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Revision of Thanerocleridae n.stat. (Coleoptera, Cleroidea)

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The subfamily Thaneroclerinae (Cleridae) is raised to the family rank – Thanerocleridae n.stat. The species *Cyrtinoclerus cyrtinoides* CHAPIN, 1924, and *Metaxina ornata* BROUN, 1909, are excluded from the family (incl. the genera *Cyrtinoclerus* CHAPIN, 1924, and *Metaxina* BROUN, 1909) and the new genus *Meprinogenus* n.gen. is established for *Cyrtinoclerus indicus* CORPORAAL, 1939. A new status is also established for the genera *Ababa* CASEY, 1897, *Lyctosoma* Lewis, 1892, and *Parathaneroclerus* PIC, 1936, (all subgenera of *Isoclerus* LEWIS, 1892). The genus *Allothaneroclerus* CORPORAAL, 1939, is synonymized with *Isoclerus* LEWIS, 1939, *Microababa* PIC, 1939, with *Compactoclerus* PIC, 1939, and the tribe Viticlerini WINKLER, 1982, with Thaneroclerini BARR, 1962, (new sense). The species *Ababa longipennis* PIC, 1947, is synonymized with *Isoclerus (Lyctosoma) parallelus* (LEWIS, 1892). Following new combinations are established: *Isoclerus (Ababa) tantillus* (LECONTE, 1865) n.comb., *Isoclerus (Parathaneroclerus) triimpressus* (Pic, 1936) n.comb., *Isoclerus (Lyctosoma) parallelus* (LEWIS, 1892) n.comb., *Isoclerus (Isoclerus) elongatus* (SCHENKLING, 1906) n.comb., *Isoclerus (Isoclerus) tuberculatus* (SCHENKLING, 1906) n.comb., *Compactoclerus sicardi* (PIC, 1939), n.comb. and *Meprinogenus indicus* (CORPORAAL, 1939) n.comb. Besides the new taxa cited above, the following new taxa are described: Zenodosini n.trib., Thaneroclerina n.subtrib., Isoclerina n.subtrib., *Isoclerus (Isoclerus) disinlei* n.sp., *Isoclerus (Isoclerus) menieri* n.sp. and *Compactoclerus davidi* n.sp. Keys to some taxa and some phylogenetical hypotheses are also provided. All higher taxa are based on transformation series and synapomorphies, the species are based on combination of the typological and mate-recognition species concepts. A concept of metataxa is used for *Lyctosoma, Compactoclerus* and *Meprinogenus* n.gen.

Keywords: Cleroidea, Thanerocleridae n.stat., new combinations, new species, phylogeny, synonymies.

INTRODUCTION

The family Thanerocleridae is a new status for the subfamily Thaneroclerinae CHAPIN, 1924. It has also nearly the same meaning as the tribe Thaneroclerini BARR, 1962. Two genera are excluded here from the old Thaneroclerinae: *Cyrtinoclerus* CHAPIN, 1924, and *Metaxina* BROUN, 1909. The first genus was introduced in Thaneroclerinae by CHAPIN (1924), the second by CROWSON (1964). For the explanation of their removal see the chapter Discussion.

There has been one complete revision of Thaneroclerinae by CORPORAAL (1939) so far. Since that time, only a few authors have published on this group: CROWSON (1964) classified the genus *Metaxina* BROUN, 1909, within Thaneroclerinae; BARR (1962) followed by EKIS & GUPTA (1971) changed the status of the subfamily into a tribus Thaneroclerini (within Clerinae); MIYATAKE (1977) described *Viticlerus formicinus* and WINKLER (1982) established the tribe Viticlerini. Larvae of Thanerocleridae were described mainly in papers of BÖVING & CHAMPLAIN (1920, 1922) and FOSTER (1976). Morphology of *Thaneroclerus buquet* SAY, 1835, was studied by KOLIBAČ (1987, 1989a, 1989b).

METHODS

Higher taxa are based on transformation series as well as on synapomorphies while species are based on two species concepts which are combined: typological (VORONTSOV, 1989) and mate-recognition species concepts (PATERSON, 1980, 1985). Both concepts (of higher taxa and species) will be explained in a separate paper (KOLIBÁČ, in press) and called the "systematic concept". As they have never been published so far I will explain them briefly here.

An establishment of species according to the "systematic concept" is as follows: (1) A type (a type series) is chosen from a group of specimens. (2) The specimens that share a common fertilization system with the type are added to the type. They compose one species together. (3) Another type is chosen from remaining specimens and the whole procedure can continue.

An establishment of higher taxa according to the "systematic concept" is as follows: (1) The ground transformation series of a (certain) character(s) or morphocline(s), which is composed of species, is found. It is a subgenus. All subgenera in one genus have transformation series of the same character(s) (Fig. C-6). (2) Synapomorphies of members of all subgenera are found. (3) Transformation series of the certain (and same) character(s) which is (are) present in all subgenera compose a genus. (4) The transformation series which is present in all genera compose a subtribe, etc. Members of each transformation series (= taxon) share common synapomorphy(ies). (5) Sometimes not all transformation series can be used because we distinguish only certain categories (e.g. genus, subtribe, tribe, subfamily) in taxonomy. Remaining series could be used only as neutral terms (cf. International Code of Zoological Nomanclature, 1985).

In other words, members of each taxon are defined by both synapomorphy(ies) and character state(s) of the transformed character(s).

The construction of a schematic drawing of phylogeny is as follows: the picture is in the horizontal position (level); no axis shows time – both axes show differences among characters. States of the transformed characters are schematically figured on particular lines. Each dichotomy is explained on the basis of (1) a character state(s) of the transformed character(s) and (2) a synapomorphy(ies). Both sister groups in a certain dichotomy have the same categorical level (sometimes more dichotomies are present than names of the systematic categories – see Fig. C-6).

For explanation of all morphological terms used in this communication see KOLIBÁČ (1987, 1989a, 1989b).

SYSTEMATICS

Family Thanerocleridae n.stat.

Thaneroclerinae CHAPIN, 1924, *Philip. Journ. Sci. 25(2):*165, 251.
Thaneroclerini BARR, 1962, *Coleopterists' Bull. 16(4):*121, 125.
Type-genus: *Thaneroclerus* LEFEBVRE, 1838.

Diagnosis: The family is based on transformation series of the tegmen, tarsus and antenna. Trogositidae (s.lat.) is probably the sister group.

Apomorphies: Front tarsomere 1 to 4 wide, tarsus compact. Tegmen without phallobasic apodeme. Pro- and mesocoxal cavities often closed. Four malpighian glands (EKIS & GUPTA, 1971) present. Mandibles with deep basal notch (Figs 56, 70). Proendosternite (furca of prothorax) with convergent arms (Fig. 87).

Plesiomorphies: Frons emarginate. Head dorsally with longitudinal wrinkles. Middle and hind tarsi with tarsomeres slender, tarsomere 5 long (similar to those in Trogositidae and Chaetosomatidae). Abdominal sternites ventrally bordered (Figs 7 and 8). Tentorium with tentorial cross-bar (Fig. 89).

As far as I know the following larvae were described within Thanerocleridae n.stat.: *Isoclerus* sp., *Zenodosus sanguineus* (SAY), *Thaneroclerus buquet* (LEFEBVRE) and *Isoclerus (Ababa) tantillus* (LECONTE) (cf. FOSTER, 1976). Having studied the descriptions of the species cited above and the new larva of Thanerocleridae from India (see below) I was unable to differentiate the genera of Thanerocleridae according to larval characters. Hence no larval characteristics are incorporated into keys.

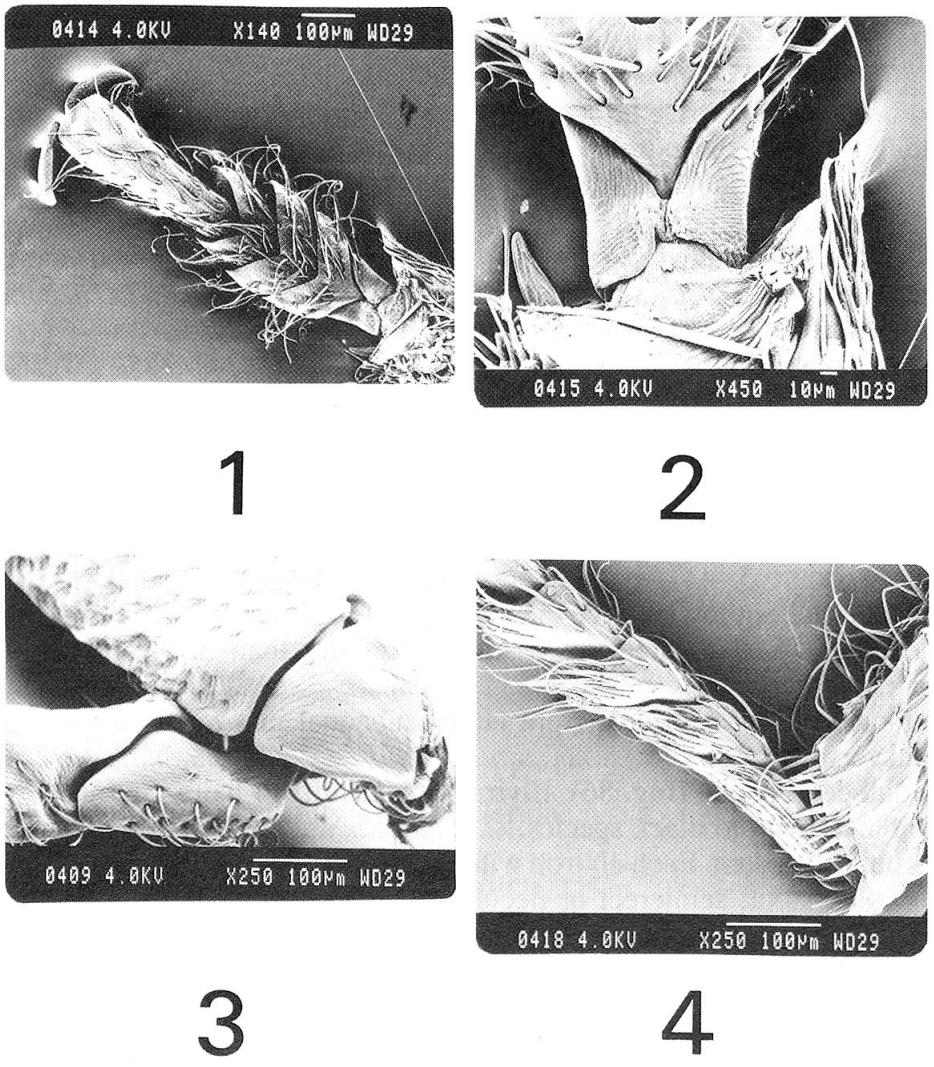
Review of several basic larval characters (according to the larvae cited above): General form clerid-like. Mandibles with only one apical tooth (Fig. 22). Five ocelli in clerid-pattern. Epicranial stem (endocarina) present in the ground plan of the family. Frontal arms present, Y-like (Fig. 24). Gular margins abruptly expanded in front of hind margin. Head capsule subrectangular. Hypostomal rods absent. Pronotum with one sclerite (and notal line), mesonotum and metanotum with paired sclerites. Tergite 9 with pigmented and sclerotized basal plate and small urogomphi either present or not (cf. Figs 23 and 25). Body pink or salmon with sparse and rather short pubescence.

Key to higher taxa of Thanerocleridae n.stat.

1. Front coxal cavities open, front coxae transverse (Fig. 14). Mesonotum wide (Fig. 17). Abdominal segment 9 present (Fig. 21). Discriminal line present. Tarsal pattern 5-5-5. ..... Zenodosini n.trib. (one subtribe Zenodosina n.subtrib, with genus *Zenodosus* WOLCOTT)
- Front coxal cavities closed, front coxae more or less spherical (Fig. 62). Mesonotum narrow (Fig. 71). Spicular fork clerid-like (Fig. 84) – segment 9 reduced. Discriminal line scarcely perceptible. Tarsal pattern 5-5-5 or 5-4-4. Thaneroclerini BARR (new sense) 2
2. Tarsal pattern 5-5-5. Round depression along notopleural suture absent. Space between front coxae rather wide. Thaneroclerina n. subtrib. 3
– Tarsal pattern 5-4-4. Round depression along notopleural suture present (Fig. 62). Space between front coxae very narrow. Isoclerina n.subtrib. 6
3. Tarsomere 4 of front tarsus distinctly smaller than 3. Nearly unicolorous species. 4
– Tarsomeres 2, 3 and 4 of front tarsus subequal in size. Elytra with distinct transverse stripes. 5
4. Radial cell present (Fig. 86). Elytra without tufts of hairs. Sternite 6 scarcely visible. Brown to black species. ..... *Thaneroclerus* LEFEBVRE
– Radial cell absent. Each elytron with humeral tuft of black hairs and three tufts of white, stout, semierect or decumbent hairs. Six visible sternites. Brown, elytra black from the second half. ..... *Meprinogenus**[1] n.gen.

[1] The asterisk behind a name of a taxon does not indicate "somebody who will die" as in the novel "Galapagos" by Kurt VONNEGUT (1985) but a metataxon. An explanation is given in the chapter "Metataxa of Thanerocleridae n.stat."

5. Antennal joints 10 and 11 subcoalescent (suture is perceptible). Elytra not depressed, without distinct humeral gibbae. Sternite 1 as long as 2 and 3 together, 2 to 6 subequal in length. ..... *Neoclerus* Lewis
– Antennal club loose. Elytra strongly depressed in anterior half, with elevated humeral gibbae. Sternite 1 as long as 2 to 4 together, 2 to 6 successively shorter. ..... *Viticlerus* Miyatake
6. Tendency to coalescence of antennal joints 10 and 11; suture between them perceptible. Prothorax heteromeran: front coxae spherical, very small; space between them minute; distance between coxal cavities and anterior margin of prosternum very long. Prosternal process below "epimera" (Fig. 62). Apical joints of labial palps coniform. Africa, Madagascar. .... *Compactoclerus** Pic
– Antennae 11-segmented with more or less distinct 3-segmented club. Prothorax not so distictly heteromeran. Prosternal process covers "epimera". Apical joints of labial palps rather securiform. America, South-eastern Asia. .... *Isoclerus* Lewis



Figs 1-4. *Zenodosus sanguineus*. 1, front tarsus dorsally. 2, dito, first tarsomere. 3, hind trochanter. 4, hind tarsus laterally.

Tribus Zenodosini n.trib.

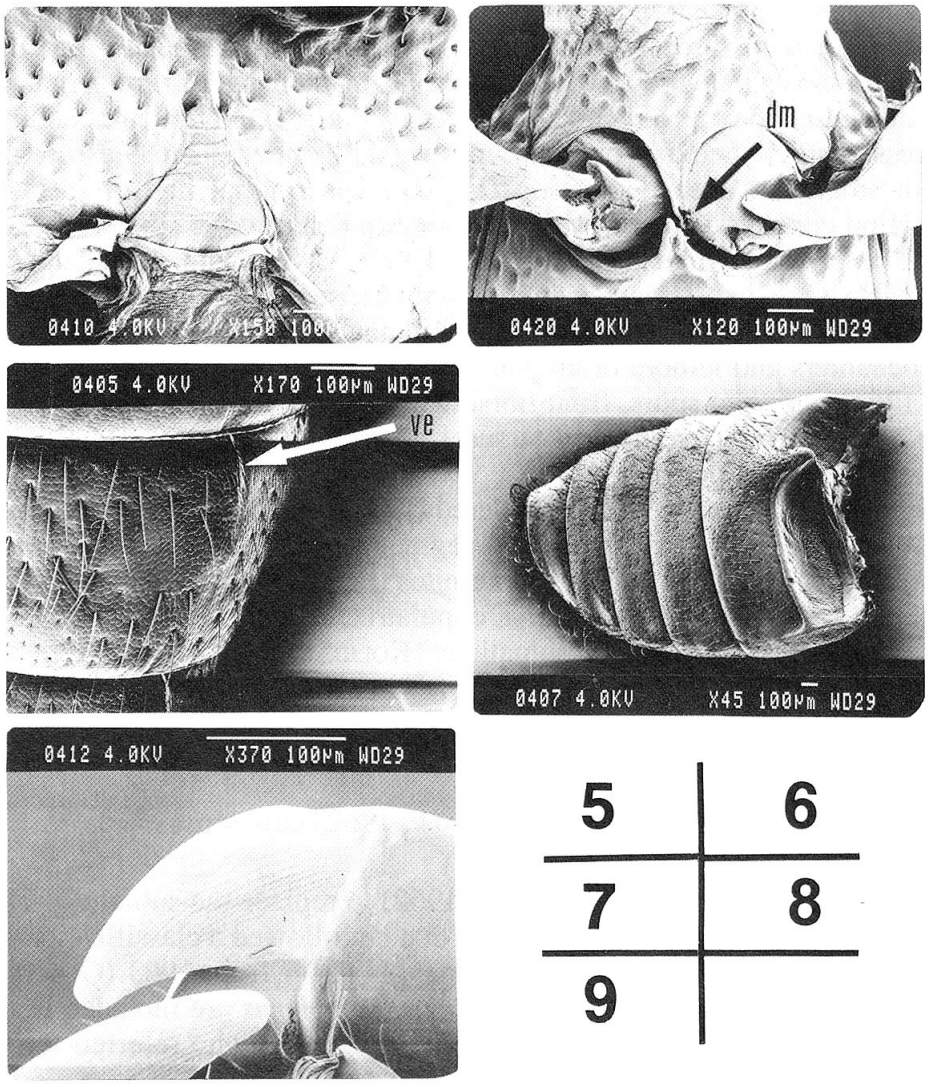
A monotypic tribe. One genus *Zenodosus* WOLCOTT with one species *Z. sanguineus* (SAY, 1835) are known.

