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**CHAETOTAXY, PHYLOGENY AND BIOGEOGRAPHY  
OF PARONELLINAE (COLLEMBOLA : ENTOMOBRYIDAE)**

**S. K. MITRA**

**ZOOLOGICAL SURVEY OF INDIA**

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(Collembola : Entomobryidae)**

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## INTRODUCTION

Chaetotaxy, although received a great deal of attention in the classification of certain groups of insects (for example, Lepidopterous larvae) in the past, it was, however, only in 1945 when Bonet first initiated the study of this character in Collembola. He studied the cephalic chaetotaxy of certain species of *Hypogastrura*. Delamare Deboutteville (1951c) was the first to attribute phylogenetic importance on the arrangement of macrochaetae and trichobothria in certain soil-type Collembola. Yosii (1956) studied the chaetotaxy of several genera of Collembola and put into use the nomenclature for designating each seta found on head and body in *Hypogastrura*. Cassagnau (1959) studied the chaetotaxy of certain species of *Tetracanthella* and emphasised the importance of this character in classification. Christiansen (1958) although classified different types of setae found on body in *Entomobrya*, he, however, did not make an attempt for studying their distribution pattern. Yosii (1959a) utilised the character in revising the genus *Seira*. Gisin (1960) used chaetotaxy to distinguish various groups and depicted the chaetotaxy of the new species he described. Yosii (1960a) studied the evolutionary trend of certain species of *Hypogastrura* on the basis of chaetotaxy. He (Yosii, 1961a) made an attempt to trace the phylogeny of higher categories of Collembola and thus proposed a new subfamily on the basis of chaetotaxy. Salmon (1964a), however, did not accept such propositions and considered chaetotaxy as of specific importance. Gisin (1961) redescribed certain species of Börner by using depictions on chaetotaxy. Gisin and da Gama (1962) recognised three species of *Seira* around Geneva on the basis of chaetotaxy and colour pattern of body. Cassagnau (1964) studied dorsal chaetotaxy of certain species of *Hypogastrura* and grouped closely related species on the basis of chaetotaxic pattern. Massoud (1964) differentiated the type-species of a new genus by using chaetotaxic table. Christiansen (1964) and Yosii (1956, 1967) discriminated the species of *Tomocerus* and other related genera by using chaetotaxy as one of the characters. He (Christiansen, 1964) also pointed out that the microchaetae adjoining each trichobothria is constant in location. Murphy (1966) discussed the taxonomy and bionomics of *Sphaeridia*; he used certain nomenclature for designating each seta found on head and body. Betsch and Cassagnau (1966) traced the evolution and form of the chaetotaxy on abdominal papillae of *Arrhopalites* from the juvenile to the adult stage. Christiansen (1966) revised the genus *Arrhopalites* of the United States and Canada and used chaetotaxy systematically for each species. Gisin (1963) discussed the pseudopores and chaetotaxy of the tribe Lepidocyrtini involving the genera like *Lepidocyrtus* and *Sinella*. Gisin (1964a, 1964b, 1965, 1967a) contributed to the understanding of the ubiquitous species of *Lepidocyrtus* on the basis of chaetotaxy of body. Sinder (1967) studied comprehensively the chaetotaxy of North American *Lepidocyrtus*. He made use certain notations for designating each seta found on body. Gisin (1967b) described a few new species of *Pseudosinella* and tried to trace their phylogeny on the basis of this character. Further, Gisin and da Gama

(1969, 1970) recognised many new species of *Pseudosinella* on the basis of chaetotaxy and other morphological characters. da Gama (1963) prepared a monograph of the species of *Isotomodes* mainly on the basis of the chaetotaxy of head and body. She (da Gama, 1966, 1967, 1968) used chaetotaxy for distinguishing species of the genera like *Hypogastrura*, *Seira*, *Lepidocyrtus*, *Xenylla* and *Tullbergia*. da Gama (1969) revised the world species of *Xenylla* on the basis of chaetotaxy. Thibaud (1969) studied the chaetotaxy of some epigeal and cavernicolous forms of Hypogastruridae during different phases of postembryonic growth. He represented the results in tabular and graphic patterns. In the same work, he further demonstrated the growth of other structures along with the linear growth of each species. Szeptycki (1967, 1969, 1972, 1973, 1977, 1978, 1979) studied chaetotaxy of Collembola in details. In Entomobryidae, he recognised and classified setae on the basis of the homology and characterised each group of setae as multiplet consisting of primary, secondary and additional setae (Szeptycki, 1979). Andre (1988) used the concept of phanerotaxy in describing a species of *Xenylla* by introducing setal nomenclature as used in mites.

Uptil now, whatever is known of the chaetotaxy of Paronellinae, it is due to the efforts of Yosii (1956, 1959b, 1960b, 1961a, b, 1966a, b, 1981, 1983, 1989) who studied the chaetotaxy of some known and new species of several genera of Paronellinae. He (Yosii, 1961b), for the first time, reiterated the importance of chaetotaxy of each tergite and suggested a rearrangement of the species of *Salina* on the basis of this character. Mitra (1973c) recorded the development of setae in the different stages of a species of *Callyntrura*. He also studied the chaetotaxy of *Salina*, *Callyntrura*, *Yosiiia*, *Dicranocentroides*, *Campylothorax* and other genera (Mitra, 1973a, 1973b, 1973c, 1974, 1975a, b, 1977, 1980).

In the present investigation it was felt pertinent to take up further studies of this character in order to find out the existence of any significance in macrochaetal number and orientation which might also complement the existing morphological differences of the genera under Paronellinae. A critical analysis of all such chaetotaxic characters has also been made to find out the phylogenetic affinities of various genera from widely different zoogeographical regions of the world including analysis of some of their ultrastructural characteristics.

## MATERIAL AND METHODS

The type-specimens of the type-species of the genera including the other species known under each genus, preserved in alcohol, were used for this study.

Specimens were first cleared in lactic acid and appendages including head were dissected out. Ventrally a longitudinal incision was given so as to get rid of the inner content of body during heat-treatment and render the specimen almost transparent. A clearing solution was made by mixing equal parts of 20% aqueous

KOH and 100% glycerol. In a drop of such solution on a grooved slide the head and body were heated separately on a spirit lamp till it started boiling. During such boiling the specimens were examined intermittently under microscope till they depigmented and the sockets were seen clearly. The material was then transferred to a drop of lactic acid and was examined under microscope without putting a coverglass. Later the specimens were put in a mounting medium prepared by mixing 40% lactic acid : 80% glycerol. Such preparations were temporarily sealed with nail polish. This technique proved excellent for studying the chaetal architecture of Paronellinae.

### GENERAL CONSIDERATIONS

In studying chaetotaxy of head the present author noted that the mode of subdivision of cephalic regions in *Hypogastrura* by Yosii (1956) is also applicable for the genera under Paronellinae. This subdivision corresponds well with the natural zonations of the distribution of setae. In addition to the subdivisions of cephalic region recognised by Yosii (*l. cit.*), in this study, area parietalis has been further subdivided into two subregions *viz.*, area postocularis, which is located just behind the ocellar field and area parietalis. Following regions can be discerned on the head of a paronelline Collembola (Fig.1).

(a) *Area Subdorsalis* :

This region is located behind the basis antennalis and continues posteriorly upto area verticalis along each ocellar field. The macrochaetae and microchaetae in this region are designated by 'SD' and 'sd' respectively.

(b) *Area verticalis* :

This region is distinct from other regions in the greater localisation of macrochaetae in the genera where they are present ; in others, having no macrochaetae, this zone is distinct in the absence of both scales and any type of setae. This area starts from the posterior limit of one ocellar field and ends at the other in the form of a "V" The macrochaetae and microchaetae in this region are designated as 'V' and 'v' respectively.

(c) *Area dorsalis* :

It is just in front of the area verticalis delimited on either side by the area subdorsalis. The macrochaetae and microchaetae in this region are designated as 'D' and 'd' respectively.

(d) *Area ocularis* :

The area inside the ocellar field; macrochaetae and microchaetae in this region are represented as 'OC' and 'oc' respectively.

(e) *Area postocularis* :

The region just behind the ocellar field ; macrochaetae and microchaetae in this region are designated by 'PO' and 'po' respectively.

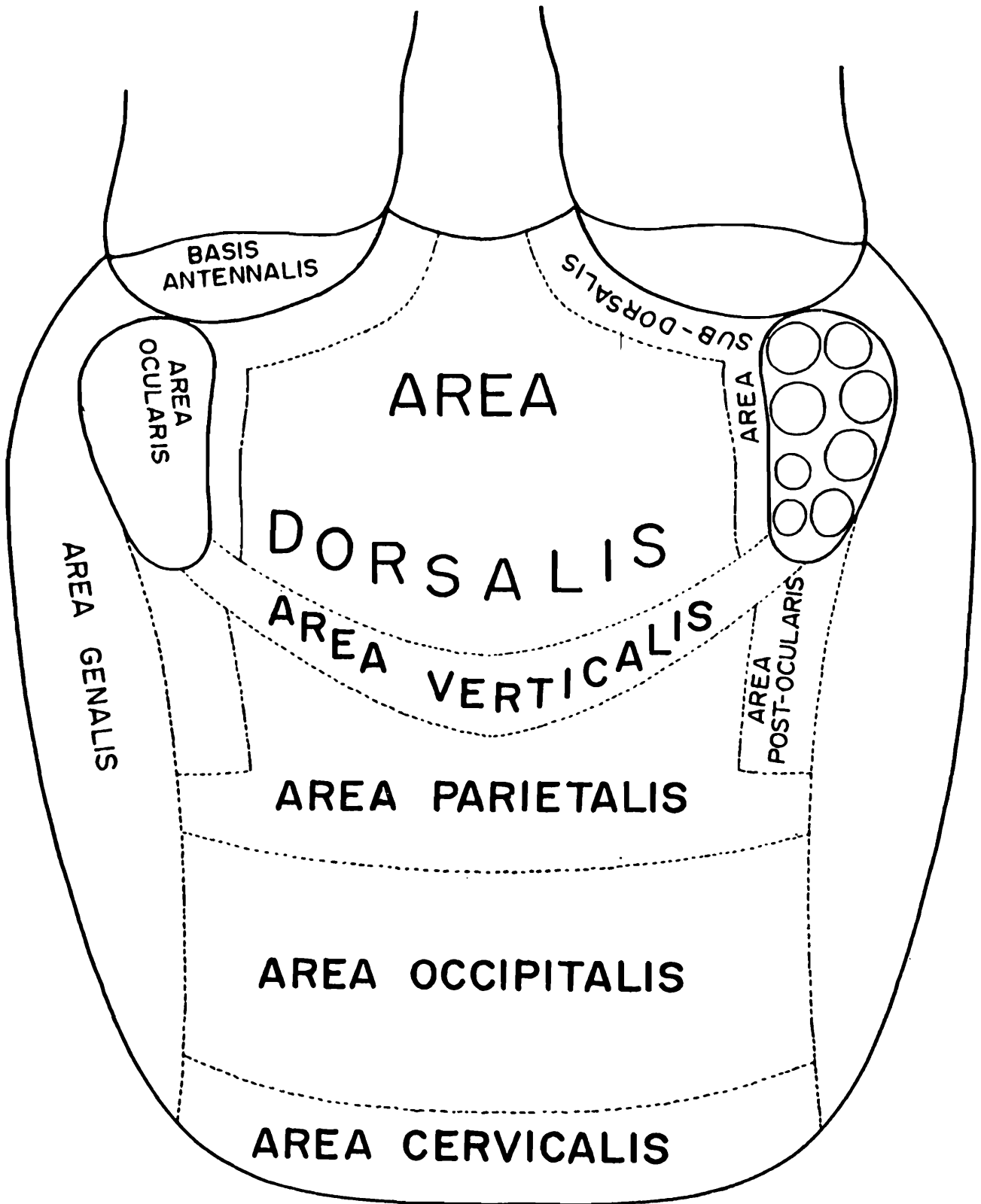


Fig. 1 : Cephalic Regions of Paronelline Collembola

(f) *Area parietalis* :

It is behind area verticalis, bounded posteriorly by area occipitalis and laterally by area genalis and area postocularis ; macrochaetae and microchaetae in this region have been designated as 'P' and 'p' respectively.

(g) *Area occipitalis* :

The region following the area parietalis, delimited posteriorly by areas cervicalis and laterally by area genalis ; macrochaetae and microchaetae in this region are designated as 'O' and 'o' respectively.

(h) *Area cervicalis* :

Region adjacent to cervix, following area occipitalis, bounded laterally by area genalis ; macrochaetae and microchaetae in this region are designated by 'C' and 'c' respectively.

(i) *Area genalis* :

The lateral region outside the outer limit of ocellar field which delimits the area parietalis, area occipitalis and area cervicalis laterally ; the macrochaetae and microchaetae in this region are designated by 'G' and 'g' respectively ; in this investigation the setae occurring in this region below the level of ocellar fields have been taken into consideration.

In studying various types of setae that occur in the cephalic region, the terms macrochaetae and microchaetae have been used in a relative sense for each zone. Thus macrochaetae of area verticalis are distinctly longer and broader than the macrochaetae occurring in the areas ocularis and subdorsalis ; such setae in the two latter regions have been termed as macrochaetae as they are distinctly longer and broader than the other setae (i.e., microchaetae) occurring in each of this respective regions. For example, the  $OC_2$  in *Salina* (Figs. 2,4), *Yosiia* (Fig. 8) and *Pseudosalina* (Fig. 6) is always distinctly larger (as indicated always by the larger setal socket) than  $oc_1$  and  $oc_3$  , although in comparison with the macrochaetae of vertex it ( $OC_2$ ) is distinctly smaller. Such relative differences in sizes of setae in each area of cephalic region (except those in area subdorsalis) is always of constant occurrence and significance. As the chaetotaxy of tergites does not follow any particular course of arrangement in the genera under Paronellinae, it has not been possible to designate such setae by using notation system. Exception being *Callyntrura* where distribution of macrochaetae on Ths. II, III and Abds. I, II, III follows a particular pattern (Fig. 20). In the present work all the macrochaetae, occurring on Ths. II, III, Abds. I, II, III have been taken into consideration, while for Abd. IV (in some genera) the anteromedial region, where the occurrence of macrochaetae follows a definite course for each genus has been studied carefully. Number of lasiotaxa is constant in all the genera, being Abd. II (2+2), Abd. III (3+3) and Abd. IV (2+2).

For each genus, the general pattern of chaetotaxy is represented. In majority genera maximum number of setae (at least in the cephalic regions) occur in the type-species. The setae, whose presence or absence is of specific importance are mentioned wherever noted. In the genera, where the distribution of macrochaetae on tergites does not follow a definite course, chaetotaxy of the type-species is illustrated as for an example.

### *Key to Tribes*

- 1 Body clothed with scales ; flexed macrochaetae present or absent .....2  
 Body not clothed with scales; flexed macrochaetae always present.....Cremastocephalini Handschin, 1926
2. Body clothed with flexed macrochaetae (usually obliquely truncated type) and darker pseudoscales, mostly with acuminate apices, heavily striated and not distinctly pedicellate; gradation from ciliated setiform scaleprimordia to scales distinctly visible; extra ocular structure absent.....  
 .....Callyntrurini New Tribe  
 Body not clothed with flexed macrochaetae (at least of obliquely truncated type) ; clothed with hyaline or finely striated true or typical scales, mostly oval or rounded in shape, secondarily may be of other configurations but always with rounded apices and distinctly pedicellate ; gradation from setiform scale-primordia to scales not visible; extra ocular structure (E.O.S) present or absent.....3
3. Extra ocular structure (E.O.S) present; ocelli 8+8, arranged in two longitudinal parallel rows, ocelli G,H vestigial but always present .....Paronellini Börner, 1906  
 Extra ocular structure (E.O.S) absent ; ocelli 8+8, reduced or absent.....4
4. Ocelli 8+8 or reduced arranged in two longitudinal parallel rows or in a circular pattern i.e. Ocellus B located almost centrally in each ocellar field; scales clothing body with prominent fine striations; forms mostly pigmented, paired inner basal tooth of unguis usually normal, not exaggerated, may be reduced.....Bromacanthini New Tribe  
 Not pigmented, ocelli absent; region near ocellar field and body sometimes faintly pigmented; clothed with hyaline scales, striations not prominent; paired inner basal tooth of unguis often exaggerated.....  
 .....Troglopedetini Börner, 1913

## CREMASTOCEPHALINI

*Salina* MacGillivray, 1894

1894. *Salina* MacGillivray, *Can. Ent.*, **26** : 105.

*Celebensis* group : This species-group occurs in the hilly tracts and have lesser number of setae on head and body as compared to the other group.

*Head* : Vertex with  $V_1, V_2$  inserted in a trapezoid fashion ; dorsal setae represented by  $do + d_{1-4}$ , none of which a macrochaeta; subdorsal region exhibits 4 macrochaetae on each side ( $SD_{1-4}$ ); ocular region has 3 setae, arranged characteristically, of which the median seta ( $OC_2$ ), a macrochaeta; postocular setae 2 ( $PO_1, PO_2$ ); parietal region represented by 4 setae, of which  $P_4$ , a macrochaeta; occipital region has a pair of macrochaetae ( $O_1 + O_1$ ); area cervicalis represented by 2+2 macrochaetae ( $C_1, C_2$ ); setae on area genalis absent (Fig.2).

*Body* : Th. II, number of macrochaetae ranges from 15-25; Th. II, 6-12; Abds. I (4-5), II (2-4), III (1+1, medially); Abd. IV anteromedially with 2+2 macrochaetae, inserted in a characteristic trapezoid fashion or in a straight line (Fig.3).

*Indica* group : This species-group occurs in tropical plains and possesses larger number of macrochaetae on head and body than the species of the *celebensis* group.

*Head* : Vertex with 5 setae,  $V_1$  and  $V_2$  macrochaetae inserted in a trapezoid fashion like the species of the *celebensis* group; dorsal setae represented by  $d_{1-4}$ ; subdorsal region with 6 setae of which  $SD_{2-6}$  macrochaetae; ocular region with 3 setae, arranged characteristically, of which the median seta ( $OC_2$ ), a macrochaeta; postocular setae 2 ( $PO_1, PO_2$ ), both macrochaetae; setae absent on parietal region; occipital region represented by 6 macrochaetae ( $O_{1-6}$ ),  $O_1, O_4, O_6$  variable; cervical region with 3 macrochaetae ( $C_{1-3}$ ); setae on genae absent (Fig.4; Pl. II,A).

*Body* : Number of macrochaetae on Th.II ranges from 28-40, Th.III from 17-26; Abds. I (9-17), II (4-6), III (1+1, medially); Abd. IV anteromedially with 2+2 macrochaetae, arranged characteristically in a trapezoid fashion (Fig.5).

