all four lineages leading to the subtribes, and that it was matched by a similar rate of extinction in three lineages but not in Cryptochilina. In a small group of Cryptochilina of the genus Cerassoma, however, an adaptation-based transformation series of extinct species can hardly be postulated.

In Cerassoma the males are very similar to some Cryptochilina species and differ only slightly from an undescribed sympatric species of that genus. It is therefore difficult to imagine a number of missing links that led to the gross morphological anomaly of the other sex only. It is difficult to imagine an adaptation-based transformation series of extinct species where the same environmental pressure did not affect the Cerassoma males, nor the females of the sympatric and a dimorphic ancestral stock.

In addition to the unusual sexual dimorphism, biological anomalies also mark the genus Cerassoma. Females of this genus are the only nocturna Cryptochilini. The significance of this change can be demonstrated by the observation that diurnal or nocturnal activity is a tribal attribute in Southern African Tentyriinae. There are no nocturnal Zophosini or diurnal Eurychorini. Although Cerassoma males were collected at night when the females were active, many were also collected in the afternoon at least on the Lamberts Bay dunes. This is the usual activity period of all Cryptochilini when they are sufficiently camouflaged by their mottled colouration. This is not the case in females with their bulky body, shiny deep red colour and slow movement on the white dunes, would be a perfect target for predators during the day. The change to nocturnal activity in Cerassoma must have been led by the female and can be viewed as an adaptation. It is suggested that this adaptation was induced by a mutation and not primarily by environmental pressure. If the phenotypic reflection of the genetic change was similar in both sexes, the placement of the group would have been difficult, not only within but also outside the tribe Cryptochilini. Is this case not similar to that of Calognathus, a curious lucanid-like tenebrionid, duly considered to constitute a tribe in its own right? In the latter case, however, the male was more affected, as is usual in many beetle families. A scenario worth investigating is that an initial macromutation manifested itself in some cosexual changes, such as the small head (which is paralleled in the genus Erodioides Knoch) and that it also grossly altered the habits of the female. At least one character change from the postulated ancestral species (stock) is the elongation of the tarsi in males. Although this feature might be useful to mount the suddenly double-sized females, it can hardly be attributed to gradual adaptation. Should such a mutation have occurred in the ancestral Cerassoma species, it was not an imminent failure, nor did it lead to a dead end, as seems to be the case in Calognathus, but was followed by adaptation-based allopatric speciation as in the Cryptochile parental stock. There are strong phenotypic indications that Cerassoma can be derived from one particular Cryptochile species, which is composed of four subspecies (Dr M.-L. Penrith, in preparation), and whose geographic range includes the same dunes where two of the Cerassoma species occur.

DEFINITION OF THE TRIBE CRYPTOCHILINI

A single unique and apomorphic character, the presence of a set of stridulatory ripples on the vertex (plectrum) and the pars stridens in the inner anterior margin of the pronotum, establishes the tribal status of the group in the subfamily Tentyriinae (Fig. 13A, 14A–C). The only exception is Calognathus, which has no stridulatory files on the vertex but only scattered tubercles. It stridulates also by moving its head dorsoventrally. Calog­nathus, however, owing to its many derived characters, cannot be considered an ancestor to the rest of the tribe. Moreover, its common ancestry with Vansonium is very likely. The absence of a stridulatory file in this monotypic genus is thus considered to be a secondary loss. The affiliation of the group to the subfamily Tentyriinae is indicated by the absence of an exposed intersegmental membrane between the last sternites and by the inverted position of the aedagus. The synonymy of the subfamily name Tentyriinae with the senior name Pimeliinae has been suggested (Watt, 1974). Watt combines these two groups in a single subfamily though recognizes the above-mentioned differences between them. The suggested change in the higher classification affects the best known name and largest group of southern African tenebrionids and has to be considered in a paper devoted to this problem.

The tribe Cryptochilini furthermore belongs to the group of tribes within the subfamily Tentyriinae which all have a narrow mentum, leaving the cardo and stipes of the maxillary palpi exposed (Fig. 2A–D). After the inclusion of two former tribes as the subtribes Calognathina and Vansonina in the tribe Cryptochilini, only two other tribes remain in the group: Molurini, with exposed trochantins, and
Stenosini, with the junction of head to pronotum pedunculato, and the temporal portion of the head extremely long.

The degree of diversity in many characters is such that without the common, unique, and undoubtedly monophyletic character (vertical stridulatory plectrum), the unity of the group would have been difficult to prove. Moreover, the character complex of any one subtribe is composed of a diversity of plesiomorphic and apomorphic characters, making a phylogenetic reconstruction virtually impossible. In some characters the different states are manifested in the proposed subtribes as their unique properties; other characters show the whole range of states in the Cryptochilini, the only markedly diverse subtribe of Tentyriinae.

**Tribe CRYPTOCHILINI sens. nov.**


Type genus: Cryptochilus Latreille, 1829

The tribe Cryptochilini, in its present composition, is composed of four subtribes: three previously recognized as tribes, Cryptochilina, Calognathina, and Vansonina, and a new subtribe Homebiina, based on a recently discovered species, Homebius kaszabi spec. nov.

Small to medium sized (3-20 mm). Body globose to elongate cylindrical, occasionally dorsoventrally compressed. Integument usually with pattern-forming scaly vestiture or dense pubescence, occasionally only with a few long setae. In some characters the dorsum is armed with rows of sharp spikes.

Head broad but usually considerably narrower than pronotum; when in a deflected, hypognathous position, retracted into the cavity of the pronotum (Fig. 12A). In two subtribes, however, the head is very broad, hardly narrower than the temporal portion of the head, with completely sclerotized surface of the proepisternum (Fig. 1A-O). Procoxal cavities usually closed behind (Fig. 3C), but occasionally open externally in Vansonini and some species of Cryptochilina (Figs 3A-B). Antennae usually 10-segmented (Fig. 4A-F, 5A), rarely 9-segmented (Vansonium, Fig. 5B; and Homebius, Fig. 5C-D). There is a general tendency in the tribe to form antennal clubs, unusual in the family, in club formation the last one (Homebiina), which has most of the plates fused (Fig. 2A). Mes- and metepisterna well demarcated (Fig. 2B); and in a single case (male Calognathus) much enlarged, giving a lucanoid appearance (Fig. 1C). It is non-functional in Homebiina, where a structure of unknown anatomy overlies it (Fig. 1D). Antennae usually small or very small, concealed beneath labrum in closed position (Fig. 1A), they might, however, be permanently exposed (Fig. 1B), and in a single case (male Calognathus) much enlarged, giving a lucanoid appearance (Fig. 1C). It is non-functional in Homebiina, where a structure of unknown anatomy overlies it (Fig. 1D). Antennae usually 10-segmented (Fig. 4A-F, 5A), rarely 9-segmented (Vansonium, Fig. 5B; and Homebius, Fig. 5C-D). There is a general tendency in the tribe to form antennal clubs, unusual in the family, in club formation the last one (Homebiina) (Fig. 5C-D), or two segments may be involved. The extremes develop in males of Cerasoma, where the combined length of the two apical segments is almost as long as the rest of the antenna, or more than a quarter of the body length (Fig. 4E).

Prosternum usually with a clear suture demarcating the proepisternum (Fig. 1A-D). Procoxa cavities usually closed behind (Fig. 3C-D), but open externally in Vansonini and some species of Cryptochilina (Fig. 3A-B). Anterior portion of the prosternum simple, with the exception of the genus Cryptochile (Cryptochilina), where it is sharply elevated, forming a collar-like structure (Fig. 2A). Mes- and metepisterna well demarcated in all species (Fig. 2A-C), with one exception (Homebiina), which has most of the plates fused and only the sterna and the mesopimeron are clearly separated (Fig. 2D).

Legs usually with small trochanters that are, however, conspicuously enlarged in Homebiina. Tarsi shorter than or as long as tibiae in most species (Fig. 12A), but conspicuously long in males of Cerasoma. Characteristic sand-adaptive features appear in species living on soft sandy substrates, for example enlarged and often explanate tibial spurs and long, soft pilosity (Fig. 19C).

Aedeagus in an inverted position in the body cavity, with completely sclerotized surface of aedeagus in a ventral position and its longitudinal...
membranous groove as well as the basal aperture in a dorsal position (subfamily character); if aedeagus curved, apex points upward. Aedeagus symmetrical, elongate and more or less parallel, consisting of basal and apical, the latter considered to be the basally fused parameres.

The unique type of stridulatory organ is the character that indicates the common ancestry and kinship between the groups of the newly defined tribe Cryptochilini. The organ is situated between the vertex of the head and the inner anterior margin of the pronotum. The finely striolate pars stridens (file) is in the pronotal margin (stable part) (Fig. 15B), whereas the plectrum (scraper) is on the vertex (moving part) (Fig. 15A). The plectrum consists of an axillary set of six to twelve sharp and narrow crests or nodules, whereas the pars stridens occupies, at its most extant form (Pachynotatus), the whole dorsal portion of the inner margin of the pronotum. The most common type of stridulation in tenebrionids is the gular-prosternal type (e.g., Platynotini, Oncotini), where the pars stridens is on the moving part (gula) (Fig. 15D). However, in Cerambycidae, for example, the plectrum is on the moving part (pronotum) and the pars stridens on the stable part (mesoscutum). The stridulatory organ is apparently subject to gradual reduction in the tribe. It is fully developed in Cryptochilina. The plectrum is reduced to a set of nodules in Vansoniina and Homebiina, the former lacking a striolated pars stridens in the pronotum. The development stage of the pars stridens in the two known specimens of Homebius was not ascertained. In Calognathina there is no trace of a specialized stridulatory organ. A similar reduction can be assumed in Drosocinii (Fig. 15C).