Diagnosis: Based on a transformation series of the tegmen. It is heteromeran, compact, with ciliation at its apex (Fig. 18).

Synapomorphies: Lacinial lamina with spines (Fig. 11). Lateral edge strongly reduced. Elytra with irregular sculpture. Phallus extraordinarily stout (Fig. 19).

Plesiomorphies: Both front (Fig. 14) and middle (Fig. 6) coxal cavities open. Antennae without distinct club. Wing with radial cell and with anal (wedge) cell in anal field (Fig. 10). Mesoscutellum wide (Fig. 17). Abdominal segment 9 with distinct both sternite and tergite (Fig. 21). Front coxae transverse (Fig. 14).

The larva is similar to *Thaneroclerus*. Urogomphi absent (BÖVING & CHAMPLAIN, 1922; FOSTER, 1976).



Figs 5-9. *Zenodosus sanguineus*. 5, gular sutures. 6, middle coxae. 7, side of abdominal sternite ventrally. 8, abdomen latero-ventrally. 9, apices of mandibles. (dm = depression at apex of mesosternal process; ve = ventral edge of sternite).

Genus *Zenodosus* WOLCOTT, 1910

*Ent. News 21:*321.
Type-species: *Clerus sanguineus* SAY, 1835.

Diagnosis: A monotypic genus without any sister group. Hence any transformation series is not distinguishable. For both apomorphies and plesiomorphies see the description of the tribe.

Zenodosus sanguineus (SAY, 1835)

Clerus sanguineus SAY, 1835, *Boston Journ. Nat. Hist. 1:*162.

Head with small, round impressions. Antennal sockets imperceptible from above. Gular sutures long, parallel along the half of their length (longer than in *Thaneroclerus*) as shown in fig. 5. Prementum with deep notch (Fig. 16), hypopharyngeal sclerite without apodeme (Fig. 15), the last joint of labial palps securiform. Antennae 11-segmented, without distinct club. Lacinia with spines on lamina (Fig. 11), the last joint of palps coniform. Labrum with connecting tormal process (Fig. 20). Mandibles with deep basal notch, their apices with furrows (Fig. 9). Eyes slightly elevated, frons straight. Submentum not elevated.

Pronotum with three shallow depressions, coarsely punctate. Lateral edge reduced. Front coxal cavities closed to the half of their width. Prosternal process slightly dilated at apex. Front coxae transverse (Fig. 14). Notopleural suture without depressions. Mesocoxae spherical, mesocoxal cavities open. Mesosternal process with small but deep depression (Fig. 6). Discriminal line of metasternum present. Hind coxae transverse, with deep longitudinal groove (Fig. 12). Metendosternite *Thaneroclerus*-like (see KOLIBÁČ, 1987). Elytra with irregular sculpture composed of dense, large impressions and with dense, short pubescens. Wings with radial cell, anal (wedge) cell and four veins in anal field (Fig. 10).

Trochanters and femora of all pairs of legs in tenebrionid position (Figs 3, 6, 12). All tibiae with two spurs, front tibiae with toothlet at apices. Tarsal pattern 5-5-5 (Fig. 4). The first tarsomere of tarsus 1 as shown (Figs 1, 2). Both dorsal and ventral faces of tibiae dentate.

Abdominal sternites laterally bordered (Figs 7, 8). Tegmen heteromeran (Fig. 18), phallus stout (Fig. 19). Abdominal segment 9 not reduced, both sternite and tergite 9 present (Fig. 21). Five visible sternites (Fig. 8). Female internal copulatory organs as shown in fig. 13, with bursa copulatrix, spermatheca and spermathecal gland – similar to those in Chaetosomatidae (KOLIBÁČ, unpubl.).

Head, pronotum, antennae and legs brown; elytra red.

Body length: 4.1-5.7 mm.

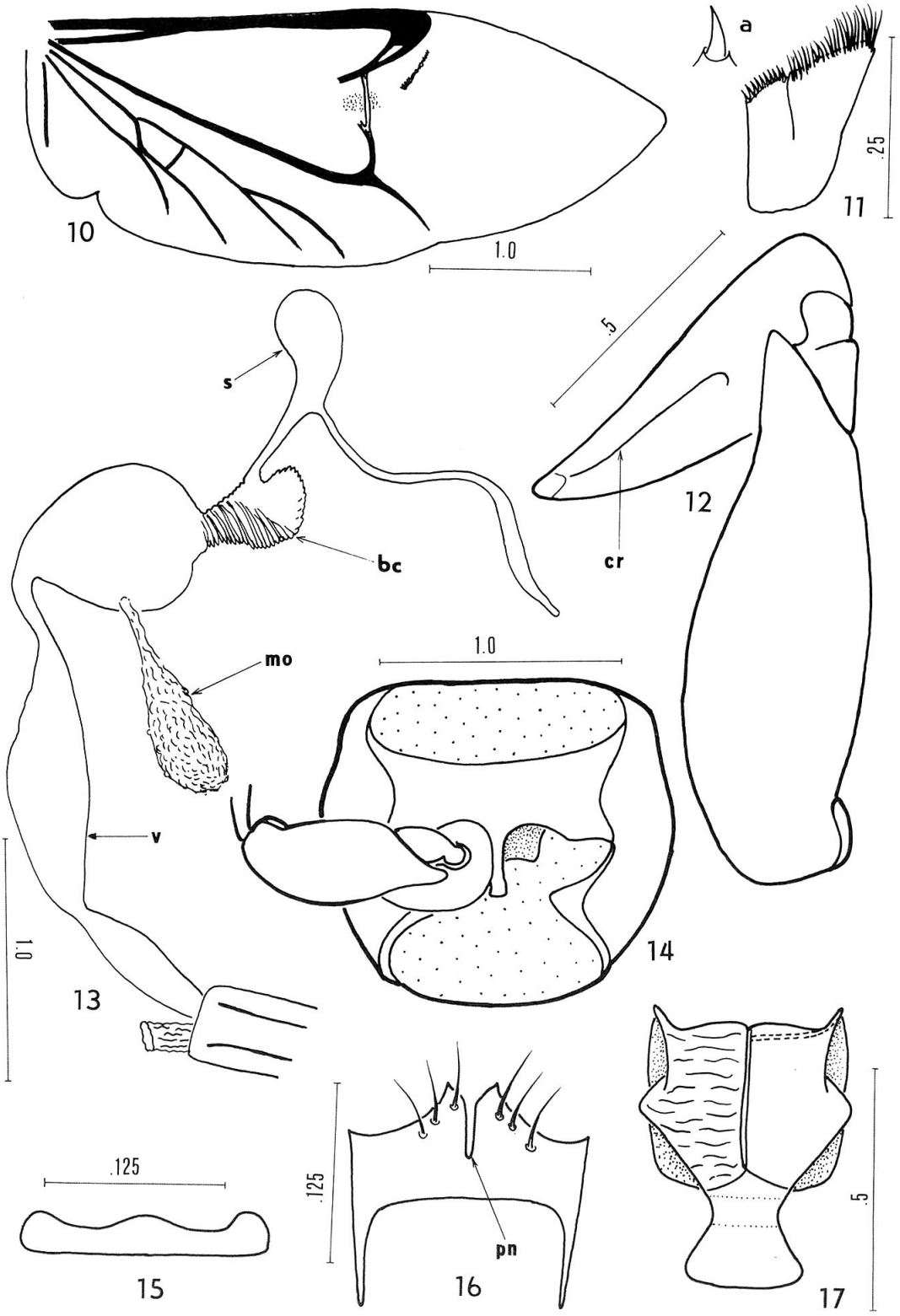
Distribution: Canada, USA.

Tribus Thaneroclerini BARR, 1962 (new sense)

*Coleopterists' Bull. 16:*121.

This tribe was established by BARR (1962) to replace the subfamily Thaneroclerinae CHAPIN, 1924. BARR himself noted that he followed a classification utilized by SCHENKLING (1910) but he cites SCHENKLING's paper from 1903 (Genera Insectorum, Cleridae) where both *Thaneroclerus* and *Isoclerus* are included in Clerini. That confusion was probably initiated by CHAPIN (1924) who referred to SCHENKLING (1910) as "Genera Insectorum".

However, the tribe Thaneroclerini has a new sense in the present communication. It is not a synonym of Thaneroclerinae auct. but one of higher taxa of the family Thanerocleridae n.stat.



Figs 10-17. *Zenodosus sanguineus*. 10, wing. 11, lacinia; 11a, spine of lacinial lamina, detailed view. 12, hind coxa, trochanter and femur. 13, female internal copulatory organs. 14, prothorax ventrally. 15, hypopharyngeal sclerite. 16, prementum. 17, mesonotum. (bc = bursa copulatrix; cr = coxal rift; mo = median oviduct; pn = premental notch; v = vagina).

Diagnosis: It is based on a transformation series of the tegmina. While the sister group Zenodosini n.trib. is polarized towards a heteromeran state of the tegmen, the tegmina of Thaneroclerini have a tendency to become loose (see *Neoclerus, Thaneroclerus* in Figs 37 and 82). It may be a homoplastic trait or a parallelism with the clerid subfamilies Tillinae and Korynetinae (cf. *Tillus elongatus*, *Enoplium serraticorne* figured in KOLIBÁČ, 1987). There are a lot of transformation series in Thaneroclerini (e.g. tarsal pattern, reduction of lateral edge, shape of antennae, reduction of radial cell, tendency to close mesocoxal cavities, etc.) but all these characters are in a plesiomorphic state in the monotypic tribe Zenodosini n.trib.

Apomorphies: Front coxal cavities closed behind, front coxae spherical (Fig. 62). Abdominal segment 9 reduced (Figs 30, 33, 35, 42, 47, 51, 54, 68, 84). Mesonotum narrow (Figs 71 and 85). Discriminal line scarcely perceptible (Figs 74 and 88).

Plesiomorphies: It is hardly possible to find one character that is in a plesiomorphic state in all genera. Such characters will be treated within particular genera, respectively.

Subtribus Thaneroclerina n.subtrib.

Diagnosis: Based on transformation series of the colour and antennae. It is interesting that the sister group Isoclerina n.subtrib. has a similar tendency in some characters (e.g. coalescence of the antennal joints 10 and 11, elytra with black stripes).

Apomorphies: They are not present in all genera of the subtribe. The depressed elytra and the closed mesocoxal cavities are the most distinct synapomorphies, but both characters are also present in some members of Isoclerina n.subtrib.

Plesiomorphies: Tarsal pattern 5-5-5. Other symplesiomorphies are not present.

Genus *Thaneroclerus* LEFEBVRE, 1838

Bull. Soc. Ent. Fr. 7:13.
Type-species: *Clerus buquet* LEFEBVRE, 1835.

Diagnosis: *Meprinogenus** n.gen. is its sister group. They differ from each other in the shape of the antennal joints 9, 10 and 11 (clubbed in *Meprinogenus** n.gen., only slightly dilated in *Thaneroclerus*) and the colour (*Thaneroclerus* is unicolorous, *Meprinogenus** n.gen. is bicolorous).

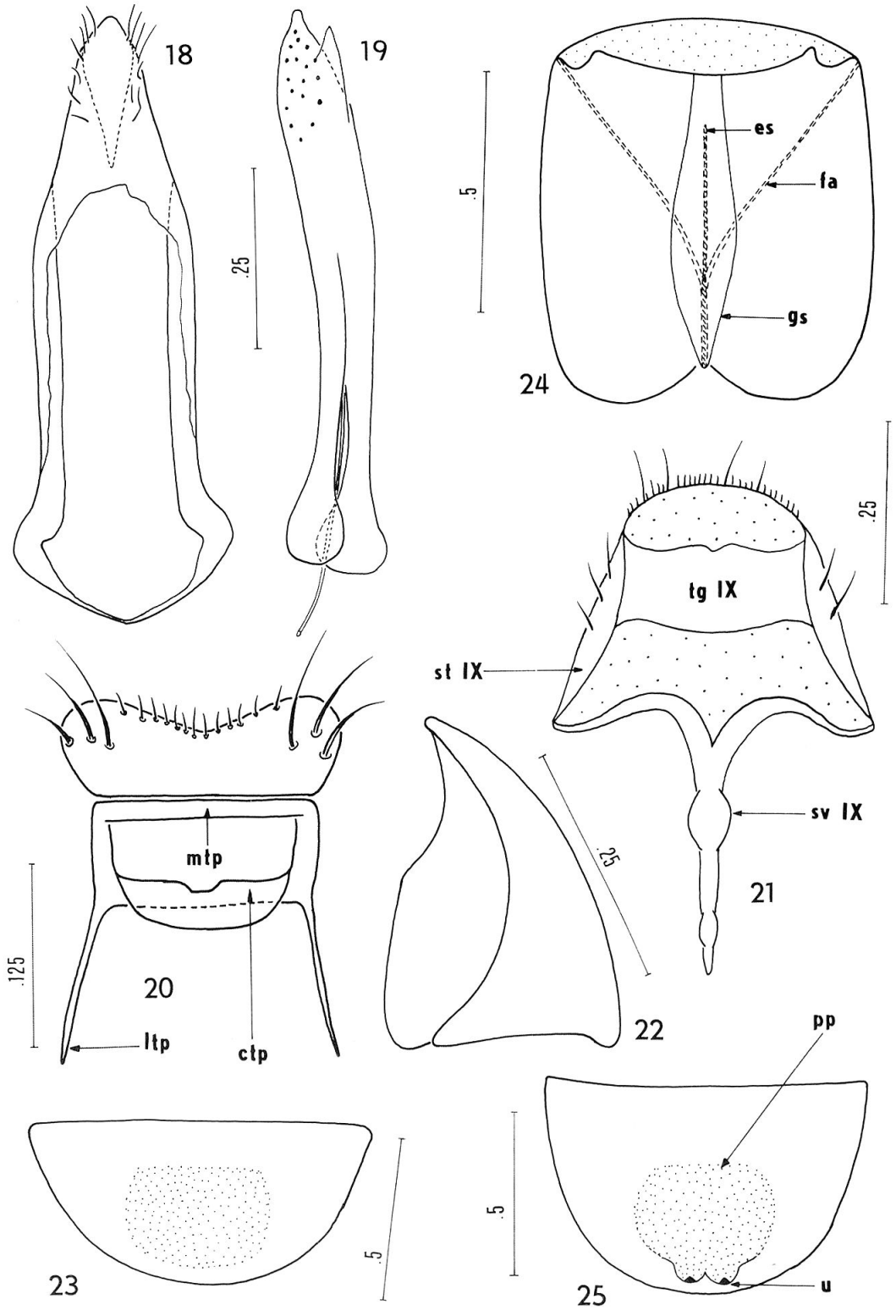
Apomorphies: Metasternum bordered (Fig. 88). Pronotum and elytra often with depressions.

Plesiomorphies: When we compare with *Meprinogenus** n.gen., nearly all character states of *Thaneroclerus* are plesiomorphic.

Head dorsally with longitudinal wrinkles, frons emarginate. Eyes flattened. Lateral edge scarcely perceptible but present. Pronotum with three more or less deep depressions. Elytra slightly depressed in the first third. Antennae 11-segmented. Labrum with connecting tormal process. Prementum with shallow notch. Hypopharyngeal sclerite without apodeme. Gular sutures long and parallel (Fig. 89).