The species of both the groups are distinct from the point of view of their nature of chaetotaxy of head and body. However, they have fundamental similarity in the number and arrangement of setae on the regions like vertex, ocular and also anteromedially on Abd. IV

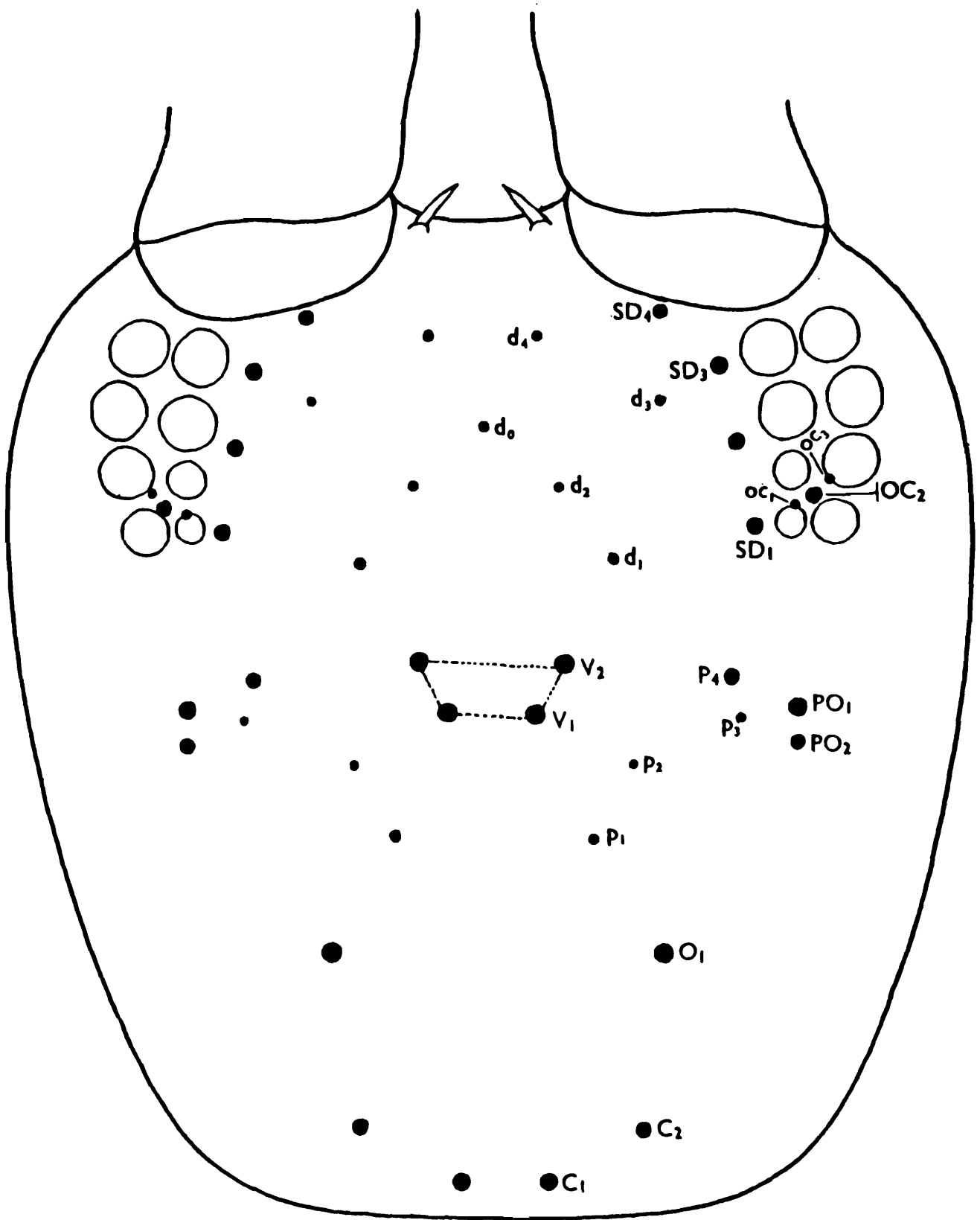


Fig. 2 : Cephalic Chaetotaxy of *Salina (celebensis group)*

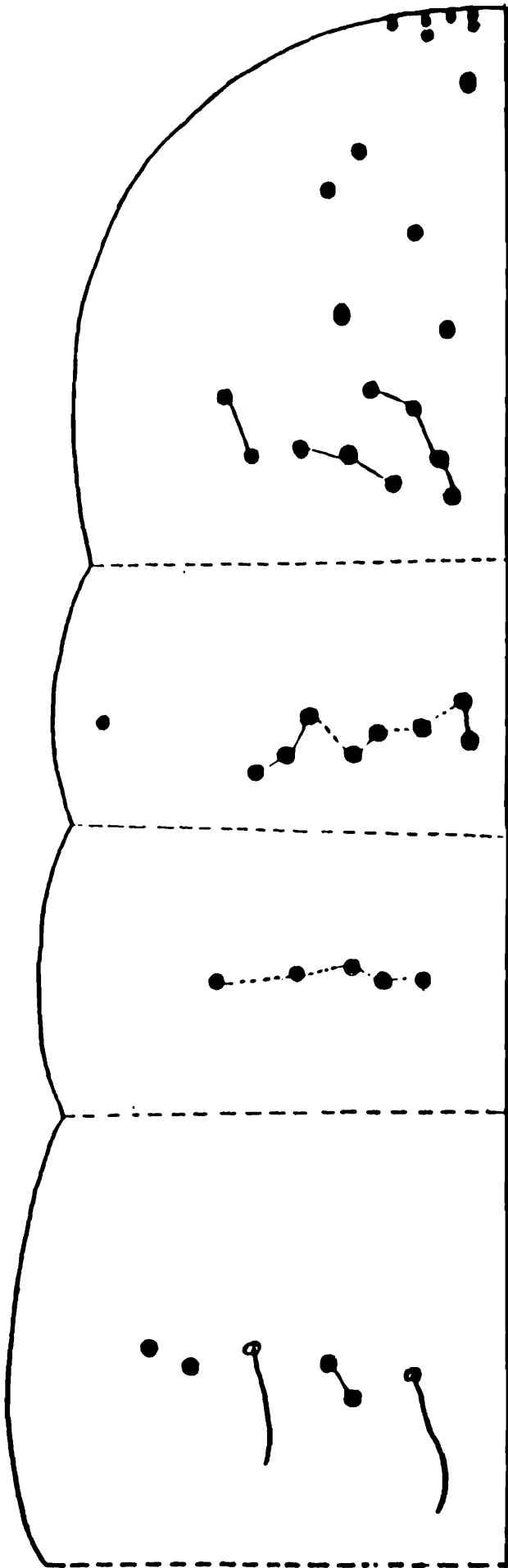


Fig. 3 : Chaetotaxy of Ths. II, III, Abds. I, II of *Salina* (*Celebensis* group)

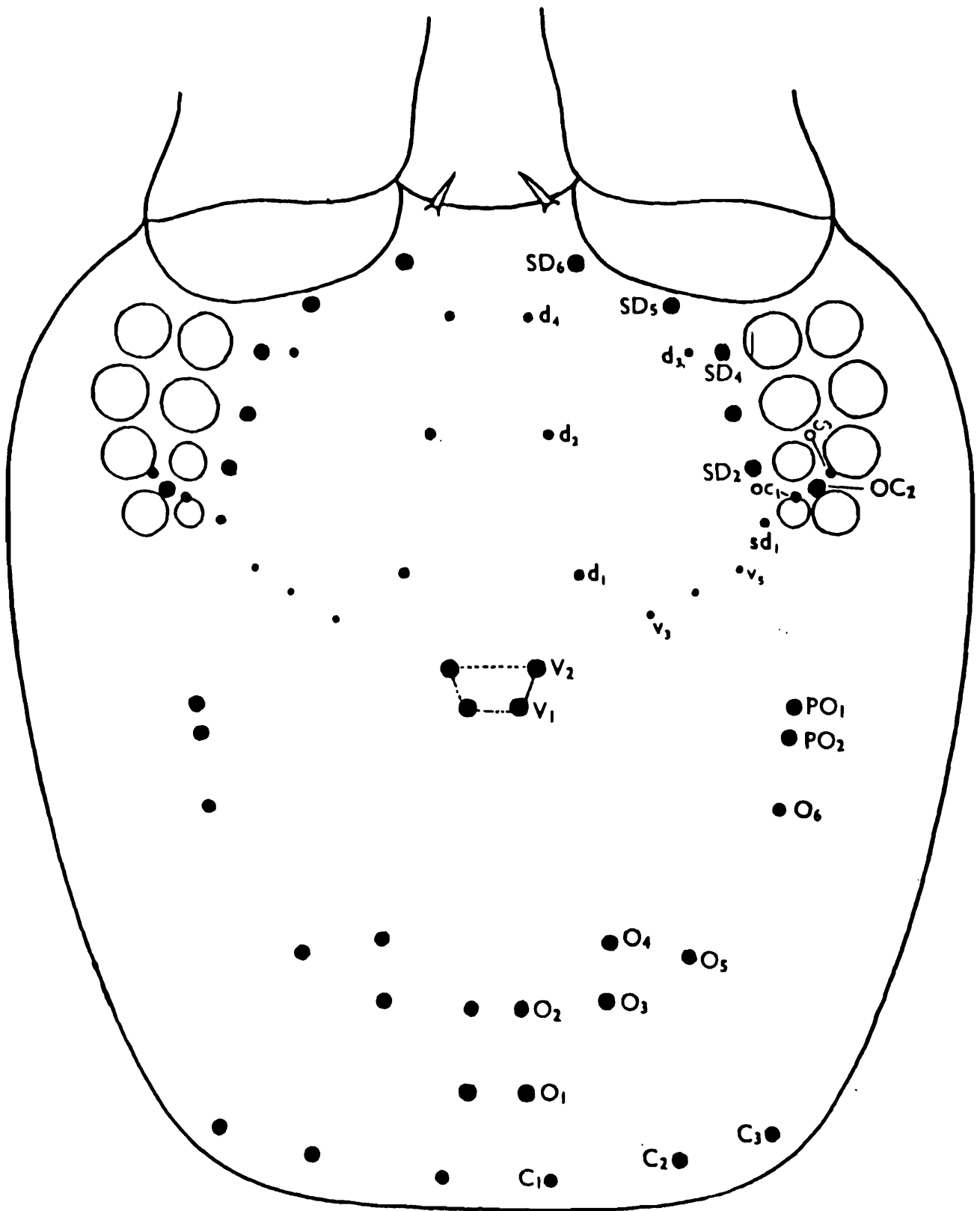


Fig. 4 : Cephalic Chaetotaxy of *Salina (celebensis group)*

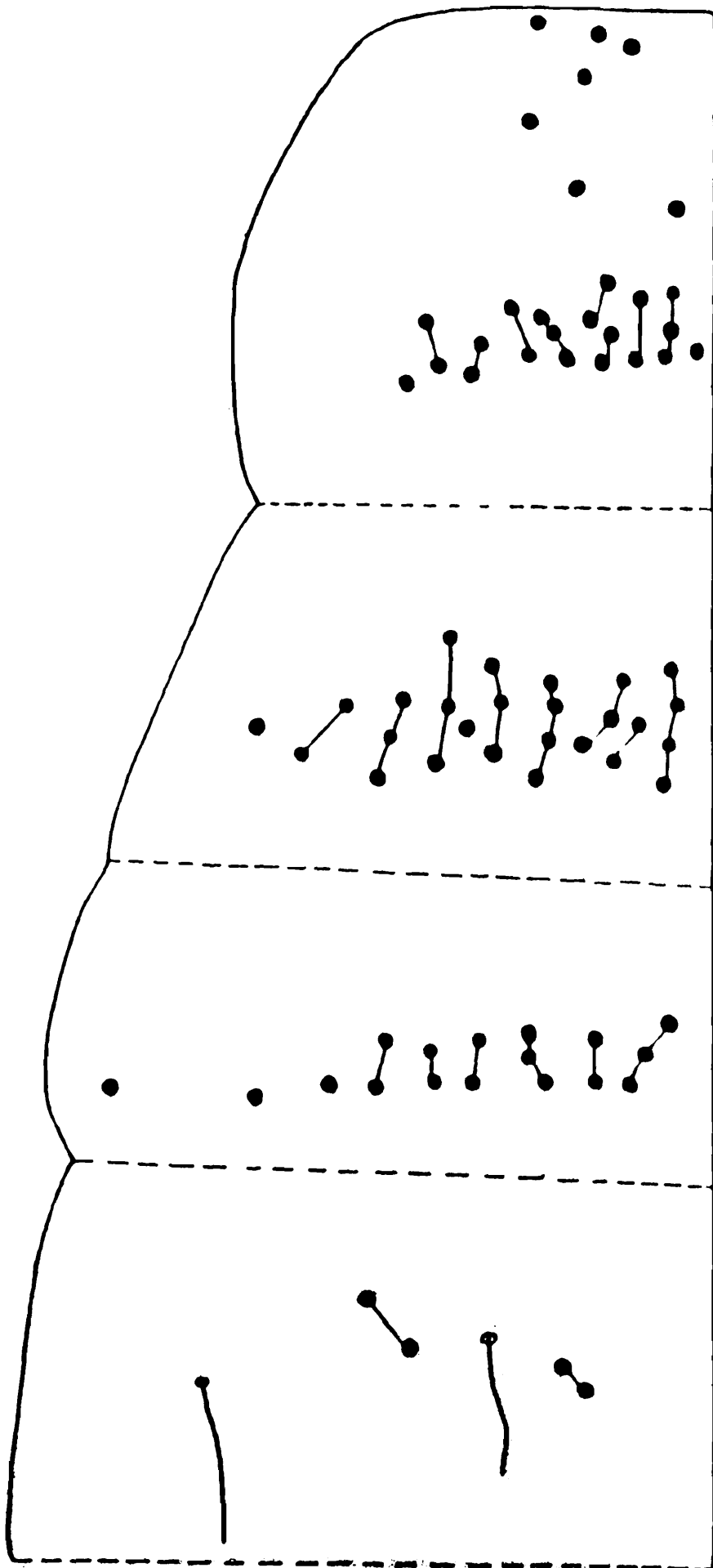


Fig. 5 : Chaetotaxy of *Ths.* II, III and *Abds.* I, II (*indica* group)

*Pseudosalina* Mitra, 1973

1973. *Pseudosalina* Mitra, *Rev. Ecol. Biol. Sol.*, **10** : 359.

**Head** : Vertex with  $V_0 + V_{1-6}$ , all of which macrochaetae and disposed in the form of a 'V'; dorsal region with  $d_{1-4}$ , all microchaetae; subdorsal region represented by 6 setae,  $SD_3$ ,  $SD_{4-6}$  macrochaetae; ocular region with 3 setae,  $OC_2$ , a macrochaeta; postocular region with 2 macrochaetae ( $PO_1$ ,  $PO_2$ ), insertion of which characteristic; parietal region represented by  $P_{1-2}$ ,  $P_1$ , a macrochaeta; occipital region represented by  $O_{1-5}$ , all macrochaetae and oriented in an inverted "V" fashion; cervical region with  $C_{1-6}$ , all macrochaetae; setae on area genalis represented by single macrochaeta ( $G_1$ ) on each side (Fig.6).

**Body** : Range of the number of macrochaetae occurring on each tergite as follows: Ths. II (43-58), III (30-40); Abds. I (17-23), II (13-18), III (5-6); Abd. IV anteromedially with 2+2 macrochaetae as in *Salina* but their orientation is quite characteristic for this genus (Fig. 7).

As compared to *Salina*, the species of the genus possess larger number of setae on head and body. Number and orientation of macrochaetae on head (specially on vertex) is a characteristic feature of the genus. Further, it is to be noted that the number of macrochaetae on any tergite is greater than both the species groups of *Salina*.

*Yosiia* Mitra, 1967

1967. *Yosiia* Mitra, *Proc. Zool. Soc. Calcutta*, **20** : 43.

**Head** : Vertex on each side with 5 setae of which  $V_1$ , a macrochaeta,  $V_1-V_1$ , if joined forms a straight line; dorsal setae  $1-3$ , all macrochaetae, a characteristic feature of the genus; subdorsal region represented by 3 setae ( $SD_{1-3}$ ), all macrochaetae; ocular region with 3 setae, arrangement of which like *Salina* and *Pseudosalina*,  $OC_2$  represented by a macrochaeta; postocular region with 2 macrochaetae ( $PO_1$ ,  $PO_2$ ); parietal region represented by 2 setae of which  $P_2$ , a macrochaeta; the occipital region with a single macrochaeta on either side ( $O_1 + O_1$ ); cervical region with 3 macrochaetae on either side ( $C_{1-3}$ ); setae absent on genal region (Fig.8).

**Body** : A typical oligochaetoid genus having single macrochaeta medially on each side of Th. II, 3 on Th. III, Abds. I and II; Abd. IV with 2-3 setae medially and 1+1 setae anteriorly (in contrast to 2+2 in *Salina*, *Pseudosalina* and *Akabosia*) (Fig. 9). The genus although exhibits very few number of setae on body, it has relatively large number of macrochaetae on head than *Salina* (*Celebensis* group).