The centre of distribution of the tribe is the central portion of the Namib, where all four subtribes occur. The highest species diversity can be observed along the western coastal area from southern Angola through the edges of the dune Namib, Richtersveld, and Namaqualand to the southwestern Cape coast. The subtribe Cryptochilina radiates further into most regions of Southern Africa and into East Africa. Of the remaining three subtribes only Vansoniina occurs further inland from the coastal regions into Bushmanland (Fig. 7).

**KEY TO THE SUBTRIBES OF CRYPTOCHILINI**

1(4) Mandibles small, in closed position concealed by labrum in both sexes (Fig. 1A) or reduced (Fig. 1D). Head small compared with rest of body, deflected (Fig. 12A). Scutellum tiny but exposed.

2(3) Antenna 10-segmented, club if distinct composed of two apical segments (Fig. 4A-F). Labrum exposed (Fig. 2A). Episterna and epimera of meso- and metasterna well demarcated (Fig. 1A). Metacoxal cavities round (Fig. 2A). Trochanters small. Mandibles functional............................. Cryptochilina

3(2) Antenna 9-segmented, last segment enlarged to form a club (Fig. 5C-D). Labrum absent. All lateral plates of meso- and metasternum with exception of mesepimeron fused (Fig. 2D). Metacoxal cavity elongate, slot-like, almost reaching lateral margin of sterna (Fig. 5D). Trochanters large. Mandibles reduced or functional ........................................ Homebiina

4(1) Mandibles in males large, of lucanoid proportions (Calognathus), or at least strongly protruding in front of mentum (Vansonium). In females, basal portions of mandibles broadly exposed on either side of mentum. Head very large compared with size of pronotum and rest of body, prognathous (Figs 17, 18). Scutellum concealed.

5(6) Antenna 9-segmented (Fig. 5B). Vertical stridulatory file present. Mandibles of males less prominent (Fig. 19). Eye scaly. Procoxal cavity open behind (Fig. 3). Metacoxal cavity round (Fig. 2B)............................ Vansoniina

6(5) Antenna 10-segmented (Fig. 5A). Vertical stridulatory file absent. Mandibles of males lucanoid (Fig. 17). Eye without scales between ocular facets. Procoxal cavity closed behind (Fig. 3C). Metacoxal cavity transverse .......................................................... Calognathina
Subtribe Cryptochilina stat. nov.


The subtribe Cryptochilina remains within the definition and composition of the former tribe Cryptochilini. Its present reduced taxonomic status is due to the inclusion of related taxa (Vansoniiina, Calognathina and Homebiina) in an enlarged concept of the tribe Cryptochilini.

This subtribe is at present the subject of a detailed revision by Dr M.-L. Penrith, Transvaal Museum. It is composed of a number of closely related genera and a considerable number of species.

Small to medium sized (3–18 mm). Body globose or elongate ovate semicylindrical, elytra sometimes flattened. Surface usually with pattern-forming scaly vestiture. Costal elements of elytra vary from virtually absent through distinct and continuous to serrate or spiky.

Head deflected, almost as broad as pronotum, to conspicuously small, vertex always with a set of narrow stridulatory scrapers (plectrum). Eye dorsoventrally elongate-ovate or more or less reniform with anterior margin indented by the genal canthus; occasionally round almost as it is in the other three subtribes, but bordered anteriorly by the laterally protruding angle of the genal canthus. Mouthparts together with mandibles inconspicuous, latter set close together; labrum well developed and exposed, in dorsal view covering the closed mandibles entirely or almost entirely. Menticum also well developed but narrow, exposing base of maxillary palpi (Fig. 1 A). Antennae always 10-segmented with a two-segmented club.

Shape and size of antennal club usually show sexual differences; the degree of dimorphism can be extremely high.

Proepisternum well demarcated (Fig. 2 A). Procoxal cavity usually closed behind but species with open cavities (Fig. 3 A) occur even in the same genus as species with externally closed ones. Anterior margin of proepisternum flat and level with gula or forming a highly elevated collar (Fig. 2 A). All lateral plates of sterna and epimera well demarcated, metepisternum a broad plate with inwardly arcuate axillary margin. Metacoxal cavity roundish (Fig. 2 A).

Legs rather short, tarsi shorter than or equal in length to tibiae, occasionally extremely short to a quarter of tibial length, length and thickness frequently sexually dimorphic. In the males of a single genus the tarsi are extremely elongate, meso- and metatarsi being much longer than corresponding tibiae (Cerasoma). Characteristic sand adaptations such as long and deplanate tibial spurs and long pilosity occur in species living on soft sandy substrata, particularly in the genus Pachynotelus.

Basic structure of aedeagus as in the other subtribes.

DISTRIBUTION. The members of the only species-rich subtribe Cryptochilina are widely distributed over most of western Southern Africa, and penetrate into tropical East Africa.

As this tribe is being revised by Dr M.-L. Penrith, here only a single genus with an unusually small head and extraordinary sexual dimorphism will be described.

Cerasoma gen. nov., Figs 2 A, 4 B–F, 6, 12 B–D, 13, 14 A–C, 15 A–B, 16 A–B

Type species: Cerasoma cerasus spec. nov.

The new genus is most closely related to Cryptochile Latreille, the male specimens of these two genera being very similar in their general habitus (Fig. 12 A–B). The most striking feature of the species of Cerasoma is the extreme and unique sexual dimorphism, both in quality and degree of morphological deviation.

Head very small in proportion to body (Fig. 12 B–C), comparable only to Homebius. Supraorbital canthus separated from eye by a smooth, usually deeply incised anterior and dorsal fossa of the latter. Pronotum with continuous lateral marginal carina (males only). Metepimeron concealed. Tarsi of male conspicuously long, up to almost twice the length of corresponding tibia (males) (Fig. 12 B). Legs and lateroventral portion of body with very long, silky pubescence (Fig. 12 B). In females, body inflated, bubble-like, unicolourous deep red (like a ripe cherry), elytra without sharp primary costae and scales (Fig. 12 C–D).

Male: head conspicuously small, much less than half the breadth of pronotum (Fig. 12 B). Supraorbital elevation distinct but not sharply crested, and separated from eye by an impression. Vertex with sharply raised stridulatory scraper (Fig. 15 A). Eye more or less reniform. Disc of head granulate (Fig. 14 A–C). Antennae 10-segmented, with two apical segments forming a distinct, sometimes striking club (Fig. 4 B–F).

Pronotum broadest at base, strongly conical (Fig. 12 B–C). Anterior angle sharply produced or pointed rectangular, posterior angle rectangular.
or slightly sharp-angled with rounded apex. Lateral carina continuous, sometimes sharply elevated. Transformed granulation of disc forms a dense pattern of elongate elevations (Fig. 12B).

Elytra ovate with rounded apex that is visible in dorsal view. Two discal carinae of each elytron sharp but not quite smoothly continuous (Figs 12B, 16A), fragmented to granules or gradually reduced and not reaching apex (Fig. 16B). Sutural carinae well marked but less elevated than discal carinae, sometimes granular, more prominent apically. Marginal row consists of somewhat irregular and coarse granulation. Integument granular and scaly with colour patterns similar to those in some Cryptochile species (Fig. 2A-B), and with some fine and silky erect hairs. Epipleura bare, upper margin largely broken up into elongate granules.

Anterior margin of prosternum with hood-like elevation as in some Cryptochile species (Fig. 2A). Front coxal cavity open behind as in Cryptochile (Fig. 3A). Median section of mesosternum broadly elevated anteriorly. Metepisternum broad, metepimeron narrowly triangular. Metepimeron not exposed (Fig. 2A).

Legs clothed with long silky pubescence. Tibial spurs large, unequal, slightly dilated. Tarsi conspicuously longer than tibiae, sometimes almost twice the length of corresponding tibiae. Tarsal claws equal, long and slender (Fig. 12B). Aedeagus with basale and apicale more or less equal in length, without generic characters.

Females of this genus do not resemble the males in general habitus at all (Fig. 12C-D); several of the specific characters are, however, similarly expressed in both sexes (Figs 13, 14).

Extremely globose, body as high as broad in dorsal view (Fig. 12C-D). Unicolorous deep red, integument entirely lacking scales but have semi-erect silky pubescence similar to that of males. Head similar in all details to that of corresponding male (Fig. 14A-B). Pronotum also similar but lateral crest prominent only basally, more rounded anteriorly and interrupted in middle (Fig. 13). Elytra inflated, apex not visible in dorsal view. Integument uniformly granular, fine sutural margination present in one species, and in some species the discal carination is marked by a more or less continuously confluent line of flat granules (Fig. 13A). Epipleural margin complete, undulating. Ventrally similar to males. Antennae much shorter than in males, all funicular segments about as long as broad, two-segmented club not conspicuous (Fig. 4). Legs similar to males but tarsi much shorter, some less than half the length of corresponding tibiae (Fig. 12C).

**DISTRIBUTION.** Southwestern Cape coastal region for a short distance on either side of the Olifants River mouth (Fig. 6).

**HABITAT.** Two of the known species were collected on soft and fine-grained dune sand, one on coastal dunes (Soutpan) and the other about 8 km from the coast (Lambert’s Bay) on dunes of undoubtedly coastal origin.

**ETYMOLOGY.** The name is a combination of the Latin noun *cerasus,* -i = cherry (masculine) and the Greek noun *soma* (neuter) = body. The name refers to the cherry-like shape and colour of the female body.

**KEY TO THE SPECIES OF CERASOMA**

1(6) Body convex but not bulbously inflated, at least elytra with scaly, pattern-forming vestiture. General appearance as in Cryptochile. Tarsi more or less twice as long as tibiae (Fig. 12B)............................................. Males

2(5) Club of antennae distinct, but the two club segments each not more than twice as long as broad (Fig. 4B-C).

3(4) Crested lateral margin of pronotum broadly reflected (Fig. 12B); striolate sculpture of disc coarser, elevations continuous longer, integument shinier. Discal carinae of elytra more continuous and shiny, the inner pair semi-parallel with the suture and each other (Fig. 13B) ............................................. *irreale* spec. nov.

