SYSTEMATICS, PHYLOGENY AND BIOGEOGRAPHY OF THE CHIEFLY AFROMONTANE GENUS *CHONDROLEPIS* MABILLE (LEPIDOPTERA: HESPERIIDAE)

by

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The five known species of the African genus *Chondrolepis* Mabille are extensively described and figured and two new species are added. Keys are given to the males and females separately.

Most species are restricted to montane habitats, mainly in East Africa. Based on their phylogeny the geographic history of the species is analyzed. It is concluded that the distribution agrees with the predictions to be derived from the hypotheses that montane forests were very much restricted during the last Glacial Period of the Northern Hemisphere, later on becoming more widespread than at present, and that the contact between the Cameroun highlands and the highlands of East Africa was through species that temporarily lived in the intervening lowland forests and not through a continuous belt of montane forest across the African continent. There are indications that for *Chrondrolepis* this contact was possible twice. Similarly, but at other periods, a contact between the montane habitats of East Zaïre and Southeast Tanzania may have occurred twice.

While the diversification of the genus is closely linked with the history of the montane forests, the origin of the genus is supposed to be the result of the desiccation of the Limpopo Valley. Testing of this hypothesis by studying the phylogeny and biogeography of other groups which should have been influenced in the same way, could lead to a better understanding of the origin of the South African fauna of forests and forest margins.

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INTRODUCTION

The genus *Chondrolepis* Mabille, 1904, though small, is interesting from the biogeographic point of view. In the first place, the species are almost entirely restricted to the margins of mountain forests in Africa, thus possibly providing additional information on the geographic history of these forests (cf. Carcasson, 1964; De Jong, in prep. a). Secondly, together with the monotypic genera *Moltena* Evans and *Ploetzia* Saalmuller, the genus seems to form a monophyletic group. *Moltena* (with the species *fiara* Butler) is restricted to the coastal districts from Port Alfred (eastern Cape Province) to Maputo (Mozambique) (Dickson & Kroon, 1978), while *Ploetzia* (with the species *amygdalis* Mabille) has only been found in northern Madagascar and the near-by island of Nossi Bé (Viette, 1956). Thus, the three genera are completely allopatric and they may be helpful in studying the relationship between Madagascar and mainland Africa as well as the origin of the butterflies of the mountainous zone. These aspects will be discussed in the chapters on phylogenetic and biogeographic considerations.

The genus was erected by Mabille (1904) to include a single species, *Pamphila murga* Mabille, 1890. Evans (1937) correctly synonymized this name with *Hesperia niveicornis* Plötz, 1883, and included four more species in *Chondrolepis*. Since then, no taxonomic notes relating to the genus have been published except for the recent publication of an unavailable name. In the present paper two new species are added.

The following abbreviations are used: BMNH - British Museum (Natural History), London; MRAC - Musée Royal d'Afrique Centrale, Tervuren; RMNH - Rijksmuseum van Natuurlijke Historie, Leiden.

DESCRIPTION OF THE GENUS

Chondrolepis Mabille, 1904

Small to medium-sized, length of forewing 12.5 to 18 mm. Termen of forewing in male almost straight, in female slightly to strongly rounded. Forewing with hyaline spots in spaces 2, 3, 6, 7 and 8 (may be absent) and in cell; opaque spot in space 1b (may be absent). Male without brand or stigma. Hindwing without spots on upperside, with indistinct or distinct markings on the underside. Hindwing with lower outer angle of cell turned up. Antennae closer together than usual, long, about two-thirds of length of costa of forewing, with distinct club and short apiculus (about as long as width of club), nudum 8-10 segments; entire antennae pure white above in male, shaft chequered and club partly or entirely white above in female. Line of white hairs between antennal bases. Palpi porrect. Coxae and hind tibiae densely fringed. Hind tibiae with two pairs of spurs, but the upper pair may be indistinct.

Male genitalia. — Tegumen with lateral folds. Uncus entire. Supra-anal sclerite (scaphium) present. Gnathos consisting of a right and left sclerite, entirely joined to ventral part of lateral fold of tegumen, distally thickly set with hairs which mainly point proximad; left and right part of gnathos separated by membrane. Aedeagus without ornamentation, no cornutus. Valvae more or less asymmetric, distal part of cucullus usually more strongly developed in right than in left valva; cucullus always spined distally.

Female genitalia. — Ostium covered by a very broad, slightly sclerotized fold which is smooth or covered with microtrichia and which laterally strongly curves back to form a deeply hollowed plate, usually with very fine spines on and near the edge. Postvaginally a large, slightly sclerotized plate, smooth or with fine knobs in proximo-lateral parts, densely set with microtrichia in distal part, where the plate is deeply indented in a V-shaped or U-shaped way; proximo-laterally the plate overlaps the hollowed part of the antevaginal plate. Laterally of postvaginal plate, slightly sclerotized or membranous folds which are densely set with microtrichia or very fine spines. Ductus bursae and bursa copulatrix membranous, no signum. Papillae anales densely set with microtrichia, apart from the normal hairs. Tergum VIII densely set with microtrichia, but smooth middorsally.

Discussion. — The genus shares the characters of the relative proximity of the antennal bases and the white line joining these bases only with the genera *Moltena* and *Ploetzia*. It can easily be distinguished from these genera by the presence of hyaline spots and the longer antennae. From *Ploetzia* it also differs in the uncus being entire. With *Moltena, Chondrolepis* shares the presence of a scaphium, quite remarkable for Hesperiidae.

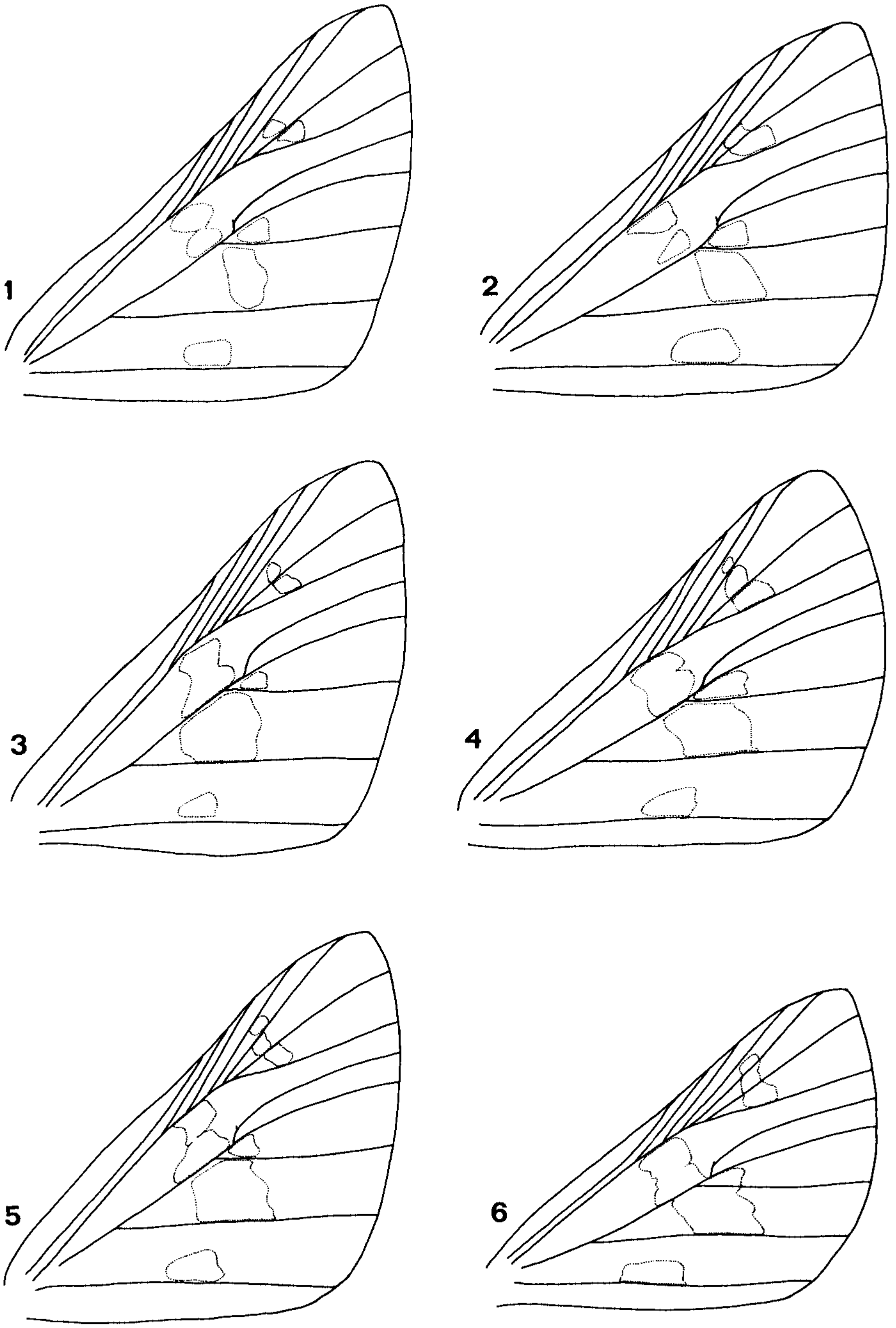
The pure white antennae of the males are very conspicuous and undoubtedly have a function as a signal. The flight is extremely fast and one often sees the antennae before the whole insect. Although they are quite active in the sunshine, it is possible that the insects also fly at dusk like *Moltena* and *Zophopetes* (see chapter on phylogeny), and in that case the white antennae could be helpful in courtship if it takes place at dusk. In this connection it is also interesting to note that the eyes usually have a reddish tinge (possibly becoming darker with age). In a paper on the related Oriental genus *Matapa* (De Jong, 1983) I noted that there seems to be a correlation between a red eye colour and activity at dusk.

The only observation on foodplants is given by Dickson & Kroon (1978) for *C. niveicornis,* which is said to live on a broad-leaved grass.

KEY TO THE SPECIES OF *CHONDROLEPIS*

MALES

1. Upperside forewing without spot in space 1b, or if present, there are three subequal subapical spots in line and spot in space 2 narrow, upright, under origin of vein 3 .... *leggei*
– Upperside forewing with yellow or creamish spot in space 1b; if spot in space 2 is narrow and upright, then only two subapical spots 2
2. Underside hindwing with conspicuous white mark on dark brown ground .... *telisignata*
– Underside hindwing without a white mark......................... 3
3. Underside hindwing dark chocolate-brown with a complete series of inconspicuous violet-grey, dark-edged, discal spots which may unite into a narrow band, and a similar spot in cell. Upperside forewing cell spot entire but much narrowed centrally, lower part rather larger than upper part; spot in space 2 large, about as wide as high, under the cell spot and with its centre well before the origin of vein 3......................... 4
– Underside hindwing ferruginous or greyish brown, with a dark, more or less wedge-shaped discal band. Upperside forewing cell spot entire or divided; spot in space 2 with its centre before or after the origin of vein 3 5
4. Length of forewing 15.3-16.4 mm. Spot in space 2 of forewing longer (wider) than high, line connecting inner edges of cell spot and spot in space



Figs. 1-6. Forewing venation and position of spots in *Chondrolepis* species, left: male, right: female; 1, 2, *C. niveicornis;* 3, 4, *C. obscurior;* 5, 6, *C. cynthia.*

2 running along inner edge of spot in space 1b. Hindwing underside, discal spots more or less separate, hardly diminishing in size from space 1c to space 4/5. Diameter of eye 1.7-1.8 mm .... *obscurior*

– Length of forewing 17-17.3 mm. Forewing, spot in space 2 slightly narrower than wide, line connecting inner edges of cell spot and spot in space 2 running along outer edge of spot in space 1b. Hindwing underside, discal spots in spaces 1c-5 fused to a wedge-shaped band. Diameter of eye 2.2 mm .... *similis*

5\. Upperside forewing, spot in space 2 with its centre after the origin of vein 3. Underside hindwing, ground colour ferruginous .... *niveicornis*

– Upperside forewing, spot in space 2 with its centre before the origin of vein 3. Underside hindwing, ground colour brown or greyish brown 6

6\. Upperside forewing, cell spot entire but narrowed medially; three subapical spots, the upper one out of line (towards apex). Underside hindwing dark greyish or violet brown with darker, wedge-shaped discal band, basally edged by a lighter area .... *cynthia*

– Upperside forewing, cell spot entire or just divided into two; two subapical spots, upper one very small. Underside hindwing brown with inconspicuous darker or violet brown, dark-edged, slightly wedge-shaped discal band .... *nero*

FEMALES

1\. Antennal club at most partly white above 2

– Antennal club completely white above 6

2\. Forewing with three subapical spots in line; cell spot entire or divided into an upper and a lower spot 3