Front coxal cavities closed, intercoxal process dilated at apex. "Epimera" covered by it. Front and middle coxae spherical. Mesocoxal cavities more or less closed by meso- and metasternum (Fig. 88). Femora not tenebrionid-like. Front tarsomere 4 not smaller than tarsomere 3. Wing with radial cell, without anal cell (Fig. 86).

Tegmen loose (Fig. 82). Female internal copulatory organs without distinct bursa copulatrix (Fig. 27).



Figs 18-25. *Zenodosus sanguineus*. 18, tegmen ventrally. 19, phallus. 20, labrum. 21, 9th abdominal segment dorsally. 22 and 23, supposed larva of *Thaneroclerus* sp. 22, mandible ventrally. 23, 9th tergite dorsally. 24 and 25, *Thaneroclerus buquet*, larva. 24, head capsule ventrally, transparent view. 25, 9th tergite dorsally. (ctp = connecting tormal process; es = epicranial stem; fa = frontal arm; gs = gular suture; ltp = lateral tormal process; mtp = medial tormal process; pp = pigmented plate; st =sternite; sv = spiculum ventrale; tg = tergite; u = urogomphi).

Body brown to black, sparsely pubescent.

Distribution: *Thaneroclerus buquet* (LEFEBVRE, 1835) is cosmopolitan, the other species live in South-eastern Asia.

For detailed description of *Thaneroclerus buquet* see KOLIBÁČ (1987, 1989a, 1989b); *Thaneroclerus quasitardatus* and *T. termitincola* are described by CORPORAAL (1939). I have not had the species *T. aino* LEWIS, 1892, at my disposal. A key to the imagoes of *Thaneroclerus* was given by CORPORAAL (1939).

Thaneroclerus impressus PIC, 1926

*Échange 42(423):*22.

Big and robust species. Pubescence dense, composed of short, erect hairs.

Frons emarginate, with longitudinal wrinkles. Eyes rather elevate. Antennae very long – they reach backwards to base of pronotum. Antennal club distinct, composed of joints 10 and 11; joints 6 to 9 successively larger.

Pronotum with rather large and shallow depressions. Elytra with large oval impressions, which are finer in the apical half. Each elytron with large depression along suture (in the half of its length).

Male copulatory organs and spicular fork see Figs 28 to 30.

Body surface brown to black.

Body length: 7.5-8.0 mm.

Distribution: North Vietnam ("Tonkin").

Description of a thaneroclerid larva from India

Epicranial stem absent. Five ocelli present in clerid pattern. Gular margins expanded. Gula narrower than in *Thaneroclerus buquet* (Fig. 24). Hypostomal rods absent. Mandible strongly depressed at ventral face, with one tooth and cutting edge expanded (Fig. 22). Head capsule rather shorter and more robust than that in *T. buquet* (Fig. 24).

Pronotum sclerotized, with notal line. Mesonotum with two sclerites (*Chaetosoma scaritides*-like). Tergite 9 with basal plate sclerotized but urogomphi absent (Fig. 23). (Tergite 9 of *T. buquet* with small urogomphi – see Fig. 25).

Body pink with sparse, medium long pubescence. The specimen described here is 10 mm long and belongs to the collection of the British Museum N.H., labelled as "in packing cases from India; May 1977; *Thaneroclerus* sp., det. J.E. MARSHALL (vide GARDNER, 1937)."

I suppose that this larva belongs either to the genus *Thaneroclerus* or *Neoclerus* (according to size, there is greater probability it is a larva of *Thaneroclerus*).

Genus *Meprinogenus** n.gen.

Type-species: *Cyrtinoclerus indicus* CORPORAAL, 1939.

Name derivation: A word-play from Latin. Masculinum.

Diagnosis: The sister group of the genus *Thaneroclerus.* They are different from each other in colour. However, there are no clear transformation series in *Meprinogenus** n.gen. and in *Thaneroclerus*; hence, *Meprinogenus** n.gen. is a metataxon.

Apomorphies: Front tarsomere 4 smaller than 3. Humeral gibbae with tufts of erect hairs. Mesocoxal cavities closed. Front tibiae without spurs. Wing without radial cell.

Plesiomorphy: Lateral edge present.

Meprinogenus indicus (CORPORAAL, 1939) n.comb.

Cyrtinoclerus indicus CORPORAAL, 1939, *Bijdr. Dierk. 27:*359.

Frons with two horns in its corners, line between them straight. Anterior part of head with fine longitudinal wrinkles. Gular sutures long and parallel. Subapical tooth of mandible very stout. The last joint of labial palps short and securiform, the last joint of maxillar one coniform. Antennae distinctly clubbed, joints from 4 to 8 successively dilated.

Pronotum constricted behind, its base bordered. Lateral edge feebly perceptible; its anterior portion is the most distinct. Front and middle coxae closed. Elytra with small humeral gibbae, each one with erect tuft of black hairs. Transversal depression occurs in middle of each elytron. The anterior half is coarsely punctate, punctation of the posterior half is finer. Impressions are in subregular rows which, by mistake, have been considered to be regular by CORPORAAL (1939). Tarsal pattern 5-5-5, tibiae 2 and 3 with two spurs at apices. Front tarsomere 4 smaller than 3. Hind trochanters and femora in tenebrionid position. Wing *Isoclerus*-like, without radial cell, but with anal cell. Six visible sternites.

Body surface red-brown but black in posterior half of elytra, with blackish tibiae and antennal joints 5 to 10. Three little fields of white stout hairs occur on each elytron.

Body length: 3.8 mm.

Distribution: India: Nilgiri Hills. Two specimens known: the holotype in British Museum N.H., one paratype in Amsterdam.

Genus *Viticlerus* MIYATAKE, 1977

*Trans. Shikoku Ent. Soc. 13(3-4):*105-106.
Type-species: *Viticlerus formicinus* MIYATAKE, 1977.

Diagnosis: It is the sister group of the genus *Neoclerus*. Although it is a monotypic genus, it is clearly defined by transformation series of the antennae (distinctly clubbed) and the wings (wingless).

Apomorphies: Six visible sternites. First abdominal sternite long, about as long as second to fourth combined. Eyes small, slightly emarginate behind. Antennal club distinct. Elytra with humeral gibbae, transversally depressed in anterior half.

Plesiomorphies: Front tarsomeres 4 as long as 3. Lateral edge weak but present. Frons emarginate. Base of pronotum constricted and bordered.

For more detailed description see MIYATAKE (1977).

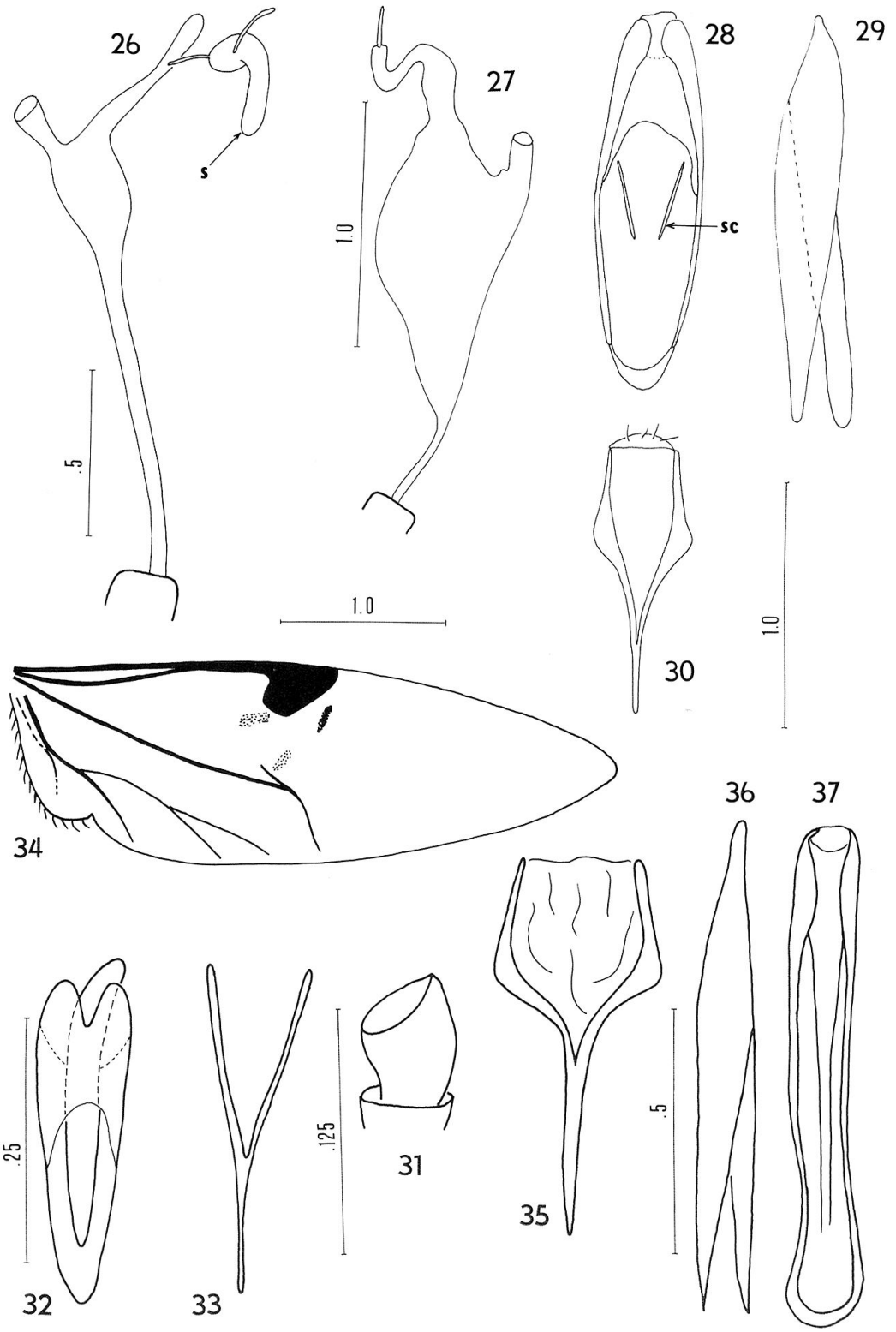
Viticlerus formicinus MIYATAKE, 1977

*Trans. Shikoku Ent. Soc. 13(3-4):*106-107.

Slender, elongate species. Body reddish brown with two testaceous bands on each elytron. Wingless species (see MIYATAKE, 1977).

Body length: 2.6-2.7 mm.

Distribution: Fiji Islands: Viti Levu.



Figs 26-37. 26, *Neoclerus nanus*. Female internal copulatory organs. 27, *Thaneroclerus termitincola*. Ditto. 28 - 30, *Thaneroclerus impressus*. 28, tegmen ventrally. 29, phallus. 30, spicular fork. 31 - 33, *Isoclerus tantillus*. 31, last joint of labial palp. 32, aedeagus ventrally. 33, spicular fork. 34 - 37, *Neoclerus ornatulus*. 34, wing. 35, spicular fork. 36, phallus. 37, tegmen dorsally. (s = spermatheca; sc = sclerite).

Genus *Neoclerus* Lewis, 1892

*Ann. Mag. Nat. Hist. 10(6):*190.
Type-species: *Neoclerus ornatulus* Lewis, 1892.

Diagnosis: Antennal joints 10 and 11 nearly coalescent, suture between them perceptible. Wing without radial cell (Fig. 34). These character states differ *Neoclerus* from *Viticlerus.*

Apomorphy: Shallow furrows for antennae present in front of eyes.

Plesiomorphy: Lateral edge present.

Distribution: South-eastern Asia.

Neoclerus ornatulus Lewis, 1892

*Ann. Mag. Nat. Hist. 10(6):*190.

Antennal sockets not visible from above. Shallow furrow for antennal joints 1 and 2 present in front of eyes. Large antennal club composed of joints 9 to 11; joint 10 and 11 coalescent together (suture perceptible). Last segment of labial palps nearly spherical. Last segment of maxillar palps coniform.

Lateral edge weak. Dilated apex of prosternal process covers apices of "epimera". Mesosternum as in *Compactoclerus davidi* n.sp. (Fig. 66). Mesosternal process long and slender, metasternal process very wide. Middle coxae large. Discriminal line scarcely perceptible. All femora strongly tenebrionid. Front tibiae extraordinarily stout. Paracoxal sutures not perceptible. Wing without radial cell, also vein r-m absent (Fig. 34).

Tegmen *Thaneroclerus*-like but longer and more slender (Fig. 37). Phallus and spicular fork see figs 36 and 35.

Red brown, wide and robust species with three black spots on each elytron.

Body length: 3.0-5.0 mm.

Distribution: Japan (Kiushiu, Nikko, Higo, Oyayanca, Ikenchaiya) and Taiwan (Taihorinsho, Fuhosho).

Neoclerus nanus (Schenkling, 1901)

Thaneroclerus nanus Schenkling, 1901, *Ann. Soc. Ent. Belg. 65:*106.

Frons strongly emarginate, *Lyctosoma*-like, with long longitudinal wrinkles. Lateral edge very distinct. Abdominal sternites laterally bordered along whole length. Tarsomeres 1 of tarsi 2 and 3 coalescent-like with tarsomere 2. Female internal copulatory organs with long bursa copulatrix as shown in fig. 26.

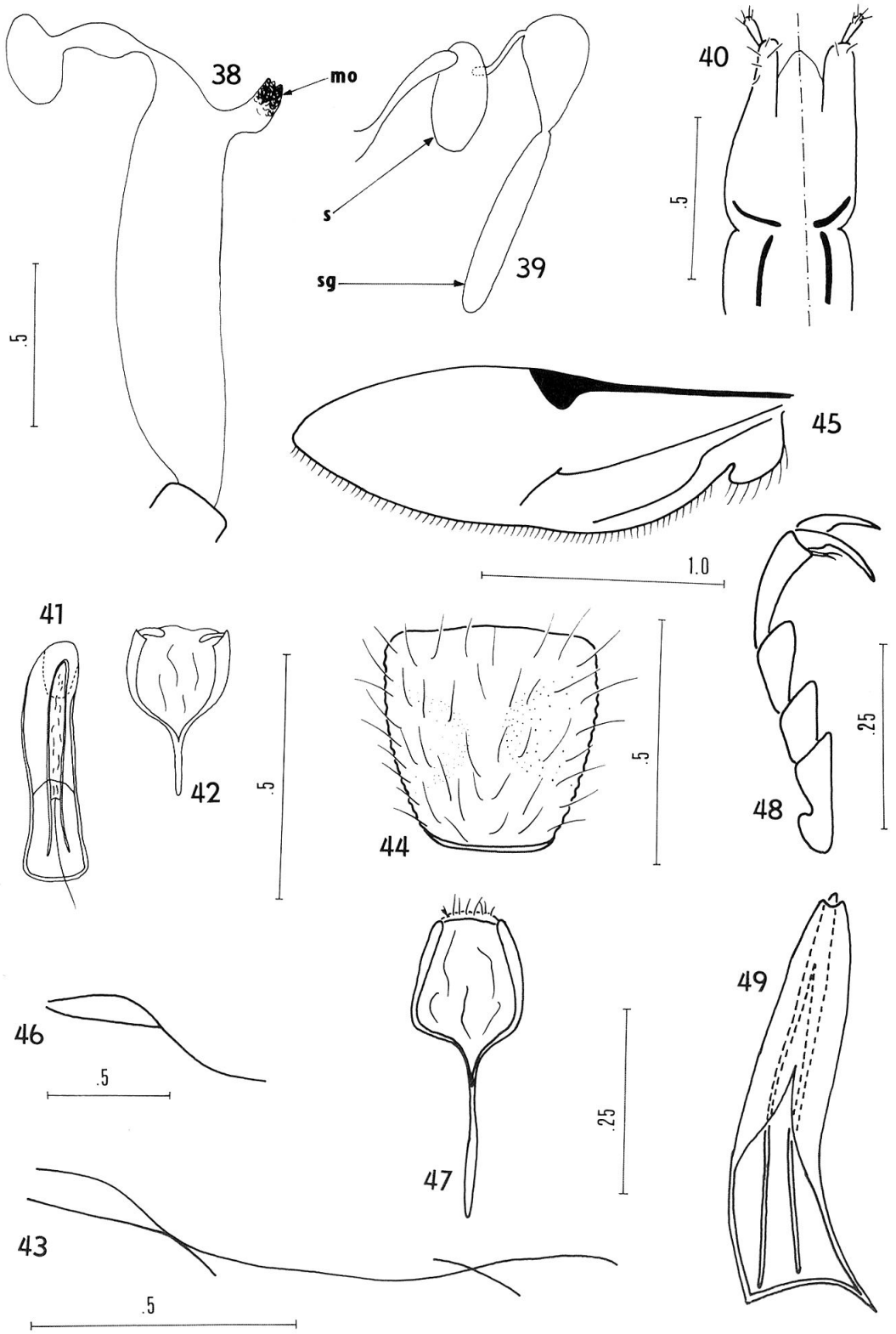
For more detailed description see Corporaal (1939) in which a key to other species is given.