4(3) Crested latera margin of pronotum much lower and only the edge reflected; reticulate sculpture of disc denser and more fragmented, integument between elevations matt. Inner discal carinae of elytra arcuate, lateral pair partly granular (Fig. 16B) ............................................. *kochi* spec. nov.
5(2) Two-segmented club of antennae unusually elongate, about as long as rest of antenna and each segment three to four times longer than broad (Figs 4E, 16A) ...................................................... cerasus spec. nov.

6(1) Unlike Cryptochile in appearance. Body bulbously inflated, bright cherry red without scaly vestiture. Tarsi extremely short, about half of tibial length (Fig. 12C-D) .................................................................................................................. Females

7(8) Posterior lateral angle of pronotum not lobi form, discal striation coarser, elevations broader. Elytral costae corresponding with those of males indicated by some confluent flat granules (Fig. 13A); Antennae shorter than half the breadth of pronotum (Fig. 4D) ......................................................... irreale spec. nov.

8(7) Posterior lateral angle of pronotum lobi form; discal sculpture finer and denser, elevations narrower. Elytral sculpture without any indication of reduced costae (Fig. 13C). Antennae as long as half the breadth of pronotum (Fig. 4F) ................................................................. cerasus spec. nov.

Female of C. kochi is unknown.

_Cerasoma irreale_ spec. nov., Figs 4C–D, 6, 12B, 13 A–B, 14 A–B

Male broadly ovate, elytra broadest just behind humeri. Head capsule very small. Lateral margins of pronotum reflected, laminate, discal sculpture coarse, straight and long vomiculate (Fig. 12B). Discal costae of elytra broad, smooth and shiny. Funicular segments of antennae short, the two club segments about twice as long as broad. Females larger than males, vestiges of sutural margination and discal carinae marked by longitudinally confluent granules (Fig. 13A).

Male: head capsule very small, if removed from pronotum about as long as broad (Fig. 14A). Clypeus sharply contracted in front of supraorbital crest. Granules coarse and large, with shiny smooth discal areas (Fig. 13A). Antennae short, only apical segment reaches beyond posterior angle of pronotum (Fig. 12B); funicular segments stout, only 3rd always longer than broad. Two apical segments large, but neither of them more than twice as long as broad, together slightly shorter than segments 3–8; funicular segments almost bare with few short hairs only, club segments densely covered with silky pubescence that adheres flatly to the surface. On one side of club segments a large triangular bare area points from base to apex (Fig. 4C).

Pronotum broad at base, strongly tapering trapezoidally towards apex. Anterior emargination in accordance with small head narrow, 10 : 19 in proportion to base. Lateral margin laminate and reflected, its edge moderately undulate, thus a prebasal lateral one not distinct. Anterior lateral angles strongly produced, sharp-angled; flat, anterior emargination deep, in the middle straight, slightly convex or flatly bilobate (Fig. 12B). Discal sculpture consists of long and straight, rather broad and regular elevations that are slightly fanned from base; intervals between sharply-edged elevations almost as broad as elevations themselves; elevations dissolved into elongate or round tubercles only at lateral and anterior margins (Fig. 13B). Disc black, shiny or sometimes opaque, with few moderately long hairs and a narrow lateral band of whitish scales. Only tiny apex of scutellum exposed.

Elytra broadly ovate with considerable variation in actual proportions, to a degree that can be mistaken for sexual dimorphism as found in the sister genus Cryptochile. Elytra broadest well in front of middle of discal section, in narrow specimens just behind humeri. Elytra moderately convex between lateral carinae, posterior declivity steep but not quite vertical. Two discal carinae of each elytron carinate, broad, smooth and shiny, carinae continuous or occasionally impressed, sometimes doubled over short sections. Sutural margination less elevated, narrower and less smoothly continuous, but not granular. Lateral margin dissolved into an irregular strip of very large granules, consisting of two or three granules transversely; not forming any distinct longitudinal lines; granules much larger than those of disc or pseudopleuron. All carinae are resolved into granules apically, only the fine granular sutural carinae reaching apex. Granulation of two inner intervals finer than that of lateral interval. Integument entirely covered by shingle-like fine scales, leaving only costae and scattered tuberculation free; basic colour of scales white, with dark brown areas along costae (on either side and not be-
versely convex, apex pointing downwards, its

erect hairs of different lengths, deflected part with
dermal margin not conspicuously lobate as

together (Fig. 12B).

Aedeagus 3.2 mm long, of which length of

Female: head capsule in all details as in male

and in both sexes differs similarly from C. cerasus

(Fig. 14A–B). The same applies to the sculpture of

the pronotum. Corresponding with males, lateral

margin of pronotum not conspicuously lobate as

in C. cerasus (Fig. 13A). Elytra reflecting the prom-

inent coarse in males with lines of confluent large

granules, which are uniformly irregular and well
defined on the rest of the elytra; granules broad

and flat, much larger than in males (Fig. 13A).

Antennae much shorter than in males, club seg-

ments small, all segments except 3rd and 10th as

broad as long, latter pointed (Fig. 14C). Bare basal

triangle of club segments present. Protibia as in

males, with identical specific characters. Tarsi

very short on all legs, less than half of the corre-
sponding tibial length (Fig. 12C) (an unknown

female character in the sister genus Cryptochile).

MEASUREMENTS. Length, male: 6.8-9.7 mm;
breadth 4.25-7.0 mm (holotype 8.55 x 5.55 mm).
Length, female: 9.0-10.3 mm, breadth 6.3-

7.8 mm (allotype 9.0 x 6.3 mm).

DISTRIBUTION. Southwestern Cape, south of

Olifants River (Fig. 6).

MATERIAL EXAMINED. 141 males and 3 females

(females 2 live specimens and 1 cadaver). All

specimens in Transvaal Museum, Pretoria.

Holotype male, allotype female and 29

paratypes: S. Afr., S W Cape Prov., Lambert's Bay,
8 km E, 32.06 S, 18.24 E, white dunes, day,
1.9.1979, leg. Endrödy-Younga, E-Y:1628 (this
sample contained a live female dug up from sand,
the allotype, and the cadaver of another female).
Further paratypes: 32, idem, but white dunes,
night, 31.8.1979, E-Y:1627 (this sample contained
the third female found); 44, idem, but Lambert's
Bay N (approximately 10 km but near coast), day,
white sand, 24.8.1981, E-Y:1841; 20, idem, day,
white sand (dunes about 300 m inland, now sepa-
rated from the coastal ridge of dunes by a rail-
road), E-Y: 1842; 16 idem, but coastal dunes, night,

ETYMOLOGY. The specific name is a modern

Latin word referring to the highly unusual sexual
dimorphism in this species (as well as genus).

Cerasoma cerasus spec. nov., Figs 2A, 4E–F, 6,
12C-D, 13C-D, 14C, 15A-B, 16A

This species is closely related to C. irreale. Their

specific characters can often be recognized in

both sexes; this type of character display provided

the final proof for the conspecific status of the

highly dissimilar sexes. Characters not repeated

below are comparable to those of C. irreale.

Body more regularly ovoid, broadest in males

around middle of elytral length, females more

elongately ovoid than in C. irreale. Pubescence of

body including that of the elytra denser, consisting

of long silky hairs in both sexes (Fig. 16A) (almost

absent in C. irreale).

Head capsule larger in both sexes. Clypeus not

contrasted in front of supraorbital crest (Fig. 14C).

In males antennal segments more elongate, both

club segments unusually enlarged, cylindrical,
together as long as rest of antenna (Fig. 4E). In

females a much larger two-segmented club, as

long as last five funicular segments together (Fig.

4F) (in C. irreale the club is only as long as three

and a half segments).

Lateral margin of pronotum less deplanate and

less reflected, deeply situated behind the middle,

forming a posterior lateral lobe in males (Fig. 13D).

In females the margin is less defined than in C.

irreale, but with a large and conspicuous postera-

lateral lobe similar to that of the male.

Discal sculpture of pronotum similarly finer in both

sexes, longitudinal elevations narrower and less

fragmented, intervals much narrower; this denser

and finer striolation gives a silky sheen to the

pronotum (Fig. 13C).

Two discal carinae of elytra less elevated in

males and not marked at all in females (Fig. 13D,
C). Dark scaly patches on elytra (male) smaller

and less prominent than in C. irreale (Fig. 16A).

Protibia similar in both sexes, dorsal surface only

moderately convex transversely, apical process

cylindrical, curved ventrad; it is more elongate

in males, with a length-breadth ratio of 20 : 6. Tarsal

segments somewhat more elongate but claws

shorter than in C. irreale.

Aedeagus very similar in shape and size to that

of C. irreale.

MEASUREMENTS. Length, male: 7.5-9.0 mm,
breadth 4.5–5.2 mm (holotype 8.0 × 4.9 mm).
Length, female: 10.3–16.0 mm, breadth 6.8–10.5 mm (allotype 11.2 × 7.4 mm).

DISTRIBUTION. Southern Namaqualand, north of Olifants River mouth (Fig. 6).

MATERIAL EXAMINED. 4 males and 19 females. All males, two alive and two dead, as well as all three live females together with nine cadavers in different stages of dismemberment, were found on 28.8.1979 (E-Y:1616). All specimens in Transvaal Museum, Pretoria.


ETYMOLOGY. Latin noun, cerasus, -i, feminine, = cherry, referring to the shape and deep red colour of live females.

**Cerasoma kochispec. nov., Figs 48,6,16B**

A single male with a rather vague locality inland from Lambert’s Bay. Its generic characters agree in all details with the other two species of Cerasoma described here. Female unknown.

Male: perfectly regularly ovate, broadest in middle of body length. Lateral margin of pronotum sharply carinate but not reflected, moderately sinuate in front of laterobasal lobe. Striolate sculpture of pronotum coarse and fragmented (Fig. 16B).
Antenna short, with two club segments moderately enlarged (Fig. 4B). Protibia moderately dilated.