– Forewing with two subapical spots, or if three, the upper one out of line; cell spot divided into an upper and a lower spot 5

3\. Forewing, spot in space 2 about twice as high as wide, its centre beyond origin of vein 3; cell spot divided............................. *leggei*

– Forewing, spot in space 2 as wide as or wider than high, its centre under or just beyond origin of vein 3; cell spot entire but constricted in middle, rarely divided 4

4\. Underside forewing, greater part of space 1b light-coloured. Underside hindwing, brown with slight violet tinge and dark brown bands and spots .... *cynthia*

– Underside forewing, a diffuse, light-coloured spot in space 1b. Underside hindwing, deep yellow or yellow-brown with ferruginous marking .... *telisignata*

5. Upperside forewing, spot in space 2 with its centre well beyond the origin of vein 3 . . . . *niveicornis*
– Upperside forewing, spot in space 2 with its centre about under the origin of vein 3 . . . . *nero*
6. Length of forewing up to 16.3 mm. Forewing, spot in space 2 slightly wider than high; underside, light-coloured area in space 1b not reaching termen (or at most along vein 1). Hindwing underside, discal spots close but separate, spot in space 2 only slightly wider than spots in space 4/5 . . . . *obscurior*
– Length of forewing 17.7 mm. Forewing, spot in space 2 narrower than high, oblique; underside, light-coloured area in space 1b more extensive, obscuring the included spot and reaching termen over vein 1. Hindwing underside, discal spots forming a continuous band from space 1c to space 4/5, wedge-shaped because the spots in space 4/5 are at most half as wide as the spots in spaces 1c and 2 . . . . *similis*

SYSTEMATIC PART

The species can be divided into two groups which are characterized as follows:

niveicornis group – ground colour of underside of hindwing sexually dimorphic, being brown in male, yellow in female; apices of lateral folds of tegumen rounded and not projecting;

similis group – ground colour of underside of hindwing brown in male and female; apices of lateral folds of tegumen rounded or pointed, more or less projecting.

Chondrolepis niveicornis (Plötz, 1883)

Hesperia niveicornis Plötz, 1883: 33. Type probably lost. Type-locality: Angola.

Pamphila murga Mabille, 1890: 31. Holotype, ♀, in BMNH (H1521). Type-locality: Kaffraria (according to original description; holotype without locality label).

Pamphila chirala Trimen, 1894: 76. Holotype, ♀, in South African Museum, Cape Town. Type-locality: Mineni Valley (Zimbabwe).

Perichares albicornis Butler, 1896: 132. Holotype, ♂, in BMNH (H1520). Type-locality: West of Lake Nyasa, Kondowi, Lower Nyika.

Kedestes (?) *miranda* Butler, 1902: 33. Holotype, ♀, in BMNH (H1522). Type-locality: E. Quaso, Masai, Kenya.

(Berger, 1984, published the name *pseudonero* for a supposed Ethiopian subspecies, based on a single male. Since the name is not accompanied by a description nor by a reference to a description, it is an unavailable name, see International Code of Zoological Nomenclature, Art. 13. The photograph of the single specimen does not show divergence from specimens caught in Kenya or elsewhere.)

Material examined. — 372♂ 150♀: 4♂ 3♀, Cameroun (Bamenda, Chang, S.of Chang, Penderu, Yaounde) (BMNH, MRAC); 41♂ 26♀, Zaïre (Kambove, L. Edward, L. Kivu, Albertville, Solwezi, Marungu Plateau, Mpala, Kundelungu Plateau, Paulis, Moto, Bambesa, Sandoa, Kolwezi, Lubumbashi, Kapanga, Kafakumba, Rungu, Kinda, Parc. Nat. Albert, Mt. Hoyo, Nioka) (BMNH, MRAC); 43♂ 30♀, Uganda (Kampala, Entebbe, Kafu Riv., Mabira Forest, Jinja, Mitiana-Entebbe, Kakindu, Kimbugu, Mpumu, Masindi, Ngusi Riv., Budongo Forest, Bugoma Forest, Kiliangore, Toro, Ankole-Toro border, Kalinzu Forest, Mpanga Forest, Fort Portal, L. Isolt, L. George, Butiaba, Buamba Forest, Pt. Alice, Kiki Country, Mubende, Namadara Forest) (BMNH, MRAC); 1♂ 1♀, Sudan (Tembura) (BMNH); 2♂ 1♀, Ethiopia (Irgalem, "Abyssinia") (BMNH); 18♂ (including holotype of *Kedestes* (?) *miranda*) 4♀, Kenya (Eldama Ravine, Kitale, Rau, Yala River, Nandi, Hoey's Bridge, Kisii Distr., Mt. Kenya, Nairobi, Kibwezi, E. Quaso (Masai), Cherangani Hills, Mt. Elgon) (BMNH, MRAC, RMNH); 70♂ 36♀, Tanzania (Kilimanjaro, Usambara, Iringa, Tukuyu, Mt. Rungwe, Uluguru Mts., Mufindi, Mabu, Kampisa, Ntakatta, Lubalisi, Luntampa, Sibweza, Kefu, Lukandamira) (BMNH, MRAC, RMNH); 2♂, Rwanda (Kisenyi, Astrida to Kigali) (MRAC); 159♂ 36♀, Burundi (Kitega) (MRAC); 18♂ (including holotype of *Perichares albicornis*) 8♀, Malawi (C. Angoniland, Zomba, Chikala, W. of L. Nyasa, Kondowi, Fwambo, Mlanje, Mlanji Boma, Lenibe, Nyassaland) (BMNH, MRAC); 4♂ 1♀, Zambia (Chambezi Valley, Karungu River) (BMNH); 10♂ 4♀, Angola (Ceramba, Pungo Andongo, Bihe, Calweha Riv., Cubal Riv., N'Dalla Tando) (BMNH).

External characters. — Male. Length of forewing 13-17.7 mm. Forewing (fig. 1), hyaline spots in spaces 2 (narrow, 1.5 times to twice as high as wide, its centre beyond the origin of space 3), 3 (small, at upper outer corner of spot in space 2), 6 and 7 (latter smaller), and in cell (almost always divided into an upper and a lower spot); a conspicuous yellow opaque spot in space 1b against vein 1; outer edge of cell spots and inner edge of spot in space 2 in line. Underside forewing, spots as on upperside; diffuse whitish spot in space 1b on the place of the yellow spot of the upperside but slightly larger; costal area same ferruginous colour as underside of hindwing, terminal area of a more violet-brown shade, separated from the ferruginous costal area by a broken dark line from vein 4 to apex. Underside hindwing ferruginous with violet, dark-edged, discal spots from vein 1b to termen in space 6, a dark dot in space 6, a violet, dark-edged outer spot and a small dark inner spot in space 7, two small dark dots in cell, fine submarginal line, area between this line and termen often a little paler; not all markings always obvious. Eye diameter, 1.4-1.9 mm.

Female. As male, but termen of forewing more convex; spot in space 2 slightly wider; in rare cases a small opaque spot in space 8, out of line (towards apex) (fig. 2). Underside, yellow where male is ferruginous and brown where male is violet. Antennal club brown, white-ringed in upper part (just under apiculus). Eye diameter as in male.

Genitalia. — Male (figs. 15-17, 36). Tegumen in dorsal view rectangular, wider (about 1.5 times) than long. Uncus in dorsal view triangular, with round top, length almost 1.5 times width at base. Hairs of gnathos not very long but conspicuous. Caecum of aedeagus less than 1.5 times as long as wide. Left valva, ratio length of cucullus : length of entire valva = 10 : 16; cucullus not bending back over costa, strongly spined dorsally, spined area at most half of length of cucullus; costa a rather indistinct, smooth sclerotization over basal half of cucullus; ventral edge of cucullus evenly curved, dorsal edge concave

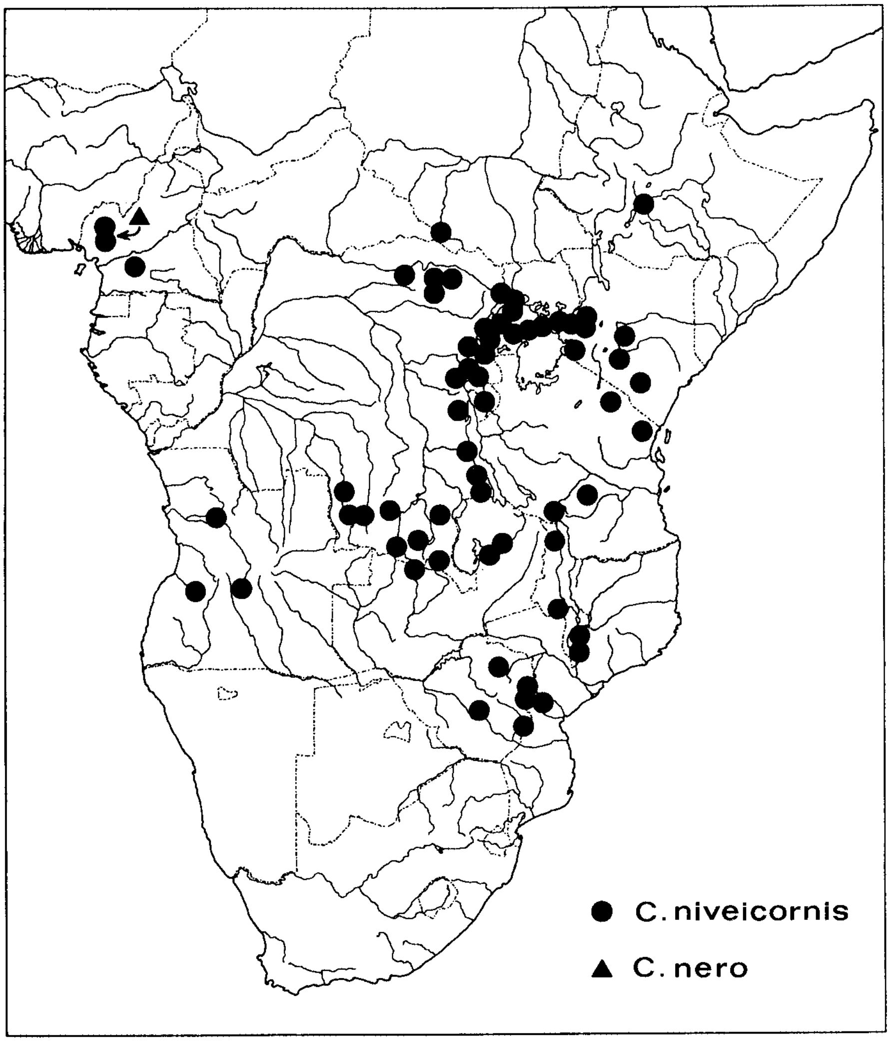


Fig. 7. Distribution of *Chondrolepis niveicornis* and *C. nero*.

in distal third. Right valva, cucullus with spined dorsal part strongly extended over costa so that spined area is about 2/3 length of cucullus, dorsal edge straight, outline of whole valva reminding of arrow-head with one barb; rest similar to left valva.

Female (fig. 46). Antevaginal fold smooth. Postvaginal plate smooth except for densely set microtrichia in apical part and reaching down alongside the U-shaped indentation to about the bottom of the indentation. Slightly sclerotized folds in membrane between sternal and tergal sclerotizations, smooth.

Habitat. — On the average not as high as the other *Chondrolepis* species, from 800 to probably not higher than 2000 m. It is a species of damp places, along streams, etc. (Congdon, in litt.; Dickson & Kroon, 1978).

Distribution (fig. 7). — Very widely distributed, from Cameroun to Ethiopia and south to Angola and Zimbabwe. Not known from most of the low-lying Congo basin. The distribution map is based on examined material, but additional records have been taken from Dickson & Kroon (1978) for Zimbabwe and Mozambique, and from Kielland (1978) for Tanzania.

Chondrolepis nero Evans, 1937

Chondrolepis nero Evans, 1937: 140. Holotype, ♂, in BMNH (H1519). Type-locality: Kumbo, Cameroun, 5500 ft.

Material examined. — 34♂ (including holotype) 11♀, all Cameroun (Kumbo, Bamenda, Banso Mts, Chang, Manengouba) (BMNH, MRAC).

External characters. — Male. Length of forewing 15-16.4 mm. Forewing with hyaline spots in spaces 2 (about as high as wide, its centre before the origin of vein 3), 3 (small, at upper outer corner of spot in space 2), 6 and 7 (the latter about half the size of the former), and cell (entire or, usually, just divided by a fine longitudinal line); conspicuous yellow, opaque spot in space 1b against vein 1; inner edges of cell spot(s) and spot in space 2 in line. Underside forewing, spots as on upperside; diffuse whitish spot in space 1b in same place as yellow spot of upperside but slightly larger; costal area brown as on underside hindwing, terminal area slightly paler brown, separated from brown costal area by diffuse line about from space 6 to apex. Underside hindwing brown with inconspicuous violet-brown, dark-edged, discal band from vein 1b to termen in space 6; other markings very obscure. Eye diameter 1.4-1.7 mm.