Subtribus Isoclerina n.subtrib.

Diagnosis: Description of its transformation series see above in Thaneroclerina n.subtrib. The colour is transformed from unicolorous brown to brown with yellow stripes. The antennae change shape of the apical joints from only slightly dilated to strongly clubbed or joints 10 and 11 subcoalescent.

Apomorphies: Tarsal pattern 5-4-4 (Fig. 48). Round depression present along notopleural suture. Space between front coxae very narrow (Fig. 62).

Plesiomorphy: Elytra without depressions (except for *Parathaneroclerus* n.stat.).



Figs 38-49. 38 - 40, *Isoclerus parallelus*. 38, female internal copulatory organs. Specimen from Bandoeng. 39, ditto. Specimen from Gunung Gedeh. 40, ovipositor ventrally. Right Bandoeng, left Gunung Gedeh. 41 - 43, *Isoclerus elongatus*. 41, aedeagus ventrally. 42, spicular fork. 43, wing anal veins. 44 and 45, *Isoclerus tantillus*. 44, pronotum. 45, wing. 46, *Isoclerus triimpressus*. Wing anal veins. 47 - 49, *Isoclerus pictus*. 47, spicular fork. 48, middle tarsus. 49, aedeagus ventrally. (mo = median oviduct; s = spermatheca; sg = spermathecal gland).

Genus *Isoclerus* Lewis, 1892

*Ann. Mag. Nat. Hist. 6(10):*191.
Allothaneroclerus Corporaal, 1939, *Bijdr. Dierk. 27:*354.
Lyctosoma Lewis, 1892, *Ann. Mag. Nat. Hist. 6(10):*192.
Parathaneroclerus Pic, 1936, *Échange 51(463):*20.
Ababa Casey, 1897, *Ann. N. York Acad. Sci. 9:*653.
Type-species: *Isoclerus pictus* Lewis, 1892.

Diagnosis: There are three distinct transformation series of the tegmen in members of this genus. The sister group *Compactoclerus** differs in the tegmen and several synapomorphies.

Apomorphies: they vary in particular subgenera.

Plesiomorphy: The last joint of labial palps securiform.

Antennae 11-segmented with loose 3-segmented club. The last joint of labial palps securiform, the last joint of maxillar ones coniform.

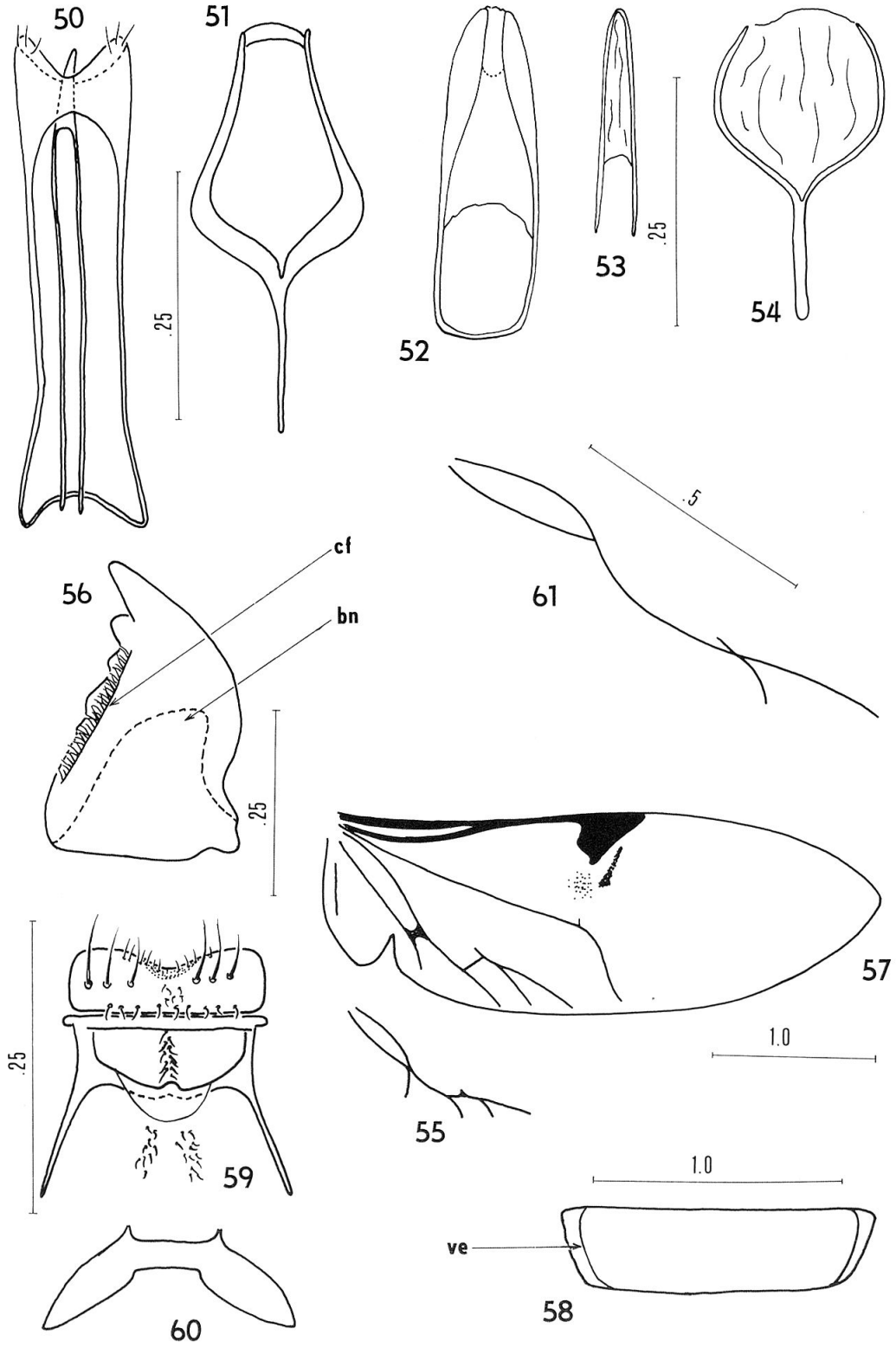
Front and middle coxal cavities closed (except in *Ababa,* with middle coxal cavities open). Front coxae spherical and small, space between them narrow. Prosternum and hypomeron with depression along notopleural suture (scarcely perceptible in the subgenus *Ababa* n.stat.). Tarsal pattern 5-4-4. Wing without radial cell, with only pigmented spot (Figs 45, 57).

Aedeagus open ventrally, without phallobasic apodeme (Figs 32, 41, 49, 50, 52). Phallus rather small and narrow (Figs 41, 49, 50, 53).

Distribution: South-eastern Asia to the southern boundary of palearctic region (China: Sichuan, Yunnan). Two species are distributed in America.

Key to subgenera and species of Isoclerus

1. Body surface brown. Eyes small, flattened (trogositid-like). 2
– Elytra with various colour patterns (Figs 90-91). Eyes bigger, more elevated. Subgenus *Isoclerus* 4
2. Frons deeply emarginate. Both sides of pronotum (Fig. 81) and elytra perfectly parallel. Both elytra and pronotum without distinct depressions. Width of pronotum equal to that of elytra. Punctation of elytra very dense and irregular. Body pubescence short. ..... Subgenus *Lyctosoma** n.stat. (one species: *Isoclerus (Lyctosoma) parallelus* (Lew.): 3.5-4.0 mm; South-eastern Asia)
– Frons slightly emarginate. Sides of pronotum subparallel: pronotum narrower towards base (Figs 44, 67, 75-80). Elytra widest at the last third. Impressions on elytra larger. Hairs on pronotum and elytra long 3
3. Pronotum with three deep depressions (Fig. 75), each elytron with two depressions. Mesocoxal cavities closed. .. Subgenus *Parathaneroclerus* n.stat. (one species: *Isoclerus (Parathaneroclerus) triimpressus* (Pic): 4.0 mm; Brazil)
– Pronotum with depressions scarcely visible (Fig. 44), elytra without depressions. Mesocoxal cavities open. ..... Subgenus *Ababa* n.stat. (one species: *Isoclerus (Ababa) tantillus* (Lec.): 1.8 mm; USA, Mexico)
4. Antennal club not distinct. Head and pronotum glabrous, with fine sparse impressions. Pronotum with depressions scarcely perceptible (Fig. 77). Elytra rather long. Anal field and male genitalia as shown in figs 41-43. 3.2 mm; China: Yunnan. ..... *elongatus* (Schklg.)
– Antennae distinctly clubbed. Head and pronotum never glabrous, with denser punctation. Pronotum with depressions. Elytra shorter. ..... *pictus* species-group 5



Figs 50-61. 50 and 51, *Isoclerus triimpressus*. 50, aedeagus ventrally. 51, spicular fork. 52 - 55, *Isoclerus disinlei* n.sp. 52, tegmen ventrally. 53, phallus. 54, spicular fork. 55, wing anal veins. 56 - 60, *Isoclerus pictus*. 56, mandible ventrally. 57, wing. 58, 4th abdominal sternite ventrally. 59, labrum. 60, hypopharyngeal sclerite. 61, *Isoclerus menieri* n.sp. Wing anal veins. (bn = basal notch; cf = ciliate furrow; ve = ventral edge).

5. Big robust species. Head only with round impressions; black. Pronotum with three deep depressions (Fig. 78); reddish. Male genitalia and anal field as shown in figs 49, 57. About 3.5 mm; Japan. ..... *pictus* LEW.
– Smaller species. Head with more or less longitudinal impressions (or wrinkles). Depressions of pronotum shallower. Head and pronotum have the same colour. 6
6. Frons deeply emarginate, with long longitudinal wrinkles. 7
– Frons nearly straight, impressions longitudinal but they do not form any wrinkles. 8
7. Pronotum cordate (Fig. 80), with fine and very dense punctation. Lateral edge absent. Antennal joints 10 and 11 paler than others, joint 11 shorter than 9 and 10 together. Each elytron with two small fields of white short hairs. 3.1-4.6 mm; Sri Lanka. ..... *tuberculatus* (SCHKLG.)
– Pronotum with subparallel sides (Fig.76). Punctation denser and coarser. Lateral edge present. All antennal joints of the same colour, joint 11 about as long as joints 9 and 10 together. Elytra without fields with ciliation. 2.9 mm; Taiwan (Fig. 90). ..... *disinlei* n.sp.
8. Head and pronotum (Fig. 67) black-brown. Dorsal side coarsely punctated. Antennae brown but joints 1 and 2 yellow. 2 mm; Sarawak. .... *sarawacensis* CORP.
– Body surface orange but elytra with two black stripes. Sculpture of dorsal side finer. Antennal joint 11 lighter. Pronotum with two deeper depressions (Fig. 79). 2.8 mm; Lombok; (Fig. 91). ..... *menieri* n.sp.

Subgenus *Ababa* CASEY, 1897 n.stat.

*Ann. N. York Acad. Sci. 9:*653.
Type-species: *Clerus tantillus* LECONTE, 1865.

Diagnosis: The subgenus is based on a character state of the tegmen.
Apomorphy: Antennal club very distinct.
Plesiomorphies: Body surface unicolorous. Mesocoxal cavities open.

Isoclerus (Ababa) tantillus (LECONTE, 1865) n.comb.

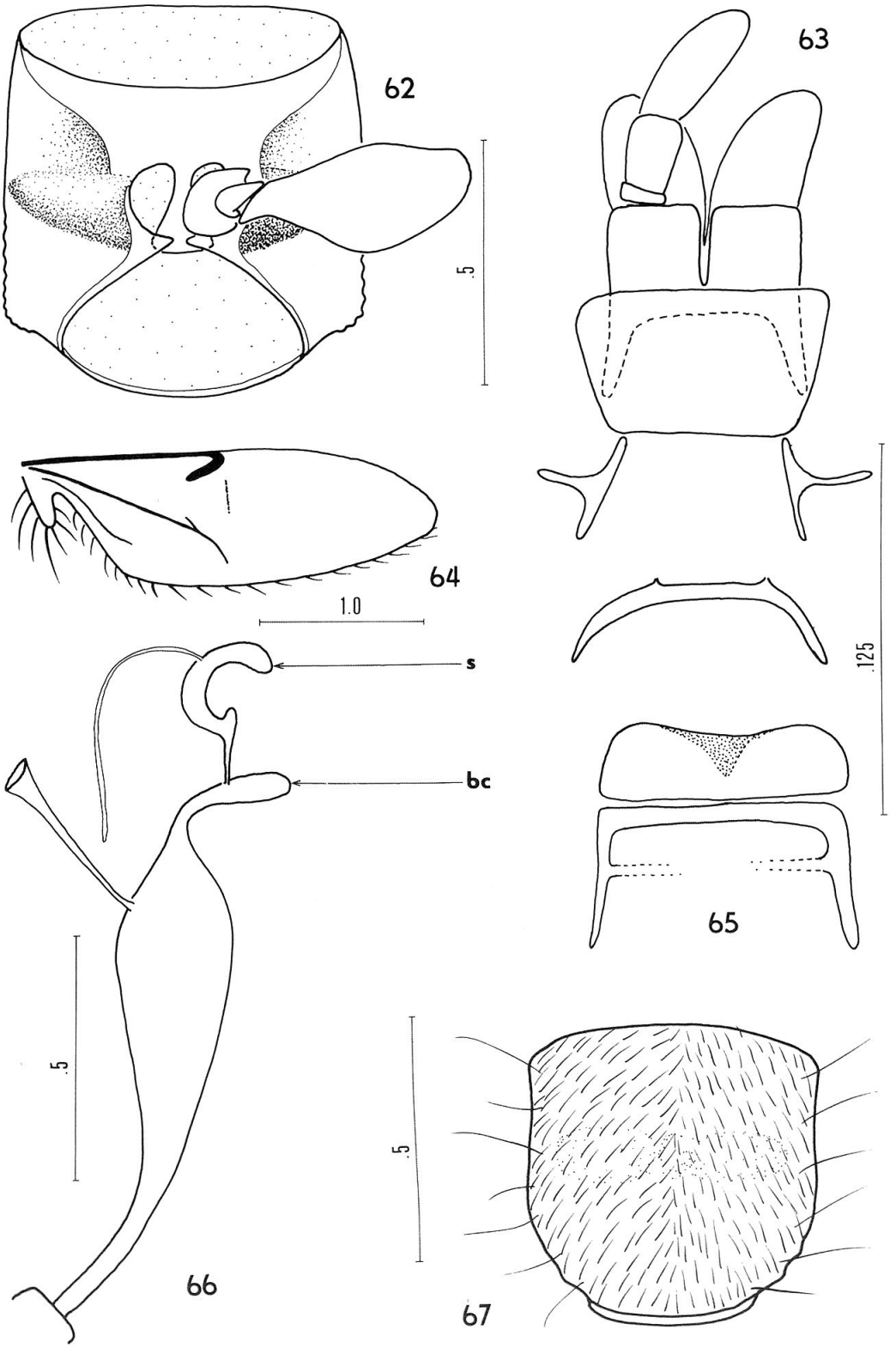
Clerus tantillus LECONTE, 1865, New Spec. Col.:96.

Gular sutures narrow, parallel. Head slightly wrinkled. Shallow furrow for antennal joints 1 and 2 in front of eyes. Antennae long, they reach backwards to base of pronotum. Club very distinct, loose, 3-segmented. All antennal joints densely and longly ciliate. Head long, frons emarginate, with two horns. The last joint of labial palp as shown in fig. 31.

Lateral edge dentate, scarcely visible. Front coxae spherical, depressions along notopleural sutures absent. Prosternal process narrow, feebly dilated at apex. "Epimera" touch that process, they are not covered by it. Mesocoxal cavities open. Pronotum see fig. 44, coarsely punctate. Elytra with about seven regular rows of large impressions which are smaller towards apices of elytra.