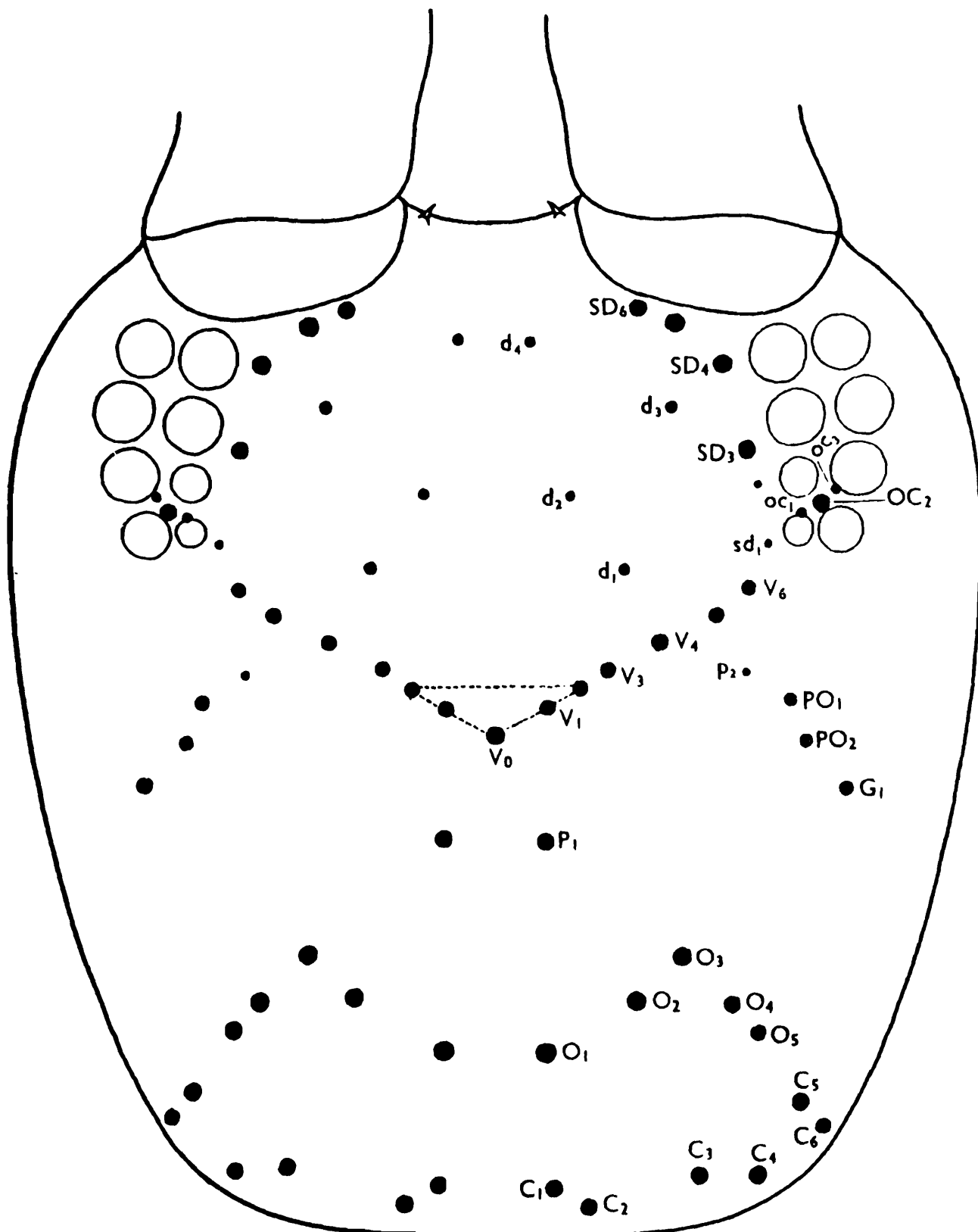


Fig. 6 : Cephalic Chaetotaxy of *Pseudosalina*

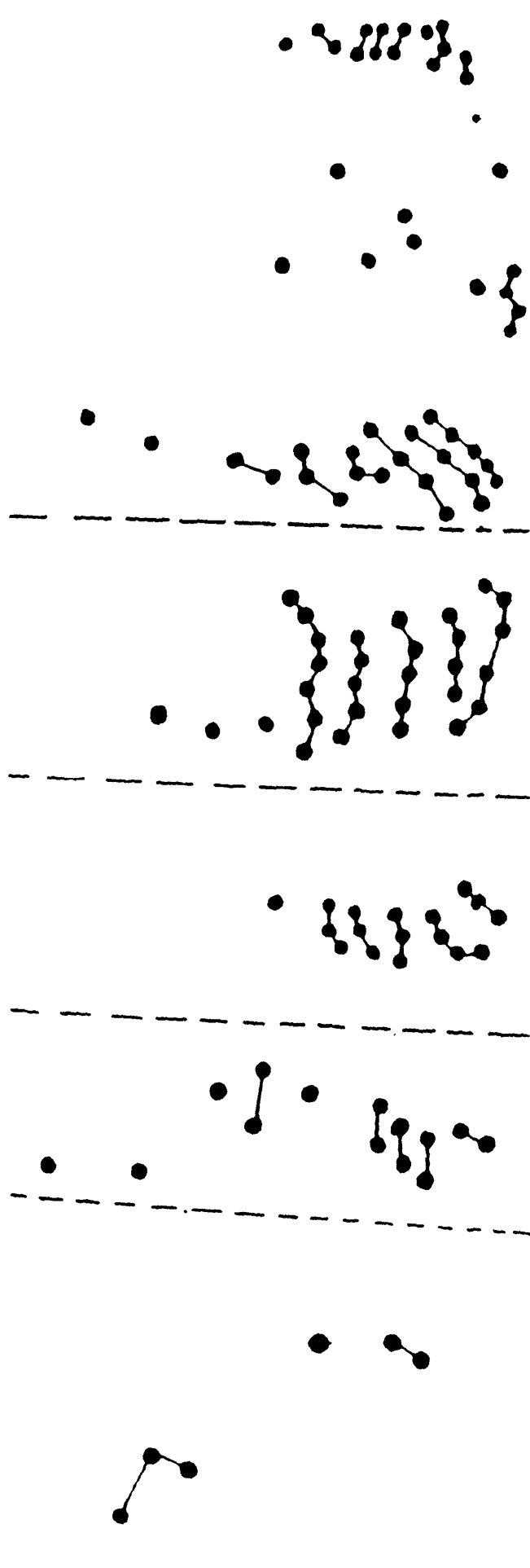


Fig. 7 : Chaetotaxy of Ths. II, III and Abds. I, II, III of *Pseudosalina*

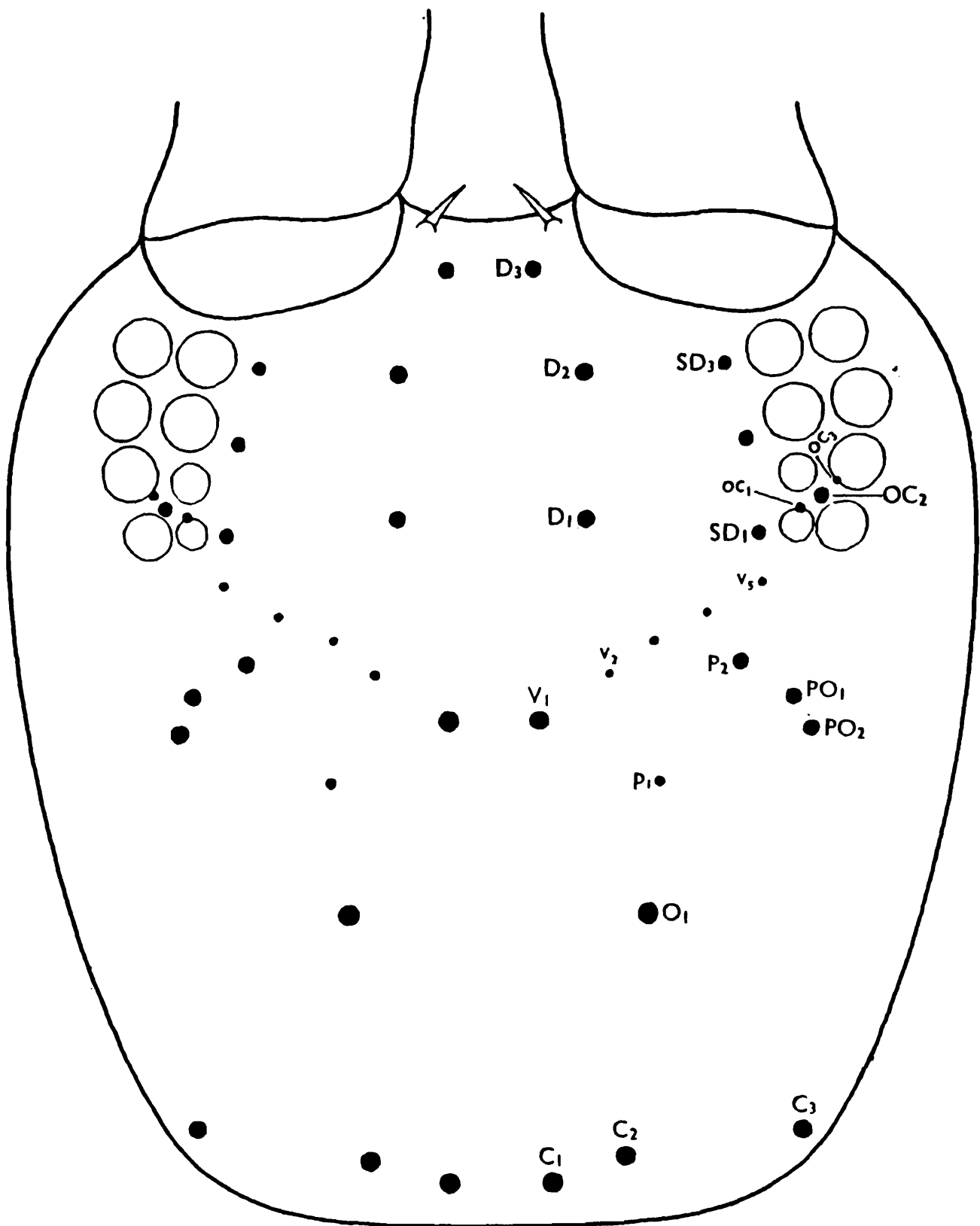


Fig. 8 : Cephalic Chaetotaxy of *Yosia*

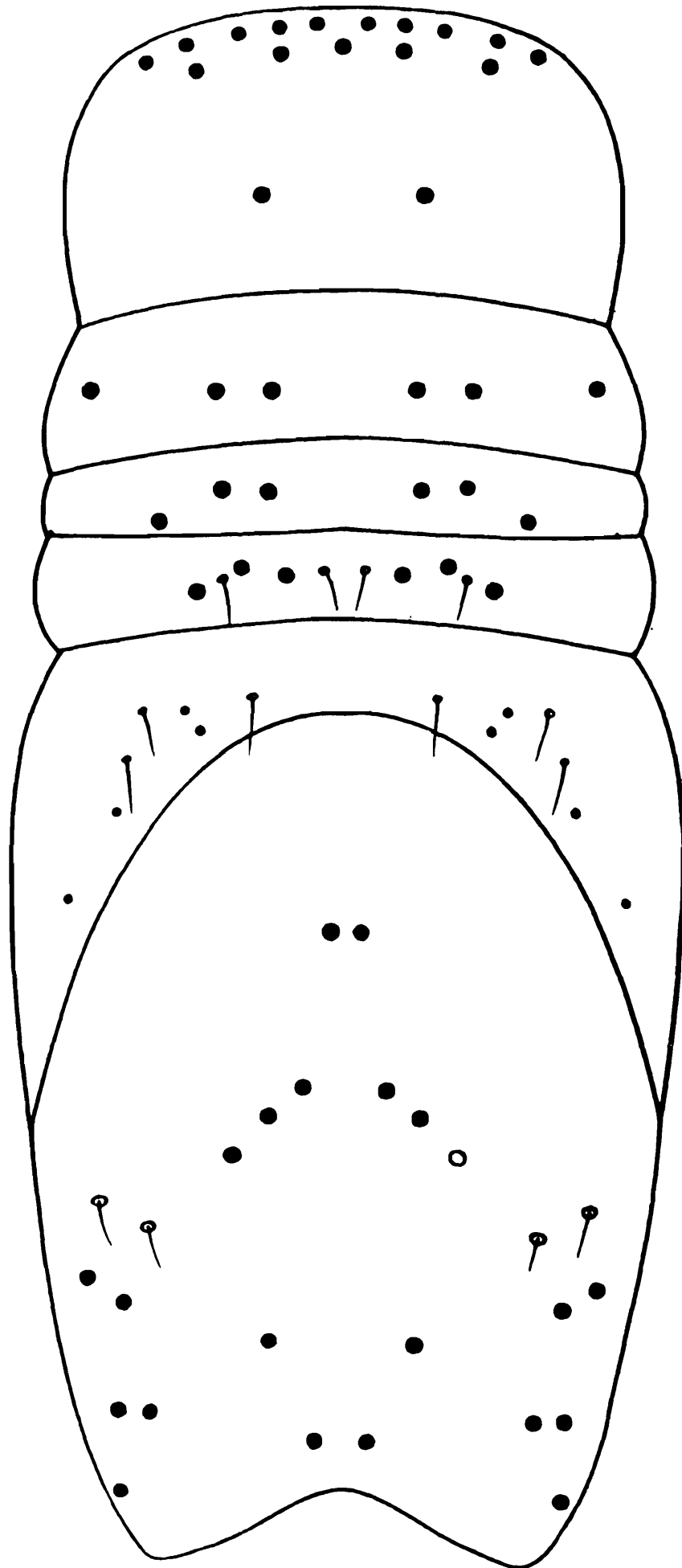


Fig. 9. Chaetotaxy of Ths. II, III and Abds. I-IV of *Yostia*

*Akabosia* Kinoshita, 1919

1919. *Akabosia* Kinoshita, *Zool. Mag.*, Tokyo, **31** : 1-20.

**Head** : Vertex with 9 setae,  $V_1$  and  $V_2$  only represented by macrochaetae and inserted in a trapezoid fashion like *Salina* ; subdorsal region represented by 6 setae of which  $SD_{1-2}$  and  $SD_{4-6}$  macrochaetae; dorsal region without macrochaetae; ocular region represented by 3 microchaetae ( $oc_{1-3}$ ); parietal region with a single macrochaeta ( $P_1$ ) on either side; postocular region represented by 2 macrochaetae ( $PO_1, PO_2$ ) ; occipital region with 3 ( $O_{1-3}$ ) and cervical region with 3 ( $C_{1-3}$ ) macrochaetae on either side (Fig. 10).

**Body** : Number of macrochaetae on each tergite and on each side as follows : Ths. II (11, including those on anterior margin), III (5) ; Abds. I (3), II (3), III (13), Abd. IV medially with 9 macrochaetae on either side in 5 distinct rows, 2+2 setae present anteriorly (first row) on the segment like *Salina* and *Pseudosalina* (Fig. 11). Yosii (1965) represented chaetal architecture of *A. matsudoensis* as Ths. II (2, posteriorly) instead of 4. III (4) instead of 5 and Abd. II (2) instead of 3.

The genus is close to *Salina* in its cephalic chaetotaxy.

*Paronellides* Schött, 1925

1925. *Paronellides* Schött, *Sarawak Mus. Journ.* , **3** : 107.

**Head** : Vertex with  $V_0 + V_{1-6}$  , all of which macrochaetae,  $V_1, V_2$  arranged in a trapezoid fashion and  $V_0$  falls medially on the line joining  $V_1-V_1$  ; dorsal region represented by  $D_0 + D_{1-9}$  , all of which macrochaetae; subdorsal region represented by 8 setae of which  $SD_{5-8}$  macrochaetae; ocular region has 4 setae ( $oc_{1-4}$ ), all microchaetae ; postocular region represented by a single macrochaeta on either side ( $PO_1$ ); parietal region represented by a single macrochaeta on each side ( $P_1$ ) ; occipital region with  $O_{1-10}$  , all macrochaetae, arrangement of which characteristic; area cervicalis represented by macrochaetae, ( $C_{1-5}$ ); area genalis represented by 3 macrochaetae ( $C_{1-3}$ ) [Fig. 12].

**Body** : Number of macrochaetae on each tergite ranges from Ths. II (68-69), III (46-47), Abds. I (23-26), II (10-11), III (9-10) ; Abd. IV medially has a transverse row of at least 7 macrochaetae on either side.

The genus is polychaetotic in the presence of a large number of macrochaetae on each tergite.

*Paronellides mioebergi*, type-species, has the largest number of macrochaetae on head and body (Fig. 13).

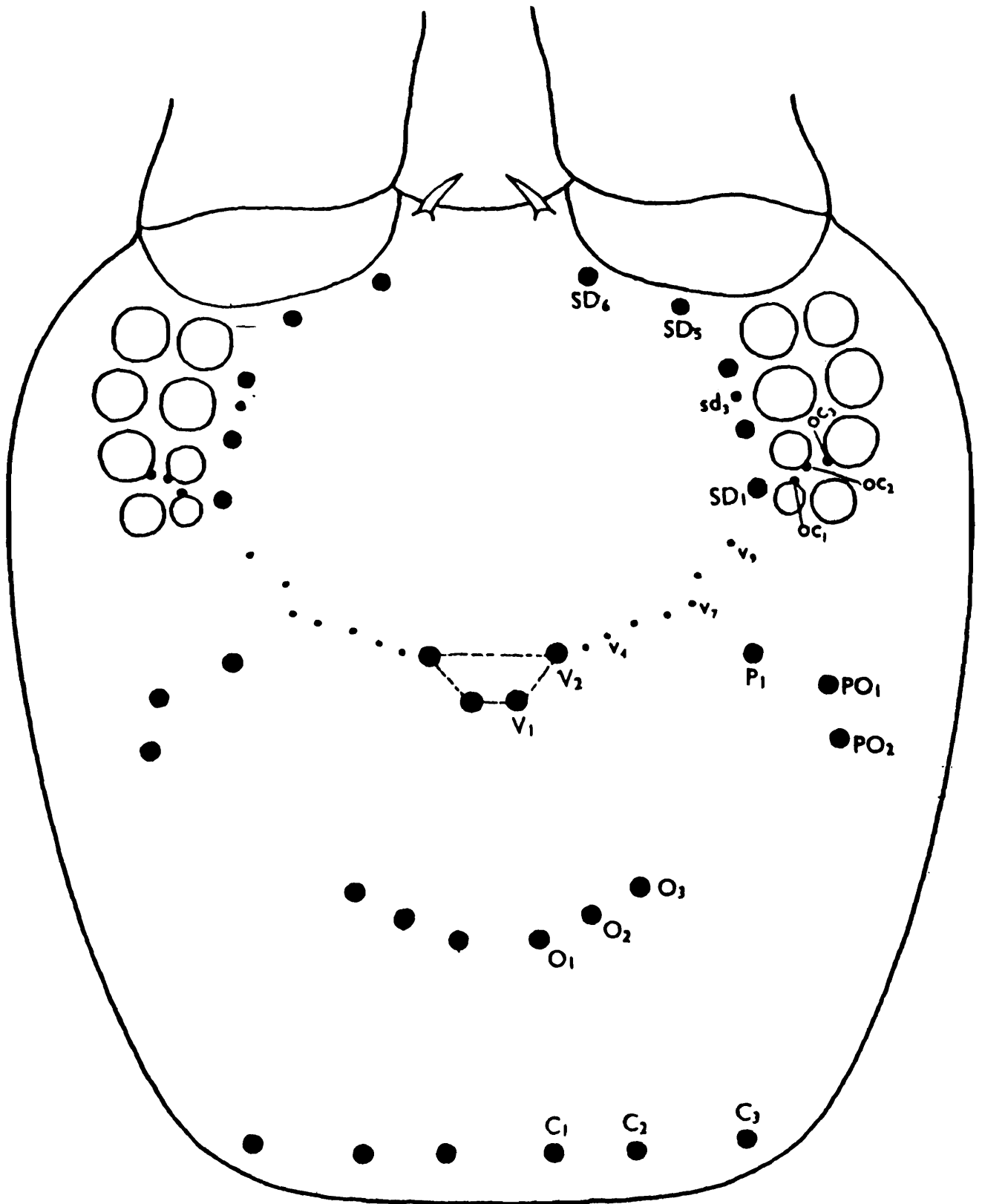


Fig. 10 : Cephalic Chaetotaxy of *Akabosia*

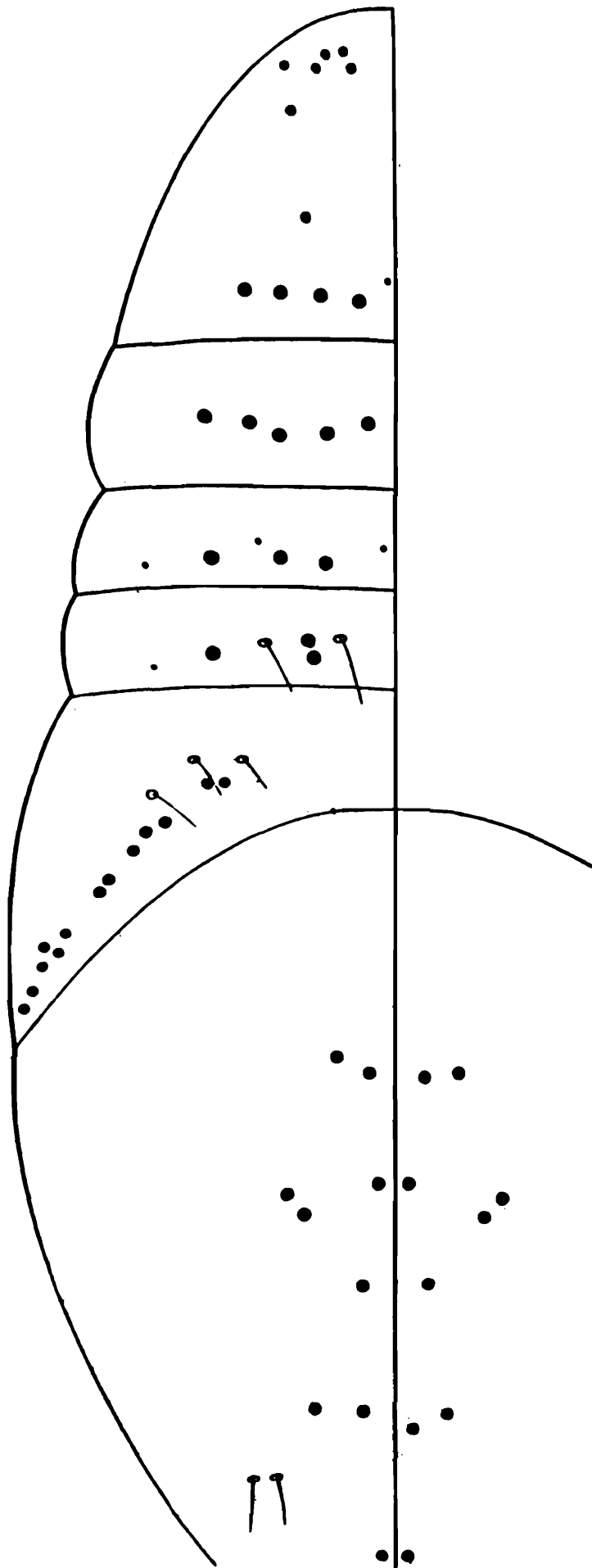


Fig. 11 : Chaetotaxy of Ths. II, III and Abds. I-IV of *Akabosia*

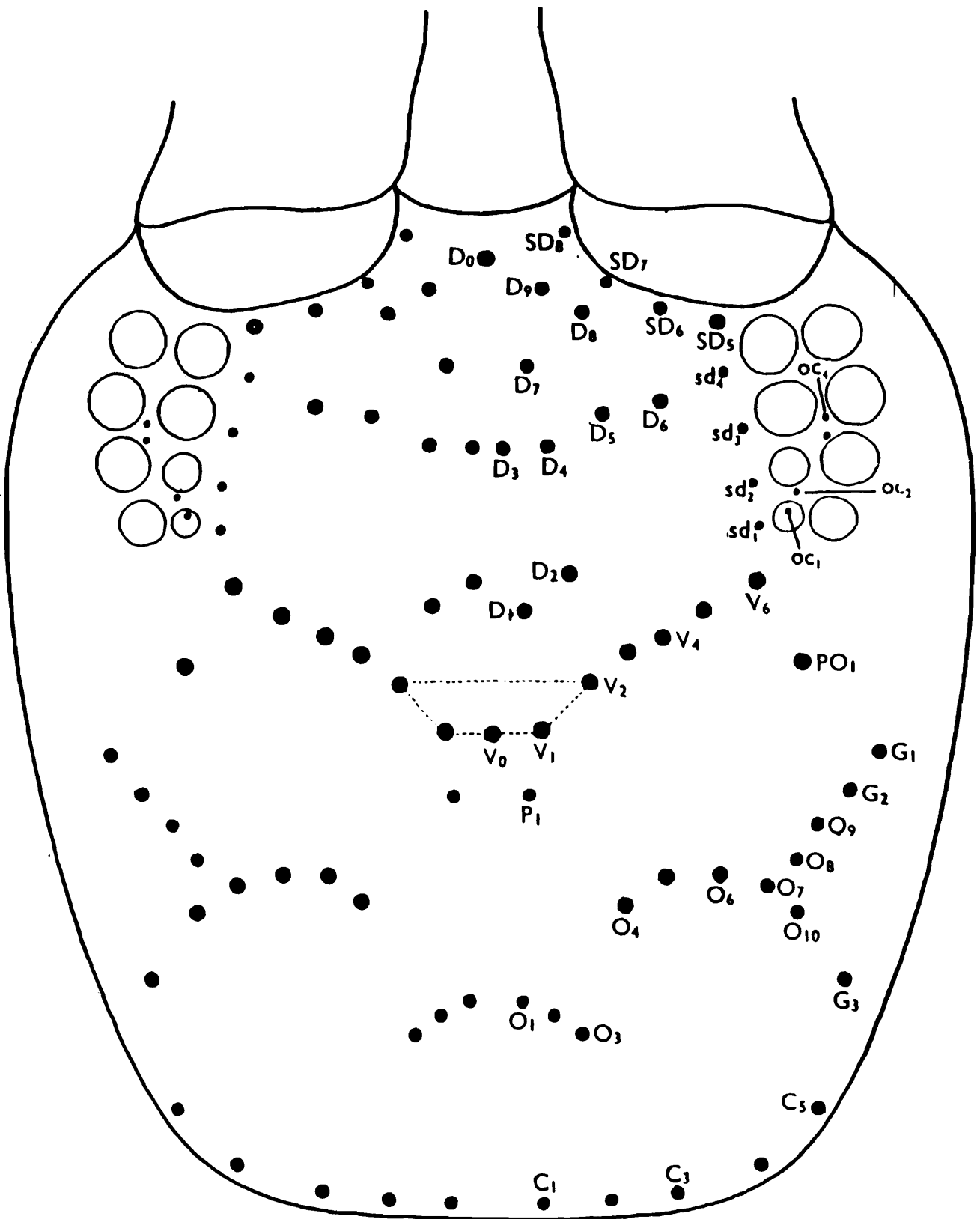


Fig. 12 : Cephalic Chaetotaxy of *Paronellides*

***Paronana* Womersley, 1939**

1939. *Paronana* Womersley, *Primitive Insects of South Australia*, Adelaide, 322 pp.