Female. As male, but termen of forewing more convex and spots slightly larger; in about half of the females a very small spot in space 8 of forewing, out of line (towards apex). Underside hindwing yellow where male is brown and brown where male is violet-brown. Antennal club brown, more lightly coloured just below apiculus. Eye diameter as in male.

Genitalia. — Male (figs. 18-20, 37). Smaller than in other *Chondrolepis* species, ratio wing length : valva length = ca. 7.7, whereas it varies from 5.1 to 6 in the other species. Tegumen rectangular in dorsal view, length about 3/4 of width; lateral fold distally about right-angled and with rounded top, outer edge slightly bumpy. Uncus narrowly triangular in dorsal view, with slightly swollen apex, length almost twice width at base. Hairs of gnathos very fine, rather indistinct. Caecum of aedeagus over twice as long as wide. Left valva, ratio length of cucullus : length of entire valva = 6.5 : 10.5; cucullus dorsally more or less rounded, not bending back over costa, rather finely spined, spined area about 0.4 times length of cucullus; costa a rather indistinct, irregular, smooth sclerotization close to cucullus; ventral edge of valva concave at base of cucullus, dorsal edge almost straight, very slightly curved. Right valva: cucullus slightly extended proximo-dorsally so as to just bending over costa, rather finely spined dorsal area about half of length of cucullus; costa as in left valva; ventral edge of valva distinctly concave at base of cucullus (or cucullus ventrally bulging in basal part), dorsal edge as in left valva.

Female (figs. 44, 45). Antevaginal fold with fine microtrichia on outer side over most of central area, laterally with fine spines. Postvaginal plate smooth except for fine spines on lateral fold and apical microtrichia; area with microtrichia reaching to about halfway the U-shaped indentation.

Habitat. — All known specimens have been caught between 1500 and 2200 m.

Distribution (fig. 7). — Only known from the highlands of Cameroun, but not from Mt. Cameroun. Evans' (1937) record from Nigeria relates to localities which once were in Nigerian territory but now belong to Cameroun.

Chrondrolepis telisignata (Butler, 1896)

Perichares telisignata Butler, 1896: 133. Holotype, ♂, in BMNH (H1518). Type-locality: West of Lake Nyasa, Kantorongonda Mt., 5900 ft.

Material examined. — 177♂ 65♀. Kenya: 49♂ 25♀, Aberdares (Kipipiri, N. Kinangop, S. Kinangop, eastern slopes, western slopes) (BMNH, MRAC, RMNH); 8♂ 16♀, Mt. Kenya (Naro Moru, Meru, Nanyuki-Meru) (BMNH, MRAC, RMNH); 41♂ 16♀, Central Kenya (Nairobi, Kikuyu, Escarpment) (BMNH); 7♂ 2♀, South Kenya (Kibwezi, Teita Hills) (BMNH). Uganda: 1♂, Mabira Forest (BMNH). Tanzania: 6♂ 6♀, Iringa Distr. (Mufindi, Njombe) (BMNH, RMNH); 4♂, Mbeya Distr. (Tukuyu, Mt. Rungwe) (BMNH, RMNH). Malawi: 1♂, Nyika Plateau (BMNH).

External characters. — Male. Length of forewing 11.7-14 mm. Forewing, hyaline spots in spaces 2 (as high as wide or, usually, wider than high; its centre before the origin of vein 3), 3 (small, at upper outer corner of spot in space 2), 6-8 (subequal, in straight line, or spot in space 6 larger than the other two spots), and cell (entire, but slightly to strongly constricted in middle, in rare cases just divided by fine, longitudinal line); conspicuous pale yellow, opaque spot in space 1b against vein 1; inner edges of cell spot and spot in space 2 in line. Underside forewing, spots as on upper side; in space 1b a diffused white area under the spot in space 2, obscuring the spot in space 1b; along termen, especially apically of subapical spots, brown as on underside hindwing, apical half of terminal area paler brown. Underside hindwing a warm brown colour, often with yellowish, sometimes whitish, scaling along termen; a conspicuous white mark from basal half vein 1b to vein 6, narrow at vein 1b, further narrowing at the origin of vein 3 and from there greatly expanding towards vein 6, the expansion being towards the wing base so that the lower edge of the mark is more or less straight (from basal half of vein 1b to outer half of vein 6) and the upper edge is concave to deeply indented; there is much variation in the width of the white mark. Eye diameter 1.2-1.4 mm.

Female. As male, but termen of forewing more strongly convex; spots generally smaller, centre of spot in space 2 under or just beyond origin of vein 3; cell spot sometimes just divided; underside forewing, spot in space 1b not enlarged to a diffused white area; underside hindwing pale yellow to yellow-brown, dark ferruginous discal area from vein 1b (almost reaching termen) strongly narrowing to vein 6, same colour in cell and basal part of space 7, area in between lightly coloured, sometimes even whitish (thus reminding of male); varies from a well-marked underside to an entirely yellow or brownish yellow underside with faint darker areas. Antennal club brown, upper half whitish. Eye diameter as in male.

Genitalia. — Male (figs. 21-23, 38). Tegumen more or less rectangular in dorsal view, about as long as wide; lateral folds not conspicuous and apices blunt. Uncus elongate pear-shaped, twice as long as greatest width, apex rounded, slightly swollen. Hairs of gnathos short and inconspicuous. Caecum of aedeagus four times as long as wide. Left valva, ratio length of cucullus : length of entire valva = 7.5 : 12.5; cucullus about parallel-sided in basal half, distally expanding upwards to well beyond dorsal edge of valva, with small spines along distal-dorsal edge; costa with well-developed, smooth, trapezoid sclerotization over basal half of cucullus; ventral edge of valva concave at base of cucullus, dorsal edge slightly concave in distal third. Right valva, cucullus gradually expanding from base, distally more strongly expanded and more strongly spined than in left valva; costal sclerotization rounded triangular; for the rest, similar to left valva.

Female (fig. 47). Antevaginal fold smooth. Postvaginal plate smooth except for apical microtrichia; area with microtrichia not reaching to halfway down the sides of the wide, shallowly U-shaped indentation. Slightly sclerotized fold between sternal and tergal sclerotizations, smooth.

Habitat. — As far as records on altitude are available the species has been caught between 1500 and 2800 m. If the species really occurs in Uganda (see below), the altitudinal range would be from about 1000 m up to 2800 m, quite exceptional for a tropical skipper. The species is especially found along forest paths and it can be quite numerous. The author found it, e.g., abundant along a road through the bamboo zone at the westside of the Aberdares (Kenya).

Distribution (fig. 8). — Widely disjunct, in Central and South Kenya and in South Tanzania/North Malawi. The disjunction does not seem to be the result of undercollecting in the intervening area, since most places where the species could be expected have been visited by collectors. The only locality in Uganda (Mabira Forest) seems to be unlikely, in the first place because it is fairly low, in the second place because no specimens are known from the well-collected western part of Kenya. Since only a single male is known from the Mabira Forest, the possibility of mislabeling must be taken into consideration until new material becomes available. Similarly there is only one male known from Kibwezi (Kenya). If not the relatively low-lying Kibwezi Forest (about 1000 m) has been meant, the specimen may have been caught in the nearby Chyulu Hills (up to over 2000 m). Also in this case more material would be welcome. From Malawi I have only seen the holotype, but more specimens have been reported by Gifford (1965). The Malawi locality nicely connects with the southern Tanzanian highlands where the species has been found in several localities.

Chondrolepis similis spec. nov.

Material examined. — Holotype, ♂, Tanzania, Mufindi, Luisenga River, 1700 m, 21.iii.1982, J. Kielland (RMNH). Paratypes: 1♂, Mufindi, Ngamalala, 1900 m, 25.iii.1983, T.C.E. Congdon (RMNH); 1♂, Luipanga River, 1800 m, 21.iii.1982, J. Kielland (coll. Kielland); 1♀, same data as holotype, but collected by T.C.E. Congdon (RMNH).

External characters. — Male. Length of forewing 17-17.3 mm. Yellowish hyaline spots of forewing in spaces 2 (slightly narrower than high; centre just before origin of vein 3), 3 (small, at upper outer corner of spot in space 2), 6-8 (diminishing in size), and in cell (entire, but outer edge sharply indented medially and inner edge very strongly concave); conspicuous yellow spot in space 1b against vein 1; inner edges of cell spot and spot in space 2 and outer edge of spot in space 1b in line. Underside forewing, spots as on upperside, diffuse light area in space 1b reaching termen; along costa and apical half of termen dark brown as on hindwing underside, crossed by faint dark line between subapical spots and termen. Underside hindwing dark chocolate-brown, violet-grey, dark-edged, discal band, narrowing from vein 1b to vein 6, indistinct spots in spaces 6 and 7 and in cell. Eye diameter 2.2 mm.

Female. As male, but length of forewing 17.7 mm; termen convex; spot in space 2 narrower and centre just beyond origin of vein 3; line connecting inner edges of spots in cell, and space 2 crosses space 1b well beyond the spot in that space. Antennal club entirely white above. Eye diameter 1.8 mm.

Genitalia. — Male (figs. 24-26, 40). Tegumen rectangular in dorsal view, slightly wider than long; lateral folds well visible, rounded apices slightly projecting distad. Uncus pear-shaped, 1.5 times as long as wide, top rounded. Gnathos with rather long and conspicuous hairs. Caecum of aedeagus 2-2.5 times as long as wide. Left valva, ratio length of cucullus : length of entire valva = 11.5 : 18.5; cucullus parallel-sided, distally expanded and spined, proximodorsal top rounded; costa with a large sclerotization over basal half of cucullus; ventral edge of valva about straight in basal third, evenly curved in distal two-third, dorsal edge straight, slightly irregular in distal third. Right valva, cucullus more strongly developed, particularly distally, proximodorsal top more angular; for the rest, as left valva.

Female (fig. 48). Antevaginal fold smooth, laterally expanded and strongly hollowed, edge and part of hollowed sclerite with bristles or fine spines. Postvaginal plate smooth except for slight apical wrinkling and apical microtrichia; area with microtrichia restricted and narrowly reaching down along sides of very wide, relatively shallow, almost semicircular indentation to about 2/3 of length of sides. Between sternal and tergal sclerites an indistinctly defined sclerotization with a small fold with fine microtrichia.

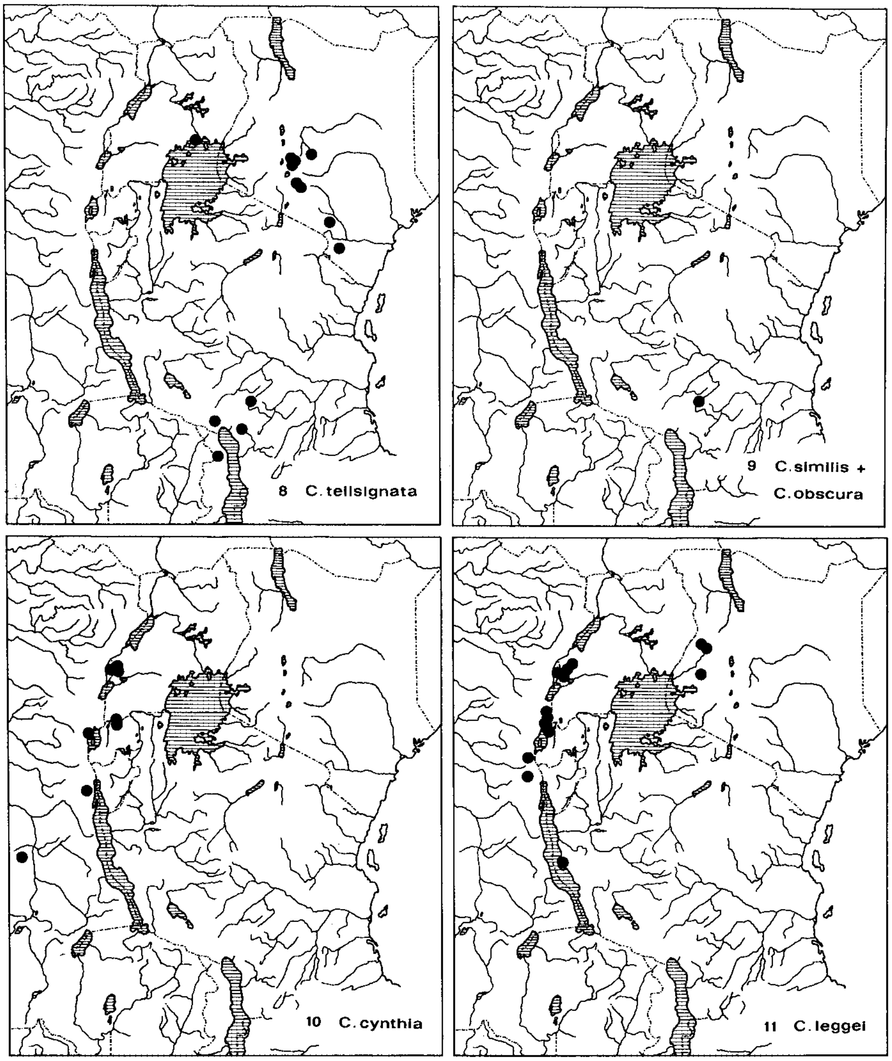
Habitat. — The four known specimens all came from a forested area, 1700-1900 m.