Legs slightly tenebrionid. Wings with only one vein in anal field (Fig. 45). Tegmen cucujoid (Fig. 32). Spicular fork as shown in fig. 33.

Dorsal side with long pale hairs. Body surface brown.
Body length: 1.8 mm.



Figs 62-67. 62 - 65, *Compactoclerus davidi* n.sp. 62, prothorax ventrally. 63, labium. 64, wing. 65, labrum. 66, *C. robustus* female internal copulatory organs. 67, *Isoclerus sarawacensis*. Pronotum. (bc = bursa copulatrix; s = spermatheca).

Larva without basal plate and urogomphi on tergite 9 (FOSTER, 1976).

Distribution: USA (Massachusetts, Washington D.C., Missouri, Alabama, Louisiana, Texas), Mexico, Bahia (?), Brazil and Mindanao (probably introduced).

Subgenus *Parathaneroclerus* PIC, 1936 n.stat.

*Échange 51(463):*20.
Type-species: *Parathaneroclerus triimpressus* PIC, 1936.

Diagnosis: The subgenus is based on a character state of the tegmen.

Apomorphy: Pronotum and elytra with deep and large depressions.

Plesiomorphy: Unicolorous body.

Isoclerus (Parathaneroclerus) triimpressus (PIC, 1936) n.comb.

Parathaneroclerus triimpressus PIC, 1936, *Échange 51(463):*20.

Head: similar to that of *Isoclerus parallelus* (Lew.) but emargination of frons shallower, sculpture finer. Antennal club slightly more perceptible than that one in *Isoclerus parallelus* (LEW.).

Pronotum subparallel, constricted at base, with three deep impressions (Fig. 75), with small denticles along base. Pubescence irregular. Elytra widest at the third quarter of their length. Two deep impressions present at the basal half of each elytron. Elytra punctated irregularly but very densely. Hairs long, but pubescence sparse. Tarsal pattern 5-4-4. Wing anal field with two veins (Fig. 46).

Tegmen characteristic, cucujoid, with sparse ciliation at apex; phallus thin (Fig. 50). Spicular fork as shown in fig. 51.

Body surface brown, elytra paler than pronotum and head.

Body length: 4.0 mm.

Distribution: Brazil (Nova Teutonia). It is possible that the species was introduced to South America from South-eastern Asia or North America. The only specimen in Paris Museum NH.

Subgenus *Lyctosoma** LEWIS, 1892 n.stat.

*Ann. Mag. Nat. Hist. 6(10):*192.
Type-species: *Lyctosoma parallelum* LEWIS, 1892.

Diagnosis: The classification of this subgenus is dubious. The character state of the tegmen is the same as in members of *Isoclerus* s.str. Hence it is classified as a metataxon.

Apomorphy: Body sides quite parallel.

Plesiomorphies: Body unicolorous. Antennal club not distinct.

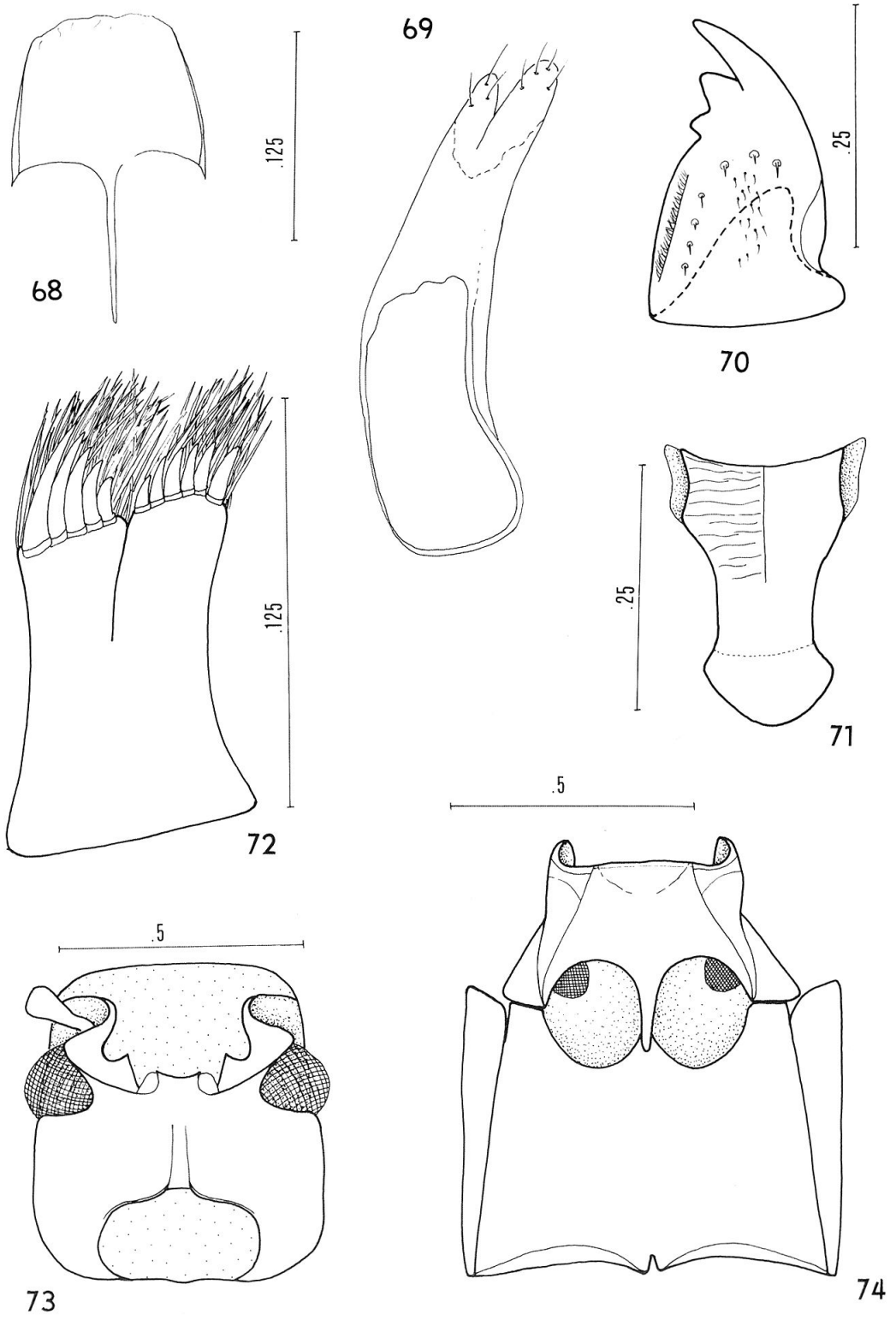
Isoclerus (Lyctosoma) parallelus (LEWIS, 1892) n.comb.

Lyctosoma parallelum LEWIS, 1892, *Ann. Mag. Nat. Hist. 6(10):*192.
Lyctosoma parvum SCHKLG., 1916, *Ent. Mitt. 5(9-12):*222 (partim).
Lyctosoma parvum var. *parvulum* CORPORAAL, 1939, *Bijdr. Dierk. 27:*352-353.
Ababa longipennis PIC, 1947, *Échange 63(508):*6 (n.syn.).

Head long, front margin of frons deeply emarginate, sculpture composed of longitudinal wrinkles, sparsely ciliate. Antennae fluently dilated, club not distinct.

Pronotum (Fig. 81) and elytra long, parallel. Elytra as wide as pronotum, with sparse pubescence, punctation very dense and irregular. Both elytral and pronotal surfaces nearly without depressions. Tarsal pattern 5-4-4.

Female internal copulatory organs as shown in figs 38 and 39. Spermatheca of the specimen from Bandoeng (Fig. 38) was probably destroyed. The ovipositor



Figs 68-74. *Compactoclerus davidi* n.sp. 68, spicular fork. 69, tegmen ventrally. 70, mandible ventrally. 71, mesonotum. 72, lacinia. 73, cranium ventrally. 74, meso- and metathorax. All coxae removed.

in fig. 40 shows differences between both Javan specimens (Bandoeng and Gunung Gedeh).

Body brown or pale brown.

Body length: 3.5-4.0 mm.

Distribution: Vietnam (Tonkin): Hoa Binh; Java (Gunung Gedeh, Bandoeng); China: Sechuan; Sumatra centr.; type specimens from Japan (Nagasaki).

Subgenus *Isoclerus* LEWIS, 1892

*Ann. Mag. Nat. Hist. 6(10):*191.
Allothaneroclerus CORPORAAL, 1939, *Bijdr. Dierk. 27:*354 (n.syn.).
Type-species: *Isoclerus pictus* LEWIS, 1892.

Diagnosis: The taxon is based on character states of the tegmen.

Apomorphy: Body bicolorous, compact (Figs 90 and 91).

Plesiomorphy: The species of the subgenus are rather advanced.

Elytra with various colour pattern. Antennae distinctly clubbed. Eyes bigger, elevated. Shape of pronotum and length of hairs on elytra and pronotum very variable (Figs 67, 76-80). Tarsal pattern 5-4-4 (Fig. 48). Six small and compact species from South-eastern Asia.

Isoclerus (Isoclerus) elongatus (SCHENKLING, 1906) n.comb.

Thaneroclerus elongatus SCHENKLING, 1906, *Deutsch. Ent. Zeitschr. 1906:*278.
Lyctosoma elongatum (SCHENKLING), CORPORAAL, 1939, *Bijdr. Dierk. 27:*352-353.

Head longitudinal, frons slightly emarginate, sculpture composed of longitudinal impressions. Eyes bigger than in *Isoclerus parallelus* Lew. Gular sutures touch each other in the half of their length, then diverge. Antennal club rather indistinct. Antennae long, they reach backwards to the first half of pronotum. Mouth foramen ventrally bordered.

Pronotum cordate, base constricted, sparsely punctate and with long pubescence (Fig. 77), *Chaetosoma*-like. Front coxae small, narrow space present between them. Lateral edge perceptible. Space in front of coxal cavities rather long. Elytra quite long, subparallel, with coarse impressions. Black transverse stripe present at the apical half of elytra[2]. Mesothorax quite wide, mesosternal process long. Both meso- and metathorax with deep impressions. This punctation sparse. Deep cut between ventral condyles present, without discriminal line. Wing anal field veins as shown in fig. 43. Legs with all femora tenebrionid, thick.

Five sternites visible, first one is the longest. Spicular fork as shown in fig. 42. Aedeagus *Isoclerus pictus*-like (Fig. 41).

Body length: 3.2 mm.

Body surface brown but black elytral stripes.

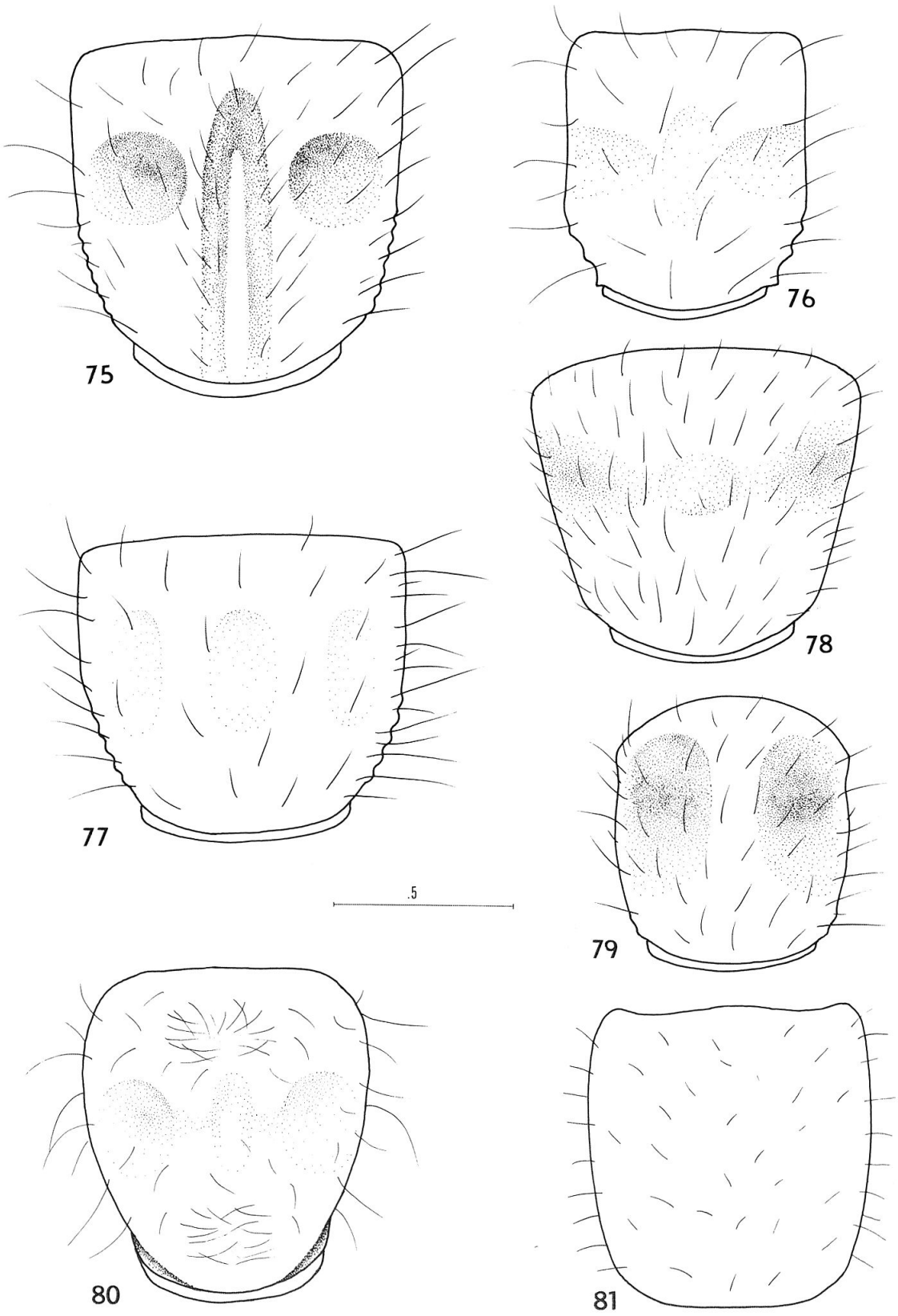
Distribution: The type specimen is from China (Yunnan). The label of the specimen described above (Paris Museum NH) is illegible.

Isoclerus (Isoclerus) pictus LEWIS, 1892

*Ann. Mag. Nat. Hist. 6(10):*191.

Head black, with fine impressions. Frons not emarginate, with long pubescence. Antennal club distinct and loose, composed of three joints. Joints

[2] CORPORAAL (1939) has pictured the type specimen from Yunnan. It has also the apex of the elytra black, according to his figure.



Figs 75-81. Pronota: 75, *Isoclerus triimpressus*. 76, *I. disinlei* n.sp. 77, *I. elongatus*. 78, *I. pictus*. 79. *I. menieri* n.sp. 80, *I. tuberculatus*. 81, *I. parallelus*.

1 and 2 lightly red, the other deep brown to black. Gular sutures narrow, parallel from the half of length. Hypopharyngeal sclerite *Thaneroclerus*-like (Fig. 60), prementum with notch. Apical joints of labial palps securiform, maxillar one coniform. Mandible with three little denticles along cutting edge, basal notch deep. Pubescent edge present at ventral side of mandible (Fig. 56). Lacinial lamina with spines. Tormal processes *Zenodosus*-like (Fig. 59).

Pronotum red with irregular dense impressions, slightly narrower towards bordered base. Lateral edge present but scarcely perceptible. Pronotum with three depressions (Fig. 78). Space between coxae narrow, coxae spherical. Prosternal process dilated, it covers "epimera". Furcasternum visible (arms slightly convergent), round depressions present along notopleural suture.

Mesosternal process without groove at apex. Coxal cavities closed by meso- and metasterna. Coxae spherical. Elytra with variable black and yellow pattern: yellow transverse tripe in the first third of elytra reaches towards their base along epipleures. The second yellow transverse stripe is situated in the second third of elytra which are rather finely and irregularly punctate and pubescent. Arms of mesendosternite split into two parts.

Intercoxal process of metasternum nearly square-shaped. Discriminal line absent, paracoxal sutures run along coxae. Anterior tendons of metendosternite distinct. Coxae with distinct furrow. Wing without radial cell, see fig. 57.

Legs rusty coloured, femora tenebrionid-like, tarsal pattern 5-4-4.