**Head** : Vertex with  $V_{1-8}$ , all macrochaetae  $V_1, V_2$  on each side located almost in a straight line and joining them with  $V_3$  on each side yields a trapezium or a rectangle; dorsal region with  $D_0 + D_{1-9}$ , all macrochaetae; subdorsal region usually represented by microchaetae ( $sd_{1-9}$ ); ocular region has 5 microchaetae ( $oc_{1-5}$ ); postocular region with a macrochaeta ( $PO_1$ ); parietal region represented by 1 macrochaeta only ( $P_1$ ),  $P_2$  usually represented by a microchaeta; occipital region represented by  $O_{1-10}$ , all macrochaetae, arranged in a characteristic manner; cervical region represented by 6 macrochaetae ( $C_{1-6}$ ); genal region represented by 3 macrochaetae on each side ( $G_{1-3}$ ) [Fig. 14].

**Body** : Number of macrochaetae on each tergite ranges as follows : Ths. II (30-52), III (20-42); Abds. I (18-20), II (8), III (7); Abd. IV medially with a transverse row of macrochaetae varying from 19-20 on either side (Fig. 15).

The genus has much resemblance to *Pseudosalina* in the presence of larger number of macrochaetae on head and body. Presence of a transverse row of macrochaetae anteromedially on Abd. IV is a characteristic feature of the genus (vs. 2+2 in *Pseudosalina*).

***Parasalina* Salmon, 1944**

1944. *Parasalina* Salmon, *Rec. Dom. Mus.*, 1 (2) : 123-182.

Material which was available for the study of the chaetotaxy of this sub-genus involved 2 paratypes, representing *Parasalina dorsanota* (Salmon) and *Parasalina dorsanota intermedia* Salmon. A careful examination of these specimens reveals that the sub-genus, in the arrangement of macrochaetae on vertex, agrees to *Paronana*. However, macrochaetae although present on dorsal, occipital, parietal and cervical regions, the number of such setae appears to be less than the species of *Paronana*. Each tergite has also less number of setae than the species of the sub-genus *Paronana*.

***Glacialoca* Salmon, 1941**

1941. *Glacialoca* Salmon, *Trans. Roy. Soc., N.Z.*, 70 ; 282.

The genus is known only by the holotype of its type-species, i.e. *Glacialoca caerulea*. Although the holotype was available for study, it has not been possible to make a detailed study of the cephalic chaetotaxy owing to the nature of its mounting. However, as far as it could be noted, it may be mentioned that the species possesses macrochaetae on areas verticalis, dorsalis, occipitalis, parietalis, genalis and cervicalis. Unfortunately, it is not possible to ascertain the actual number of setae occurring in each region along with their nature of insertions.

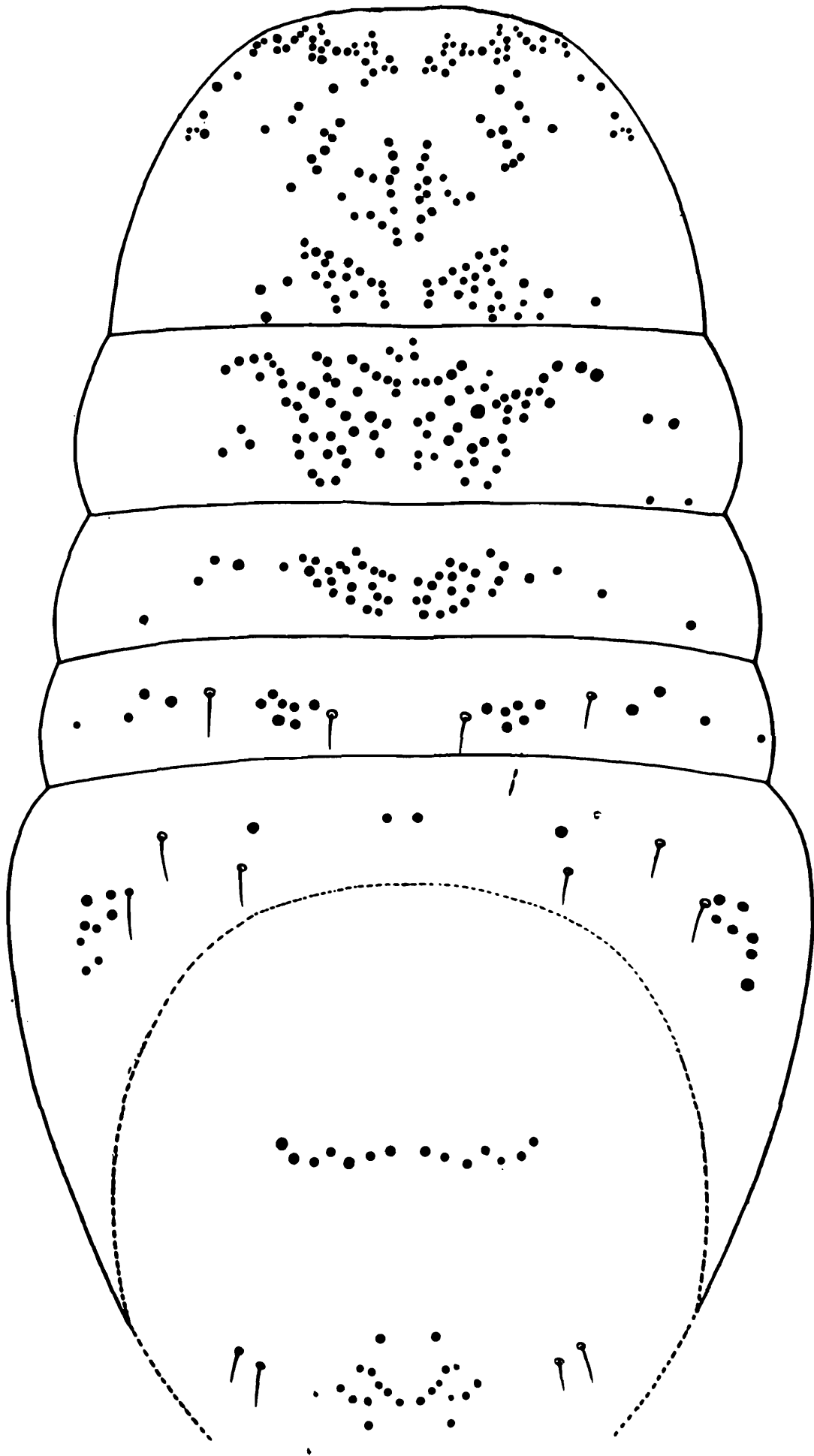


Fig. 13 : Cephalic Chaetotaxy of *Akabosia*

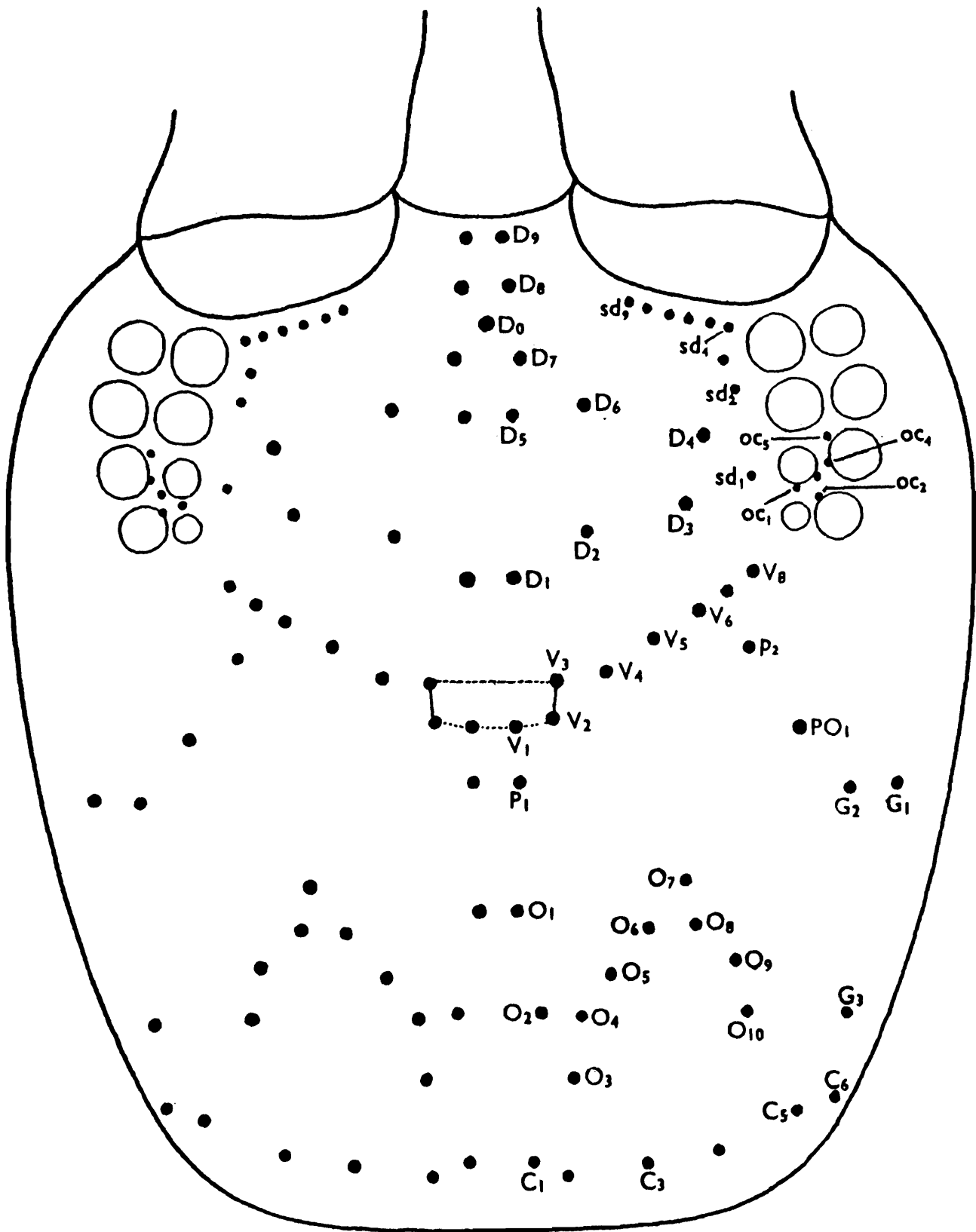


Fig. 14 : Cephalic Chaetotaxy of *Paronana*

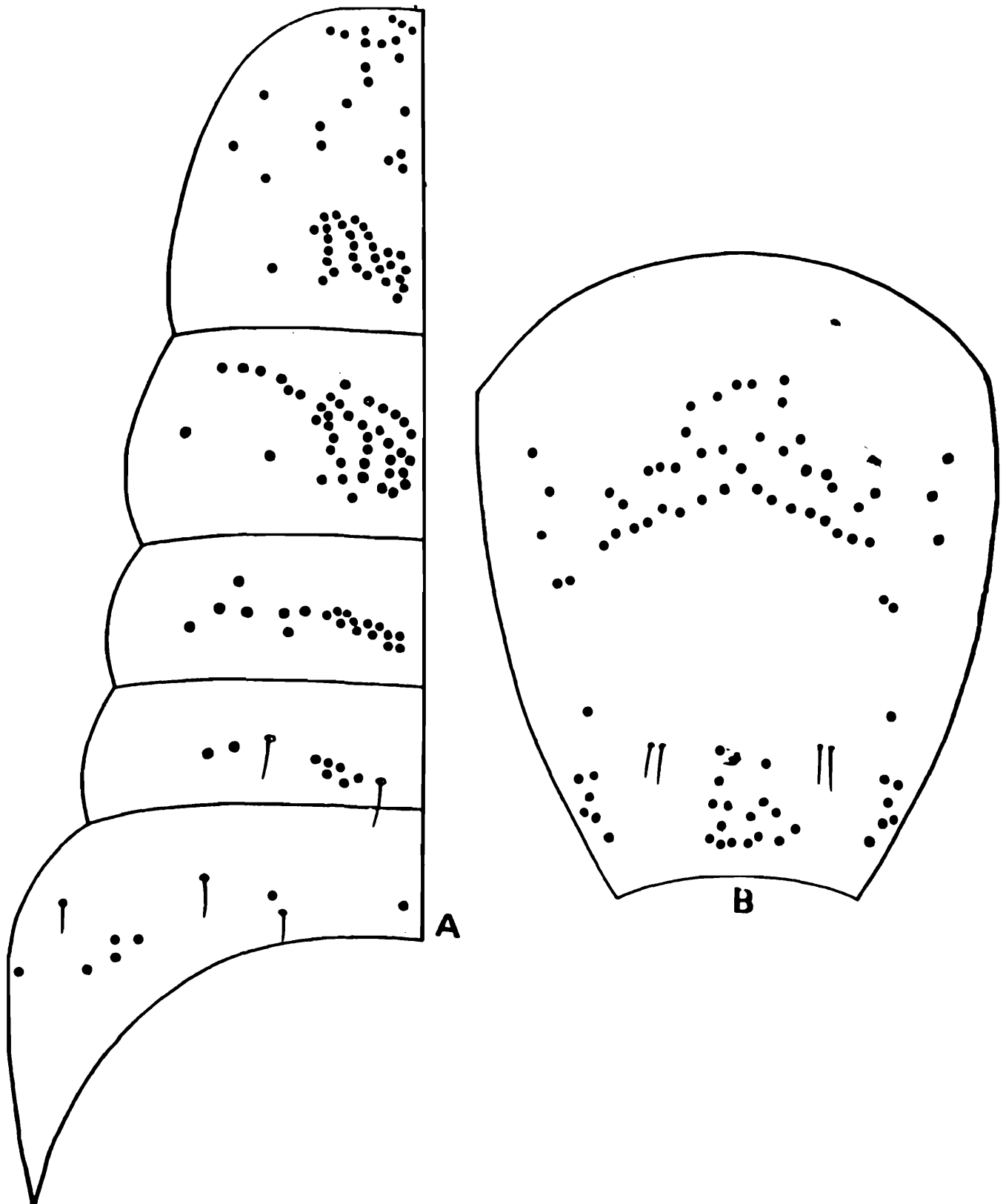


Fig. 15 : Body Chaetotaxy of *Paronana*. A, Ths. II, III, Abds. I-III ; B, Abd. IV.

Though number of macrochaetae could not be studied accurately by clearing the tergites, nevertheless, the macrochaetal sockets were distinctly visible through pigmented surface (Fig.16). The number of macrochaetae given below segment-wise represents the minimum number of setae that could be noted through pigmented surface : Ths. II (16), III (23); Abds. I (3), II (6), III (8). Medially on Abd. IV a transverse row of macrochaetal sockets could be seen (cf. *Paronana*).

### *Metacoelura* Salmon, 1951

1951. *Metacoelura* Salmon, *Zool. Publ. Vict. Univ. Coll.*, (8) : 1-82.

**Head** : Vertex with  $V_0 + V_{1-6}$ , arrangement of  $V_1, V_2$ , as in *Paronellides*; dorsal region with  $D_{1-3}$ , all macrochaetae; subdorsal setae not noted; ocular region represented by  $oc_{1-4}$ , all microchaetae; postocular region represented by a single macrochaeta ( $PO_1$ ) on each side; parietal region with  $P_1$  macrochaeta on each side; occipital region represented by  $O_{1-7}$ , all macrochaetae; cervical region represented by 4 macrochaetae on each side ( $C_{1-4}$ ); genal region with 3 macrochaetae ( $G_{1-3}$ ) on each side (Fig. 17).

**Body** : Number of macrochaetae on the segments as follows : Ths. II (38), III (30); Abds. I (18), II (7), III (3, medially); Abd. IV anteromedially has a transverse row of 10 macrochaetae on either side (Fig. 18).

### CALLYNTRURINI

#### *Callyntrura* Börner, 1906

1906. *Callyntrura* Börner, *Mitt. naturh. Mus.*, Hamburg, 23 : 147.

**Head** : Vertex represented by  $V_0 + V_{1-7}$ , all macrochaetae,  $V_0$  and  $V_7$  differ among species,  $V_1, V_2$  usually arranged in a trapezoid fashion with  $V_0$  located medially on the line joining  $V_1 - V_2$ ; dorsal region usually with 5 microchaetae ( $d_{1-5}$ ) and a single macrochaeta ( $D_6$ ),  $d_5$  sometime represented by a macrochaeta, other setae ( $d_{1-4}$ ) always microchaetae,  $d_{1-3}$  unpaired ones, located on the middorsal line of head, number of microchaetae in this region variable; subdorsal region with 10-14 variable macro- and microchaetae,  $SD_1, SD_5, SD_9-14$  usually macrochaetae; ocular region always with 3 macrochaetae ( $oc_{1-3}$ ), the orientation of which almost similar to *Salina*, *Pseudosalina* and *Dicranocentroides*; postocular region represented by a single macrochaeta ( $PO_1$ ); genal region represented by a single macrochaeta ( $G_1$ ) on each side, presence or absence of this macrochaeta of specific significance; parietal, occipital and cervical regions without any setae (Fig. 19).

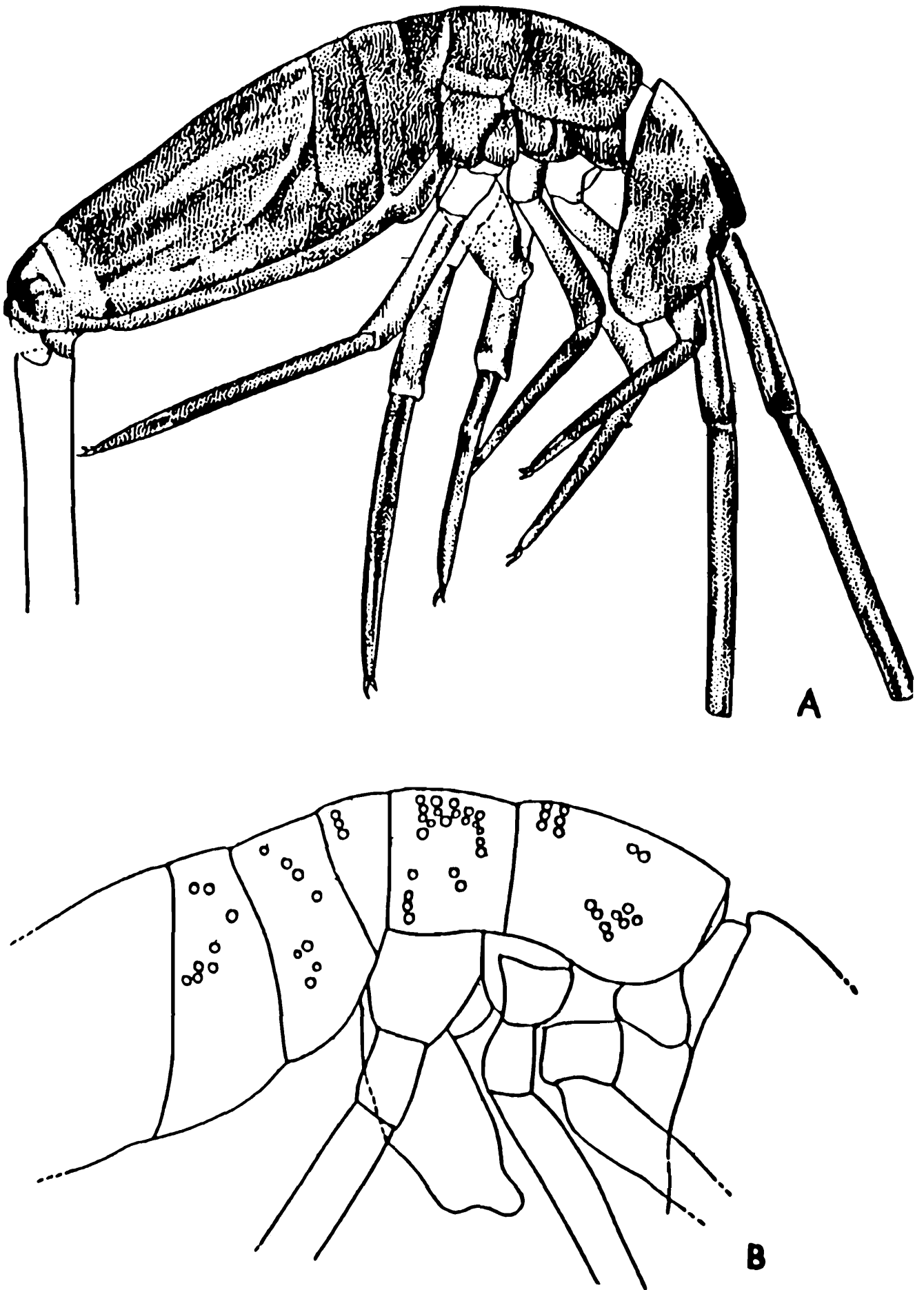


Fig. 16 : *Glacialoca caerulea* Salmon (Holotype). A, Profile showing pigmentation ; B, chaetotaxy of Ths. II, III, Abds. I, II, III..