Distribution (fig. 9). — Only known from the surroundings of Mufindi in the southern highlands of Tanzania.

Chondrolepis obscurior spec. nov.

Material examined. — Holotype, ♂, Tanzania, Mufindi, Lupeme, 6500', 19.i.1983, T.C.E. Congdon. Paratypes, 18♂ 23♀, all Mufindi and surroundings. Holotype and 13♂ 19♀ paratypes in RMNH, 5♂ 4♀ paratypes in Coll. Kielland.

External characters. — Male. Length of forewing 15.3-16.4 mm. Forewing (fig. 3), yellowish hyaline spots in spaces 2 (large, slightly wider than high, centre well before origin of vein 3), 3 (small, at upper outer corner of spot in space 2), 6, 7 (slightly to obviously smaller), and 8 (very small, may be absent), and in cell (entire but constricted medially, the lower part being the larger; rarely just divided by a fine longitudinal line); conspicuous pale yellow opaque spot in space 1b against vein 1; inner edges of cell spot and spots in



Figs. 8-11. Distributions of *Chondrolepis* species.

spaces 2 and 1b in line. Underside forewing, spots as on upperside; in space 1b a diffuse lighter area around the spot, not clearly reaching termen; along costa and apical half of termen dark chocolate-brown as on underside of hindwing, crossed by an indistinct darker line between subapical spots and termen. Underside hindwing dark chocolate-brown; complete series of small, dark-ringed, violet-grey discal spots, and such a spot in cell; a very indistinct dark line between discal spots and termen. Eye diameter 1.7-1.8 mm.

Female. As male, but length of forewing up to 16.3 mm; termen of forewing strongly convex; hyaline spot in space 8 always present but small; spot in space 2 rather wider than high with its centre under or beyond the origin of vein 3; spot in space 3 larger than in male; line connecting inner edges of cell spot and spot in space 2 crosses space 1b at or beyond outer edge of spot in space 1b (fig. 4). Underside hindwing not as dark as in male, spots more conspicuous. Antennal club entirely white above. Eye diameter as in male.

Genitalia. — Male (figs. 27-29, 41). Tegumen trapeziform in dorsal view, basal width about 3/4 distal width, slightly longer than basal width; lateral folds conspicuous, with rounded, projecting and incurving tops. Uncus elongate pear-shaped, twice as long as wide, top rounded. Hairs of gnathos short, rather inconspicuous. Caecum of aedeagus three times as long as wide. Left valva, ratio length of cucullus : length of entire valva = 10.5 : 16.5; cucullus almost parallel-sided, distally expanding and shallowly indented so as to form a bipartite, spined head; costa with elongate sclerotization, ventrally with fine knobs, apical edge irregular; ventral edge of valva concave at base of cucullus, dorsal edge evenly curved, but with a shallow indentation at about 1/3 from apex. Right valva, cucullus gradually expanding towards the dorsodistal part which is more strongly spined and more angular then in left valva, and not as clearly indented and bipartite; for the rest rather similar to left valva.

Female (fig. 49). Antevaginal fold smooth, laterally broadly expanded and edge here irregular to finely spined. Postvaginal plate smooth except for apical microtrichia; area with microtrichia reaching down along sides of wide, U-shaped indentation almost to bottom of indentation. Sclerotized area in lateral membrane, passing into small fold with very fine microtrichia.

Habitat. — All specimens have been caught in forested area at an altitude of 1700 to 2000 m.

Distribution (fig. 9). — So far only known from the surroundings of Mufindi in the southern highlands of Tanzania.

Chondrolepis cynthia Evans, 1936

Chondrolepis cynthia Evans, 1936: 185. Holotype, ♂, in BMNH (H1524). Type-locality: Kisiba, Bugoie Forest, W. Kivu, 8500 ft.

Material examined. — 18♂ 15♀. Uganda: 5♂ 6♀, Ruwenzori area (Namwamba, Bwamba Pass) (BMNH); 2♀ Kigezi Distr. (Mafuga Forest, Mt. Mahinga) (BMNH). Zaïre: 11♂ (including holotype) 5♀, Kivu Distr. (Kisiba, Ngesho, Riv. Lulimbaha, Mt. Muhi, Mt. Biega, Mwana, Tshiaberimu, between Luemba and Mukera) (BMNH, MRAC); 2♂ 1♀, Ruwenzori area (BMNH, MRAC); 1♀, Katanga (Katompe) (MRAC).

External characters. — Male. Length of forewing 14-15.9 mm. Forewing (fig. 5), hyaline spots in spaces 2 (about as wide as high, its centre before the origin of vein 3), 3 (small, at upper outer corner of spot in space 2), 6-8 (subequal, the spot in space 6 slightly larger; in a straight or slightly curved line), and in cell (entire, but constricted in middle); small but conspicuous yellow spot in space 1b against vein; inner edges of cell spot and spot in space 2 in line. Underside forewing, spots as on upperside; terminal area pale brown; greater part of space 1b creamish from base to about outer edge of spot in space 2, obscuring the spot in space 1b. Underside hindwing brown with discal band (narrowing from vein 1b to vein 6) and costal area dark brown, area basally of discal band pale brown. Eye diameter 1.5-1.7 mm.

Female. As male, but termen of forewing much more convex; spots slightly larger and spot in space 2 with its centre under or beyond the origin of vein 3 (fig. 6); underside hindwing, ground colour a bit paler so that markings are sharper. Antennal club brown, apical half whitish. Eye diameter as in male.

Genitalia. — Male (figs. 30-32, 42, 43). Tegumen slightly trapeziform in dorsal view, at base about 3/4 distal width; lateral folds well-developed, with slightly irregular edges and projecting, rounded tops. Uncus elongate pear-shaped with rounded apex, over twice as long as greatest width. Hairs of gnathos relatively short. Caecum of aedeagus about four times as long as wide. Left valva, ratio length of cucullus : length of entire valva = 9 : 15; cucullus parallel-sided over most of its length, distally finely spined, apex upturned, not reaching dorsal line of costa; costa with large, trapezoid sclerotization over middle of cucullus, very fine spines or knobs in ventral part; ventral edge of valva slightly concave at base of cucullus, dorsal edge very slightly concave in distal part. Right valva with cucullus more expanded distally, reaching beyond dorsal line of costa, more strongly spined here; costa with rounded triangular sclerotization; dorsal edge of valva evenly curved; for the rest, similar to left valva.

Female (fig. 50). Antevaginal fold smooth but projecting lateral parts with many small spines. Postvaginal plate smooth except for microtrichia at apices, the area with microtrichia reaching to about halfway U-shaped indentation; lateral slight sclerotization also with microtrichia.

Habitat. — All specimens have been caught between 2000 and 2800 m.

Distribution (fig. 10). — From the Ruwenzori area south to north end of Lake Tanganyika, and in Katanga. Very local and never caught in large numbers.

Chondrolepis leggei (Heron, 1909)

Chioneigia leggei Heron, 1909: 107. Holotype, ♂, in BMNH (H1523). Type-locality: E. Ruwenzori.

Material examined. — 20♂ 16♀: 3♂ 6♀, Kenya (Kitale, Hoey's Bridge, Nandi Plateau) (BMNH); 8♂ (including holotype) 4♀, Uganda (Mpanga Forest, Namwamba Valley, Ruwenzori) (BMNH); 8♂ 5♀, Zaïre (Ruwenzori, Karissimbi Volcano, Ngesho, Rutshuru, Mulungu, Rumangabo, Mutsora, Mwenga) (BMNH, MRAC); 1♂, Rwanda (Gisenye) (BMNH); 1♀, Tanzania (Lukandamira) (MRAC).

External characters. — Male. Length of forewing 14.5-16 mm. Forewing, hyaline spots in spaces 2 (narrow, upright, at least twice as high as wide, under origin of vein 3 and under lower cell spot), 3 (small, apically of spot in space 2, not overlapping it), 6-8 (subequal, in straight line), and in cell (an upper and a lower spot); no spot in space 1b (in two males out of 18 a small yellow dot). Underside forewing, spots as on upperside, inconspicuous lighter suffusion in basal half of space 1b; dark brown along costa, violet-brown along termen in apical half. Underside hindwing violet-brown, discal band (of about equal width) and basal area dark brown. Eye diameter 1.5-1.7 mm.

Female. As male, but termen of forewing much more convex; spot in space 2 a bit broader, 1.2-1.5 times as high as wide, its inner edge under origin of vein 3, overlapped by spot in space 3; always a small, yellow, opaque spot in space 1b on the upperside, this spot being obscured by a light suffusion on the underside; underside hindwing as in male or slightly paler. Antennal club brown, apical half white. Eye diameter as in male.

Genitalia. — Male (figs. 33-35, 39). Tegumen almost rectangular in dorsal view, slightly wider than long; lateral folds well-developed, with irregular edges, distally pointed and projecting; in centre of tegumen a rounded outgrowth pointing distad. Uncus elongate pear-shaped, parallel-sided in distal third, length about 1.3 times greatest width, top rounded. Hairs of gnathos relatively long and conspicuous. Caecum of aedeagus about five times as long as wide. Left valva with strongly developed cucullus; ratio length of cucullus : length of entire valva = 9.5 : 10.5; cucullus elongate and almost parallel-sided in basal two-third, apically expanding to a two-headed, condyloid shape, the proximal head larger and with stronger spines than the distal head; costa with large, more or less trapezoid sclerotization over basal half of cucullus, in ventral part with area of closely set, small tubercles; ventral edge of valva slightly concave at base of cucullus, dorsal edge slightly concave at costal sclerotization. Right valva similar to left; proximal head of cucullus more elongate; tubercles of costa hardly more than fine knobs or irregularities in the sclerotization.

Female (fig. 51). Antevaginal fold smooth but slightly projecting lateral parts with small spines. Postvaginal plate largely smooth, proximo-laterally with fine bumps, apices with microtrichia down to bottom of V-shaped indentation. Membrane distally of postvaginal plate with slight sclerotization. Between lateral extension of antevaginal fold and tergal sclerotization a small membranous fold with microtrichia.

Habitat. — As far as there are exact altitudinal records, all specimens have been caught between 1200 and about 2200 m.

Distribution (fig. 11). — Disjunctly distributed in western Kenya, the Ruwenzori range and adjoining Uganda, around Lake Kivu, and in the central part of the east side of Lake Tanganyika. Apparently a rare insect, since from most localities only a single specimen or at most very few specimens are known.

PHYLOGENETIC CONSIDERATIONS

Relationship with other genera

Evans (1937) distinguished the *Ploetzia* group for 15 genera of African Hesperiidae, one of which is *Chondrolepis*. The group is rather well-defined by the shaggy appearance of the ventral side of the thorax and the densely fringed coxae and hind tibiae. There seem to be links with genera in the Oriental region, like *Matapa, Gangara* and *Erionota,* but the relationship is still uncertain and for the present study it seems to be a good working hypothesis to suppose that the African genera form a monophyletic group. The group can be subdivided on the basis of an array of characters. One of the subgroups, containing *Chondrolepis, Moltena* Evans, *Ploetzia* Saalmuller and *Zophopetes* Mabille, is characterized by the following combination:

- lower outer angle of cell of hindwing turned up;
- palpi porrect;
- third segment of palpi short;

- antennae partly or entirely white or creamish above (less conspicuous in *Ploetzia*).

A phylogenetic reconstruction of the group must await future investigation. For the present study it is supposed that this subgroup of four genera is monophyletic. The first three genera share two apparently unique characters (i.e., unique in the Hesperiidae) which are therefore considered apomorphic:

1. Antennae at base closer together than usual, especially in the male.
2. Line of white hairs between the antennae, most conspicuous in the male.