Abdomen: Sternites laterally bordered (Fig. 58). Aedeagus see fig. 49. Tegmen open laterally. Spicular fork as shown in fig. 47.

Head black, pronotum and ventral part of body are rusty, elytra as described above.

Body length: 3.5 mm.

Distribution: Japan (Tovada – Aomori; Nikko).

Isoclerus (Isoclerus) disinlei n.sp.

Name derivation: The name is a word-play from Chinese.

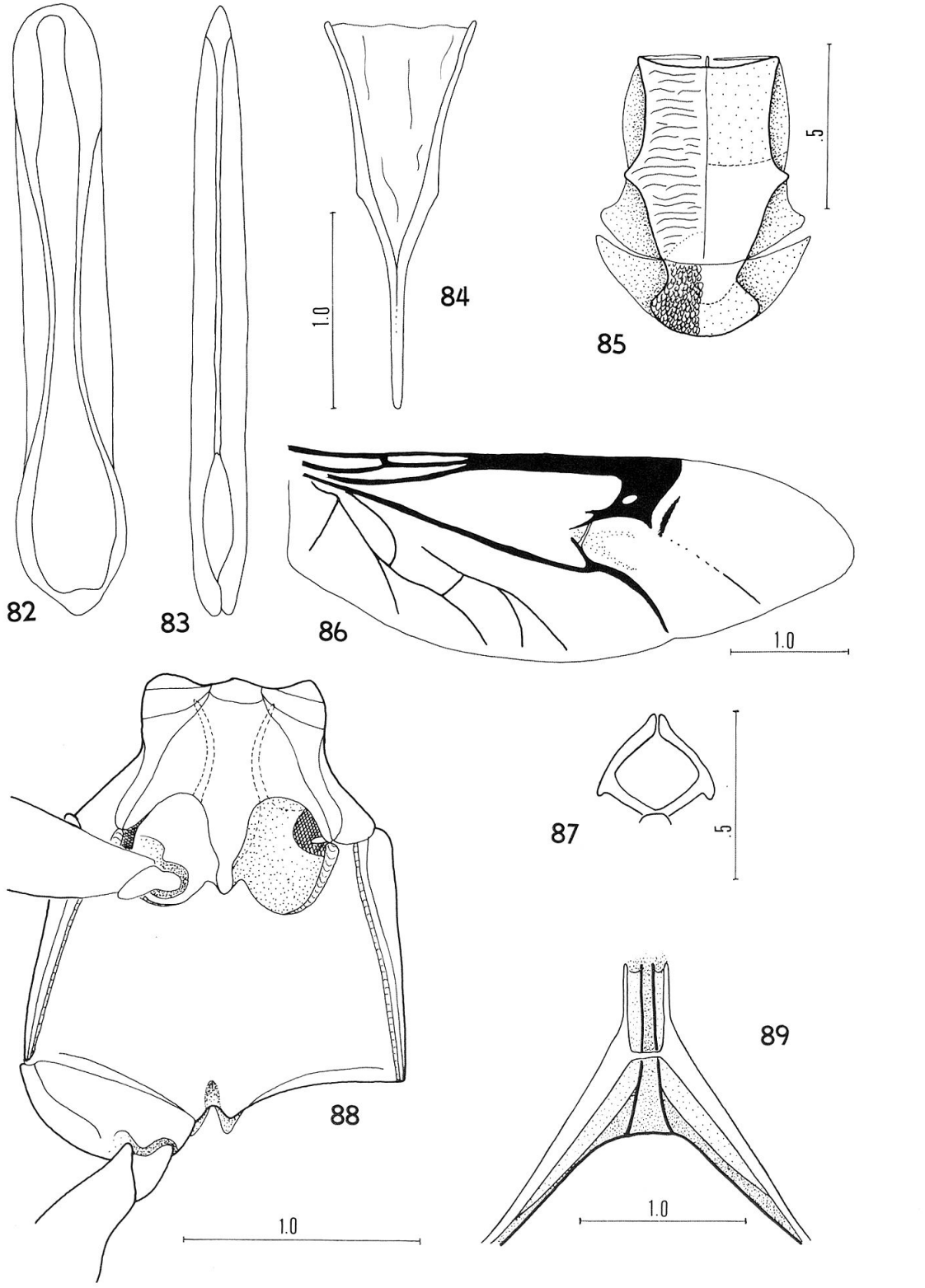
Frons very deeply emarginate. Eyes large. Extraordinarily long longitudinal furrows reach to the half length of head. The last antennal joint as long as joints 9 and 10 together.

Pronotum with parallel side to the second third of length (Fig. 76). Its three depressions very shallow, punctation dense. Pale pubescence of head and pronotum the longest of all *Isoclerus* species. Lateral edge distinct. Elytral colour pattern similar to that in *I. pictus* Lew.: smaller part of elytra yellow; little black spot present at base; transverse black stripe at the half of elytra connected along epipleura and suture with black apical spot (Fig. 90). Hairs on elytra black. Head, pronotum and antennae red brown; all parts of legs lighter but bases of tibiae blackish.

Anal field veins and aedeagus as shown in figs 52 to 55. Body shape see fig. 90.

Body length: 2.9 mm.

Distribution: Taiwan: Shanmei. The only specimen (male holotype) is in the author's collection.



Figs 82-89. *Thaneroclerus buquet*. 82, tegmen dorsally. 83, phallus. 84, spicular fork. 85, mesonotum. 86, wing. 87, proendosternite or furca of prothorax. 88, meso- and metasternum ventrally. 89, tentorium dorsally. (Figs 82-84 and 86 according to KOLIBAČ, 1987; Figs 85 and 87-89 according to KOLIBÁČ, 1989a; modified).

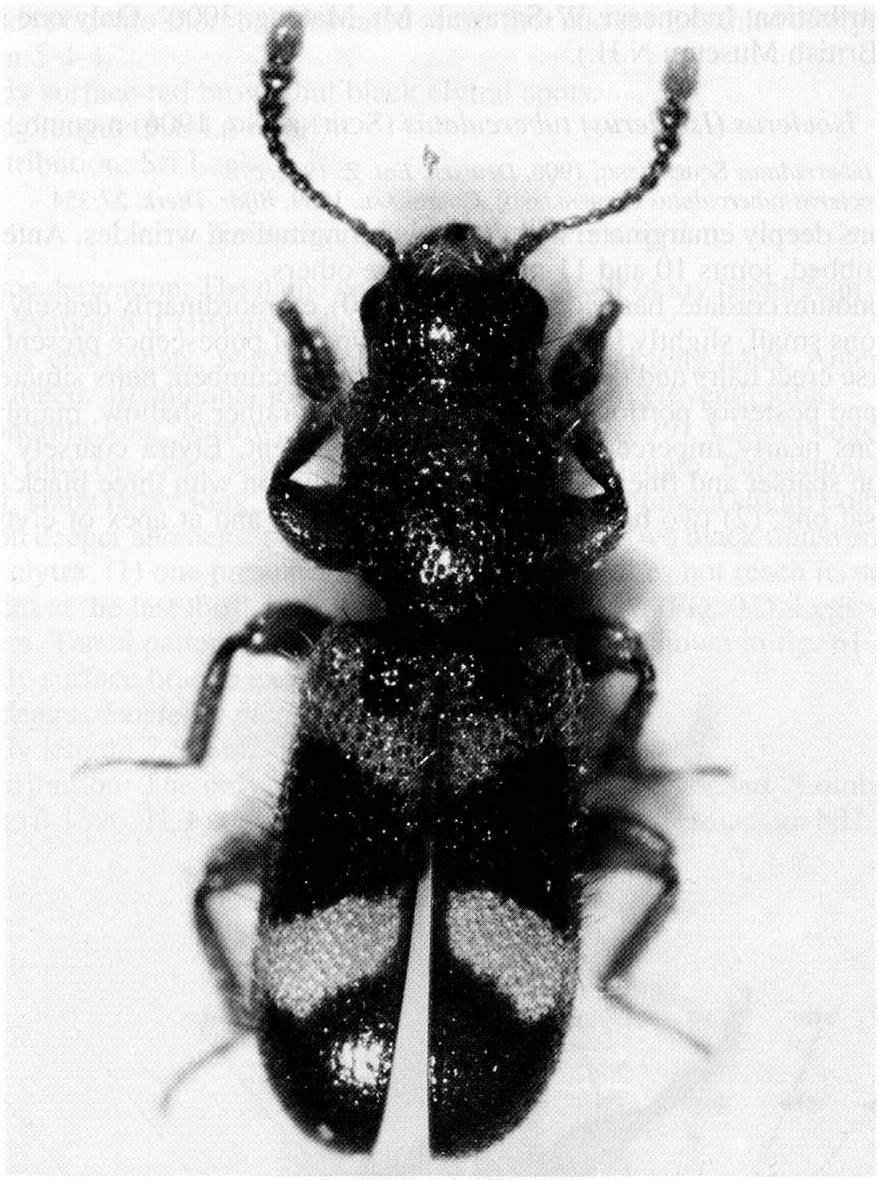


Fig. 90. *Isoclerus disinlei* n.sp. (Photo by author).

Isoclerus (Isoclerus) sarawacensis CORPORAAL, 1939

Bijdr. Dierk. 27:354.

Frons slightly emarginate, with fine longitudinal wrinkles. Head rather long. Antennae distinctly clubbed, joints 1 and 2 yellow, the others brown.

Pronotum brown, with very shallow depressions only, quite long, parallel-sided, not constricted at base (Fig. 67), lateral edge distinct. Two kinds of pubescence present: (1) long erect hairs and (2) long decumbent ones. Elytra brown, with two yellowish transverse stripes. Sculpture deeper and denser than in *Isoclerus pictus* Lew. Dense pubescence present. Tarsal pattern 5-4-4. Both femora and tibiae pale brown, tarsi yellow.

Body length: 2.0 mm.

Distribution: Indonesia: W-Sarawak, Mt. Matang, 3000'. Only one specimen known (British Museum N.H.).

Isoclerus (Isoclerus) tuberculatus (SCHENKLING, 1906) n.comb.

Neoclerus tuberculatus SCHENKLING, 1906, *Deutsch. Ent. Z. 1906:*278.
Allothaneroclerus tuberculatus (SCHENKLING), CORPORAAL, 1939, *Bijdr. Dierk. 27:*354.

Frons deeply emarginate, with very long longitudinal wrinkles. Antennae distinctly clubbed, joints 10 and 11 paler than the others.

Pronotum cordate, base constricted (Fig. 80), extraordinarily densely punctate. Impressions small, slightly longitudinal. Two types of pubescence present: (1) very long sparse erect hairs and (2) two areas of shorter decumbent hairs situated at both anterior and posterior portions of disc. Depressions rather shallow, mainly median depressions nearly imperceptible. Lateral edge absent. Elytra coarsely punctate, punctation sparser and finer towards apex. Each elytron with three black spots: (1) small basal one, (2) two big ones situated at the half and at apex of elytron. Two

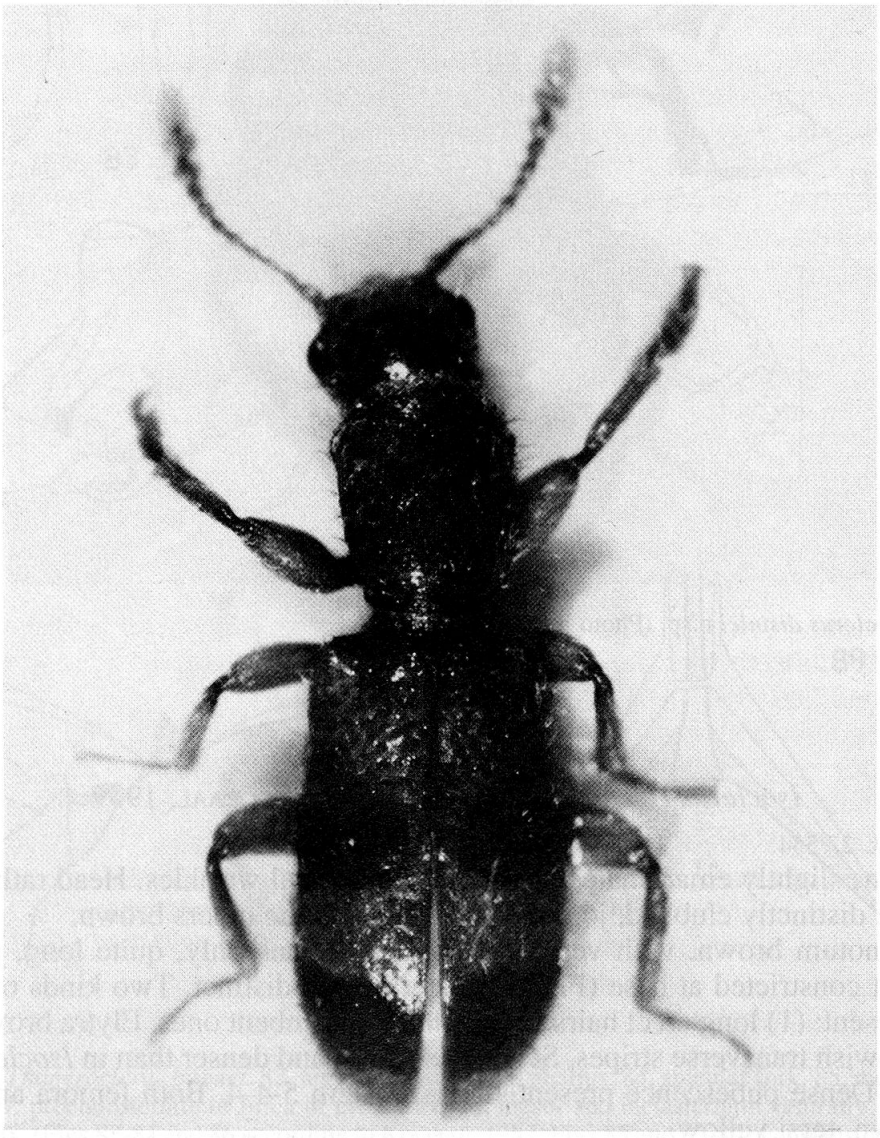


Fig. 91. *Isoclerus menieri* n.sp. (Photo by author).

small fields of white short hairs situated at the first and the last third of elytron. Tarsal pattern 5-4-4.

Body surface red brown but black elytral spots.

Body length: 3.1-4.6 mm.

Distribution: Sri Lanka.

Isoclerus (Isoclerus) menieri n.sp.

Name derivation: The name was derived in honour of my friend Jean J. MENIER (Muséum National d'Histoire Naturelle, Paris).

Frons emarginate, with longitudinal wrinkles and long hairs. Antennae distinctly clubbed, all antennal joints orange but yellowish eleventh joint.

Pronotum long, narrow, its sides subparallel (Fig. 79). Lateral edge distinct. Disc with only two deep depressions at the half of its length. Punctation denser at basal half. Hairs rather long. Base bordered. Elytra with humera slightly tuberculate. Punctation deeper and denser at the first third of elytra. Two black transverse stripes occur on elytra: (1) one present in the anterior half, it does not reach its suture; (2) one present at the last third, it runs over the whole width (Fig. 91). Legs with long white hairs. Tarsal pattern 5-4-4. Anal field of wings as shown in fig. 61.

Body surface orange except elytral black stripes.

Aedeagus *Isoclerus pictus*-like.

Body length: 2.8 mm.

Distribution: The only specimen (male holotype) is labelled "Lombok, Sapit 2000', April 1896, H. FRUHSTORFER", deposited in the Paris Museum NH.