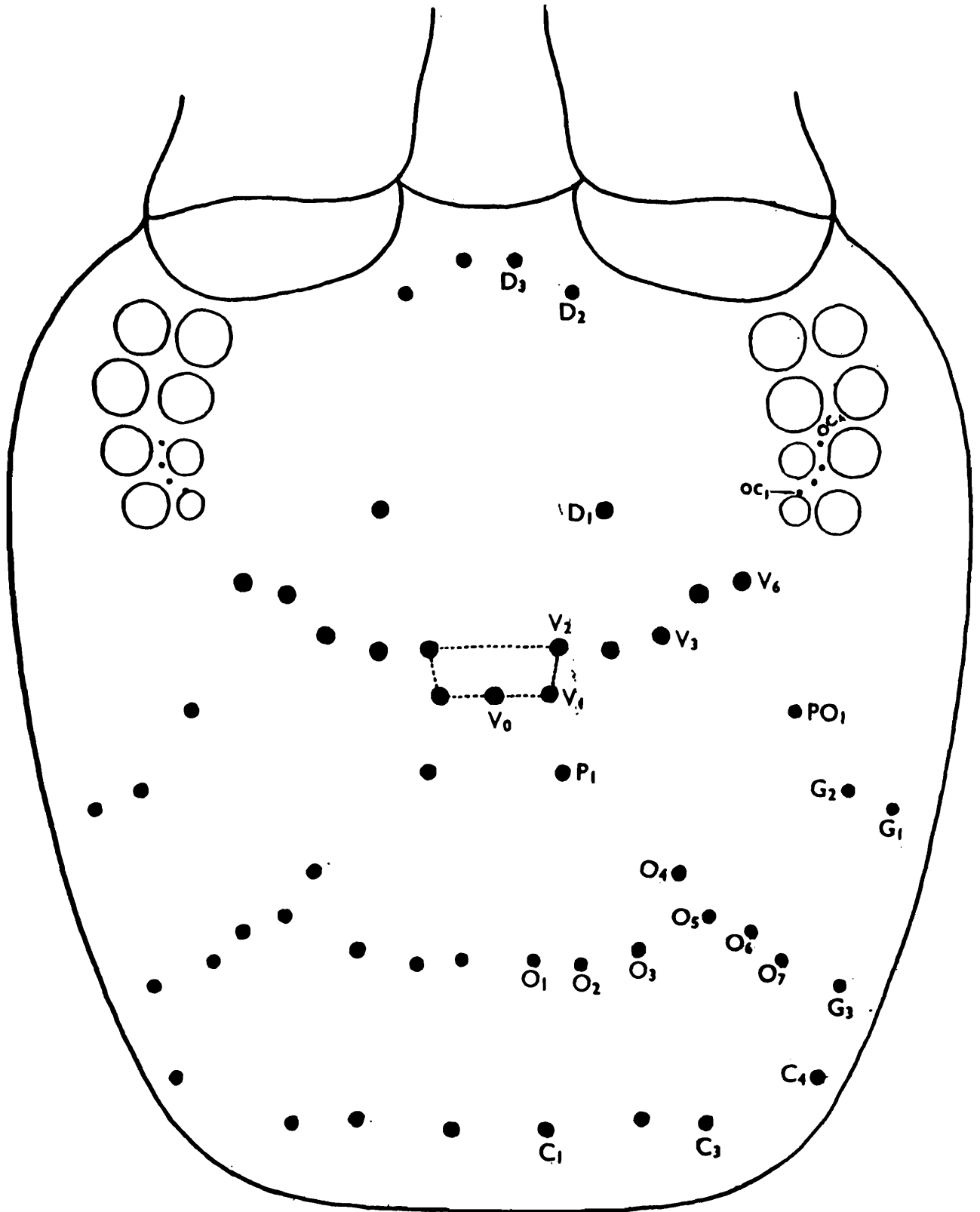


Fig. 17 : Cephalic Chaetotaxy of *Metacoelura*

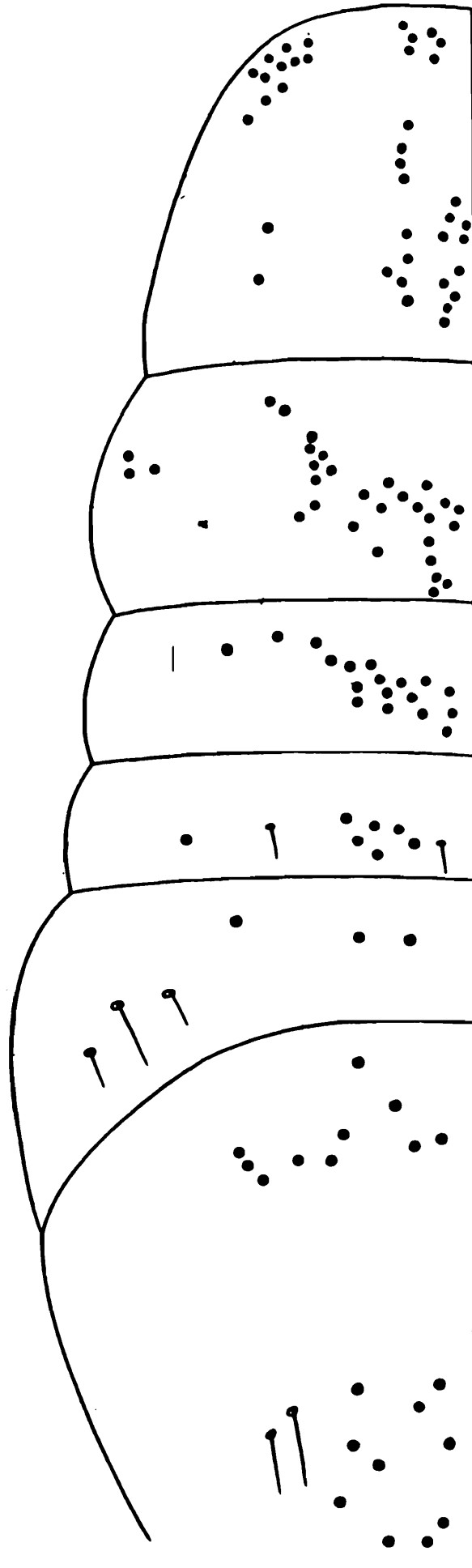


Fig. 18 : Chaetotaxy of Ths. II, III and Abds. I-IV of *Metacoelura*

**Body** : The range of the number of macrochaetae occurring on body as follows : Ths. II (8-26), III (11-23) ; Abds. I (5-15), II (5-12), III (4-11) and Abd. IV medially with a transverse row (seldom in 2 transverse rows) of 9-16 macrochaetae on each side.

In the species of *Callyntrura* the body segments can be subdivided into 3 longitudinal regions, viz., medial, paramedial and lateral regions like the species of *Lepidocyrtus* (Snider, 1967). This can be done by drawing two longitudinal parallel lines, 2 passing perpendicularly through 1<sub>1</sub> on Abd. II and the other through 1<sub>2</sub> on Abd. II and 1<sub>2</sub> on Abd. III. The medial region can be further subdivided into 4 subregions (*via.*, Pa, Pb, Pc and Pd zones) taking advantage of the orientation of macrochaetae in 4 distinct rows in all the species examined (Fig. 20 ; Pl. III, C).

No difference so far has been observed in the basic pattern of chaetotaxy on head and body in the species belonging to the two subgenera of *Callyntrura*, viz., *Callyntrura* (*Callyntrura*) and *Callyntrura* (*Handschinphysa*). The Species living on herbs and shrubs exhibit reduction in the number of macrochaetae on head and body in contrast to the species found in the humid forest floor.

### *Dicranocentroides* Imms, 1912

1912. *Dicranocentroides* Imms, *Proc. zool. Soc.*, London, 1912 : 80-125.

**Head** : Vertex represented by V<sub>0</sub> + V<sub>1-7</sub> , all macrochaetae, presence or absence of V<sub>7</sub> of specific significance, V<sub>1</sub>, V<sub>2</sub> usually arranged in a trapezoid fashion with V<sub>0</sub> located medially on the line joining V<sub>1</sub>-V<sub>1</sub> (cf. *Callyntrura*). In one species, viz., *Dicranocentroides flavescens* Yosii, some variable macrochaetae occur on vertex, dorsal and parietal regions in addition to the usual number of constant setae (Fig.21); dorsal region with 3 microchaetae (d<sub>1-3</sub>) and a single macrochaeta (D<sub>6</sub>), d<sub>1-3</sub> unpaired, located anteriorly on the middorsal line, number of microchaetae in this region variable; subdorsal region represented by 11-17 (variable) setae, SD<sub>9-12</sub> near the base of antennae usually macrochaetae; ocular region represented by 3 microchaetae (oc<sub>1-3</sub>), arrangement of which similar to *Callyntrura*, *Pseudosalina*, *Salina* and *Yosii* ; postocular region represented by a single macrochaeta (O<sub>2</sub>) and a variable microchaeta (o<sub>1</sub>) ; cervical region without setae, in some species 1+1 variable microchaetae seldom occur; genal region represented by 2 macrochaetae (G<sub>1-2</sub>).

**Body** : *Dicranocentroides* has relatively larger number of macrochaetae on body segments than *Callyntrura*, as follows : Ths. II (35-53), III (33-49) ; Abds. I (18-31), II (12-20), III (2, medially) ; Abd. IV has medially a transverse row of 10-14 macrochaetae on either side (Fig. 22).

Cephalic chaetotaxy is although reasonably constant in the species of *Dicranocentroides*, some specimens of *D. flavescens* exhibit a few variable macrochaetae in the area verticalis. This is, however, an exceptional example as regards the variation in cephalic chaetotaxy. Number of macrochaetae on each tergite is variable even in the examples from the same population in most of the species of this genus.

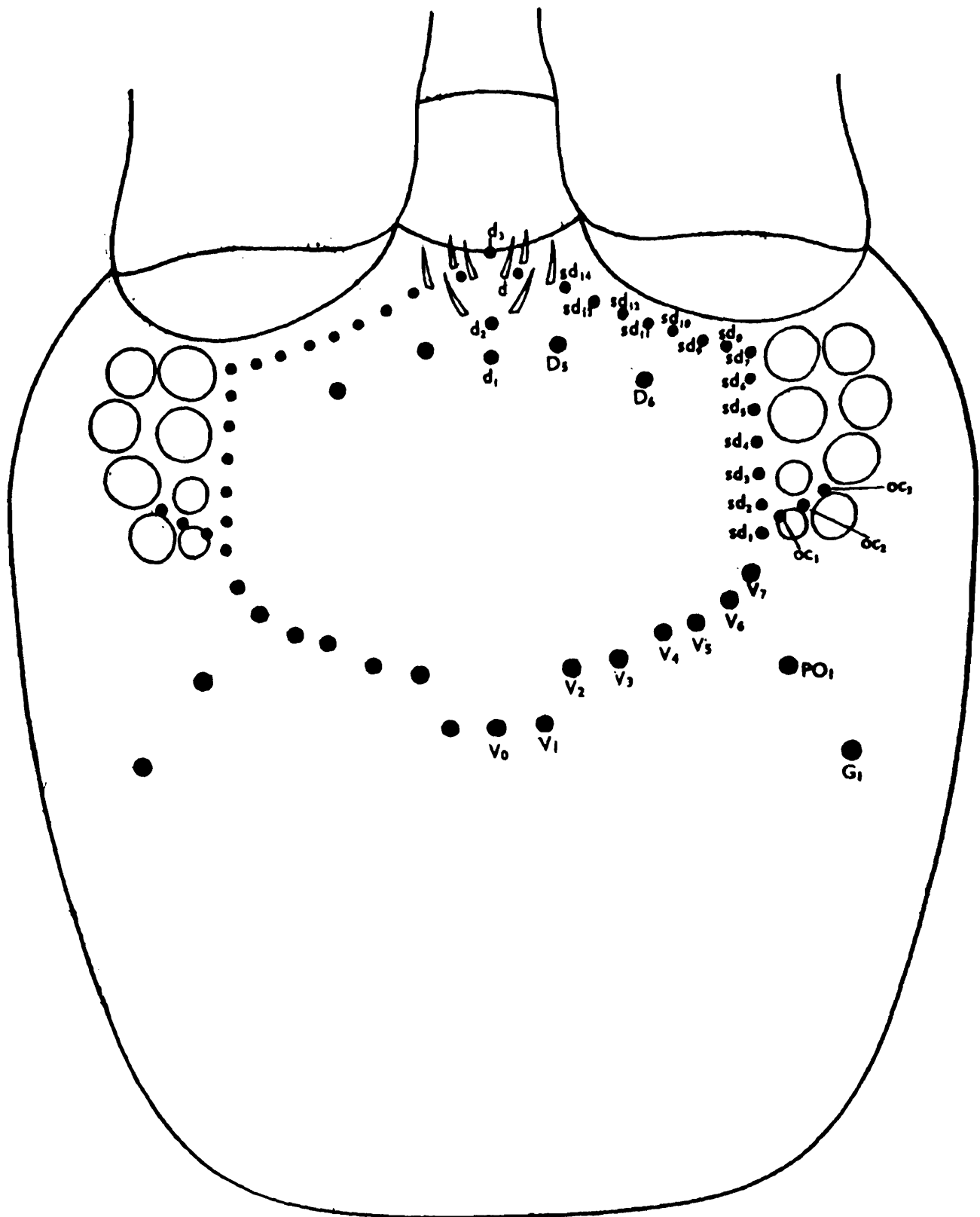


Fig. 19 : Cephalic Chaetotaxy of *Callyntrura*

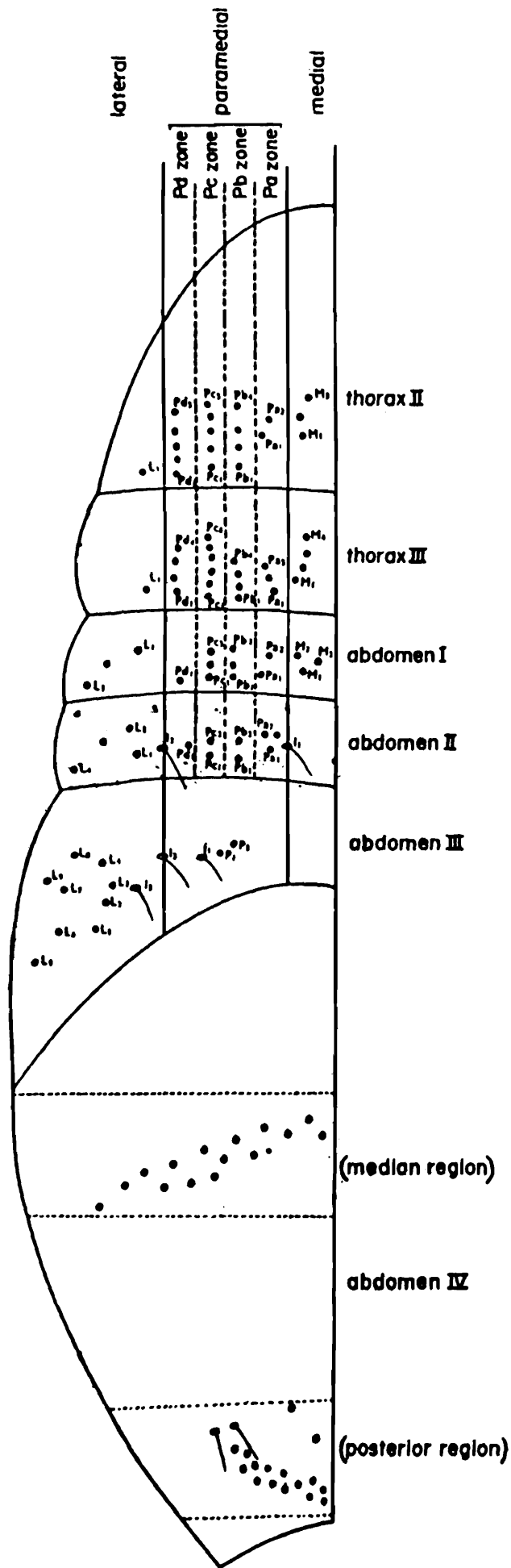


Fig. 20 : Basic Chaetotactic Plan of Ths. II, III and Abds. I-IV of *Callyntrura*