Head very small but not as narrow as in *C. irreale*. Clypeus contracted in front of supraorbital crest. Granulation coarse, sharp and shiny. Antenna short, only 1st segment reaches beyond basal corner of pronotum. Third segment more than twice its breadth. 4th to 7th stout, moderately longer, 8th as long as broad. Two-segmented club indistinctly smaller than in *C. irreale* (Fig. 4B).

In all segmental proportions *C. kochi* is closer to the latter species than to *C. cerasus*. Basal triangle of apical segment bare but that of preapical segment finely pubescent. Dense leaning pubescence of club segments dark golden brown.

Pronotum broad trapezoid in shape, more contracted from base than in *C. cerasus*. Anterior emargination evenly arcuate; anterior lateral angles slightly sharp-angled, pointed. Posterior lateral angle lobate. Lateral margin sharply carinate but only narrow edge finely reflected, moderately sinuate in front of basal lobe. Discal striolation only slightly finer and denser than in *C. irreale*, but much more fragmented, crested elevations short (Fig. 16B).

Shape of elytra closer to *C. cerasus*, broadest at about anterior third of length, evenly arcuate to roundly produced apex. Inner discal carina sharp and narrow, moderately elevated, slightly undulating, with few breaks in its smooth crest. The two inner carinae are not semiparallel as in the other two species, but distinctly arcuate. Lateral discal carinae broad, more elevated, fragmented and made up of longitudinal as well as granular elements, at places in three or four irregular longitudinal rows. Granulation of rounded marginal carina is coarse but granules are much smaller and less shiny than in *C. irreale*. Few elongate fragments of a continuous carina appear at the inner margin of the granular marginal carina. This fragmented carina is only marked by a few larger granules in the other two species. Granulation of intervals similar to that of *C. irreale*. Pilosity of disc uniform, moderately long and erect, long and silky in the deflected lateral portions, particularly in the humeral section. Disc with dense scaly vestiture, scales yellowish, with dark brown costal dots and smaller dots on the intervals (Fig. 16B).

Dorsal surface of prothorax strongly convex transversely but not as triangularly dilated as in *C. irreale*. Legs otherwise do not differ significantly from the latter species.

The only male was not dissected.

MEASUREMENTS. Length 10.0 mm, breadth 6.3 mm.

DISTRIBUTION. Southwestern Cape Province (Fig. 6).

MATERIAL EXAMINED. 1 male. Holotype in Transvaal Museum, Pretoria.

Holotype male: S. Walters, Clanwilliam, 24.4.1947. According to the definite sand-adaptive characters the specimen must have been collected on soft sand in the vicinity of Clanwilliam.

ETYMOLOGY. This new species is named in honour of Dr C. Koch, brilliant student of Southern African Tenebrionidae, who marked this specimen as belonging to a new genus.
Subtribe Vansoniina stat. nov., Figs 1B, 2B, 3B, 5B, 7, 19A–B


Type genus: Vansonium Koch, 1950.

Vansoniina is a monogeneric subtribe of Cryptochilini. Head conspicuously large, prognathous with strong mandibles particularly in males (Fig. 19A–B), vertex with fine stridulatory file. Antenna 9-segmented (Fig. 5B). Procoxal cavity open behind (Fig. 3B). Scutellum completely concealed. The species is composed of two distinct subspecies. The differential subspecific characters are discussed under the subspecies.

Head very large, surface area about equal to that of pronotum, width together with eyes broader than apical margin of pronotum and considerably broader than pronotum at base. Genal canthus forms a sharp process in front of eye. Eye very small, perfectly circular, Vertex with narrow axillar stridulatory file. Labrum very large, bilobate, with long and flat apical setae. Mandibles large, broadly exposed around labrum. Mentum well developed, bilobate (Figs 1B, 16A B).

Pronotum short, broad and flat, only anterior part of lateral margins deflected, short cordiform with angular posterior angles; posterior margin produced backwards in a broad triangle, concealing scutellum entirely (Fig. 16A–B).

Elytra elongate cordiform with roundly deflected lateral margins.

Pars stridens in inner margin of pronotum reduced to fine tubercles against plectrum of vertex.

DISTRIBUTION. Northern and eastern margins of the central dune Namib and Bushmanland.

Vansonium Koch

References and description as for species below.

Vansonium bushmanicum Koch, Figs 1B, 2B, 3B, 5B, 7, 19A–B


Medium sized, dorsum deplanate over deep body; except for parts of mandibles, closely covered with squamiform pubescence. Mandibles moderately large, prognathous (Fig. 19A–B), eyes small, antennae 9-segmented (Fig. 5B). Procoxal cavity open behind (Fig. 3B). Scutellum completely concealed. The species is composed of two distinct subspecies. The differential subspecific characters are discussed under the subspecies.

Head very broad, together with eyes hardly narrower than pronotum, prognathous (unlike Cryptochilina). Disc deplanate in front, moderately convex behind eyes. Clypeus emarginate in a broad V-shape, edge here bare and shiny. Backwardly slanting anterolateral margin meets gena in a sharply pointed angle. Vertex with fine stridulatory file. Eye conspicuously small, protuberant and perfectly round, with dense and erect squamiform pubescence between ocular facets. Mandibles moderately large, apex slightly curved, each mandible with an inner median tooth. Labrum very large, anteriorly emarginate and densely pubescent (Fig. 19A). Mentum transverse, bilobate with broad and shallow anterior emargination (Fig. 1B). Antennae 9-segmented; basal segment elongate, 2nd very small, 3rd as long as two subsequent segments together. Apical segments do not form an appreciable club (Fig. 5B).

Pronotum broadly cordiform with deplanate dorsum, basal margin with large triangular median process covering scutellum. Anterior lateral angles rounded, posterior ones sharply obtusangular (Fig. 19A–B).

Elytra ovate, apex roundly pointed, broadest in front of middle of length. Humeral angle sharp, obtusangular. Disc moderately convex, more so posteriorly than laterally. Lateral portion with few erect hairs (Fig. 19A–B). Pars stridens in inner margin of pronotum reduced to fine tubercles against spectrum of vertex.

Round procoxal cavities externally open behind (Fig. 3B). Mesosternum and mesepimera large, mesepimera narrow, its sutures covered by scales in fresh specimens. Mesocoxal cavity round, the posterior one moderately transverse (Fig. 2B). First three visible sternites very convex transversely, bearing the only long and erect setae of the body. Fourth visible sternite less convex and fifth deplanate.

Pro- and mesocoxae globose and strongly produced from coxal cavities, metacoxa largely embedded. Trochanters well developed but not particularly large. Femora long, cylindrical, pro- and metatibia somewhat thickened distally, meso- and metafemur narrower, Tibiae straight, semiparallel.
from protibia gradually somewhat longer. Protibia always, mesotibia in one subspecies, denticulate, metatibia simple. Tibial spurs large and depen­ate, unequal in length, largest on metatibia and smallest on mesotibia. Metatibia also with an apicodorsal semicircle of conspicuous long setae. Tarsi rather short, only slightly longer than half of the corresponding tibiae. Tarsal claws fine, equal in size, somewhat shorter than claw seg­ments.

Aedeagus small, 1.2 mm long, apicale slightly longer than basale, apicale strongly arcuate in middle.

Length: 5.3–9.0 mm.

Distribution: type material and localities as listed under subspecies.

**Vansonium bushmanicum bushmanicum**
Koch, Figs 7, 19A


Protibia with four lateral teeth, three large and one small. Prosternal apophysis broader, as broad as procoxa cavities. Median portion of mesosternum shorter and broader, as long as its posterior margin between mesoscocxae. Anterior portion of deflected sides of pronotum with vestiges of a lateral carina. Posthumeral section of elytra with rounded lateral margination and disc usually with indistinct and flatly rounded vestiges of a costal structure. Additional characters given by Koch (1962: 128) such as shape of head and proportions of antennal segments are either minimal or appear variable.

**MEASUREMENTS.** Length: 7.8–8.0 mm. Fairly consistent in size and in the middle of the range of variation of *V. b. namibense*.

**DISTRIBUTION.** Bushmanland from Kakamas westwards into southern South West Africa/Namibia.

**TYPE MATERIAL.** Holotype and 26 paratypes: Farm Nabeis (on some labels Nabeis), 30 m W. of Kakamas, Bushmanland, 17.12.1948, Koch & van Son. All in Transvaal Museum, Pretoria. The rest of the original type series of 96 specimens were distributed by Koch in the major museums.

**MATERIAL EXAMINED.** 36 specimens including type series.

**Additional localities:** 1 Steinkopf (28°15'S, 17°44'E), 3 Achab (29°15'S, 19°03'E), 2 Pofadder (29°09'S, 19°25'E), 1 Nabeis (28°51'S, 20°09'E), 1 Fish River Canyon (27°37'S, 17°36'E), 1 Kakamas (28°45'S, 20°33'E).

**MONTHS RECORDED.** May (cadavers), August, October, December.

**HABITAT.** All specimens were found in stony areas with fine wind-blown sand. The only live specimens were found by Koch, who noted that they were collected under stones resting on soft sand in congregations of up to 10 specimens under a stone.

**Vansonium bushmanicum namibense** Koch, Figs 7, 19B


Protibia with five lateral teeth, four large and one small. Mesotibia with two sharp lateral teeth. Prosternal apophysis narrower than procoxa cavities. Median portion of metasternum narrower, the ratio between its length and posterior breadth between mesocoxal cavities is 18:14. Anterior portion of deflected sides of pronotum evenly rounded, without a trace of a vestigial carina. Disc of elytra usually even, without a longitudinal elevation.

**MEASUREMENTS.** Length: 5.3–9.0 mm. Both the smallest and largest specimens of this species were found in *V. b. namibense*. It appears that most specimens (mostly cadavers) found around Gobabeb are markedly smaller than those from further south.