As a consequence the genus *Zophopetes* can be used as outgroup (cf. De Jong, 1980) for considerations of the relationship between any two of the other three genera.

Chondrolepis and *Moltena* share three apomorphies:

3. Presence of scaphium (dorsal sclerotization of anal tube in male). This is unique in Hesperiidae (so far known); it occurs in many lepidopterous groups, apparently a parallel development, the only similarity being the place of the sclerotization.

4. Hindwing vein 2 arises as far from wing base as vein 7. This is not unique in Hesperiidae, but in the other genera of the *Ploetzia* group vein 7 arises nearer the wing base. On the basis of the argument of outgroup comparison the situation in *Chondrolepis* and *Moltena* can be considered apomorphic.

5. Uncus entire, with unindented apex. The uncus comes in many forms in the Hesperiidae and an entire uncus as well as an indented or bipartite one can be found in many species. Therefore this character does not seem to be very helpful. The argument of outgroup comparison, however, shows that the entire and unindented uncus can be considered apomorphic in *Chondrolepis* and *Moltena,* the uncus being apically indented in *Ploetzia* and *Zophopetes* (as usual in the other genera of the *Ploetzia* group).

From the discussion above a cladogram arises as depicted in fig. 12. It is apparently contradicted by an apomorphic character present in *Moltena* and *Ploetzia,* and absent in all other members of the *Ploetzia* group (though widespread outside the group), viz.,

6. Forewing without spots. This is however a very unreliable character in Hesperiidae. Not only may the development of spots vary considerably within a species, but presence or absence may be a differentiating character between congeneric species or it may even be a sexually dimorphic character. The loss of spots is apparently a frequent parallel development. Possibly the spots are easily suppressed, and the suppression may also easily be undone. Therefore, the three other characters uniting *Moltena* and *Chondrolepis* are given more weight than the absence of spots in *Moltena* and *Ploetzia.* It does not alter the fact, however, that for both genera, *Moltena* and *Ploetzia,* this character is an apomorphy.

Another apparently apomorphic character of *Moltena* is:

7. Many short and fine, dark brown striae on the underside of the wings. It is not found in any other species of the *Ploetzia* group (nor in any other Hesperiidae, for that matter).

For the sake of completeness and not essential for the present discussion, another apomorphy of *Ploetzia* is mentioned here without discussion:

8. Proboscis vestigial.

The characters that define *Chondrolepis* as a monophyletic group are inconspicuous. This is rather surprising since a *Chondrolepis* species is not easily mistaken for a species of another genus. This is, however, because of a combination of characters, several of which also occur outside *Chondrolepis*. Since at this stage we are trying to define *Chondrolepis* as a monophyletic subgroup of the monophyletic group *Chondrolepis* + *Moltena, Ploetzia* could be taken as outgroup. Because one of the apomorphies of *Chondrolepis* concerns the position of a spot, and spots are completely absent in *Ploetzia,* the outgroup is enlarged so as to include *Zophopetes* as well. Where appropriate a comparison will be made with other genera of the *Ploetzia* group. The apomorphies of *Chondrolepis* based on the argument of outgroup comparison are:

9. Costa of forewing slightly concave (in male more obvious than in female). In the outgroup it is straight or slightly convex.

10. Forewing spot in space 2 displaced basad. In the outgroup, where present, the spot in space 2 is well beyond the origin of vein 3, separated therefrom by about its own width. In *Chondrolepis* the spot in its most distad position still has its inner edge under the origin of vein 3. Where in the other genera of the *Ploetzia* group the spot in space 2 reaches basad to before the origin of vein 3, this is because it is enlarged in basal direction and not because the whole spot is displaced.

11. Male genitalia asymmetric. The asymmetry only concerns the valvae. In the outgroup (*Ploetzia* and *Zophopetes*) as well as in *Moltena* the genitalia are symmetric. Asymmetric valvae are also found in species of some other genera of the *Ploetzia* group (*Gamia* Holland, *Artitropa* Holland, *Pteroteinon* Watson), as well as in some other Hesperiidae.

12. Tegumen with longitudinal lateral folds. Unique in the *Ploetzia* group. Lateral extensions of the tegumen of different shapes are sometimes found in Hesperiidae species, apparently independently developed.

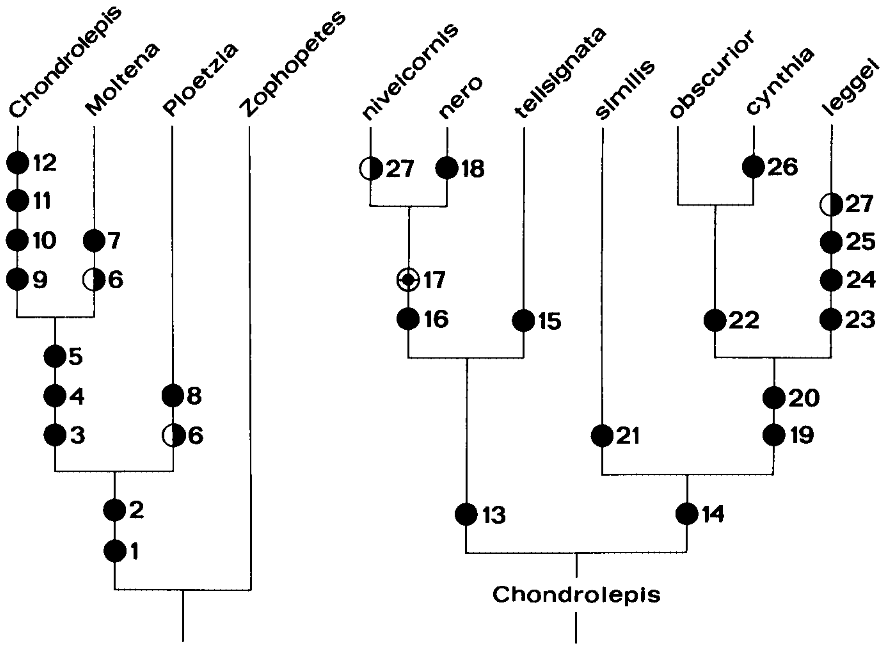
The serial numbers of the characters discussed above have been used in fig. 12.

Relationship between the species

The seven species of *Chondrolepis* easily fall into two groups, each of which has a single apomorphy and is therefore considered monophyletic. The apomorphies are as follows:

13. Ground colour of underside of hindwing sexually dimorphic, brown in male, yellow in female. It occurs in *niveicornis, nero* and *telisignata,* together called the *niveicornis* group. The dimorphism is not found in other members of the *Ploetzia* group; in *Zophopetes* the female has a white stripe on the underside of the hindwing which is absent in the male, but this is quite different from the dimorphic ground colour found in the *niveicornis* group.

14. Lateral folds of tegumen with projecting apices. It is found in what is called the *similis* group: *similis, obscurior, cynthia,* and *leggei.* Under 12, it was stated that the presence of lateral folds of the tegumen was an apomorphy of *Chondrolepis.* The differentiation with projecting apices is considered a



12 13

Figs. 12, 13. Phylogenetic trees. The numbers refer to the discussion of the characters in the text. Indicated are apomorphies (black dots), parallelisms (half-filled circles), and one uncertain apomorphy (nr. 17).

further development (and thus an apomorphy) rather than that the less differentiated folds of the *niveicornis* group would mean a reversal towards the plesiomorphic state (i.e. no folds at all).

The *niveicornis* group can be subdivided on the basis of the following four characters (15-18):

15. Hindwing underside of male with a conspicuous and typical white mark, in the form of an oblique anvil with narrow foot. Only found in *telisignata,* not found in any other species of Hesperiidae.

16. Uncus triangular in dorsal view, because the sides are straight. Found in *niveicornis* and *nero.* In *telisignata,* the *similis* group and *Moltena* the sides of the uncus are concave in dorsal view. On the basis of the argument of outgroup comparison the triangular uncus of *niveicornis* and *nero* is considered an apomorphy.

17. Forewing with two subapical spots. Found in *niveicornis* and *nero.* Since *telisignata* and the *similis* group have three subapical spots (in *obscurior* males sometimes two), two spots can be considered apomorphic (outgroup comparison). It must be remarked, however, that the character is rather problematic. No spots are found in *Moltena* and *Ploetzia,* one subspical spot is found in one species of *Zophopetes,* the other species of the genus having no subapical spots at all. Also in other genera, within as well as outside the *Ploetzia* group, the number can be quite variable. Because of the instability of the character the situation in *niveicornis* and *nero* is marked in fig. 13 as an uncertain apomorphy.

18. Male genitalia small in relation to wing length. In *nero* the male genitalia are conspicuously small: length of forewing is 7.7 times length of valva, whereas it varies from 5.1 to 6 times in the other *Chondrolepis* species (about 5.4 times in *niveicornis*). On the basis of the argument of outgroup comparison the small size in *nero* can be considered apomorphic.

The first division of the *similis* group is based on three apomorphies: characters 19-21.

19. Cucullus of right and left valvae dorsally indented, leading to a differentiation in a proximal and a distal part. A slight indentation can be found in the cucullus of one valva in *similis* and *niveicornis,* and possibly occurred in the ancestor of *Chondrolepis.* The occurrence of the character in both valvae (though not equally well developed) must, then, be considered a further differentiation.

20. Costa of valvae with fine knobs in ventral part. Found in *obscurior, cynthia* and *leggei.* By outgroup comparison this must be considered apomorphic.

21. Male with large eyes. The eye diameter of the males of *similis* is relative-

ly larger than in the other species of the genus: in *similis* the ratio length of forewing/diameter of eye is 7.7 to 7.9, in the other species it varies from 9 to 9.7 (with a single extreme value of 10.7).

For the next subdivision of the *similis* group characters 22-25 are the arguments, all based on outgroup comparison.

22. Tegumen trapezoid in dorsal view (i.e., lateral folds diverging distally) instead of rectangular. Found in *cynthia* and *obscura.*

23. Lateral folds of tegumen apically (distally) pointed. Only found in *leggei.*

24. Tegumen with a central lobe. Only found in *leggei.*

25. Cucullus differentiated into rounded prongs, a larger proximal one and a smaller distal one. Only found in *leggei.*

Finally, the last subdivision of the *similis* group is based on a single apomorphy, leaving *obscurior* without autapomorphic characters for the moment.

26. Cucullus with a curved and pointed distal part. Only found in *cynthia.*

Finally an apparently parallel development must be mentioned:

27. Reduction of spot 2 of forewing. As stated under 10, the basad displacement of spot 2 is an apomorphy of the genus. In the females of all species the centre of the spot is under or well beyond the origin of vein 3, in the males it is before, under or beyond the origin of vein 3. This is in agreement with the often found situation that the females are more conservative than the males. It suggests that the species in which the males have the centre of spot 2 beyond the origin of vein 3 (*niveicornis* and *leggei*) show the most primitive condition. However, I doubt it. In these species, and particularly in *leggei,* spot 2 is narrow and its outer edge is not remarkably further distad than in the other species of the genus. I rather think that the inner edge of spot 2 has moved outwards, reducing the width of the spot. As a consequence the centre of the spot is a bit displaced outwards, but not the spot itself. Thus the relatively narrow spot 2 in *leggei* and *niveicornis* is an apomorphy. Since spot size is very variable throughout the Hesperiidae I do not attach much weight to this character and depict it as a parallel development in fig. 13.

Similarly the cell spots are variable and since it is not always easy to decide whether there is one or two, this character is not further discussed here.

The resulting cladogram is found in fig. 13.

BIOGEOGRAPHIC CONSIDERATIONS

The *Chondrolepis* species

There are two opposing hypotheses to explain the disjunct distribution of montane forest organisms in Cameroun on the one hand and East Africa on the other, viz.,

a. Depression of the montane forest belt in the Pleistocene by up to 1000 m during the Ice Ages of the Northern Hemisphere, resulting in a continuous belt of montane forest from Cameroun to East Africa along the Congo-Nile watershed and possibly a southern belt via Angola and southern Zaïre. Proponents of this view are, e.g., Carcasson (1964), Moreau (1963, 1966), Van Zinderen Bakker (1967). The view is based on the assumption that there is a sharp distinction between species of montane and lowland forests.

b. There is no clear-cut boundary between species of montane and lowland forests, instead there is a large range of overlap in ecological requirements. A number of montane forest species could therefore live in the intervening lowland forest (perhaps especially along the northern and southern edges of the Congo Basin), as long as competition was low (during an expanding phase of the forest). Proponents of this view are, e.g., Diamond & Hamilton (1980), Hamilton (1982), Hedberg (1969). Some downward shift of the montane forest belt must have occurred, but the extent still has to be established. For the explanation of the present disjunctions in the distribution of montane forest species the acceptance of an extensive montane forest belt across the continent is not necessary.