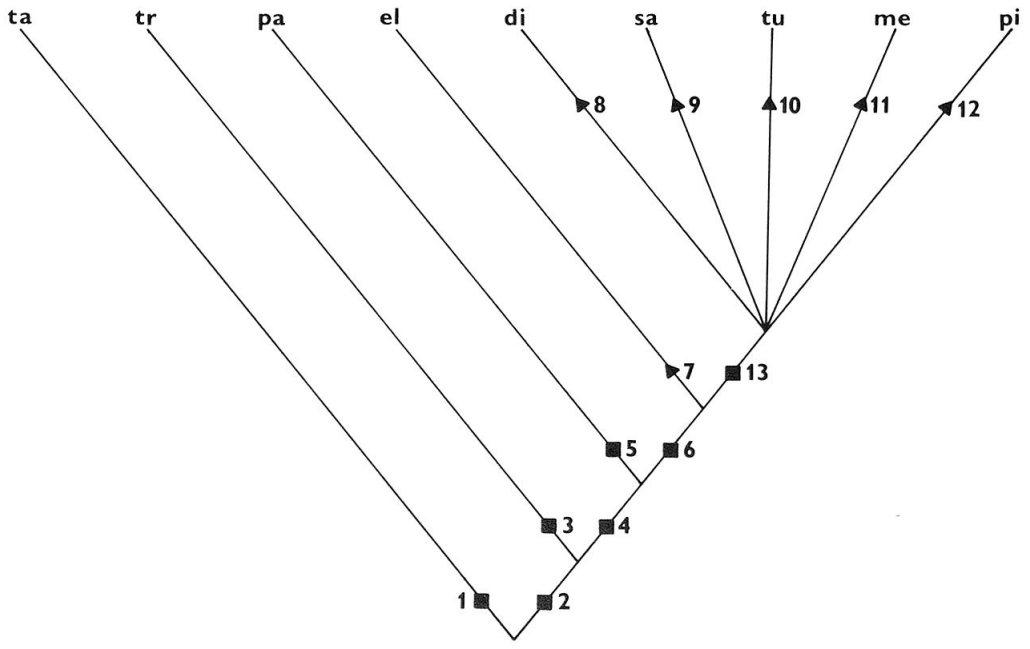


Fig. C-1. Partially resolved cladogram of the genus *Isoclerus*. *I. pictus*-group not resolved (bush). For details of the apomorphies see tab. 1 and text. (Square = synapomorphy, triangle = autapomorphy; ta = *tantillus*, tr = *triimpressus*, pa = *parallelus*, el = *elongatus*, di = *disinlei;* sa = *sarawacensis*, tu = *tuberculatus*, me = *menieri*, pi = *pictus*).

Phylogeny of Isoclerus

The inner classification of the genus *Isoclerus* is not quite clear. There are several alternatives as to how to classify species of *Isoclerus* into subgenera. The species form two distinguished groups: the group of unicolorous species (*I. tantillus, I. triimpressus, I. parallelus*) and the group of bicolorous ones (all other *Isoclerus* species), see partially resolved cladogram in fig. C-1. The latter group composes a direct transformation series of the colour – from *I. elongatus* (red with on black stripe on elytra) to *I. pictus* (black colour dominates). A sequence of the bicolorous species based on a transformation series of the colour is shown in fig. C-3.

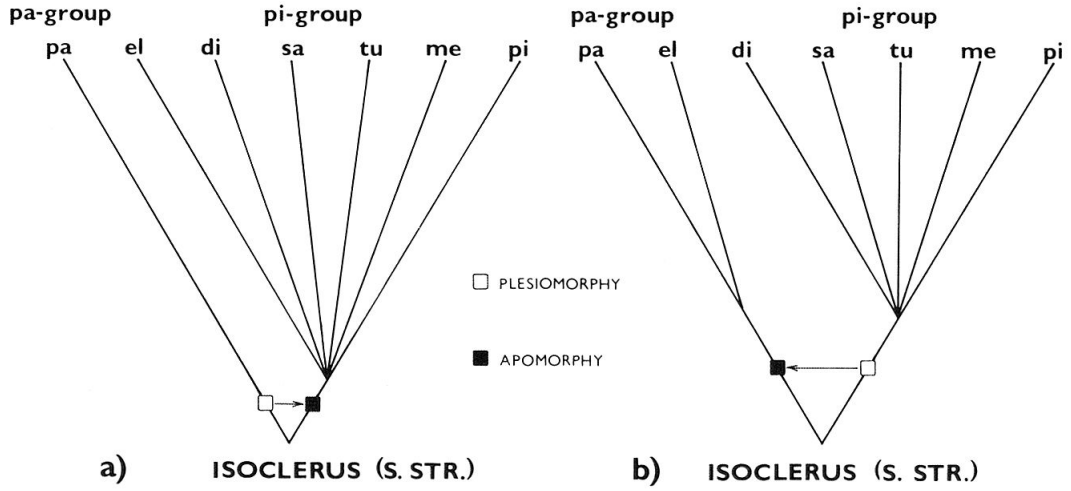


Fig. C-2. Other alternatives for a classification of the subgenus *Isoclerus* s.str. a) *Isoclerus elongatus* is classified within the *pictus*-group on the basis of its colour patterns. b) *I. elongatus* is classified within the *parallelus*-group on the basis of the subparallel body shape. See text for details.

The subgenera *Ababa, Parathaneroclerus* and *Isoclerus* (s.str.) are based on independent trends of the morphology of the tegmina. However, this character is also dubious because both the first and second subgenera are monotypic and a character state of the tegmen in *Isoclerus* (s.str.) is the same in all species (there are no transformation series in the subgenera cited above). However, both subgenera *Ababa* and *Parathaneroclerus* are probably monophyletic: although they are rather primitive taxa, both their members, *I. tantillus* and *I. triimpressus*, have autapomorphies which are not present in more advanced taxa of *Isoclerus*. It could be explained by the heterobathmy of characters (or the mosaic pattern of evolution; see Ax, 1984) but such a hypothesis would be unprovable.

The monotypic subgenus *Lyctosoma** has the same character state of the tegmen as species of *Isoclerus* (s.str.). The species *I. (Lyctosoma) parallelus* (Lew.) has another body shape and sculpture than other members of the latter subgenus but it does not form any transformation series *(Lyctosoma** is a monotypic subgenus). Both *Isoclerus* and *Lyctosoma** were described in the same paper so that they could be paraphyletic taxa. In spite of this fact I decided to establish *Lyctosoma** as an

Tab. 1. List of apomorphies in *Isoclerus* species.

Apomorphy No.	Character state
1	antennae strongly clubbed
2	middle coxal cavities with deep impressions
3	pronotum and elytra with deep depressions
4	parameres imperceptible
5	sides of both pronotum and elytra parallel
6	elytra with colour pattern
7	elytra subparallel
8	antennal joint 11 as long as joints 9 and 10 together
9	pronotum coarsely punctated
10	lateral edge absent
11	pronotum with only 2 shallow depressions
12	frons without longitudinal wrinkles or impressions
13	small, compact species

independent metataxon which indicates that its characters differ from *Isoclerus* (s.str.). Similar methods are sometimes used in paleontology.

It would be possible to classify the species *I. parallelus* (LEW.) within the subgenus *Isoclerus* s.str. and the species *I. elongatus* (SCHKLG.) within the *parallelus*-group on the basis of the subparallel body shape (Fig. C-2b). The second alternative is a classification of *I. parallelus* within the subgenus *Isoclerus* in an independent species group (Fig. C-2a). Then *I. elongatus* would be classified within the *pictus*-group on the basis of its colour patterns.

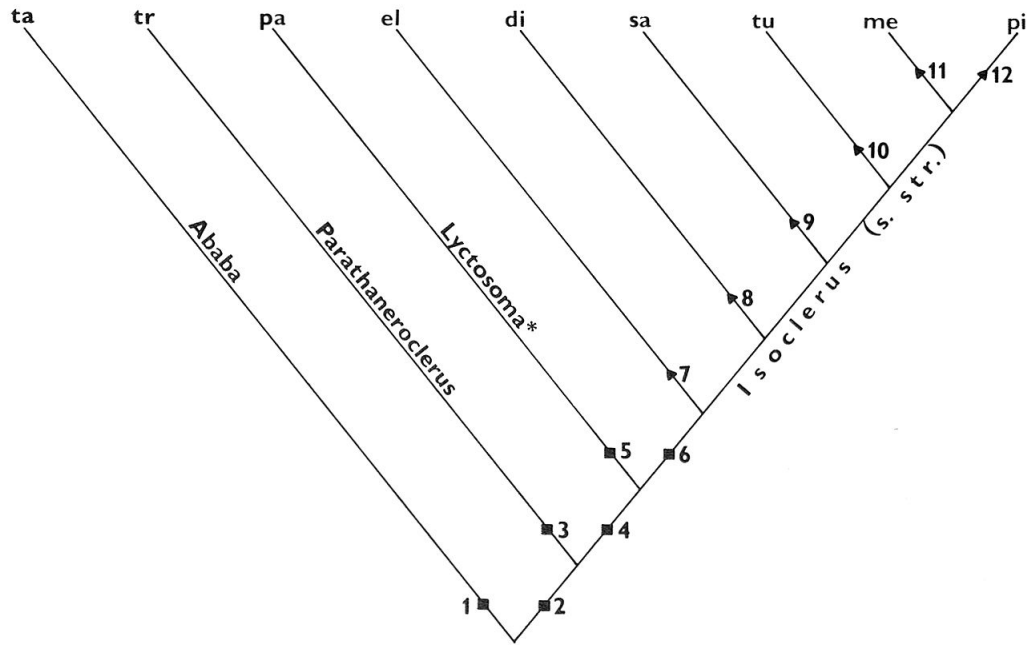


Fig. C-3. Fully resolved cladogram of the genus *Isoclerus*. Symbols as in fig. C-1. See text for details.

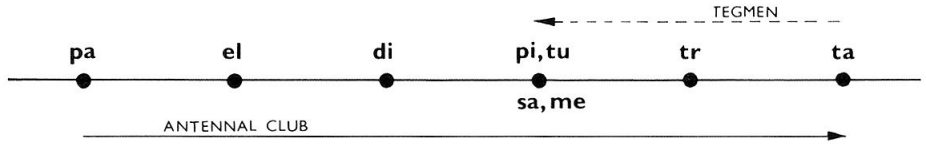


Fig. C-4. Two transformation series in the genus *Isoclerus*. The sequence of the species is based on a transformation series of the antennal club. See text for details.

The distinct antennal club is, according to HENNIG's criterion of frequency of occurrence (HENNIG, 1966), an apomorphic character in Thanerocleridae. Then a transformation series of the antennal shape runs through the whole genus *Isoclerus* (Fig. C-4) against a transformation series of the tegmen. The criterion cited above had often been questioned (e.g. KOLIBÁČ, 1989b) and besides, the species *I. tantillus* and *I. triimpressus* have a greater number of plesiomorphic characters than other species (see their descriptions). Hence I decided to use the transformation series of the tegmen.

Genus *Compactoclerus** PIC, 1939

*Mélang. exot. ent. 71:*18.
Microababa PIC, 1939, *Revue fr. Entomol. 6(3-4):*187 (n.syn.).
Type-species: *Compactoclerus robustus* PIC, 1939.

Diagnosis: Three species of the genus do not form a transformation series of the tegmen although they have a different state from all members of the genus *Isoclerus* (Fig. 69). Hence *Compactoclerus** is a metataxon.

Apomorphies: The last joint of labial palps coniform (Fig. 63). Mesonotum wide (Fig. 71). Femora in heteromeran position.

Plesiomorphy: Body surface more or less unicolorous.

Mouth foramen strongly bordered (Fig. 73). Antennal joints 10 and 11 nearly coalescent (suture between them visible). Subapical tooth (premolar) not situated exactly in axis of the cutting edge (rather slightly *Peltis*- or Heteromera-like). Last joint of both maxillar and labial (Fig. 63) palps coniform. Apices of "epimera" cover dilated apex of prosternal process (Fig. 62). Mesocoxal cavities closed (Fig. 74). Anterior part of mesothorax not as narrow as in other Thanerocleridae (Fig. 74). Femora tenebrionid-like. Radial cell and vein r-m absent. Margin of jugal field with extremely long ciliation (Fig. 64).

*Key to species of Compactoclerus**

1. Pronotum parallel-sided (Fig. 62). Eyes rather elevate. Body surface coarsely sculptured, not glabrous, with rather long and dense pubescence. Yellow, unicolorous species. 1.9 mm. Congo. ..... *davidi* n.sp.
– Pronotum narrower towards base. Eyes flattened, small. Body surface finer sculptured, moderately glabrous, with shorter pubescence. Yellow brown, elytra lighter than head and pronotum. 2
2. Big, robust species. Pronotum becomes narrow from anterior corners. Frons deeply emarginate. Labrum extraordinarily small. 4.0 mm. Congo. .... *robustus* PIC

– Smaller species. Pronotum becomes narrow from middle. Frons feebly emarginate. Labrum medium-sized. 2.5 mm. Madagascar. .... *sicardi* Pic n.comb.

Compactoclerus robustus Pic, 1939

*Mélang. exot. ent. 71:*18.

Frons deeply emarginate, with fine wrinkles. Mouth foramen strongly bordered. Apical joints of all palps small and coniform. Eyes small, flat. Gular sutures parallel. Mandibles with basal notch deeply incised. Long, ciliate line present on ventral side in median portion (in level of cutting edge). Little denticle situated below subapical tooth. Antennal joints 10 and 11 coalescent-like. Labrum small, not emarginate.

All coxal cavities closed, dilated prosternal process covered by apices of "epimera". Lateral edge present. Pronotum with round impressions and erect hairs. Space between front coxae narrow. Mesosternal process short; it reaches to about middle of coxae. Mesonotum *Thaneroclerus*-like. Elytra densely, irregularly punctate. Metasternum with large ventral condyles. Wings with radial cell and r-m vein. Anal field with only one vein.

Six sternites, but sixth scarcely visible. Ovipositor typically thaneroclerid – coxital styli thin and long, coxitae narrow. Female internal copulatory organs as shown in fig. 66.

All pairs of legs tenebrionid. Body surface brown, but pronotum and head blackish.

Body length: 4.0 mm.

Distribution: The unique specimen (female) from Congo (Paris Museum NH).

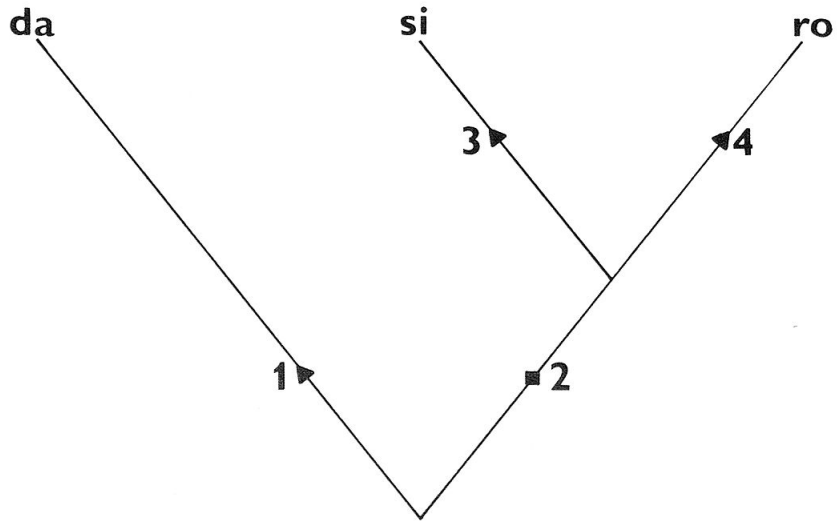


Fig. C-5. Cladogram of the genus *Compactoclerus**. Symbols as in fig. C-1. Apomorphies numbered as in tab. 2. (da = *davidi,* ro = *robustus,* si = *sicardi*).

Compactoclerus sicardi (Pic, 1939) n. comb.

Microababa sicardi Pic, 1939, *Revue fr. Entomol. 6(3-4):*187.

The sister species of *C. robustus*. Space between antennal joints 10 and 11 wider. Head longer. Elytra very slightly depressed in anterior portion. Five sternites visible in the three specimens under study. One specimen without elytral pubescence (artifact?). Emargination of frons slightly variable. Other characters as in *C. robustus*.

Body length: 2.5 mm.

Distribution: Madagascar (Mt. d'Ambre). The holotype is deposited in Paris Museum NH.

Compactoclerus davidi n.sp.

Name derivation: The name was derived from the name of my son.

Head orthognathous, mouth foramen strongly bordered (Fig. 73). Frons feebly emarginate, eyes rather elevated. Subapical tooth large (Fig. 70). Ligula deeply incised, hypopharyngeal sclerite without apodeme (Fig. 63), submentum flat, scarcely visible. Lacinial lamina with about five spines (Fig. 72). Connecting tormal process imperfectly developed (both branches not coalescent at middle) (Fig. 65). Antennal joints 10 and 11 coalescent-like (similar to *C. robustus*).

Lateral edge distinct. Proendosternite perceptible. Ventral part of prothorax with two depressions as in *Isoclerus* (Fig. 62). Space between front coxae extraordinarily narrow, coxae spherical and small. "Epimera" cover apices of dilated prosternal process. Pronotum with subparallel sides (Fig. 62). Mesothorax without "neck" (see e.g. *Thaneroclerus,* Fig. 88), but wide (Fig. 74). Mesosternal process long. Middle coxal cavities closed. Anepisterna not long and narrow (cf. Figs 74 and 88). Mesoscutum rather wide.