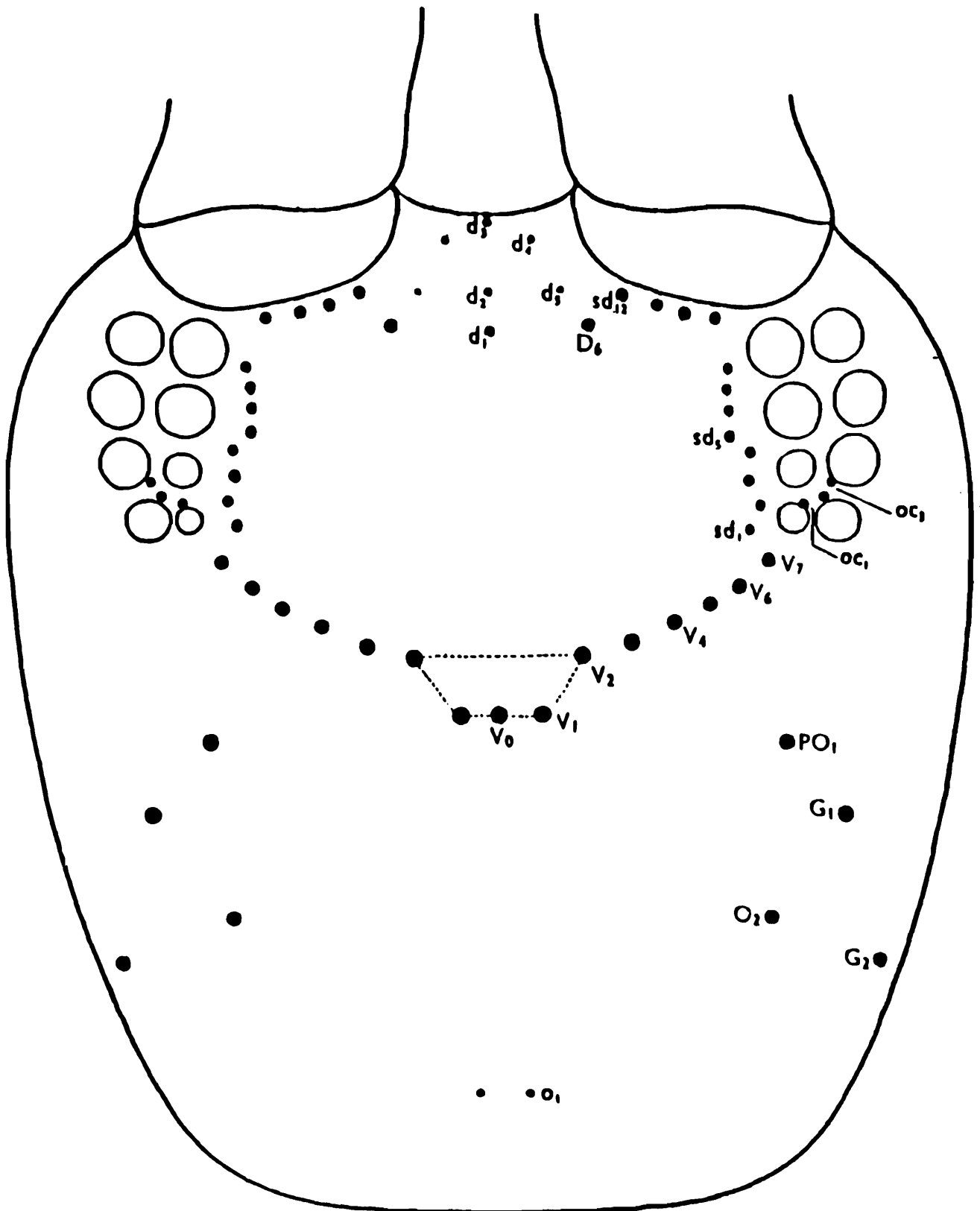


Fig. 21 : Cephalic Chaetotaxy of *Dicranocentroides*

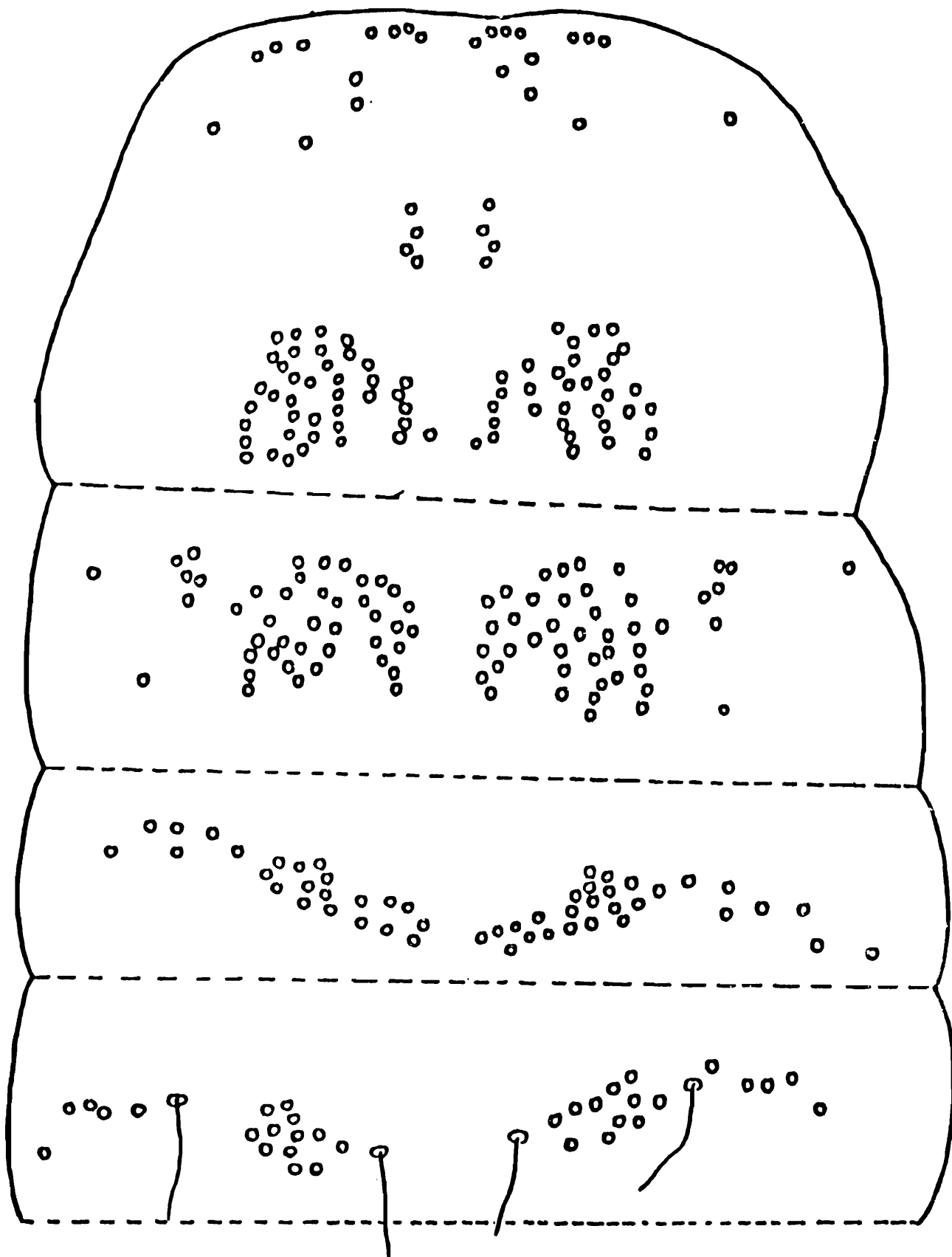


Fig. 22 : Chaetotaxy of Ths. II, III and Abds. I, II of *Dicranocentroides*

*Pseudoparonella* Handschin, 1925

1925. *Pseudoparonella* Handschin, *Treubia*, 6 : 225 (*nec, s. str.*).

**Head** : Vertex with  $V_0 + V_{1-6}$ , all macrochaetae,  $V_1, V_2$  arranged in a trapezoid fashion with  $V_0$  located medially on the line joining  $V_1-V_1$ ; dorsal region with 7 macrochaetae ( $D_{1-7}$ ), arrangement of which characteristic for the sub-genus; subdorsal region represented by 8 setae of which  $SD_4$  and  $SD_{6-8}$ , usually macrochaetae; ocular region with 5 microchaetae ( $oc_{1-5}$ ), arrangement of which characterisitc; postocular region on each side with a single macrochaeta ( $PO_1$ ); parietal region medially represented by 1+1 macrochaeta ( $P_1 + P_1$ ); postocular region on each side with a single macrochaeta ( $PO_1$ ); occipital region has 5 macrochaetae on each side ( $O_{1-5}$ ), arrangement characteristic; cervical region represented by 6 macrochaetae on each side ( $C_{1-6}$ ); genal region with 2 macrochaetae on each side ( $G_{1-2}$ ) [Fig. 23].

**Body** : Usually with lesser number of macrochaetae on tergites than its nearest ally, *Lawrenceana*, (New Subgenus). Thus, Ths. II (11-17), III (12-20); Abds. I (3-5), II (4-5), III (10) and Abd. IV anteromedially on each side with a transverse row of 8 macrochaetae (Fig. 24; Pl. III, B).

*Lawrenceana* Mitra (In press)

**Head** : Vertex with  $V_0 + V_{1-7}$ , all of which macrochaetae, arrangement of  $V_0, V_1, V_2$  like the sub-genus *Pseudoparonella*; dorsal region with 5 macrochaetae ( $D_{1-5}$ ); subdorsal region represented by 17 setae of which  $SD_4, Sd_5, SD_{10-17}$  macrochaetae; ocular region represented by 5 microchaetae ( $OC_{1-5}$ ); postocular region represented by a single macrochaeta on each side ( $PO_1$ ); parietal region without any setae; occipital region with 6 macrochaetae on each side ( $O_{1-6}$ ); cervical region with 4 macrochaetae on each side ( $C_{1-4}$ ); genal region represented by 2 macrochaetae on each side ( $G_{1-2}$ ), insertion of which quite characteristic for the sub-genus (Fig. 25; Pl. II, C).

**Body** : Usually with relatively more macrochaetae on each tergite than *Pseudoparonella*, range of macrochaetae on each segment as follows : Ths. II (12-18), III (15-21); Abds. I (5-12), II (4-8), III (4-7); Abd. IV anteromedially with transverse rows of 13-16 macrochaetae on either side (Fig. 26; Pl. I, A; III, B).

*Idiomerus* Imms, 1912

1912. *Idiomerus* Imms, *Proc. Zool. Soc.*, London, 1912 : 80-125.

The genus is known by its type-species *Idiomerus pallidus* which is now represented by the lectotype remaining in the collection of the British Museum (Natural History), London and several topotypes, collected by the author.

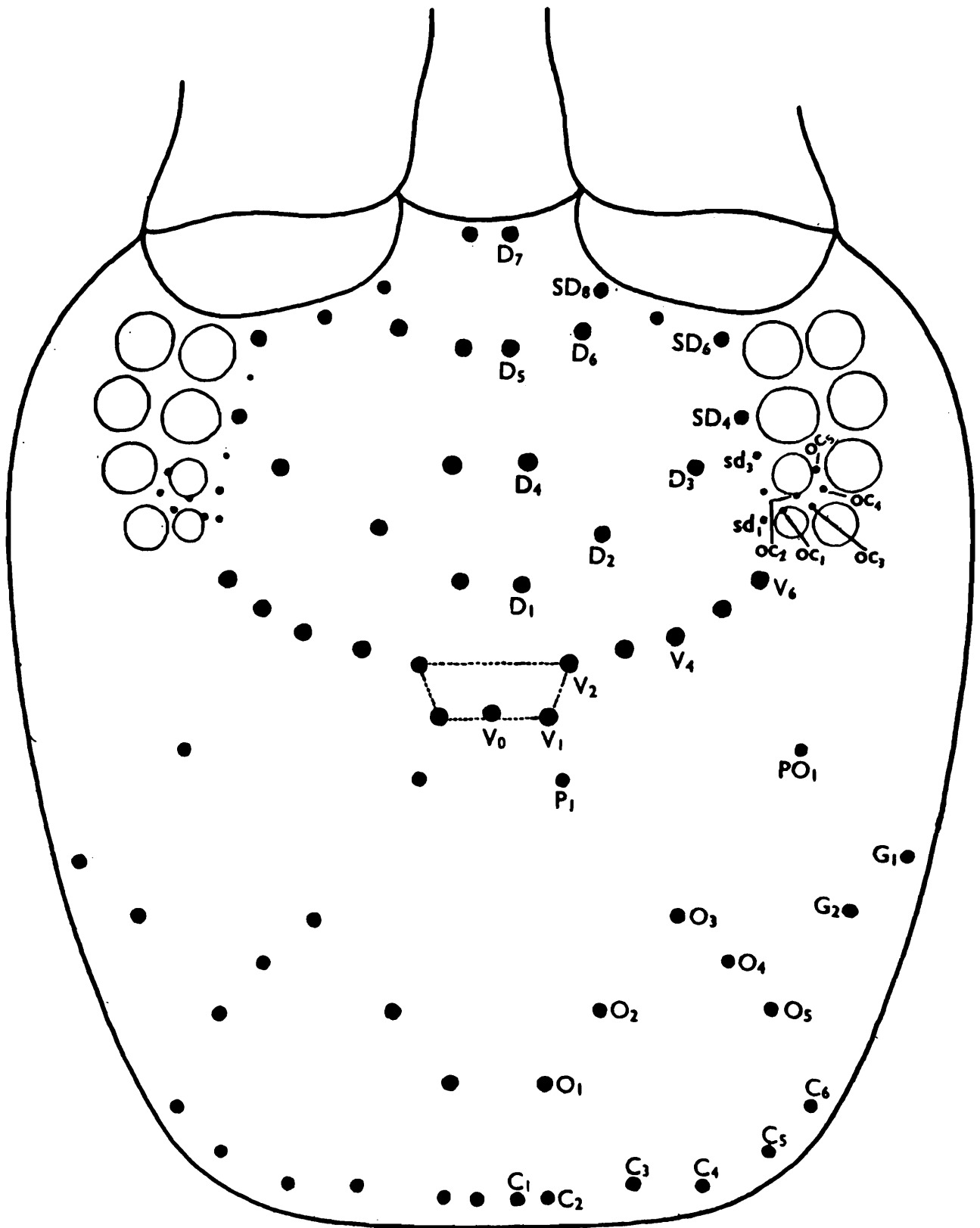


Fig. 23 : Cephalic Chaetotaxy of *Pseudoparonella* (*Pseudoparonella*)

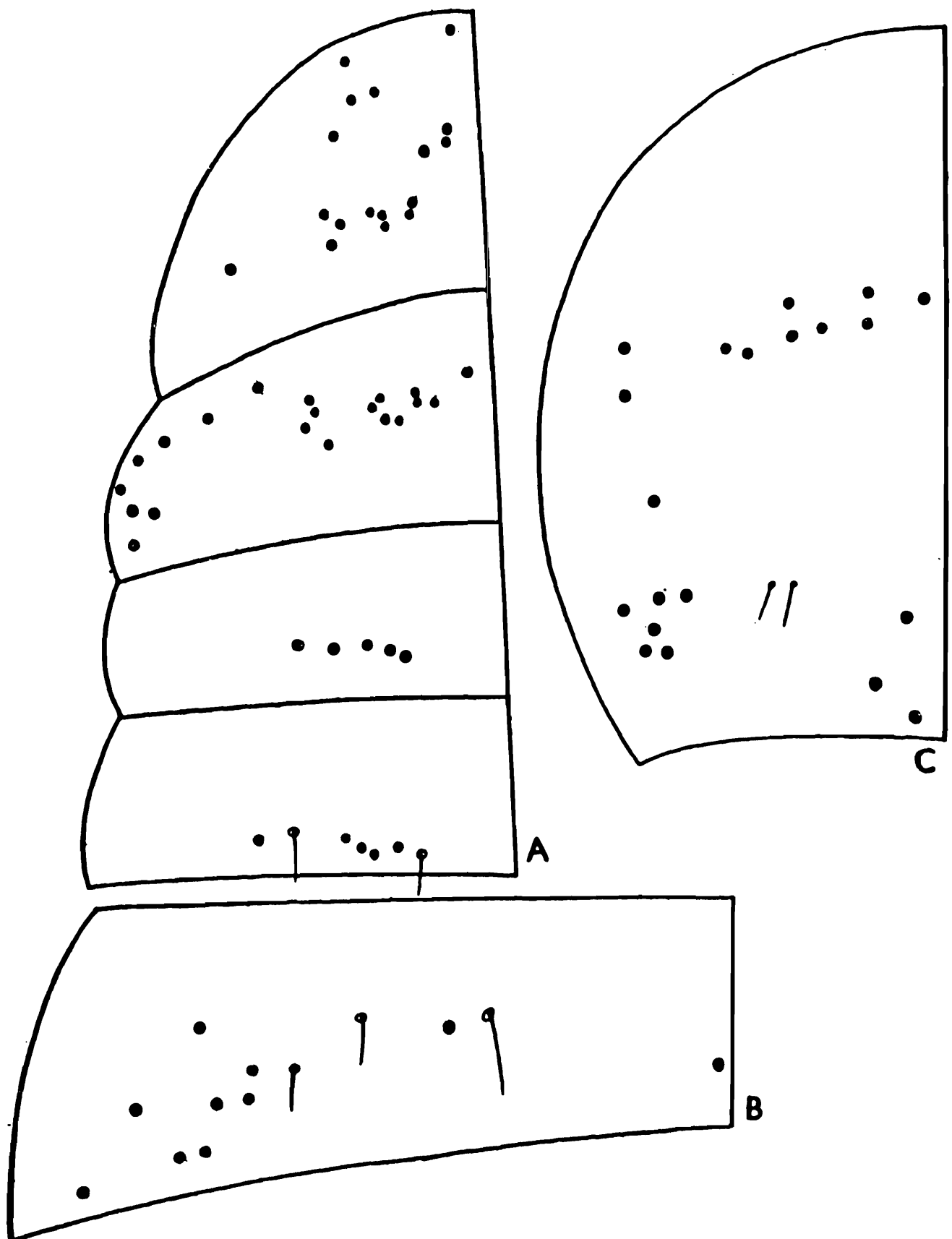


Fig. 24 : Body Chaetotaxy of *Pseudoparonella* (*Pseudoparonella*). A. Ths. II, III, Abds. I, II ; B, Abd. III ; C, Abd. IV.

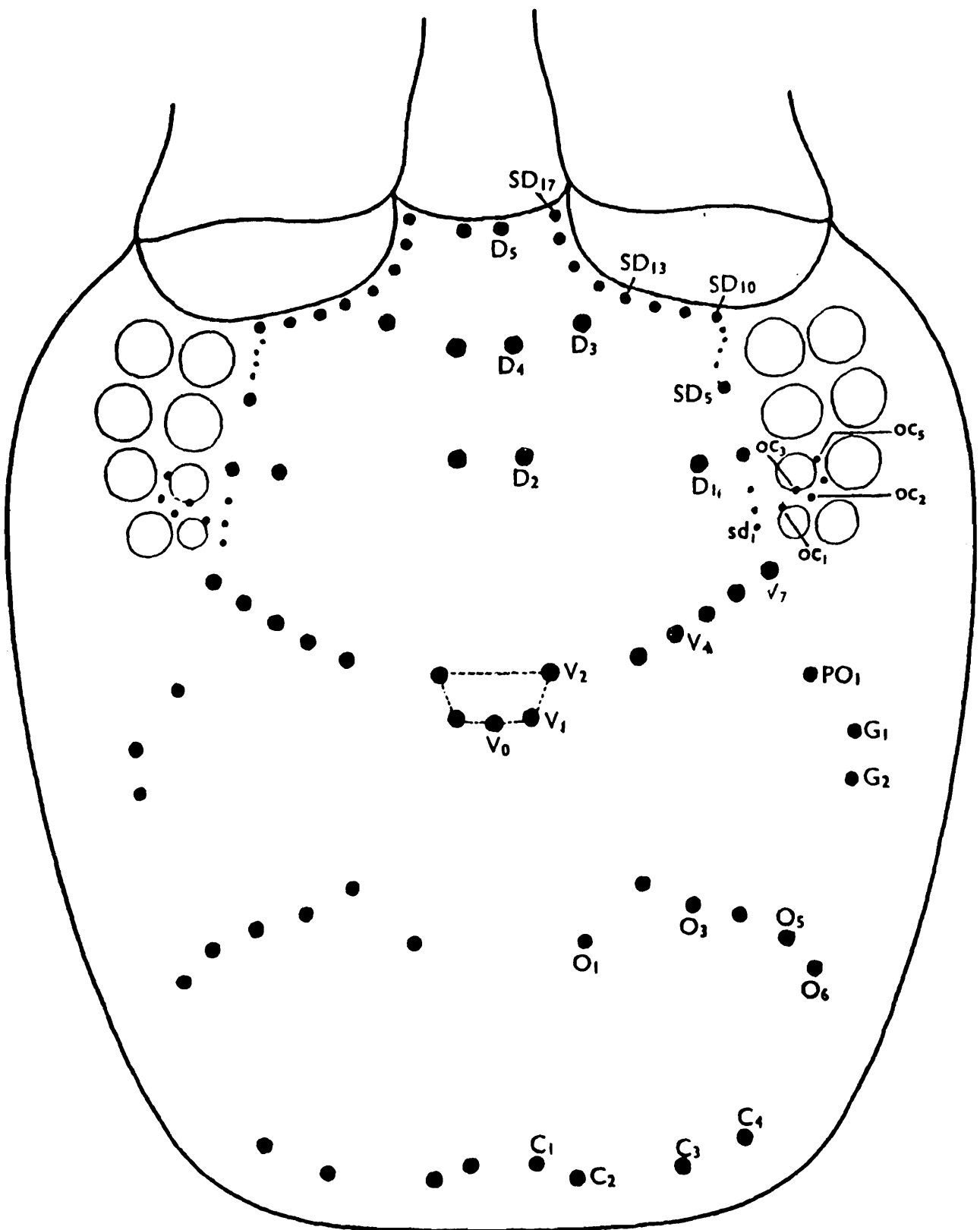


Fig. 25 : Cephalic Chaetotaxy of *Pseudoparonella (Lawrenceana)*

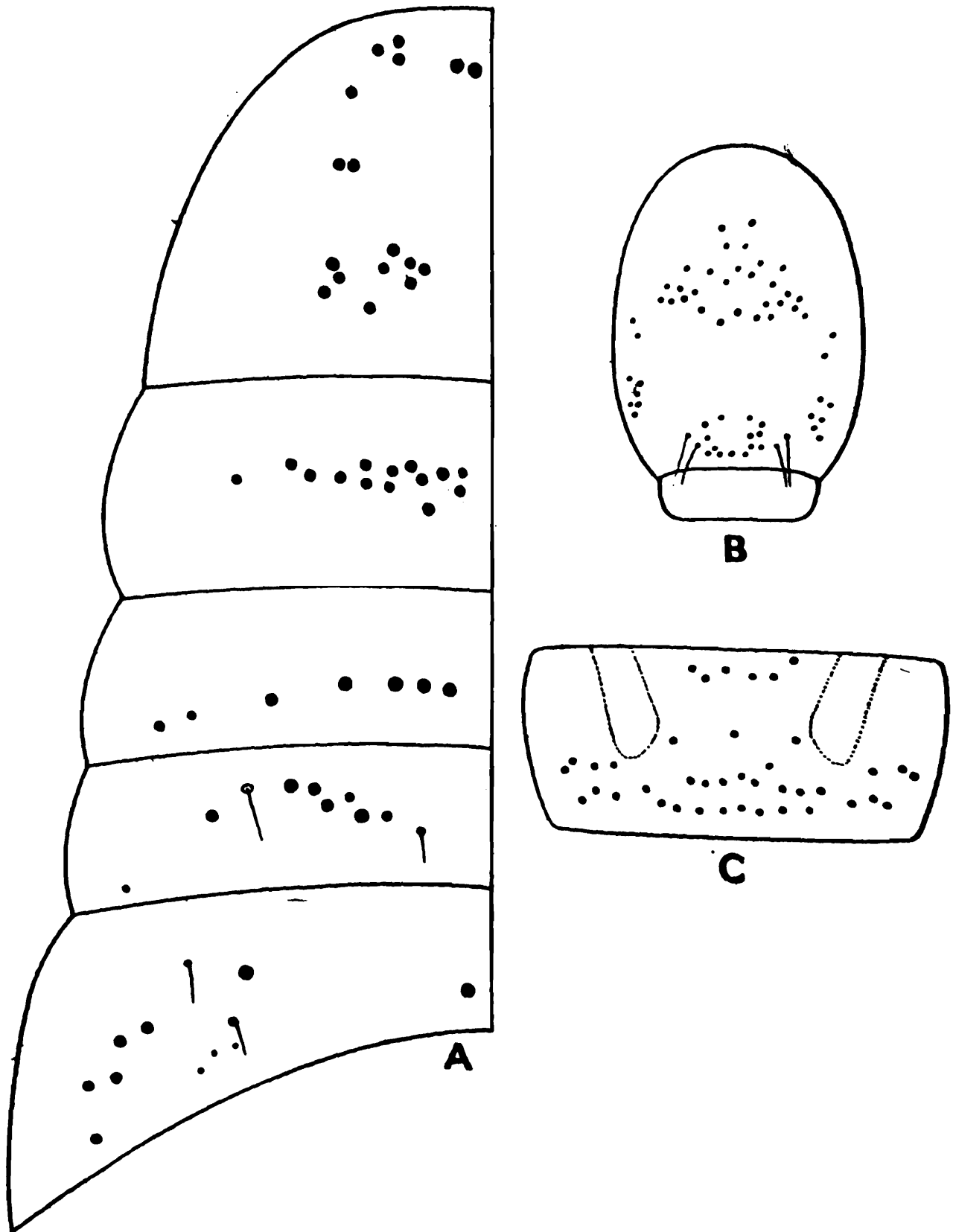


Fig. 26 : Body Chaetotaxy of *Pseudoparonella (Lawrenceana)*. A, Ths. II, III, Abds. I-III ; B, Abd. IV ; C, Abd. V