In my opinion the second hypothesis is the most likely one. The first hypothesis reminds of the many landbridges built across almost any stretch of water to explain similarities between separated land masses, and it has the same defect: it does not explain why so many species did not make use of it. This will be discussed more extensively in a wider context (biogeography of East African forest butterflies, De Jong, in prep. a). Here it may suffice to note that the distribution of the *Chondrolepis* species is in accordance with the predictions to be derived from the second hypothesis: not all species show the disjunction and the species that does (*niveicornis*) is not restricted to montane forest. Moreover, the Cameroun endemic (*nero*) is the sister species of *niveicornis*. Thus, contact between Cameroun and East Africa only occurred in one of the upper branches of the cladogram (fig. 13). Apparently *Chondrolepis* (and its ancestor, judged from the distribution of *Moltena*) is a group that originated and diversified in the eastern half of Africa. After at least two speciation events in East Africa the line with the greatest tolerance to lowland conditions twice expanded its range to the Cameroun highlands where the populations became isolated by extinction in the Central African lowland. Double colonization of islands from the same stock is well-known, e.g. the Chaffinch, *Fringilla coelebs* Linnaeus, and the Blue Chaffinch, *F. teydea* Webb, Berthelot & Moquin-Tandon in the Canary Islands (see Voous, 1960).

For this vicariance explanation (in accordance with the second hypothesis) no assumptions need to be made about a broad east-west forest belt, nor about jump dispersal. The same pattern can be found, e.g., in the genus *Metisella* (Lepidoptera: Hesperiidae) (De Jong, in prep. b), the genus *Issoria* (Lepidoptera: Nymphalidae) (Bernardi, 1980), and many plants (White, 1981).

The situation within East Africa is rather different. The montane forests, now much fragmented, were probably much more coherent in rather recent times, i.e. during the relatively wet period about 12.000-4.000 yrs BP (Hamilton, 1982; Hedberg, 1969). At the height of the Last Glacial, ca. 18.000 yrs BP, vegetation belts on the mountains may have shifted about 1.000 m downward, but apart from being cooler the climate was also much drier and the plateau of East Africa was devoid of forest and covered with arid vegetation or very open woodland (Livingstone, 1975; Van Zinderen Bakker, 1982). Forests could only survive in the wettest areas such as the mountains of eastern and southern Tanzania and eastern Zaïre. Thus, much of the present distribution area of the montane ecosystem may be quite young. The present fragmentation probably started about 4.000 yrs BP when the climate became drier, but it was apparently much reinforced by human intervention from ca. 3.000 yrs BP onward (Hamilton, 1982).

If this picture, which is mainly based on palynological and climatic evidence, is true, then we can expect to find in the montane Hesperiidae (as well as in other groups of montane organisms, of course) a concentration of species (among which endemics) in the refugial areas (East Zaïre, East and South Tanzania), and lower diversity and no endemics in other montane areas, with the number of species decreasing with increasing distance from the refugial areas. Of course, the small genus *Chondrolepis* is not very well suited for testing such predictions. In spite of the low number of species, however, the distribution of the *Chondrolepis* species fits the predictions surprisingly well: with the exception of *niveicornis,* which is not so much restricted to the montane level, each species is limited to one of the supposed refugial areas with at most an extension into non-refugial areas, showing the low degree of intermingling of the refugial populations. On the other hand, the sistergroup relationship between *obscurior* and *cynthia* (in South Tanzania and East Zaïre to West Uganda, respectively) indicates that contact between the two areas has been possible in the past and the same vicariance event may have occurred earlier leading to the origin of *similis* (South Tanzania) and its sistergroup (East Zaïre to West Kenya, and South Tanzania).

The distribution of *telisignata* is puzzling. It is sympatric with its sistergroup and allopatric with two not so closely related species, *cynthia* and *leggei.* The disjunct distribution, South Tanzania/North Malawi and Kenya/Uganda is not found in any other butterfly or skipper, species occurring in both areas also occurring elsewhere. It therefore calls for a special rather than a general explanation. Here we could think of competition, especially from the side of *leggei,* since the latter species has been found on Mt. Elgon whereas *telisignata* occurs east and west of that locality but not on Mt. Elgon itself. To test this idea we need, however, to know much more about the ecological requirements of both species. If the Uganda specimen of *telisignata* has not been mislabeled, the limited distribution in lowland forests west of Kenya could also be the result of competition by *niveicornis,* one of the two species of the sistergroup of *telisignata.*

Biogeographic relations with other genera

The complete allopatry of *Chondrolepis, Moltena* and *Ploetzia* (fig. 14), which form a monophyletic group, suggests that it would be an ideal case to apply vicariance biogeography to. On closer examination, however, the case is not so simple. Vicariance biogeography, like other approaches to biogeography, looks for general patterns to be explained by general causes. Special cases need special explanations which are difficult to test in a hypothetico-deductive way. Indeed, the *Chondrolepis* + *Moltena* + *Ploetzia* case is a special one because this distribution pattern is not found in other Lepidoptera nor in any other animal group I know of. The explanation, I think, must be sought in the larval foodplant requirements. These are different for the three genera. For *Chondrolepis* only Gramineae have been reported as larval foodplant (Dickson & Kroon, 1978), *Moltena* lives on *Strelitzia nicolai* Regel & Koern. (Strelitziaceae) (Dickson & Kroon, 1978), and *Ploetzia* has been reported from the Cocos palm (Palmae) (Viette, 1956). If indeed *Zophopetes* is the sistergroup of the three genera combined (see Phylogenetic considerations), Palmae probably were the original foodplants of the ancestor of *Chondrolepis* + *Moltena* + *Ploetzia,* since *Zophopetes* is only known from *Phoenix* species (Palmae) (Carcasson, 1981; Dickson & Kroon, 1978). Why the ancestor of *Chondrolepis* + *Moltena* changed foodplants is unclear, but obviously it enabled *Chondrolepis* to colonize higher altitudes where Palmae are scarce or absent.

The foodplant choice of *Moltena* restricts it to the coastal area of southeastern Africa, since this is the area where *Strelitzia* occurs*. The same distribution pattern can only be expected in phytophagous groups with the same original distribution, where the same change of foodplants occurred in the same period. Such cases are not known so far. If the genus *Strelitzia* never occurred further north, it is most likely that the ancestor of *Chondrolepis* + *Moltena,* being distributed over a much wider area, lived on Gramineae and that it changed to *Strelitzia* in the south after break-up of the distribution area. The break-up was possibly caused by increasing desiccation of the broad and hot, low-lying Limpopo valley, the present boundary between *Chondrolepis* and *Moltena.* If so, the *Chondrolepis* + *Moltena* distribution pattern may be a special case of a more general pattern: vicariance due to desiccation of the Limpopo valley. The generality of such an explanation can be tested by studying the phylogeny and biogeography of other groups for which the Limpopo valley is a boundary. The outcome could be interesting as it might give a partial answer to the question of the derivation of the South African fauna, viz., whether it was colonized from the north or is a split-off part of a former, more widely distributed biome. This clearly falls outside the scope of the present paper.

Whether it was the desiccation of the Limpopo valley or another event that caused the break-up of the *Chondrolepis* + *Moltena* ancestor, the roots of *Chondrolepis* must apparently be sought in the eastern part of Africa in the first place, and the genus probably arose by a north-south vicariance event. It would be interesting to compare this with the origin of other montane butterflies and if differences are found (e.g., origin by east-west vicariance events), to study how far this is correlated with differences in ecological requirements.

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* The Strelitziaceae have an interesting distribution. There are only four genera, with the following distribution: *Strelitzia* (4 species) in southeastern Africa, *Ravenala* (1 species) in Madagascar, *Phenakospermum* (1 species) in Guyana, and *Heliconia* (ca. 50 species) in tropical America (Heywood, 1979). It is apparently a relict distribution. I don't know the relationship between the genera, but if *Strelitzia* and *Ravenala* are sistergroups, there has not been any coevolution between these plants and *Moltena/Ploetzia,* the skipper genera undoubtedly being very much younger than the genera of the Strelitziaceae.

History, London), and U. Dall'Asta and F. Desmet (Musée Royal d'Afrique Centrale, Tervuren) kindly placed the collections in their care at the author's disposal and were helpful in various ways. The valuable discussions on biogeographic implications with Mr. J. Krikken (RMNH) are gratefully acknowledged. The Uyttenboogaart-Eliasen Stichting financially supported one of the author's expeditions to the Kenyan highlands where one of the *Chondrolepis* species was studied in the field.

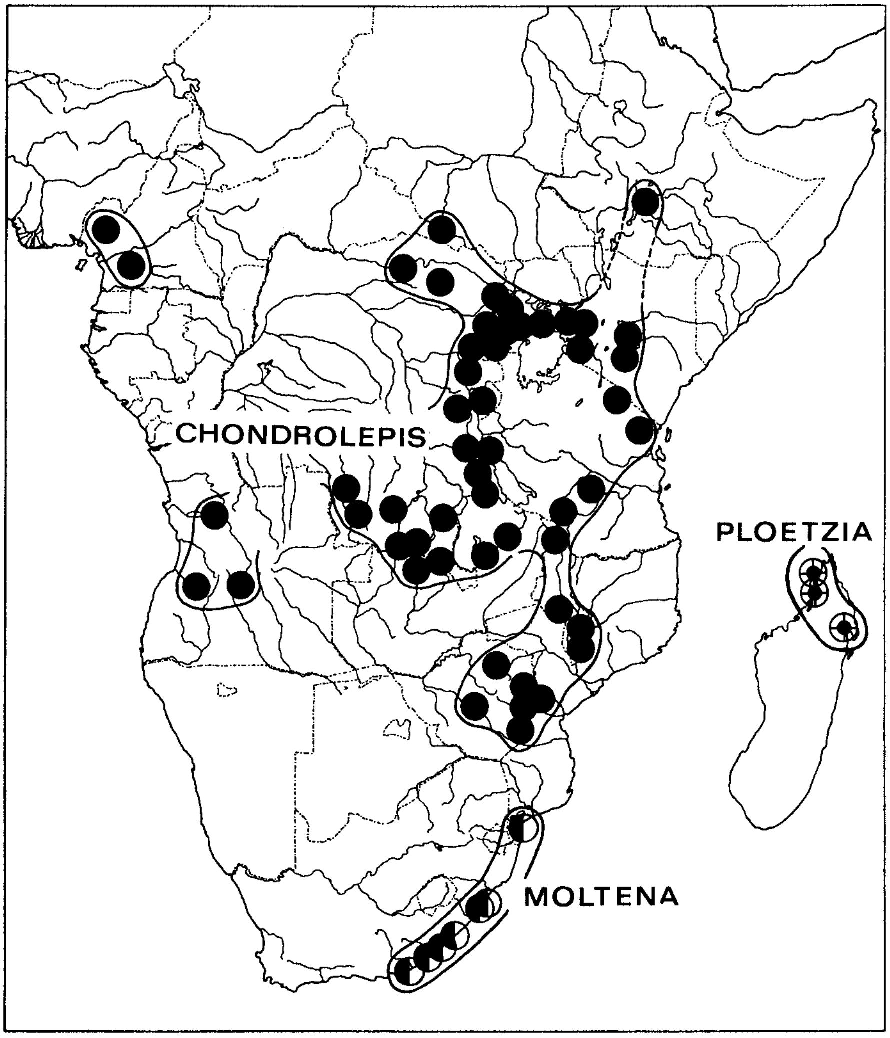

Fig. 14. Vicariant distribution of *Chondrolepis, Moltena* and *Ploetzia,* which are supposed to form a monophyletic group.