Whole dorsal surface longly pubescent and coarsely punctate. Paracoxal sutures distinct. Metendosternite *Thaneroclerus*-like. Wings without radial cell and r-m, with only one vein in anal field. Jugal lobe very distinct, with long hairs (Fig. 64).

All femora in tenebrionid position, hind empodium very strongly projecting, middle one rather retracted.

Sternites bordered. Phallus similar to that of *Isoclerus,* tegmen open ventrally, parameres slightly divided, ciliate (Fig. 69). Spicular fork as shown in Fig. 68.

Body surface yellowish.

Body length: 1.9 mm

Distribution: Congo (Ndelele).

The holotype and one paratype are deposited in the author's collection.

*Phylogeny of Compactoclerus**

A presumed phylogeny of the genus *Compactoclerus** is shown in fig. C-5. The species *C. robustus* and *C. davidi* n.sp. have a common character state (Tab. 2) of the antennal club (joints 10 and 11 nearly coalescent). *C. sicardi* and *C. robustus* have more common apomorphies than *C. robustus* and *C. davidi* n.sp., hence the character state of the club should be considered a parallelism (homoplastic character).

Tab. 2. List of apomorphies in *Compactoclerus** species.

Apomorphy No.	Character state
1	pronotum parallel-sided
2	elytra lighter than head and pronotum
3	frons only feebly emarginate
4	labrum extraordinarily small

Phylogeny of Thanerocleridae n.stat.

A presumed phylogeny of the family Thanerocleridae n.stat. is shown in fig. C-6.

Explanation:

1) The tribes Zenodosini n. trib. and Thaneroclerini are determined by a transformation series of the tegmen. The plesiomorphic tegmen is probably cucujoid-

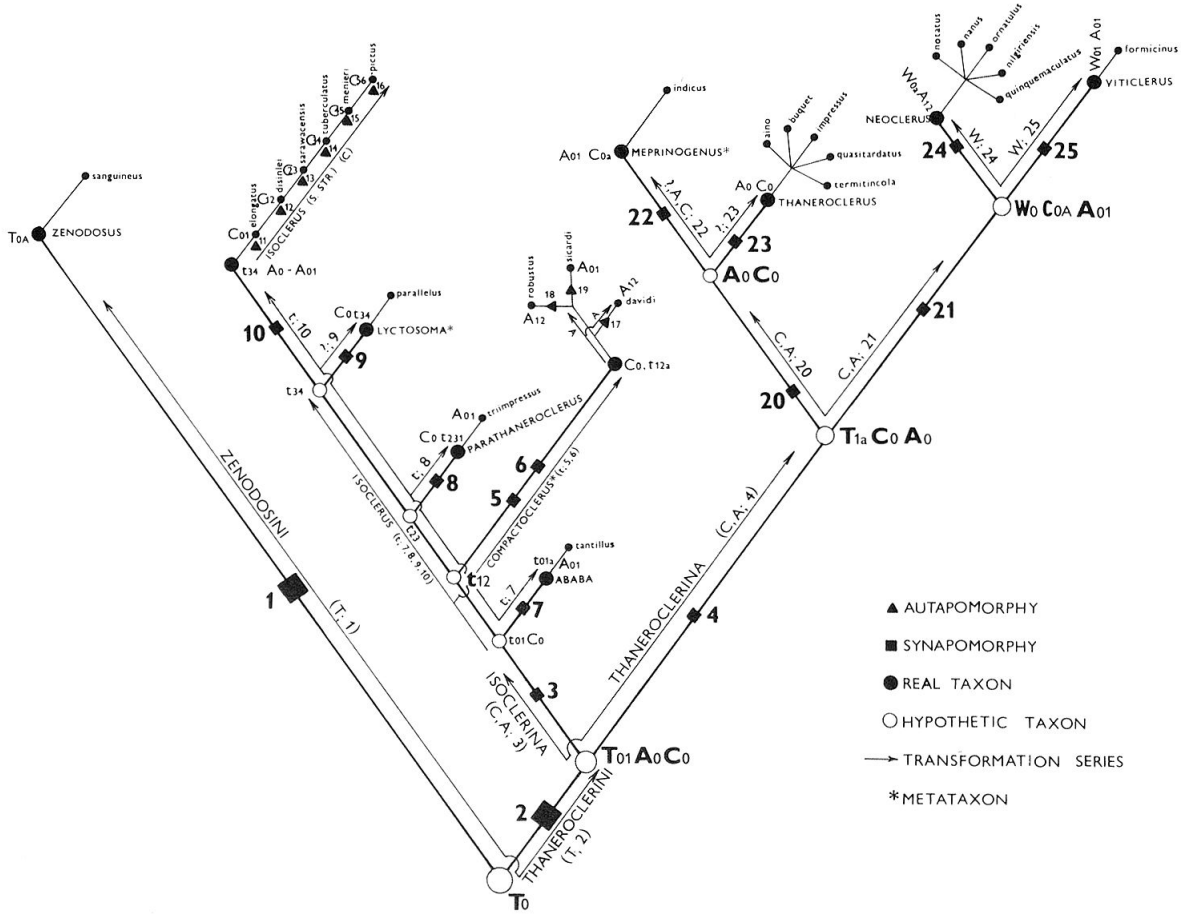


Fig. C-6. A presumed phylogeny of the family Thanerocleridae n.stat. Numbers correspond to apomorphies 1 to 25. Letters correspond to transformation series as follows: T/t, tegmen; A, antennal club; C, colour; W, wing. See text for details.

like (T01). The nearest character state occurs in *Isoclerus (Ababa) tantillus* (t01a) (without the phallobasic apodeme, of course) (Fig. 32). The character state of *Zenodosus sanguineus* (T0A) is apomorphic, tenebrionid- (salpingid-)like (Fig. 18). The most derived state in Thaneroclerini is the loose tegmen of *Thaneroclerus* or *Neoclerus* (T1a; Figs 28, 37, 82). Intermediate states between both the cucujoid and loose tegmina are probably the states of *Isoclerus* (t01a, t231, t34; Figs 41, 49, 52) and *Compactoclerus** (t12a; Fig. 69).

Members of both tribes differ from each other in the synapomorphies 1 and 2: Zenodosini n.trib. has spines on the lacinial lamina (Fig. 11), the species of Thaneroclerini have the front coxal cavities closed (Fig. 62).

Comment: The lacinia with the spines occurs also in the subtribe Isoclerina n.subtrib. (Fig. 72). I consider it to be a homoplasy.

2) The subtribes Isoclerina n.subtrib. and Thaneroclerina n.subtrib. are determined by transformation series of the colour and antennae. It is interesting that tendencies in both characters are the same in members of both subtribes. The colour change from unicolorous brown (C0) (in *Ababa, Parathaneroclerus, Lyctosoma**, *Compactoclerus**, *Thaneroclerus*) to various bicolorous patterns (C01-C56, C0a, C0A; e.g. Figs 90 and 91) (in *Isoclerus* s.str., *Meprinogenus** n.gen., *Neoclerus, Viticlerus*). The antennae change from non-clubbed (A0) (in *Thaneroclerus, Meprinogenus** n.gen., *Isoclerus elongatus*) through clubbed (A01) (in all *Isoclerus* species except *I. elongatus, Compactoclerus sicardi, Viticlerus formicinus*) to a compact club with antennal joints 10 and 11 subcoalescent (A12) (in *Compactoclerus robustus*, *C. davidi* n.sp., *Neoclerus*).

Members of both subtribes differ from each other in the following synapomorphies (3 and 4): Isoclerina n.subtrib. has the tarsal pattern 5-4-4 (Fig. 48), Thaneroclerina n.subtrib. has the middle coxal cavities always closed by the meso- and metasternum (Fig. 88).

Comment: Regarding the number of synapomorphies of Isoclerina n.subtrib. and their scarcity in Thaneroclerina n.subtrib., it is possible to consider the latter subtribe the more primitive one.

3) The genera *Compactoclerus** and *Isoclerus* differ from each other in a transformation series of the tegmen. It occurs from nearly cucujoid-like (t01a) in *Isoclerus (Ababa) tantillus* (Fig. 32) through the tegmen of *Isoclerus (Parathaneroclerus) triimpressus* (t231; Fig. 50), which is also quite similar to the cucujoid one, to the tegmen of the subgenera *Lyctosoma** and *Isoclerus* s.str. (t34; Figs 41, 49). Members of *Compactoclerus** have the tegmina in an intermediate state between the states of both *Ababa* and *Isoclerus* s.str. (t12a; Fig. 69).

Members of both genera are determined by the synapomorphies 5 to 10. The subgenera of *Isoclerus* have some of the following synapomorphies: antennae strongly clubbed (7, *Ababa*), both pronotum and elytra with deep and large depressions (8, *Parathaneroclerus*), body quite parallel-sided (9, *Lyctosoma**), or body with various colour patterns (10, *Isoclerus* s.str.). *Compactoclerus** has the last joints of the labial palps coniform (Fig. 63) and the anterior part of the mesothorax wide (Fig. 74).

Comments: One could consider the genus *Compactoclerus** an ancestor of *Isoclerus*. It is not possible to decide if it is a mono- or paraphyletic taxon. That is why it is marked with an asterisk as a metataxon.

4) The subgenera of *Isoclerus* also differ from each other by a transformation series of the tegmen. *Ababa* has the tegmen nearly cucujoid but without the phallobasic apodeme (cf. KOLIBÁČ, 1987, 1989b) (t01a; Fig. 32), *Parathaneroclerus* has

it as shown in fig. 50 (t231). The tegmina of *Lyctosoma** and *Isoclerus* s.str. are the same (t34; Figs 41, 49, 52).

Members of the particular subgenera are determined by the following synapomorphies: *Ababa* has the antennae strongly clubbed (7), *Parathaneroclerus* has both the elytra and the pronotum with extraordinarily deep and large depressions (8), *Lyctosoma** has its body quite parallel (9) and all members of *Isoclerus* s.str. have the elytra with color patterns (10; Figs 90 and 91).

Comments: The subgenus *Lyctosoma** is also a metataxon. It has no transformation series and it could be synonymized with the subgenus *Isoclerus* s.str.

5) There are two groups of genera in Thaneroclerina n.subtrib. They differ from each other by transformation series of the colour and shape of the antennal club. The first group *(Meprinogenus** n.gen., *Thaneroclerus*) has the unicolourous body in *Thaneroclerus* (C0) and the elytra with the colour pattern in *Meprinogenus** n.gen. (C0a, see description). *Thaneroclerus* has the apical antennal joints scarcely dilated (A0) while *Meprinogenus** n.gen. has these joints more distinctly clubbed (A01).

The second group of genera (*Neoclerus, Viticlerus*) has the elytra with stripes (C0A) in both of its members. *Viticlerus* has the antennae clubbed (A01) and *Neoclerus* has the joints 10 and 11 subcoalescent (A12).

Both *Meprinogenus** n.gen. and *Thaneroclerus* share the synapomorphy 20: the small tarsomere 4 of the front tarsi. Both *Neoclerus* and *Viticlerus* share the synapomorphy 21: a reduction of either the wing membrane or the radial cell (Fig. 34).

6) The genera *Meprinogenus** n.gen. and *Thaneroclerus* differ from each other in a character state of the body colour (see above) and in the synapomorphies 22 (the radial cell reduced in *Meprinogenus** n.gen.) and 23 (the metasternum bordered in *Thaneroclerus*; Fig. 88).

Comments: The genus *Meprinogenus** n.gen. is the last metataxon of the family Thanerocleridae n.stat. It is monotypic so that it has not any transformation series. *Thaneroclerus* is a very primitive genus, nearly without any apomorphies. It could be an ancestor of *Meprinogenus** n.gen.

7) The genera *Viticlerus* and *Neoclerus* differ from each other in transformation series of the wing and antennal club. The wing is reduced (W01) in *Viticlerus* or the radial cell is reduced (W0a; Fig. 34) in *Neoclerus.* The antennal club is distinct in *Viticlerus* and it has subcoalescent joints 10 and 11 in *Neoclerus.*

Members of the genus *Neoclerus* have the synapomorphy 24 (frons with the grooves for antennae) and the species *Viticlerus formicinus* has the synapomorphy 25 (six visible sternites).

Comments: The fact of a reduction of the wings in *Viticlerus* does not mean that a reduction of the radial cell did not occur before the loss of wings. Hence both advanced states of the wing characters need not form two independent transformation series.

Metataxa of Thanerocleridae n.stat.

The term "metataxon" was used by DONOGHUE (1985) for taxa with unknown monophyletic or paraphyletic status. KLUGE (1989) defined metataxa as taxa without synapomorphies.

The taxa *Lyctosoma*, Compactoclerus** and *Meprinogenus** do not have their own transformation series and are considered as metataxa in this communication. These taxa were described later than their sister groups so that they could be

synonymized. For example: *Thaneroclerus* does not share any common transformation series with *Meprinogenus** n.gen. Thus, the metataxon *Meprinogenus** n.gen. was established so that it can be synonymized with the latter genus. However, both genera have their own synapomorphies (22, 23) hence this approach is different from the cited approach of KLUGE.

The status of *Lyctosoma** is explained in the chapter "Phylogeny of *Isoclerus*". The genera and subgenera of Isoclerina n.subtrib. differ from each other by a transformation series of the tegmen. But all members of *Compactoclerus** have nearly the same state of the above-mentioned character so that they do not form any transformation series. Nearly the same situation exists in the sister group *Meprinogenus** n.gen. – *Thaneroclerus*. It is not possible to form any transformation series in *Meprinogenus** n.gen. because it is a monotypic genus.

Also the tribe Zenodosini n.trib. is monotypic. That is why neither the tegmen nor any other trait can form some transformation series. In spite of this fact I consider the tribe to be valid because its character state of the tegmen is very distinguished (and advanced) and it is aimed in another direction than in the members of Thaneroclerini n.stat.

DISCUSSION

Phylogenetical hypotheses on relationships among Thanerocleridae n.stat. and other Cleroidea (especially Trogositidae s.lat., *Metaxina* BROUN, Chaetosomatidae, *Lesneoclerus* CORPORAAL and Cleridae) will be established in a subsequent paper. Some members of Thanerocleridae n.stat. share many common homoplastic characters with Heteromera (Tenebrionoidea): e.g. shape of bases of femora, spherical front coxae, tegmen, etc. Some characters are common to (or derived from) Cleridae and Chaetosomatidae (mouth parts), others resemble Trogositidae (tarsi, shape and sculpture of head, margin of abdominal sternites, etc.). The sister group will probably rather be among Trogositidae than Cleridae.

The old subfamily Thaneroclerinae (sensu CORPORAAL, 1939, and CROWSON, 1964, respectively) also contains the genera *Cyrtinoclerus* CHAPIN, 1924, and *Metaxina* BROUN, 1909. The first (with one species *C. cyrtinoides* CHAPIN, 1924) I have never myself seen (the unique specimen from Washington Museum was not borrowed). I consider this species a member of the superfamily Tenebrionoidea according to the picture in CORPORAAL (1939). It has the tarsomeres 4 of the front and middle legs very short, resembling the situation in e.g. some members of the family Elacatidae. The hind legs are missing. This classification is, of course, tentative.

The second genus is also represented by one species, *Metaxina ornata* BROUN, 1909. The addition to Thaneroclerinae was based on unconvincing larval characters. The characters of imagoes are nearer to Chaetosomatidae than to Thanerocleridae n.stat. but it is not impossible that this genus will compose a special family.

The number of higher taxa (for example genera) decreases with the increasing knowledge of mutual relationships, morphology, ecology, etc. This fact was shown by EHRLICH & MURPHY (1983) in Lepidoptera (cf. MOUND, 1985). Systematics of Thanerocleridae n.stat. shows a similar tendency. The number of genera listed in CORPORAAL (1950) plus the genera described after that date[3], incl. *Metaxina,* are

[3] CROWSON (1964) considered the genus *Cleridopsis* CHAMPION, 1912, to belong to Thaneroclerinae. This genus is not included in any subfamily in CORPORAAL (1950) and I did not study it.

13. In my present revision there are only 7 genera. In my opinion it is because the "systematic concept" of higher taxa was used; consequently knowledge of the morphology of members of the genera increased.

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This paper was not supported by anyone but my wife. Hence my thanks belong also to her.

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