**Head** : (Fig. 27) : Vertex with  $V_{1-4}$ , all macrochaetae,  $V_1-V_1$  located in a straight line, chaetotaxy of vertex characteristic; subdorsal region represented by 25 microchaetae ( $Sd_{1-25}$ ), dorsal region with  $d_{1-4}$ ,  $d_{1-2}$  unpaired,  $D_4$  represented by a macrochaeta. Besides, 5-6 variable microchaetae occur in this region; ocular region with  $oc_{1-3}$ ,  $OC_2$ , a macrochaeta (cf. *Salina* MacGillivray, *Callyntrura* Börner, *Yosiia* Mitra); parietal region with  $P_{1-3}$ ,  $P_3$  a macrochaeta; postocular region with  $PO_1$ , a macrochaeta; occipital, cervical and genal regions without any setae.

**Body** : (Fig. 28) : Th. II (20), Th. III (13), Abd. I(3), Abd. II (4) And 1 pseudopore on each side, Abd. III (1), Abd. IV medially with 13 macrochaetae on each side arranged in a transverse row and posteromedially with 18 localized setae on each side, Abd. V with 2 unpaired median and 10 setae on each side.

### *Parachaetoceras* Salmon, 1941

1941. *Parachaetoceras* Salmon, *Trans. Roy. Soc. N.Z.*, **70** : 282.

The genus is known by its type-species, *Parachaetoceras pritchardi* (Womersley). The material available to the author involves one specimen mounted on a slide from the Dominion Museum, New Zealand, det. Salmon and 3 specimens mounted on slides from the South Australian Museum, Adelaide. In view of the specimens all being mounted, it has not been possible to ascertain the exact number of setae on vertex, occipital and cervical regions. Following details, however, may be given on the basis of observations on those slides : Vertex with macrochaetae, viz.,  $V_0 + V_{1-3} \dots \dots$ ,  $V_1-V_1$  and  $V_2-V_2$  arranged in a trapezoid fashion with  $V_0$  located medially on the line joining  $V_1-V_1$ ; ocular setae, 5; dorsal region with many macrochaetae; subdorsal setae near antennal joints represented by macrochaetae; postocular region represented by one macrochaeta on each side ( $PO_1$ ); parietal region apparently without any setae; occipital region with many macrochaetae and its arrangement somewhat similar to that of *Lawrenceana*; area cervicalis also with many macrochaetae; area genalis represented by 3 macrochaetae on each side ( $G_{1-3}$ ).

**Body** : Polychaetotic; Ths. II, III/Abds. I, II, III each at least with : 20 (excluding those on anterior margin), 21/10. 7,2 (medially) macrochaetae; Abd. IV anteromedially with a transverse row of 10 macrochaetae on either side.

Unlike Cremastocaphalini and Callyntrurini, the genera under Paronellini, Bromacanthini and Troglopedetini do not possess well developed, flexed macrochaetal clothing (brush setae). However, certain stiff setae occurring on head and body in the genera under these three tribes can be classified into two categories : longer (macrochaetae) and shorter (microchaetae). It may be noted that the nature of macrochaetae of Paronellini and Bromacanthini is different from that of Cremasto-

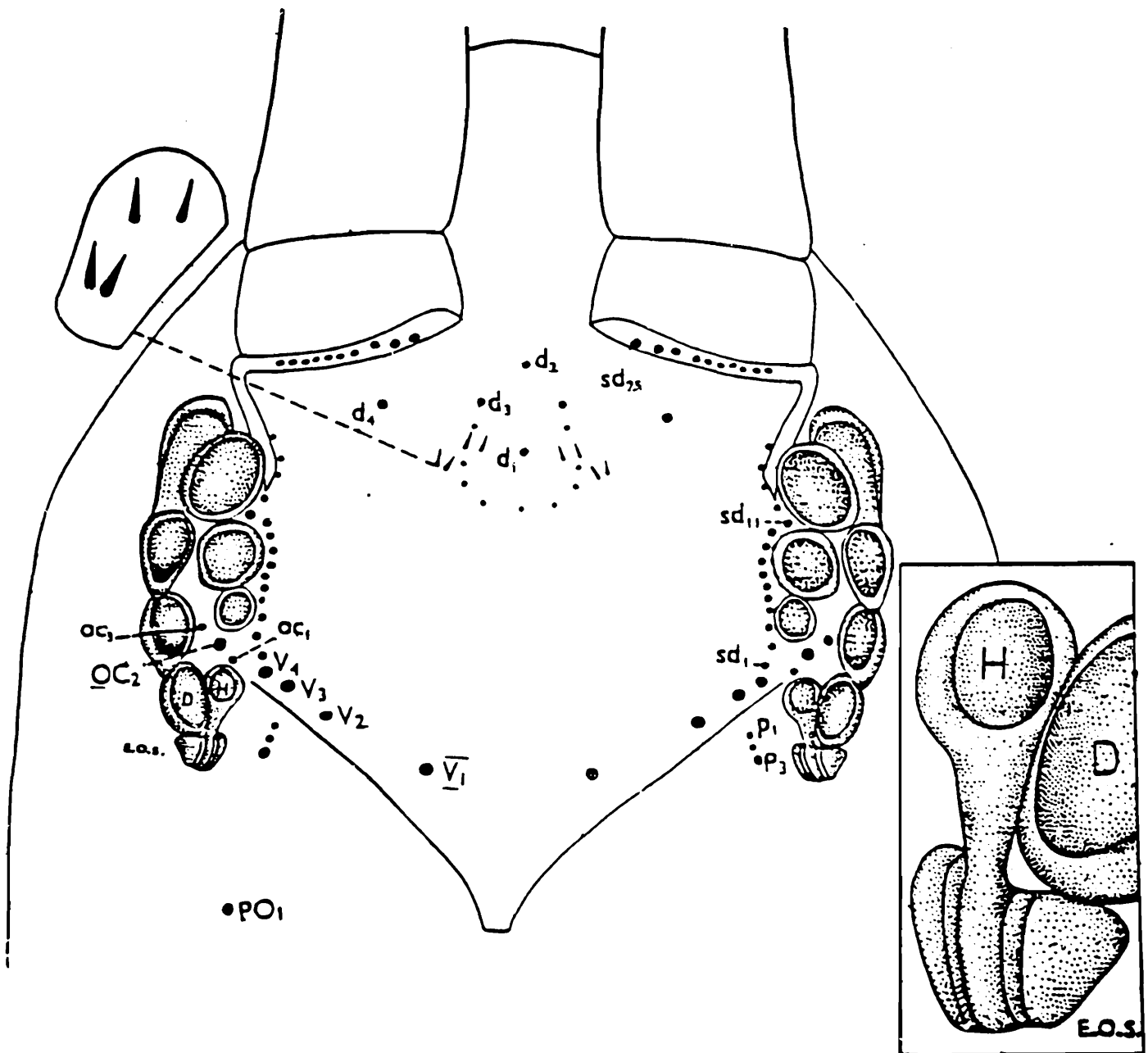


Fig. 27 : Cephalic Chaetotaxy of *Idiomeres*

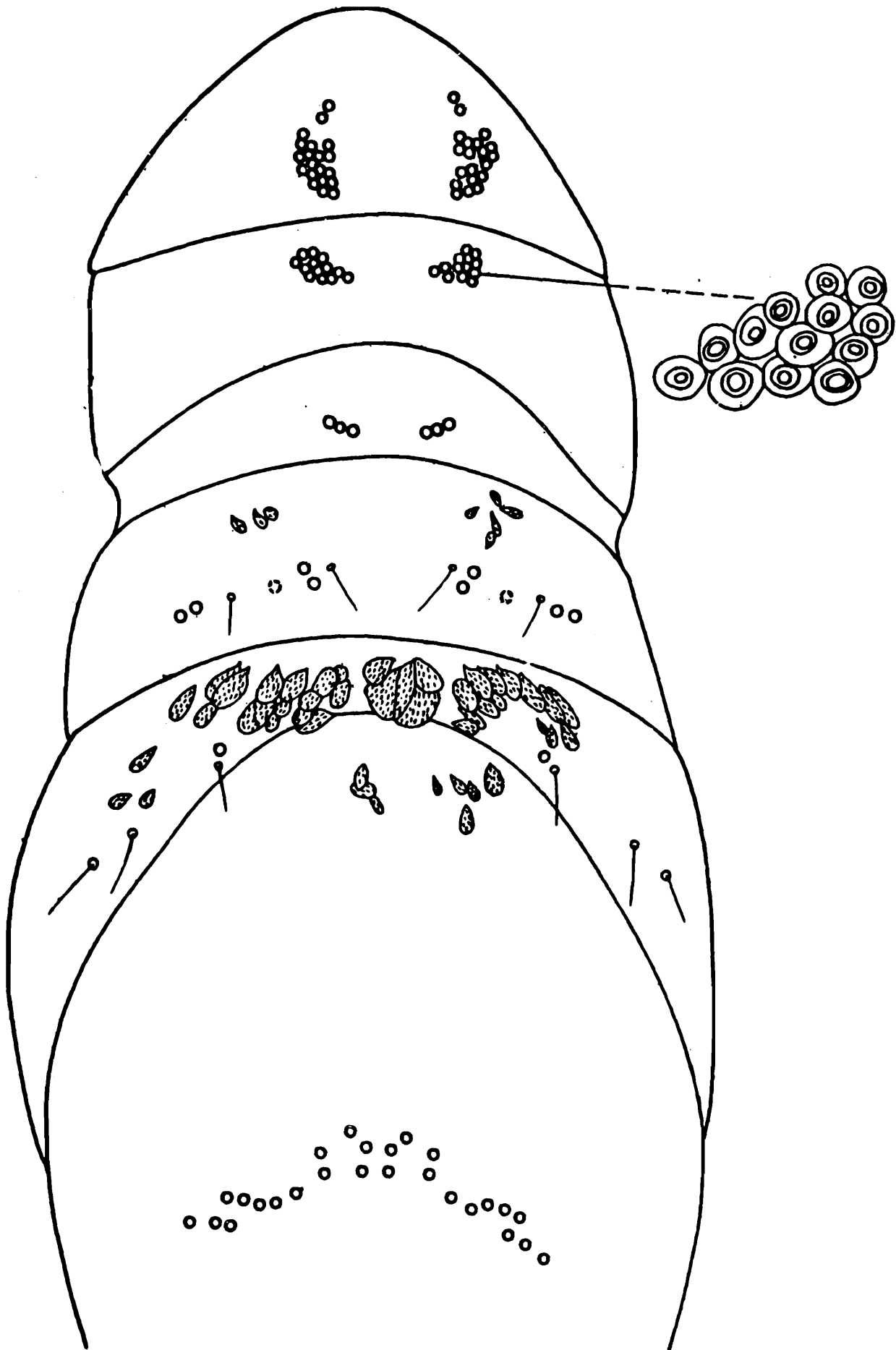


Fig. 28 : Chaetotaxy of Ths. II, III and Abds. I-IV of *Idiomerus*

cephalini and Callyntrurini not being flexed. In *Campylothbrax*, such macrochaetae, however, are distinctly different from those of stiff bristle-like macrochaetae occurring in the other genera of Paronellini and Bromacanthini. Microchaetae in Paronellini, for their variable nature, not considered here, except those which occur in the ocular, parietal and subdorsal regions and exhibit a state of near constancy.

## PARONELLINI

### *Paronella* Schött, 1893

1893. *Paronella* Schött, *Bih. K. Svenska Vet. Akad. Handl.*, **19** (2) : 1-28.

**Head** : Vertex devoid of any setae and scales ; dorsal region represented by  $D_1$ - $D_3$ , distance between  $D_1$  and  $D_2$  on each side closely approximated and their joining forms a narrow rectangle, right  $D_5$  located slightly above the left ; subdorsal setae c. 22, extremely variable in number and nature; ocular region with 5 microchaetae ( $oc_{1-5}$ ) on each side ; parietal region without setae ; postocular region with a single macrochaeta ( $PO_1$ ) on each side ; occipital and cervical regions without macrochaetae; area genalis represented by a single macrochaeta ( $G_1$ ) on each side, a characteristic feature of *Paronella* (Fig. 29).

**Body** : Th. II medially with 6 short, stiff and localised setae, arrangement asymmetrical ; Th. III and Abd. I without any setae ; Abd. II with 2 setae on each side in close proximity of lasiotrichia ; Abd. III with 8 setae on either side ; no distinct transverse row of setae occurs in the anteromedial region of Abd. IV, general surface of the segment with 6 setae on either side (Fig. 30).

### *Diranocentruga* Wray, 1953

1953. *Diranocentruga* Wray *J. Agric. Univ., Puerto Rico*, **37** (2) : 140-150.

**Head** : Vertex devoid of setae and scales ; dorsal region represented by  $D_0 + D_{1-5}$ , joining of  $D_1$ ,  $D_2$  of both sides yields a broad and wide rectangle, presence or absence of  $D_3$  of specific significance, while  $D_0$ ,  $D_4$  variable ; number and nature of subdorsal setae extremely variable and in most cases it varies between 10-20,  $SD_{1-7}$ ,  $SD_{10}$ ,  $SD_{17}$  usually represented by macrochaetae ; ocular region represented by microchaetae, number of which extremely variable, thus in the same species the number may vary from 6-11 ; parietal region represented by a single variable microchaeta ( $P_1$ ) ; postocular region with a single macrochaeta ( $PO_1$ ) on each side; genal, occipital and cervical regions devoid of macrochaetae (Fig. 31 ; P1. II, B).