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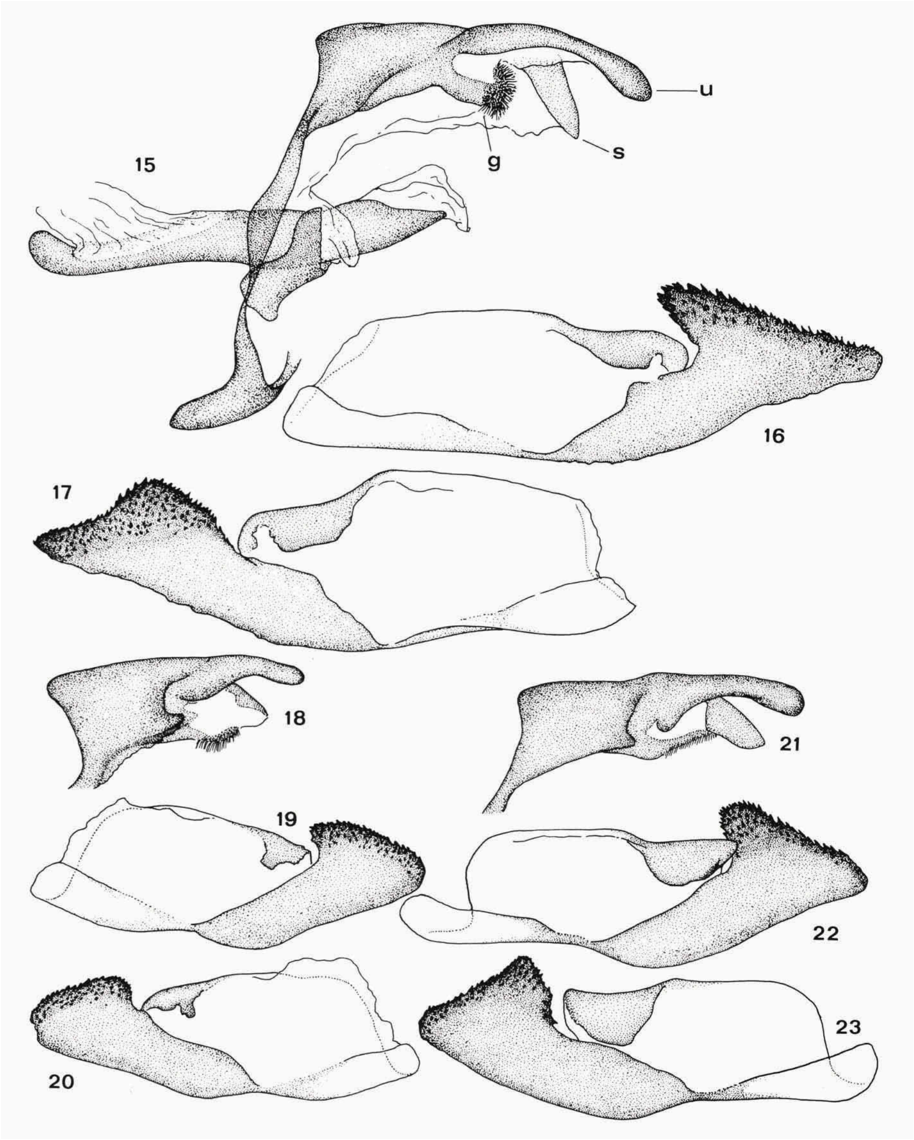
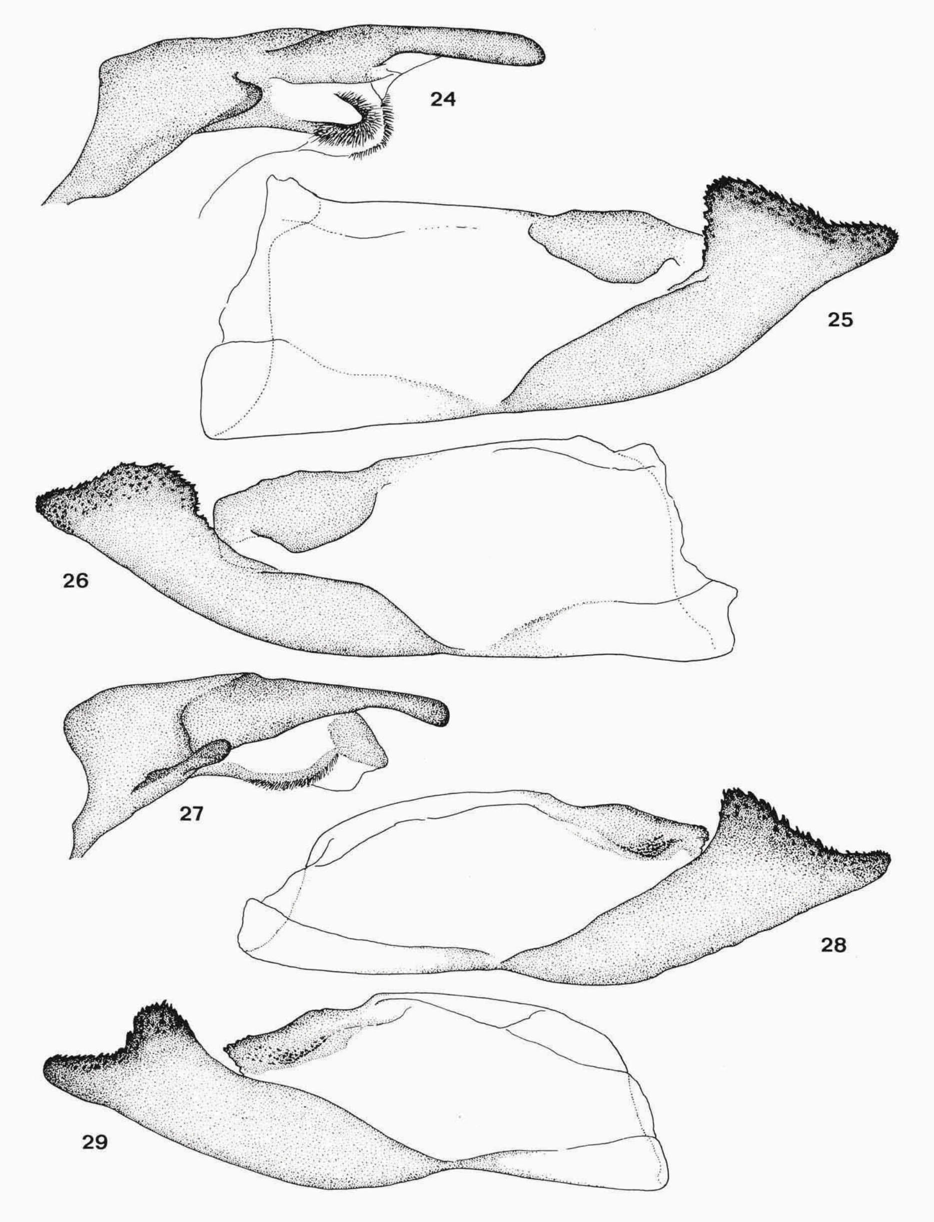
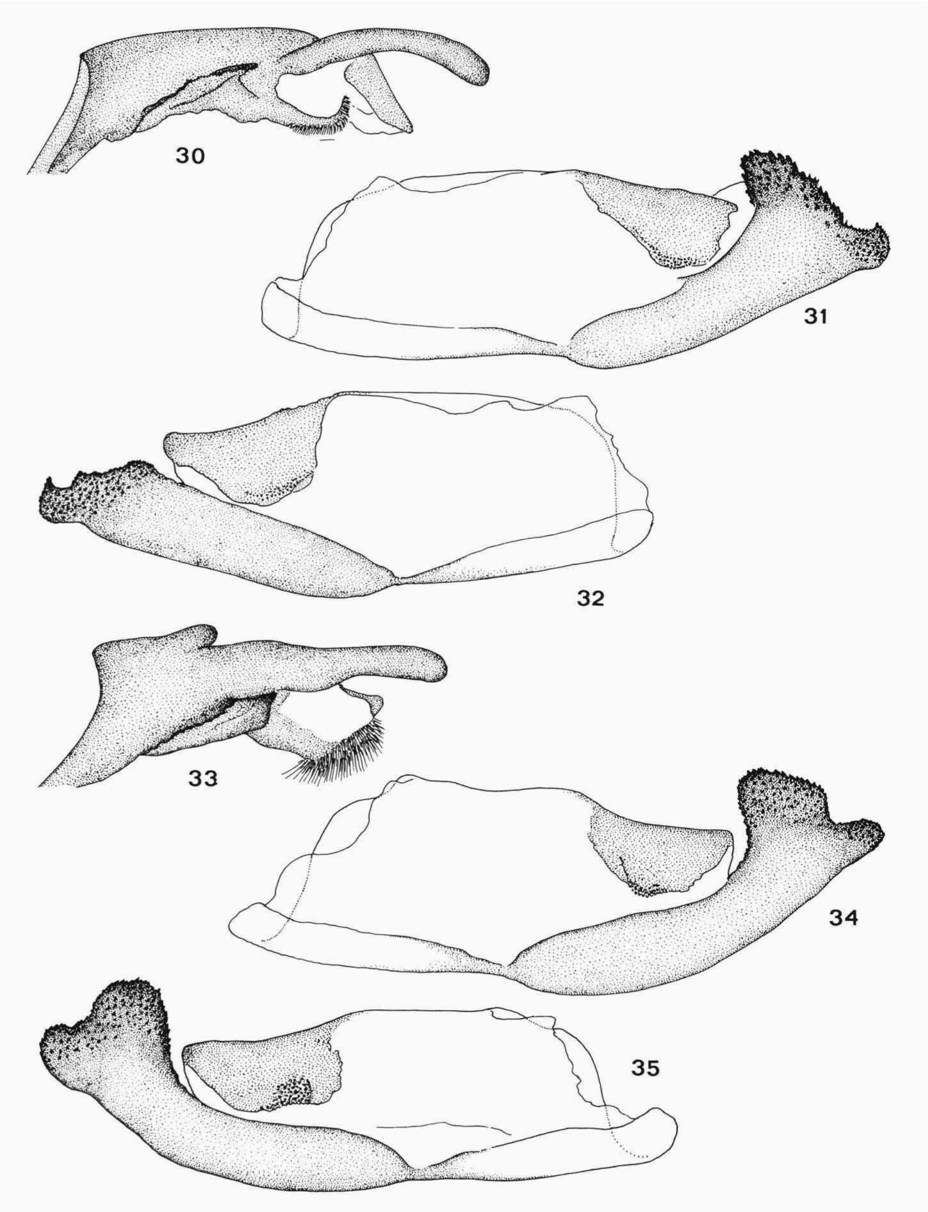


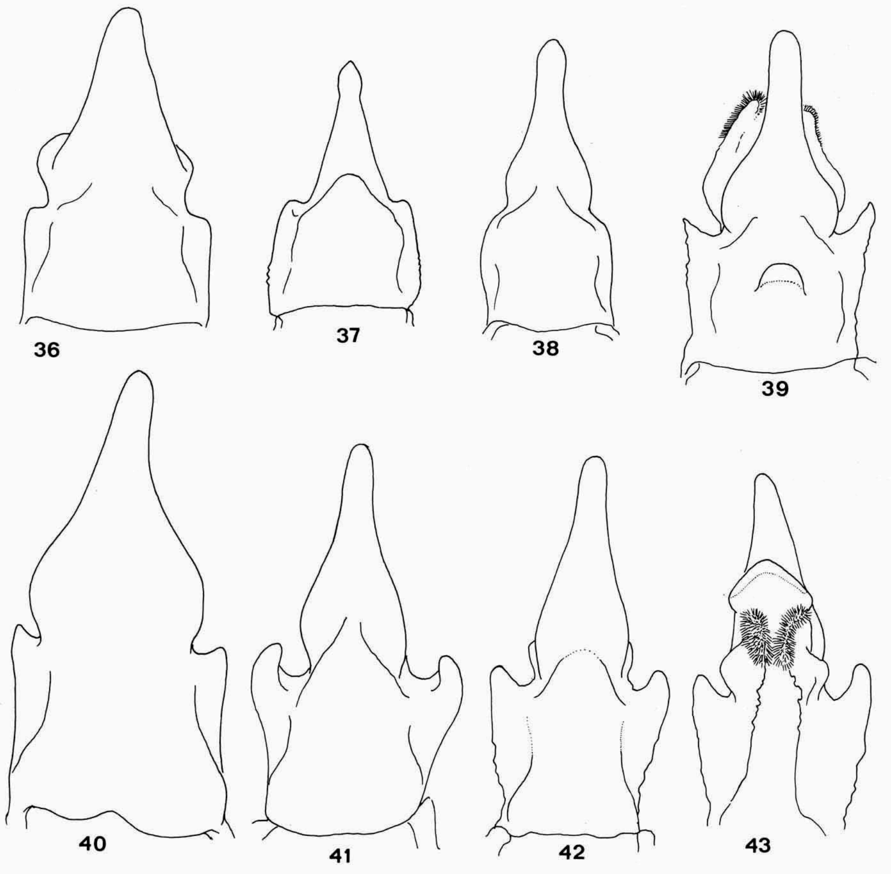
Figs. 15-23. Male genitalia of *Chondrolepis* species; 15-17, *C. niveicornis;* 18-20, *C. nero;* 21-23, *C. telisignata.* The following parts are shown: left side of tegumen, uncus (u), scaphium (s) and gnathos (g) (15, 18, 21; in 15 also vinculum and aedeagus); inner side right valva (16, 19, 22); inner side left valva (17, 20, 23). All drawings at same scale.