**DISTRIBUTION.** Inland margins of central dune Namib.

**TYPE MATERIAL.** Holotype and 3 paratypes: Tschauchab Riv. (dunes 30 m W. Sesriem), X.1957, Koch, all in Transvaal Museum, Pretoria.

**MATERIAL EXAMINED.** Including types, 15 more or less intact specimens and 18 cadavers.

**Additional localities:** 4 Tsondab Vlei (23°59'S, 15°26'E), 2 Mirabib (23°28'S, 15°17'E), 23 Gobabeb (23°34'S, 15°03'E), 5 Gorras (farm 99) (25°19'S, 15°56'E).

**MONTHS RECORDED.** January, February, June, October.

**HABITS AND HABITAT.** Crepuscular and nocturnal in activity. Live specimens were collected in river beds, ow vegetated dunes and flat fine...
sandy areas, usually in bare places. They were observed cleaning their burrows in the same fashion as sand-burrowing wasps. They do not occur on barren sand dunes. Months recorded (live): October and January.

Subtribe Calognathina stat. nov., Figs 1C, 2C, 3C, 5A, 8, 9, 16D, 17, 18


Monogeneric subtribe of Cryptochilini. Head very large, prognathous. Mandibles unusually large in males, stout and broad in females. Eyes small, round. Labrum large, bilobate and setose (Figs 17, 18). Vertex without stridulatory file. Antenna 10-segmented (Fig. 5A). Pronotum short and broad. Elytra elongate cordiform (Figs 17, 18). Procoxal cavity closed behind (Fig. 3C). Mesocoxal cavity small and round, the metacoxal one broad, outwardly pointed, ovate (Fig. 2C).

Head very large, covering about the same surface area as pronotum, transversely oblong in males, produced anteriorly in females. Eyes small, round. Labrum large, bilobate and setose (Figs 17, 18). Vertex without stridulatory file. Antenna 10-segmented (Fig. 5A). Pronotum short and broad. Elytra elongate cordiform (Figs 17, 18). Procoxal cavity closed behind, the metacoxal one broad, outwardly pointed, ovate (Fig. 2C).

DISTRIBUTION. Interdune valleys and marginal, vegetated dunes of the dune Namib from southern Angola into the Richtersveld south of the Orange River.

Calognathus Guérin-Ménéville

References and description as for species below.

Calognathus chevrolati Guérin-Ménéville


Male: head very large, pronotum broader only by its lateral triangular dilations. Disc deplanate or depressed in middle, more or less slanting to clypeal margin. Clypeal emargination U-shaped with produced lateral angles. Preocular canthus angularly produced. Disc bare at clypeal declivity and postmentum, the rest of the head capsule being covered by hair-like or hyaline scales (see subspecies). Dorsum of head with numerous large and shiny tubercles, each of them carrying a long and erect bristle. Eyes round, almost vertical on sides of head, convex and bare; composed of very numerous small and convex corneal facets. Mandibles extremely large, lucanoid, with large transverse ventrobasal teeth more or less concealed by labrum. Labrum large, bilobate and setose (Figs 17, 18). Labrum large, broad, with emarginate anterior margin, integument light reddish brown, pubescence long, particularly at anterior margin. Mentum transverse, most of it fitting into an emargination of postmentum. Central sclerite of ligula transversely oblong (Figs 1C, 2C, 17, 18).

Pronotum transverse, twice or more than twice as broad as long. Lateral margins angularly tilted, anterior margin slightly emarginate, posterior margin slightly arcuate or straight. Dorsum with coarse setiferous granules which are more densely set laterally. Scaly covering of pronotum similar to that of head. Procoxa cavities closed behind. Scutellum completely concealed. Elytra cordiform to ovate with rounded pointed apex. Margin of lateral deflection set with three irregular rows of sharp and decumbent small spikes. Epipleura not marked at ventral edge of elytra. Suture line, a broad lateral band on disc, and deflected margin of elytra with dense scale-like pubescence. A darker discal band of elytra at least posteriorly with sparser scales; integument, where exposed, not covered by hyaline scales. Discal setiferous granules smaller than those of pronotum. Mesosternum convex between mesocoxal cavities. Mesepisternum very large, mesepimeron elongately triangular, mesocoxal cavity round.
Metasternum broad; metepisternum large with arcuate inner margin; metepimeron small, triangular (Fig. 2C).

Antennae 10-segmented, basal segment the largest, second segment the smallest of all segments. Third segment elongate, 4th to 10th gradually decreasing in length. Last two segments, although slightly broader, do not form a distinct club (Fig. 5A). Protibia and in some subspecies also mesotibia sharply denticate, teeth spike-like. Metatibia only sharply granular. Tarsi strongly bilaterally compressed, claw segments of all legs the longest of all tarsal segments. Claws sharp and arcuate, slightly unequal in length, in the protarsus the inner, in the meso- and metatarsus the outer claw longer. Tibial spurs large, almost straight, slightly deplanate, unequal in length. All legs excepting protarsus with extremely long ptilosity (sand shoes).

Female: in general appearance, including subspecific characters, similar to the males, but mandibles small, of 'normal' size (Fig. 18). Clypeal margin of head with four processes (two in males).

The species is composed of four subspecies distributed in partly isolated areas from the Richtersveld (northwestern Cape Province) through the Namib area to southwestern Angola. Habitat selection and habits are similar in all four subspecies. They are diurnal to crepuscular, avoiding the hottest hours of the day. They occur on vegetated dunes or vegetated sandy flats or in vegetated parts of interdune valleys, but avoid shifting and barren sand dunes or gravel plains.

Additional information is given in the subspecies accounts.

An interesting case of morphological hermaphroditism was found in a specimen belonging to C. c. eberlanzi from the Keis in the Richtersveld. In this specimen the external sexually dimorphic characters are split between the two sexes. It has only been ascertained (without actual dissection) that the specimen has an ovipositor, thus the sexual organs at least are closer to the female ones. The mandibles of the specimen are three to four times larger than in a female but are distorted. The clypeal margin is produced into two blunt processes in males and two pairs of smaller processes in females. The mandibles of the specimen are broader and arcuate with sharp basal crest characteristic of male mandibles and are also smooth and shiny. The clypeal margin is produced into two blunt processes in males and the double processes on the right-hand side and the double processes on the left-hand side. The shape of the elytra is more cordiform, as in females (Fig. 16).

**KEY TO THE SUBSPECIES OF C. CHEVROLATI**

1(2) Scaly pubescence of dorsal surface bicolorous: evenly dense reddish brown on vertex and disc of pronotum, whitish yellow behind clypeus and at all lateral margins. Richtersveld and southern Namib (Figs 17A, 18A) .......................................................... chevrolati Guérin

2(1) Scaly pubescence where present uniformly silvery white. Scales of vertex and disc of pronotum small and round, in contrast to elongate lateral scales, sometimes providing these surfaces with a shiny black and bare impression.

3(4) Mandibles of males angularly arcuate with sharp basal crest on their inner dorsal surface. Clypeal processes broad and blunt. Elytra flattened. Central Namib (Figs 17B, 18B) ............................................ eberlanzi Koch

4(3) Mandibles moderately and evenly arcuate, basal crest vestigial or absent. Clypeal processes sharply pointed. Elytra more convex transversely.

5(5) Silvery scaly margination of head, pronotum, and elytra distinct. Scales of vertex and of anterior part of pronotal disc round, adherent and hyaline. South bank of Kunene River (Figs 17C, 18C) ......................... lucanoides subsp. nov.

6(5) Silvery scales of dorsal surface scattered, with very little aggregation at margins. Dense scales of vertex and pronotum dark silvery. Southern Angola (Figs 17D, 18D) .............................................................. atricolor Pic
Calognathus chevrolati chevrolati Guérin-Méneville, Figs 17A, 18A, 8, 9

The entire dorsum of the head with the exception of the clypeal margin, as well as entire disc of pronotum, densely covered with scale-like hairs; pubescence bicoloured: off-white behind clypeal margin and lateral sections of pronotum, brown on vertex and median section of pronotum. A broad lateral band and broad sutural margin of elytra with similar pubescence to that of head and pronotum, in an off-white to light brown colour. A narrow, almost rectilinear V-shaped area of each elytron either completely bare (males), or brown pubescent as middle of pronotum and only apically bare and black (females). - Mandibles of males stronger and more angularly arcuate, with strong and long basal crest. Preocular angle of genal canthus as well as lateral process of pronotum rounded. - Pronotum more than twice as broad as long, basal margin doubly arcuate, and in large males edge sharply reflected. - Elytra almost as broad as long, cordiform, strongly deplanate.

MEASUREMENTS. Largest male 20.0 mm (mandibles 5.0 mm), breadth 8.5 mm. Smallest male 11.0 mm (mandibles 1.9 mm), breadth 5.4 mm. Females: length 11.5-14.3 mm, breadth 5.7-7.7 mm.

DISTRIBUTION. Richtersveld in northwest Cape Province and southern Namib desert (Figs 8, 9).

TYPE MATERIAL. Guérin’s type specimen has not been seen. Chevrolat sent the single male with the locality Cap de Bonne-Esperance to Guérin, who described it in 1836. His description leaves no doubt even about the subspecific identity of the nominal race, as he writes about the pubescence of the head and pronotum: ‘couverte d’un duvet soyeux tres fin a reflets metaliques’, presumably referring to the golden or bronze colour of the scaly pubescence.


MONTHS RECORDED. July to December, and May.