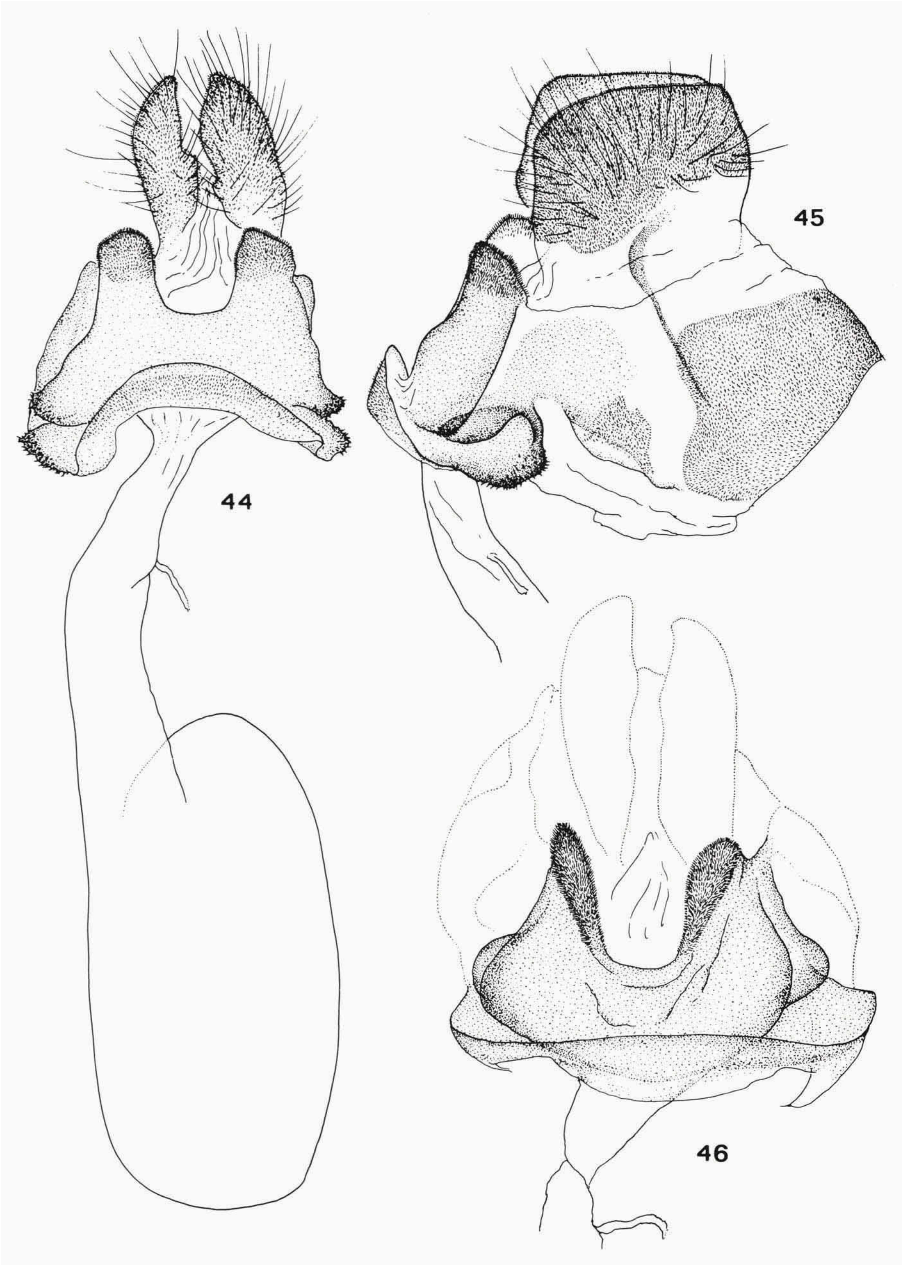
Figs. 24-29. Male genitalia of *Chondrolepis* species; 24-26, *C. similis;* 27-29, *C. obscurior*. The following parts are shown: left side of tegumen, uncus, scaphium (turned over, hidden in 24) and gnathos (24, 27); inner side right valva (25, 28); inner side left valva (26, 29). All drawings at same scale.



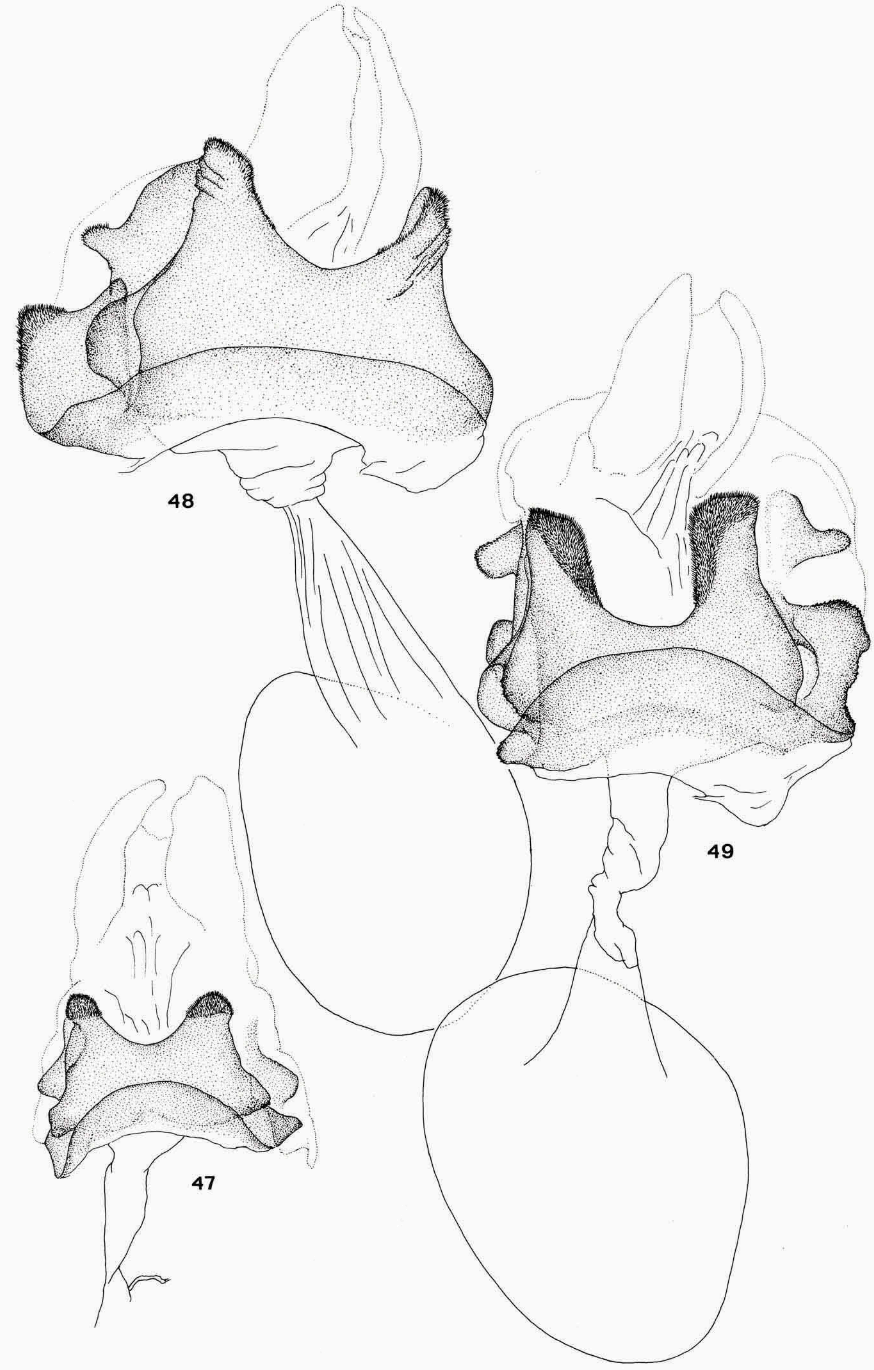
Figs. 30-35. Male genitalia of *Chondrolepis* species; 30-32, *C. cynthia;* 33-35, *C. leggei.* The following parts are shown: left side of tegumen, uncus, scaphium and gnathos (30, 33); inner side right valva (31, 34); inner side left valva (32, 35). All drawings at same scale.



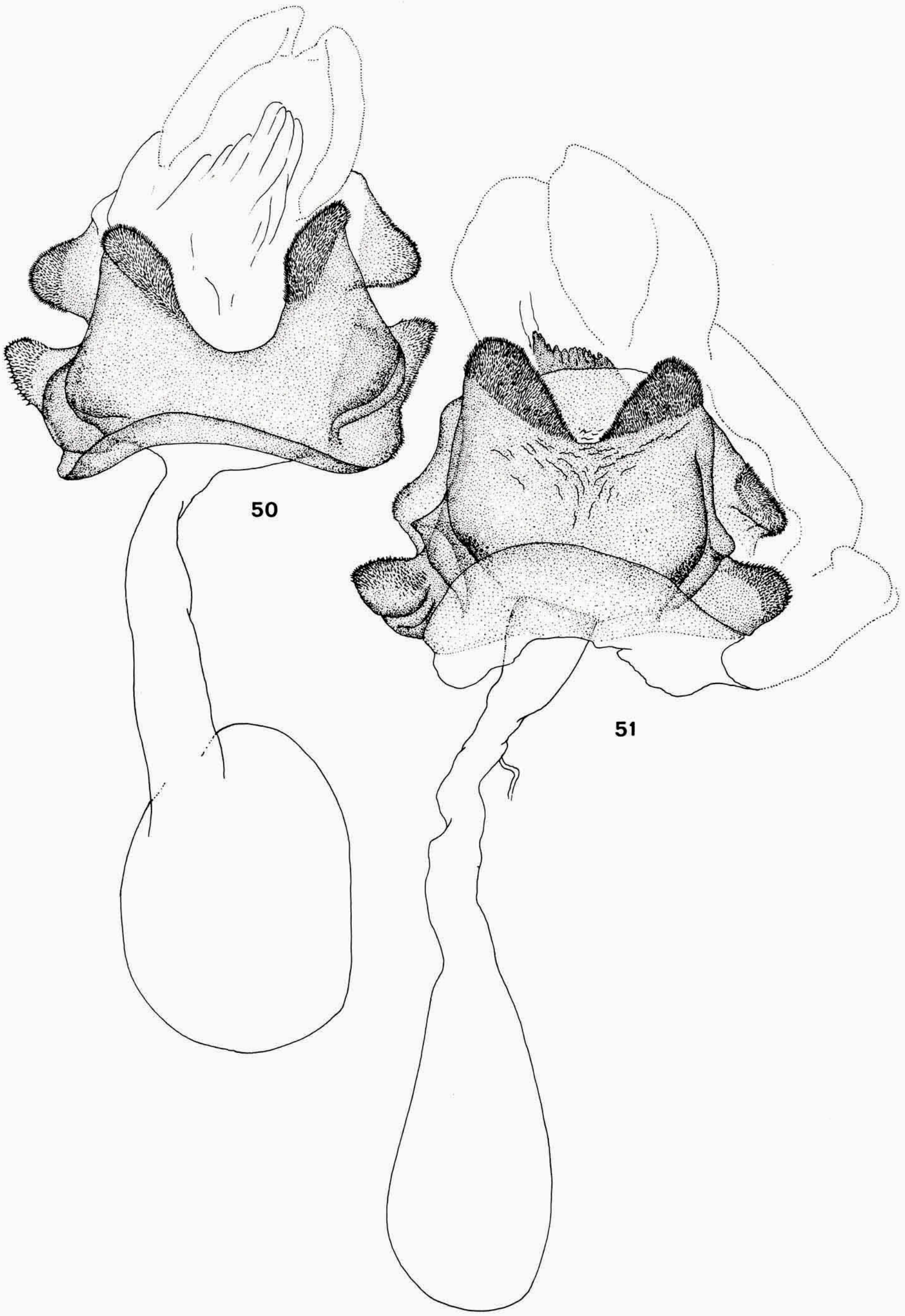
Figs. 36-43. Upperside (36-42) and underside (43) of tegumen and uncus of *Chondrolepis* species; 36, *C. niveicornis;* 37, *C. nero;* 38, *C. telisignata;* 39, *C. leggei;* 40, *C. similis;* 41, *C. obscurior;* 42, 43, *C. cynthia.* All drawings at same scale.



Figs. 44-46. Female genitalia of *Chondrolepis nero* (44, 45) and *C. niveicornis* (46); ventral view (44, 46) and lateral view (45).



Figs. 47-49. Female genitalia of *Chondrolepis telisignata* (47), *C. similis* (48) and *C. obscurior* (49); ventral view.



Figs. 50-51. Female genitalia of *Chondrolepis cynthia* (50) and *C. leggei;* ventral view.