Calognathus chevrolati eberlanzi Koch, Figs 17B, 18B, 8, 9

Vertex and disc of pronotum black, covered by small, round, perfectly fitting hyaline scales, providing surface with a greasy sheen. A pair of bilateral, post-clypeal patches and lateral margins of head, as well as lateral bands on disc of pronotum, covered by white scale-like hairs. Marginal white pubescent band of elytra distinctly narrower than in C. v. chevrolati; sutural band also narrower, thus black discal area broader, not rectilinearly V-shaped. In females, bare discal area of elytra with fewer scales restricted to basal section, and they are also white. - Mandibles of males less angularly arcuate, basal crest at their inner dorsal margin sharp as in C. v. chevrolati but shorter. Preocular angle of genal canthus more narrowly rounded, lateral angle of pronotum pointed. Proportions and basal margin of pronotum as in C. v. chevrolati, elytra somewhat more elongate.

MEASUREMENTS. Largest male 25.0 mm long (mandibles 6.0 mm), breadth 9.5 mm; smallest male 14.0 mm long (mandibles 3.0 mm), breadth 6.5 mm. Females: length 12.8-17.0 mm, breadth 7.0-9.2 mm.

DISTRIBUTION. Richtersveld, southern and central Namib (Figs 8, 9).

TYPE MATERIAL. Holotype male, allotype female and 3 paratypes: Namib, S.W. Africa, leg. F. Eberlanz (framed printed labels), Further paratypes: 2, 50 km radius fr. Lüderitz. F. Eberlanz (photoprint labels) and 7 idem (but handwritten).

MATERIAL EXAMINED. 110 males, 45 females and 1 morphological hermaphrodite. 101
specimens in Transvaal Museum, Pretoria. 49 in State Museum, Windhoek, and 7, University of Pretoria.


MONTHS RECORDED, September to November and March, May, July, August.

**Calogonathus chevrolati lucanoides subsp. nov.**, Figs 8, 17C, 18C

The new subspecies is in the smaller size range of *C. chevrolati*. It resembles in habitus, although in some characters it appears to be closer to *C. v. eberlanzi* in *C. v. lucanoides*.

- Scaly pubescence of head uniformly silvery, only clypeal projection bare. Scales of vertex almost round, becoming gradually longer and pointed towards lateral margin. Scales nowhere tightly adherent to integument or hyaline, black colour of integument not showing through scales. Scale cover of head thus more similar to that of the southern *C. v. lucanoides* than to the two spatially intervening subspecies.

**MEASUREMENTS**. Largest male 17.5 mm long, breadth 7.0 mm. Smallest male 14.0 mm long (mandibles 3.0 mm). Females: length 10.5–13.8 mm, breadth 5.5–7.7 mm. Holotype 15.8 mm long.

**DISTRIBUTION**. Kaokoveld, south bank of Kunene River between coastal dunes and Hartmann'sberge (Fig. 8).

**MATERIAL EXAMINED**. 30 males and 14 females. All specimens in Transvaal Museum, Pretoria.


**Calogonathus chevrolati atricolor** Pic, Figs 8, 17D, 18D


Males somewhat smaller than in the two previous subspecies, not reaching their maximum sizes. Females about in the same size range.

- Scaly pubescence of head uniformly silvery, only clypeal projection bare. Scales of vertex almost round, becoming gradually longer and pointed towards lateral margin. Scales nowhere tightly adherent to integument or hyaline, black colour of integument not showing through scales. Scale cover of head thus more similar to that of the southern *C. v. chevrolati* than to the two spatially intervening subspecies.

**MEASUREMENTS**. Largest male 17.5 mm long (mandibles 4.0 mm), breadth 7.0 mm. Smallest male 14.0 mm long (mandibles 3.0 mm). Females: length 10.5–13.8 mm, breadth 5.5–7.7 mm. Holotype 15.8 mm long.
male 11.3 mm long (mandibles 1.5 mm); breadth 5.7 mm. Females 12.0-15.0 mm long and 6.2-9.5 mm broad.

**DISTRIBUTION.** Southwestern Angola between the Kunene and Coroca Rivers (Fig. 8).

**TYPE MATERIAL.** Pic's type specimen (male) has not been seen. Its locality 'Guinea' refers to 'southern Guinea', often applied to the Angolan coast by early travellers.

**MATERIAL EXAMINED.** 10 males and 11 females; 20 in Transvaal Museum, Pretoria, and 1 in State Museum, Windhoek.

**Localities:** 1 Rio Coroca (15.43 S, 11.45 E), 3 south of Rio Coroca, 1 Lago de Carvalhao (15.46 S, 12.01 E), 14 Porto Alexandre (15.48 S, 11.50 E), 1 Baia dos Tigres (16.36 S, 11.43 E) and 1 without locality.

**MONTHS RECORDED.** March, June, and September.

**Subtribe Homebiina subtrib. nov.,** Figs 1D, 2D, 3D, 5C-D, 9, 19C-D

**Type genus:** Homebius gen. nov.

The only known member of this subtribe shows the highest number of apomorphic characters in the tribe.

- Head extremely small, prognathous (Fig. 19C-D), vertex with narrow, transverse axillar stridulatory file. Labrum and mandibles apparently absent or reduced. Submentum square, strongly projecting, largely concealing feebly scierotized and small mentum (Fig. 1 D). Eyes small but protruding, ovate, small mandibles and concealed labrum. - Pronotum almost flat, transversely ovate with anterior emargination. Scutellum exposed. - Elytra elongate ovate, moderately convex. Posterior femora deplanate, posterior tibiae bilaterally compressed, tarsal claws fine and small (Fig. 19C). Further characters of the genus are to be found in the diagnosis of the subtribe Homebiina, and in the description of its only species, *Homebius kaszabi* spec. nov.

**ETYMOLOGY.** The Latin name is derived from the name of the nearest named area between the type locality and Gobabeb in the Kuiseb valley, Homeb.

*Homebius kaszabi* spec. nov., Figs 1D, 2D, 3D, 5C, D, 9, 10, 11, 19C,D

**Male:** head conspicuously small, prognathous, with rather long collar section which might be retracted into the thorax in live specimens. Disc deplanate, genal angle almost evenly arcuate with clypeus between eyes. Vertex with narrow axillar stridulatory file, the main character for placing this species in the tribe Cryptochilini. Clypeus thick and rounded at its anterior margin, in lateral view. Labrum apparently absent. Eyes small, black, dorsoventrally elongate ovate, about three times broader than long. The eye is not reduced anteriorly by the genal canthus but has a collar-like posterior 'support' from the evenly shaped postgena. Corneal facets are small and very coarse, suggesting nocturnal or subterranean habits, as does the pale, feebly sclerotized integument of the whole body. Dense and very short setae emerge from between the facets. Submentum strongly produced in middle, forming two very deep bilateral emarginations for the vertical movement of the maxillary palpi (Fig. 1D). A similar formation of the submentum has not been found.
verse. Metasternum very long, emarginate be-
as coxa, mesocoxal cavities thus well separated;
sis roundly elevated, apophysis almost as broad
the cavities are almost round, only slightly trans­
medially separated from each other by the vertical
mesepimeron is not fused. Median portion of
metasternum together with mesosternal apophy­
jecting and virtually touching (an extremely
unusual character). The cavities themselves are
narrowly separated from each other by the shape of
the body. Surface, particularly ventrally, with scat­
tered, darker reddish and small tubercles. Metati­
tubercles. Tibial spurs unequal, both somewhat
broadest in middle and slightly bent. Outer sur­
bia gradually dilated and bilaterally compressed,
segments very long, slightly conical, broadest
strongly elevated above sternites posteriorly. Tro­
tal view, the fifth (ana) sternite is rounded trian­
gular, as long as two preceding sternites together
(Fig. 2D). Integument of ventral surface similar to
that of pronotum, pubescence short with long silky
hairs on lateral portions of prosternum and
metasternum only.

Procoxae projecting oviform, trochanters rather
broad, taking most of the breadth of femoral base.
Proternum elongate ovate, laterally slightly com­
pressed. Protibia short, dilated and extended to a
pointed apical process. Two long, thin and un­
equal tibial spurs originate from a surface where
the thickness of the tibia abruptly reduces. Tarsal
insertion is about at the middle of the process of
the tibia, well removed distally from the protruding
surface with the spurs. Tarsal segments narrow,
elongate and cylindrical. Claws very unequal, thin,
bristle-like, the external one half the length of the
other, hair-like. Pubescence consists of a combi­
nation of short leaning and long silky hairs. First
tarsal segment long, with a row of granules, each
giving rise to a moderately long but strong bristle.
Mesocoxae round, projecting from the anterior
surface; trochanters slightly larger but not broader
than in the anterior leg. Femur longer but otherwise
similar to the profemur; tibia simple, with more
distinct bristle granulation. Tibial spurs unequal,
narrow and simple, the longer one somewhat
longer than half of first tarsal segment. All tarsal
segments very long, slightly conical, broadest
distally. Claws very unequal, inner one about as
long as the claw segment, slightly bent, bristle-
like, external one much shorter and hair-like.
Metacoxa level with metasternum anteriorly but
strongly elevated above sternites posteriorly. Tro­
chanter very broad and completely separates
coxa and femur (unusual character). Femur very
broad, bilaterally strongly compressed and
slightly bent so as to accommodate the shape of
the body. Surface, particularly ventrally, with scat­
tered, darker reddish and small tubercles. Metati­
bia gradually dilated and bilaterally compressed,
broadest in middle and slightly bent. Outer sur-
face with conspicuous, projecting reddish brown
tubercles. Tibial spurs unequal, both somewhat
deplanate, with rounded apices. First tarsal seg­
ment cons derably longer than the three subse­
quent ones together. Three distal segments rather
broad and short, these are the shortest of all tarsal segments. Metatarsi apparently with a single claw that is similar to the larger one of the mesotarsus. The only known male has not been dissected.

Female (Fig. 19D), considerably larger, showing few dimorphic differences. Antenna slightly stouter, 3rd segment only three times longer than broad. 8th segment perfectly joins the base of the moderately enlarged apical segment (Fig. 5D). Legs shorter in comparison to body length than in the male but very similar in proportions.

MEASUREMENTS. Length: male 4.75 mm, female 7.45 mm. Breadth: male 2.7 mm, female 3.2 mm.

DISTRIBUTION. Hummocky areas on the eastern margin of the central dune Namib (Fig. 9).


Holotype male: South West Africa, central Namib desert 32 km E Gobabeb, 23.41 S, 15.22 E, pitfall trap, 7 Jan. 1981, leg. L. Praetorius (the locality called Elephant Valley is near the north bank of the Kuiseb River at the southernmost edge of the dune sea). Allotype female: idem, but Diamond Area 2, 25.20 S, 15.28 E, under Stipagrostis sabulicola, 22 June 1982, leg. J. Irish (the locality is in the vicinity of the Awasib mountain).

HABITAT. The male was found in a pitfall trap between the foot of a barren dune and Stipagrostis hummocks of the adjoining sandy flat area. The female was dug up from a hummock. The extremely reduced and non-functional mandibles suggest that the adults of Homebius kaszabi can only take soft food material, or do not feed at all. Soft food in their desert environment might only be found in nests or burrows of other animals. The fact that this species has avoided discovery for about 40 years in the desert's best researched area suggests a nearly permanently subterranean way of life. The extreme morphological reductions and virtual absence of pigmentation also indicate a subterranean symbiotic or semiparasitic lifestyle. My strongest suspicion, in preference to ants' nests, is that it inhabits the burrows of the golden mole or rodents such as Gerbillurus paeba.

ETYMOLOGY. This remarkable new species is dedicated to the memory of Dr Zoltán Kaszab, the most prominent student of tenebrionids, my teacher and good friend, who died during the course of the present study.

RELATIONSHIPS AND CLADISTIC ANALYSIS

The definition of higher categories in Tenebrionidae is often problematic. This is probably due to the unusually high rate of speciation in some of the major evolutionary lineages. It is feasible, then, to assume that an average rate of natural extinctions left much larger morphological gaps in the historic continuum than in a less diverse group. An alternative possibility to an exceedingly high rate of speciation is that an unusually high level of character transformations accompanied some of the speciation events. Thus today we find a number of often very well-defined groups with little indication of their kinship. For the same reason we must often be content with a single group character equally applicable to all taxa to delimit the supposedly monophyletic higher taxon.

In the case of the newly defined tribe Cryptochilini: this single adult character is the unique vertico-pronotal stridulatory organ described in the diagnosis of the tribe. Even for this character there is a single exception: it is not present in the genus Calognathus. The interpretation of this absence as a secondary loss will be explained below. The common possession of the vertico-pronotal stridulatory organ defines the tribe adequately, but all attempts to relate the tribe more closely to one or another kinship group failed. If the small size of the mentum should prove to be a monophyletic grouping character within the subfamily Tentyriinae, the remaining tribe in kinship with Cryptochilini is only Stenosini, with hardly any general morphological resemblance to it.

In determining the apomorphic states of the transformation series a similar conclusion could be drawn if either the Stenosini or another tribe of Tentyriinae could have been identified as a sister group of the Cryptochilini. In ascertaining the plesiomorphic state of several characters, the tentryiid tribe Molurini was often used, although a definite link between this tribe and Cryptochilini cannot be established. The uniformly exposed mesochoanin in Molurini, however, secures a unique position of plesiomorphy for this tribe in Tentyriinae as the subfamily is understood at present. In a few cases the characters had to be considered in an even wider context; these transformation series will be discussed below. For the purpose of a cladistic analysis, 26 adult morphological characters were evaluated. In the analysis all four subtribes are compared, using three of the genera of Cryptochilina, the only generically subdivided subtribe.
The following transformation series or character states were used in the cladistic analysis.

<table>
<thead>
<tr>
<th>Character</th>
<th>Plesiomorphic state</th>
<th>Apomorphic state</th>
</tr>
</thead>
<tbody>
<tr>
<td>1. Head orientation</td>
<td>prognathous</td>
<td>hypognathous</td>
</tr>
<tr>
<td>2. Body shape</td>
<td>flattened</td>
<td>box-like</td>
</tr>
<tr>
<td>3. Procoxal cavity</td>
<td>closed</td>
<td>open</td>
</tr>
<tr>
<td>4. Metacoxal cavity</td>
<td>transverse</td>
<td>round</td>
</tr>
<tr>
<td>5. Prosternum</td>
<td>simple</td>
<td>with collar</td>
</tr>
<tr>
<td>6. Eye</td>
<td>reniform</td>
<td>round</td>
</tr>
<tr>
<td>7. Elytral disc</td>
<td>carinate</td>
<td>smooth</td>
</tr>
<tr>
<td>8. Mandibles</td>
<td>normal</td>
<td>enlarged</td>
</tr>
<tr>
<td>9. Protibia</td>
<td>tuberculate</td>
<td>dentate</td>
</tr>
<tr>
<td>10. Scutellum</td>
<td>exposed</td>
<td>concealed</td>
</tr>
<tr>
<td>11. Antennae</td>
<td>10-segmented</td>
<td>9-segmented</td>
</tr>
<tr>
<td>12. Metatibial apex</td>
<td>simple</td>
<td>callose</td>
</tr>
<tr>
<td>13. Head size</td>
<td>large</td>
<td>small</td>
</tr>
<tr>
<td>14. Metapleuron</td>
<td>separate</td>
<td>fused</td>
</tr>
<tr>
<td>15. Body dimorphism</td>
<td>uniform</td>
<td>sexually dimorphic</td>
</tr>
<tr>
<td>16. Female antennae &amp; tarsi</td>
<td>normal</td>
<td>shortened</td>
</tr>
<tr>
<td>17. Male antennae &amp; tarsi</td>
<td>normal</td>
<td>lengthened</td>
</tr>
<tr>
<td>18. Pronotal margin</td>
<td>rounded</td>
<td>with lateral carina</td>
</tr>
<tr>
<td>19. Specialized stridulatory organ</td>
<td>present</td>
<td>absent</td>
</tr>
<tr>
<td>20. Labrum</td>
<td>present</td>
<td>absent</td>
</tr>
<tr>
<td>21. Mentum</td>
<td>well developed</td>
<td>vestigial</td>
</tr>
<tr>
<td>22. Submentum</td>
<td>truncate</td>
<td>projecting</td>
</tr>
<tr>
<td>23. Mesepisternum</td>
<td>separate</td>
<td>fused</td>
</tr>
<tr>
<td>24. Metepisternum</td>
<td>separate</td>
<td>fused</td>
</tr>
<tr>
<td>25. Trochanters</td>
<td>small</td>
<td>large</td>
</tr>
<tr>
<td>26. Metacoxae</td>
<td>embedded</td>
<td>projecting</td>
</tr>
</tbody>
</table>

The directions of transformations shown are in most cases evident and can be confirmed in other tenebrionid tribes. Three characters, however, deserve further discussion.

_Homebius kaszabi_ shows unusually large trochanters, that of the metacoxa taking the whole width of the metatibial base. Such large trochanters are unusual in the Tenebrionidae, but general in, for example, families of Adephaga. It is considered that the large metatrochanter in _Homebius_ is a secondary development.

Open procoxal cavities appear several times in the Coleoptera. Whereas it is a rather common condition in plesiomorphic suborders (Adephaga, Myxophaga), it appears only sporadically in the Cucujidae, e.g., in the families Cryptophagidae and Mycetophagidae in which the externally open cavity is a family character, or at least the common property of a subfamily (Merophyinae of Endomychidae). In Cryptochilini, however, it is at best a generic character, of which both states occur in Cryptochilini, in _Cryptochile_ it is not even generically consistent. There is an indication that the opening of the cavity is a secondary anatomical adjustment in connection with the inflation of the body (apomorphy) and the permanent attachment of the pronotum to the hind body (apomorphy). By these evolutionary events in some cryptochilide groups, the posterior margin of the proepisternum and that of the prosternal apophysis turned inward to the coxal cavity, exposing the coxae to or beyond the posterior margin of prosternum. The approaching apices of the above-mentioned plates can be clearly seen even in the case
of open cavities (Fig. 3A–B). The open coxal cavity in Cryptochilina is therefore considered to be apomorphic.

The vertico-pronotal stridulatory organ, consisting of a complex plectrum on the vertex (Fig. 15A) and pars stridens on the inner surface of the anterior pronotal margin (Fig. 15B) is not only unique in the Tenebrionidae but probably in Coleoptera as a whole. The repeated and independent appearance of such an organ within a subfamily must be ruled out as a possibility. The common ancestor of Cryptochilina must have possessed this organ. This character is thus used to support the monophyletic origin of all the Cryptochilina subtribes as presented here. A specialized stridulatory organ is best developed in the subtribe Cryptochilina. Here both the scraper (plectrum) (Fig. 15A) and the pars stridens (Fig. 15B) are fully developed. The plectrum is present on the vertex of Vansonium but the pars tridens lost its characteristic striation and appears as a set of fine but sharp tubercles against the plectrum. The rest of the anterior inner margin of the pronotum is almost entirely smooth. In Calognathus the organ is further reduced. Neither the vertex nor the inner margin of the pronotum shows a specialized structure. The sound here is apparently produced by the scattered sharp tubercles of the vertex that are moved against the perfectly smooth, longitudinally somewhat convex inner margin of the pronotum. Homebius has the characteristic scraper of the vertex, but its pronotal structure could not be studied. The sound production of the Cryptochilina species is regularly noticed and can be heard from a distance of about 0.8 m in larger species, being obviously produced by the dorsoventral movement of the head. There was no record of stridulation of Calognathus until my 1989 expedition to the Namib. Then being aware of the problem I first noticed the rhythmic movement of the head of a captured specimen, and then heard the sound from a distance of 10–15 centimetres. Thus the sound production in Cryptochilina is general and is produced by the movement of the same body parts, but the development stage of specialized sound organs differs between the subtribes. The indications that Calognathus has lost it secondarily are very strong. Calognathus can be ruled out as representing the ancestral lineage, as it is one of the most apomorphic species (monotypic genus), with a high number of character states from which none of the other groups of the tribe could possibly be derived. The correct phylogenetic position of Calognathus is furthermore well demonstrated by its close cladistic relationship to Vansonium, with which it has the highest number of shared apomorphies found between any pair of genera in the tribe. Vansonium has the characteristic plectrum, indicating that the common ancestor of Vansonium and Calognathus also possessed it during the course of cryptochiline evolution, and Calognathus must have lost it after their separation.

The shared apomorphies between the genera studied are shown in Fig. 10. Characters 1–11 are those which show the highest numbers of synapomorphies, thereby indicating the closest kinships between the individual genera. Characters 12–14 show shared apomorphies between genera whose relationship is more remote, and are indicators of the tribe's common ancestry. Characters 15–26 represent autapomorphies and to a lesser extent Calognathus. No autapomorphy could be found for Vansonium, indicating that apart from the character transformations shared with Calognathus and Homebius, it has deviated least from the ancestral phenotype in Cryptochilina. In the cladogram (Fig. 11) constructed from the above data, the figures enclosed in squares give the numbers of shared apomorphies in the lineages distal to the square. The figures in circles give the numbers of autapomorphies found in each genus analysed.

The cladogram indicates an early divergence between Cryptochilina and the ancestor of the other three subtribes. In the second lineage, Calognathus and Vansonium appear to be closely related, whereas Homebius is further removed from the pair. Homebius actually has one more shared apomorphy with Vansonium than with Calognathus. This might be an indication that the common ancestor was more similar to Vansonium. Homebius could actually hardly be recognized as a cryptochiline if it did not possess the characteristic vertico-pronotal stridulatory organ. The peculiar shape of its antenna does not recur in the tribe, but the last antennal segments in the tribe seem to be subject to evolutionary changes unparalleled elsewhere in the subfamily. Another peculiar character of Homebius is its head, which is extremely reduced in size, very unlike most cryptochilines. Many other apomorphic characters in Homebius, such as reduction of mouthparts and fusions in the sternal structures could best be understood if its biology could be shown to be
linked with the subterranean burrows of desert mammals.

HISTORIC BIOGEOGRAPHY

The general distribution of the tribe Cryptochilini is restricted to parts of the African mainland. The highest species diversity is found in Southern Africa, with only a few species in the eastern parts of Kenya, Tanzania and northern Mozambique. These species of the tribe are at present apparently isolated from the main Southern African distribution area.

Within Southern Africa the highest species diversity is in coastal Namaqualand through the Richtersveld to the inland margins of the central Namib desert. From this area the diversity gradually decreases northwards, where the tribe's distribution ends in southern Angola. In the same way, with a gradual reduction in species diversity, members of the tribe reach the coastal areas of the southern Cape Province. They appear again in a small area of the northeastern Transvaal, where they seem to be geographically isolated.

Climatologically, only the high rainfall tropical zone and high mountain ranges with regular winter snow cover are excluded from their distribution. These restrictions leave a wide range of climatic conditions both in terms of temperature and humidity as acceptable for the dispersion and persistence of cryptochilines.

The edaphic requirements are more restricted to sandy soils, although the substrate might range from consolidated to soft. Heavy soils are excluded from habitation. Coastal dunes in the Namaqua area are vegetated, even if sparsely, and well inhabited by cryptochilines. In the Namib only marginal and vegetated dunes and interdune valleys are inhabited, but the highest species diversity is found on vegetated sandy flats bordering the dune Namib.

Although no sister group to the Cryptochilini could be determined to prove it, it seems to be likely that the tribe's centre of origin is nearest to the area identified as holding the highest species diversity. In the central part of the subcontinent's west coast, not only are the most conservative extant genera present, but also all the highly derived Cryptochilina and all three derived subtribes live in close proximity.

ACKNOWLEDGEMENTS

My sincere thanks are due to Dr M.-L. Penrith, who is engaged in a revision of the subtribe Cryptochilina, for her communications on this conservative subtribe that were particularly of great help in the evolutionary treatment. I also thank Dr M. Báriska (formerly C.S.I.R., Timber Research Institute) for his invaluable help in scanning micrography. I am grateful to Mr J. A. Irish and Mrs Hella Rust of the State Museum, Windhoek, for the loan of their material.

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Fig. 1
Mouthparts in Cryptochilini. A = Cryptochile sp.; B = Vansomium bushmanicum Koch; C = Calognathus chevrolliat chevrolliati Gaérin; D = Homebus kaszabi spec. nov. Anatomical parts: 1 = mentum; 2 = labium; 3 = labial palp; 4 = mandibula; 5 = maxillary palp; 6 = antennae; 7 = labrum; 8 = clypeus; 9 = mouthpart of unknown anatomy and function.
Fig. 2
Ventral structure in Cryptochilini. A = Cerasoma carasus spec. nov.; B = Vansonium bushmanicum Koch; C = Calognathus chevrolati chevrolati Guérin; D = Homatius kassabi spec. nov. Anatomical parts: 1 = foramen; 2 = prosternum; 3 = episternum of prosternum; 4 = prosternal apophysis; 5 = procoxal cavity; 6 = mesosternum; 7 = episternum of mesosternum; 8 = epimeron of mesosternum; 9 = mesocoxal cavity; 10 = episternum of metasternum; 11 = epimeron of metasternum; 12 = metasternum; 13 = metacoxal cavity; 14 = 1st visible sternite; 15 = elytron, X marks fused plates.
Fig. 3
Procoxal cavities in Cryptochilini. A–B = cavity open behind; C–D = cavity closed behind. A = Cryptochile sp.; B = Vansonium bushmanicum Koch; C = Calognathus chevrolati chevrolati Guérin; D = Homebius kaszabi spec. nov. Prosternal plates framing the procoxal cavity; horizontal shading = episternum of prosternum; vertical shading = prosternum and its apophyses.

Fig. 4
Antennae in Cryptochilini. A = Cryptochile sp. (undescribed, from Lambert’s Bay dunes); B = Cerasoma kochi spec. nov. male; C = C. irreale spec. nov., male; D = C. irreale spec. nov., female; E = C. cerasus spec. nov., male; F = C. cerasus spec. nov., female.

Fig. 5
Antennae in Cryptochilini. A = Calognathus chevrolati chevrolati Guérin; B = Vansonium bushmanicum Koch; C = Homebius kaszabi spec. nov., male; D = H. kaszabi, female.
Fig. 6
Distribution of the Cerasoma species on the Atlantic coast of the southwestern Cape. ■ = Cerasoma irsulae spec. nov.; ○ = C. cerasus spec. nov.; ▲ = C. kochi spec. nov.

Fig. 7
Distribution of Vansonium bushmanicum Koch subspecies in Bushmanland and in the Namib desert. ● = V. b. bushmanicum Koch; ▲ = V. b. namibense Koch.
Fig. 8
Distribution of Calognathus chevrolati Guérin subspecies. 1 = C. chevrolati chevrolati Guérin; 2 = C. chevrolati eberlanzi Koch; 3 = C. chevrolati lucanoides subspec. nov.; 4 = C. chevrolati atricolor Pic.

Fig. 9
Localities of some Cryptochilini species in the southern half of the Namib desert area. • = Calognathus chevrolati chevrolati Guérin; • = C. chevrolati eberlanzi Koch; ● = Homelius kassabi spec. nov.
Fig. 10
Distribution of synapomorphies in Cryptochilinae.
Fig. 11
Cladogram of Cryptochilini subtribes. Figures in squares indicate the numbers of synapomorphies, those in circles the number of autapomorphies.
Fig. 12

A = Cryptochile sp. (undescribed assumed ancestor of Cerasoma species), B = Cerasoma irreale gen. et spec. nov., male, C = C. cerasus spec. nov., female, dorsal view, D = C. cerasus spec. nov., female, lateral view.
Fig. 13
Scanning electron micrographs showing specific sculptural characters in both sexes of two Cerasoma species. A = C. irenea spec. nov., female; B = C. irenea, male (A and B with pronotal reticulation coarser and less continuous, elytra with traces of costal elements in female or heavy costae in male); C = C. cerasus spec. nov., female; D = C. cerasus, male (C and D with pronotal reticulation denser and more continuous, elytra without costal elements in female, male with narrower costae).
Fig. 14
Head sculpture in Cryptochilina. A = Cerastoma irreale spec. nov., male; B = C. irreale, female (coarse, sparse sculpture); C = C. cerasus spec. nov., female (finer, denser sculpture; male similar, but not available for coating for electron microscopy); D = Cryptochile sp., with dense, scaly cover.
Fig. 15
Stridulatory organs in Tenebrionidae. A-B = Cerassoma cerasus gen. et spec. nov., female; C = Drososchrus sp., Drosochlini; D = Oroclinini. A = stridulatory plectrum on vertex consisting of a set of short transverse crests. B = pars striata in anterior inner margin of pronotum; C = apparently reduced and non-functional gular plectrum; D = functional gular plectrum.
Fig. 16

A = Cerasoma cerasus spec. nov., male; B = C. kochi spec. nov., male; C = Calognathus chevrolati aberlanzi Koch, male with distorted mandibles (possibly a hermaphrodite).
Males of Calognathus chevrolati Guérin subspecies. A = C. c. chevrolati Guérin, B = C. c. aebelani Koch, C = C. c. lucanoides subspec. nov.; D = C. c. atricolor Pic.
Fig. 18
Females of Calognathus chevrolati Guérin subspecies. A = C. c. chevrolati Guérin, B = C. c. eberlandi Koch, C = C. c. lucanoides subspec. nov.; D = C. c. atricolor Pic.
Fig. 19
Vansoniina and Homebiina. A = Vansornium bushmanicum namibense Koch, male; B = V. bushmanicum bushmanicum Koch, female; C = Homebius kaszabi gen. et spec. nov., male; D = H. kaszabi, female.