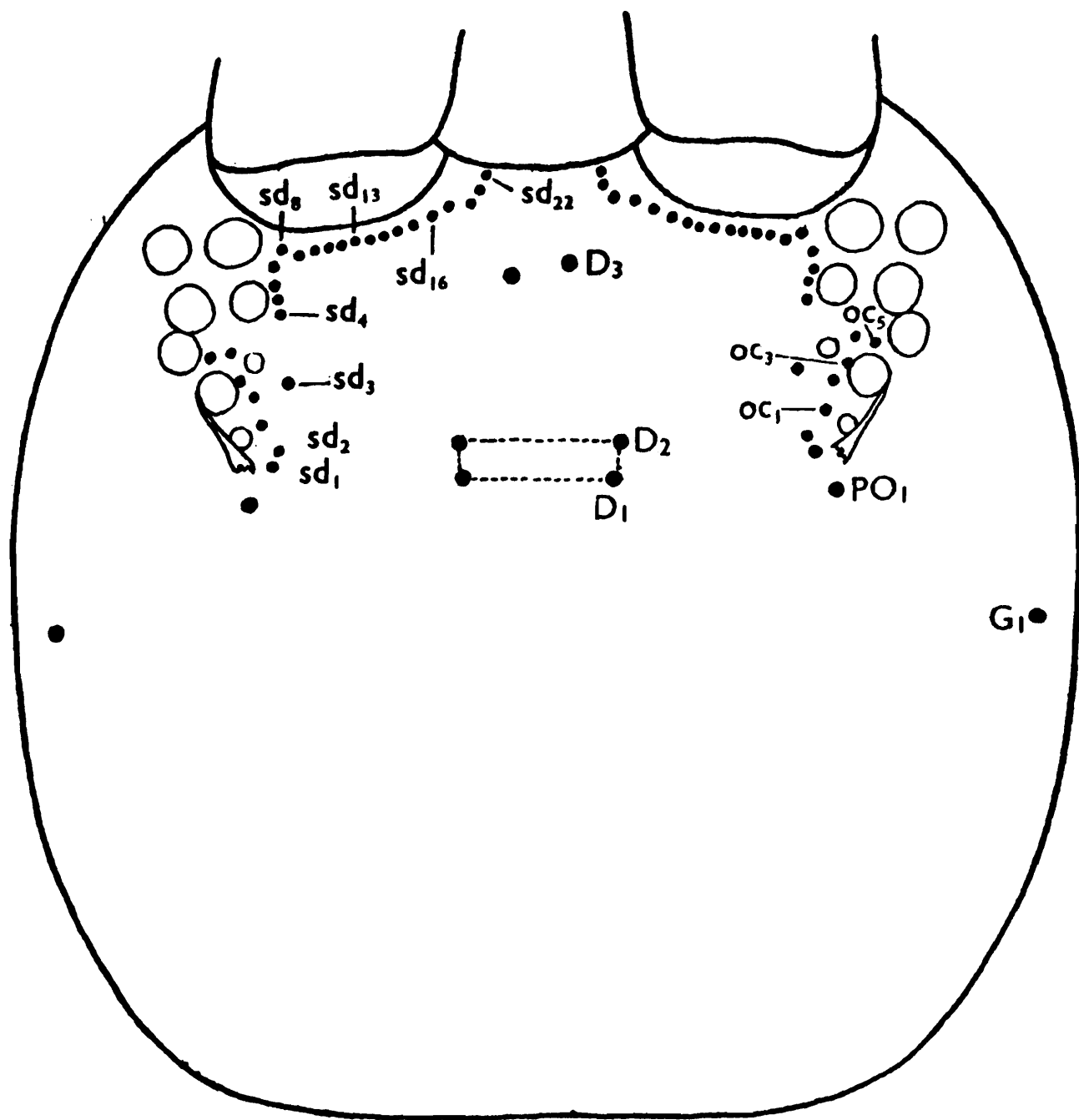


Fig. 29 : Cephalic Chaetotaxy of *Paronella fusca*

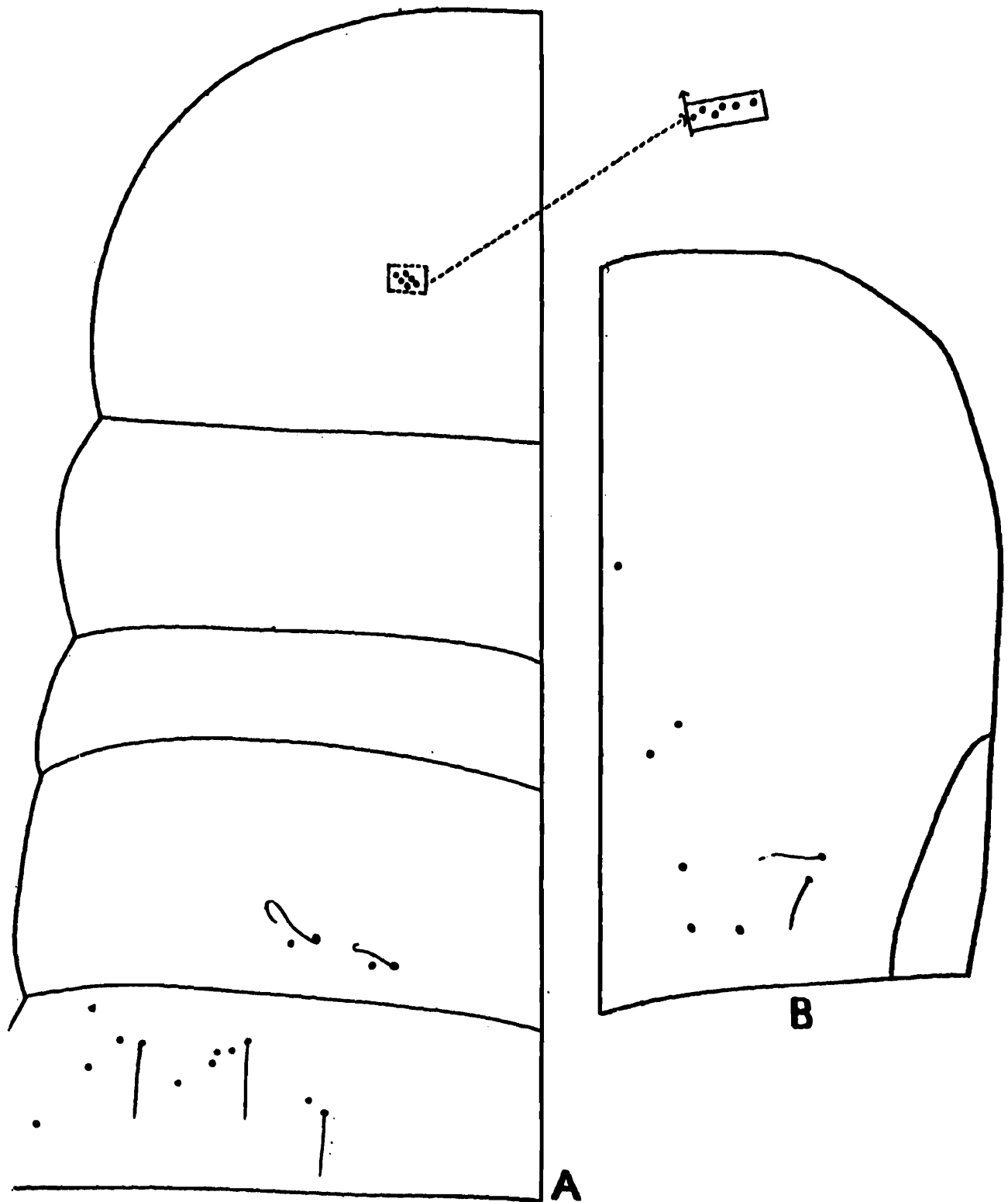


Fig. 30 : Body Chaetotaxy of *Paronella fusca*. A, Ths. II, III and Abds. I-III ; B, Abd. IV.

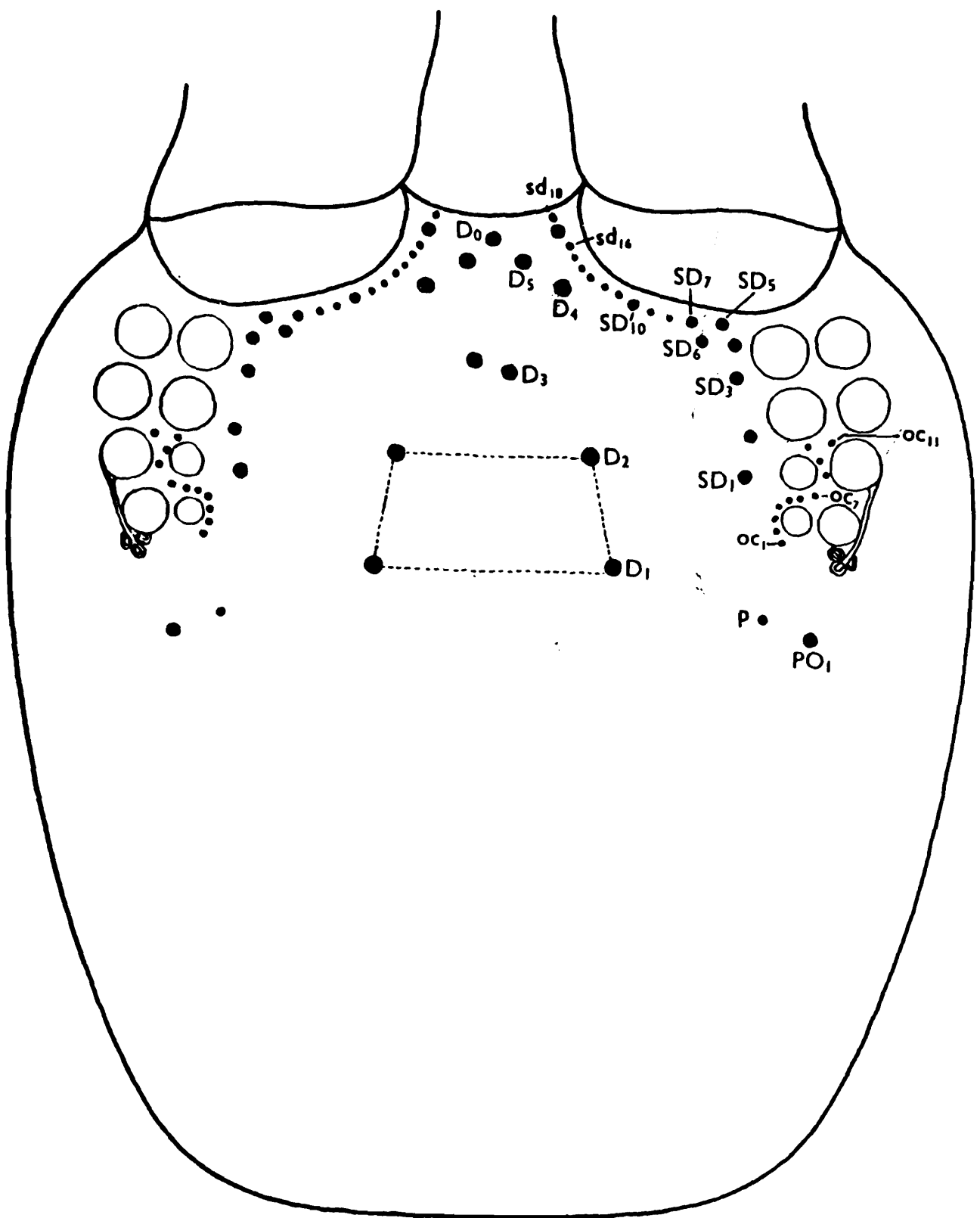


Fig. 31 : Cephalic Chaetotaxy of *Dicranocentruga*

*Body* : Th. II with 6 localised setae like *Paronella*; Th. III and Abds. I, II without setae ; Abd. III usually with 7 setae on either side distributed on its general surface ; no distinct transverse row of setae occurs medially on Abd. IV, but the general surface with 5 setae on either side ; 1+1 pseudopores present on each segment (Fig. 32 ; P1. I, B).

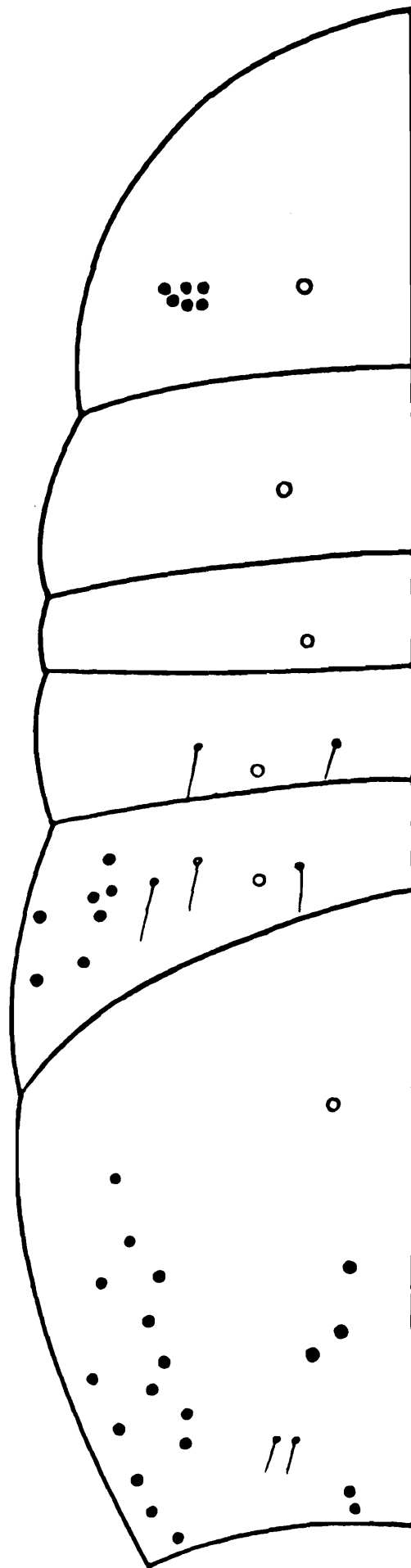


Fig. 32 : Chaetotaxy of Ths. II, III and Abds. I-IV of *Dicranocentrus*

***Campylothorax* Schött, 1893**

1893. *Campylothorax* Schött, *Bih. K. Svenska Vet. Akad. Handl.*, **19** (2) : 1-28.

**Head** : Vertex represented by  $V_{1-5}$ , all macrochaetae ; dorsal region represented by  $D_{1-4}$ , all macrochaetae ; subdorsal region represented by 10 setae on each side,  $SD_1$  only may be represented by a macrochaeta ; ocular region represented by 6 microchaetae on each side ( $oc_{1-6}$ ) ; postocular region represented by a single macrochaeta on each side ( $PO_1$ ) ; parietal region represented by 3 microchaetae ( $P_{1-3}$ ) ; occipital, cervical and genal regions without any setae (Fig. 33).

**Body** : Th. II posteriorly with 6 closely localised macrochaetae on each side in the arrangement of a "V" with a seta located within (P1. 1, C) ; Th. III with 4 localised macrochaetae on each side, Abds. I, II devoid of any setae, Abd. III on either side with 8 setae ; Abd. IV medially with a transverse row of 6 setae on either side (Fig. 34 ; P1. 1, E).

Setae found in this genus specially on body are distinct from those found in the other genera of Paronellini; they are cylindrical, folded and sometime with a distinct knob apically and are not so stiff as those in *Paronella* and *Dicranocentruga*.

**BROMACANTHINI, new tribe*****Bromacanthus* Schött, 1925**

1925. *Bromacanthus* Schött, *Sarawak Mus. Journ.*, **3** : 107-127.

**Head** : Vertex, occipital, genal and cervical regions without any setae ; area dorsalis anteriorly with 1 microchaeta on each side ( $d_1$ ) ; ocular region represented by 5 microchaetae ( $oc_{1-5}$ ) ; subdorsal region on each side with 7 microchaetae ( $sd_{1-7}$ ) ; parietal region represented by 3 microchaetae ( $p_{1-3}$ ) ; postocular region represented by a single macrochaeta ( $PO_1$ ) on each side (Fig. 35).

**Body** : Achaetotic in the total absence of setae at least on Ths. II, III and Abds. I-III; Abd. IV medially and laterally with a few setae (Fig. 36); each lasiotrichia at its base on each segment with some specialised scales, number and arrangement of which constant for each segment, thus : Abds. II [  $1_1$  (3),  $1_2$  (2) ], III [  $1_1$  (3),  $1_2$  (7) ], IV [  $1_1$  (4),  $1_2$  (5) ], accessory scales at the base of  $l_3$  on Abd. III, not noted (P1. 1, F).

***Lepidonella* Yosii, 1960 b**

1960. *Lepidonella* Yosii, *Bull. Osaka Mus. Nat. Hist.*, **12** : 9-38.

**Head** : Vertex, parietal, occipital, genal and cervical regions without setae; ocular region with 5 microchaetae ( $oc_{1-5}$ ) ; subdorsal region with 15 microchaetae ( $sd_{1-15}$ ) ; dorsal region represented by 3-4 macrochaetae located anteriorly ( $D_{1-4}$ ) [ Fig. 37].

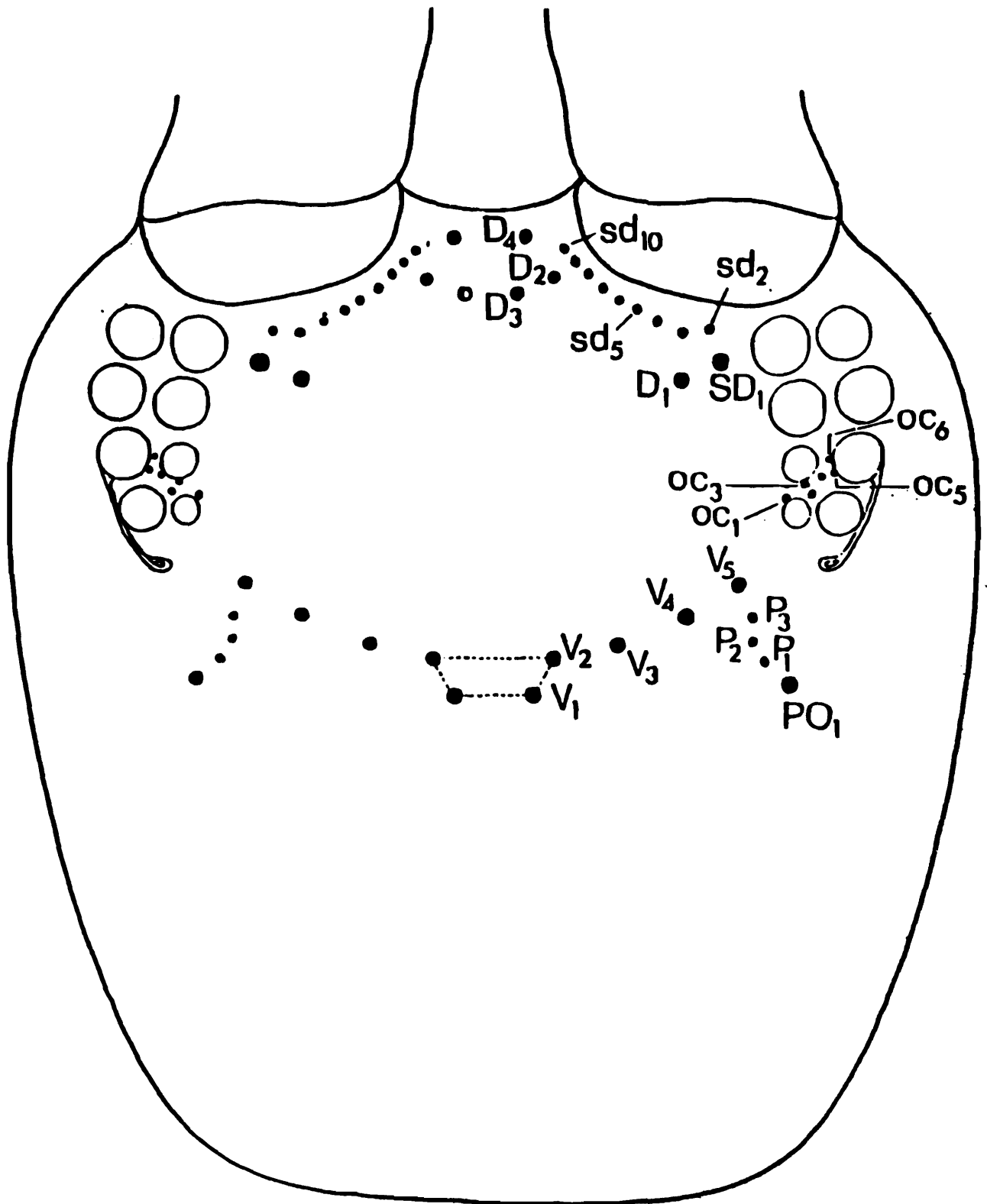


Fig. 33 : Cephalic Chaetotaxy of *Campylothorax*

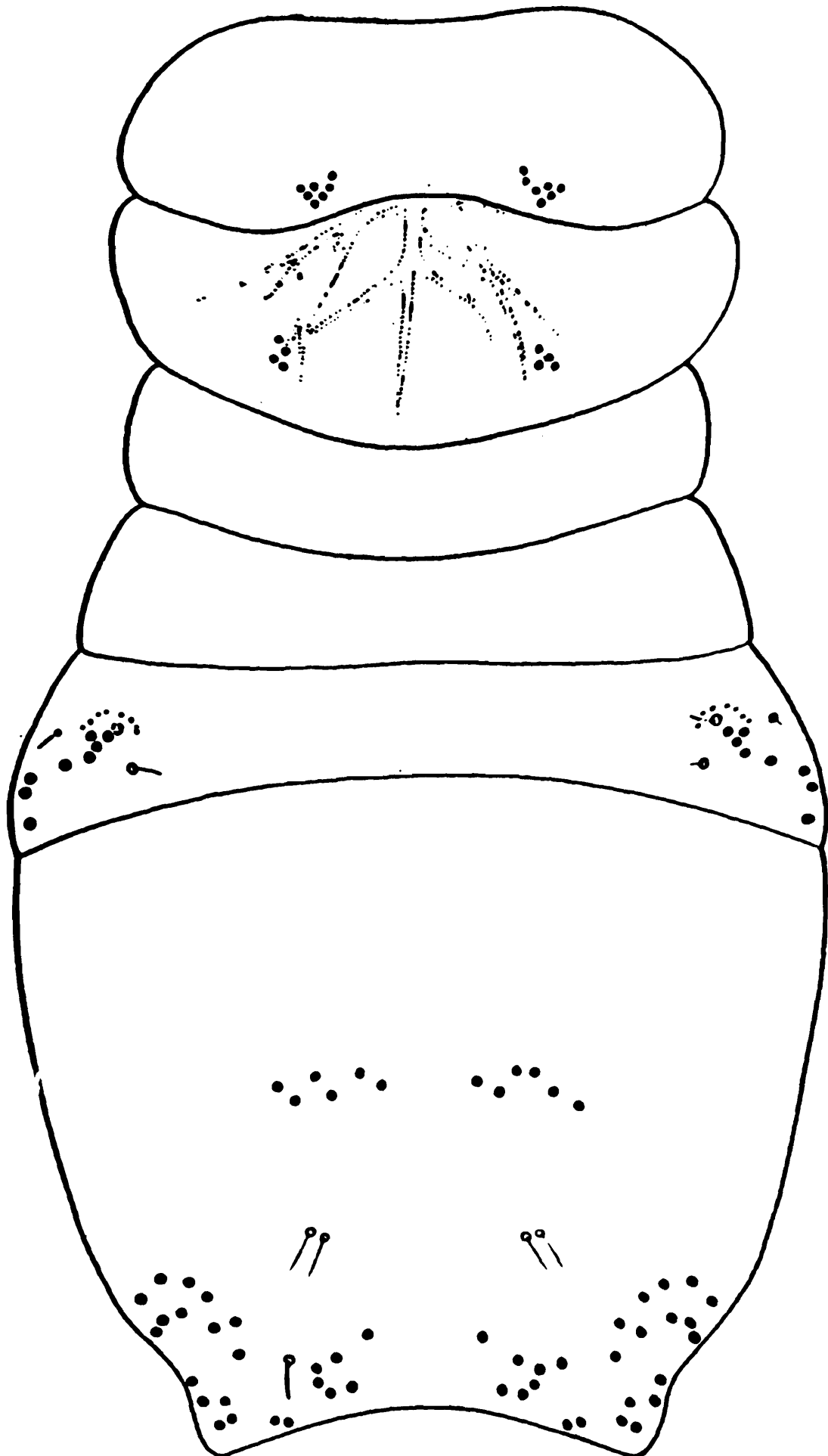


Fig. 34 : Chaetotaxy of Ths. II, III and Abds. I-IV of *Campylothorax*

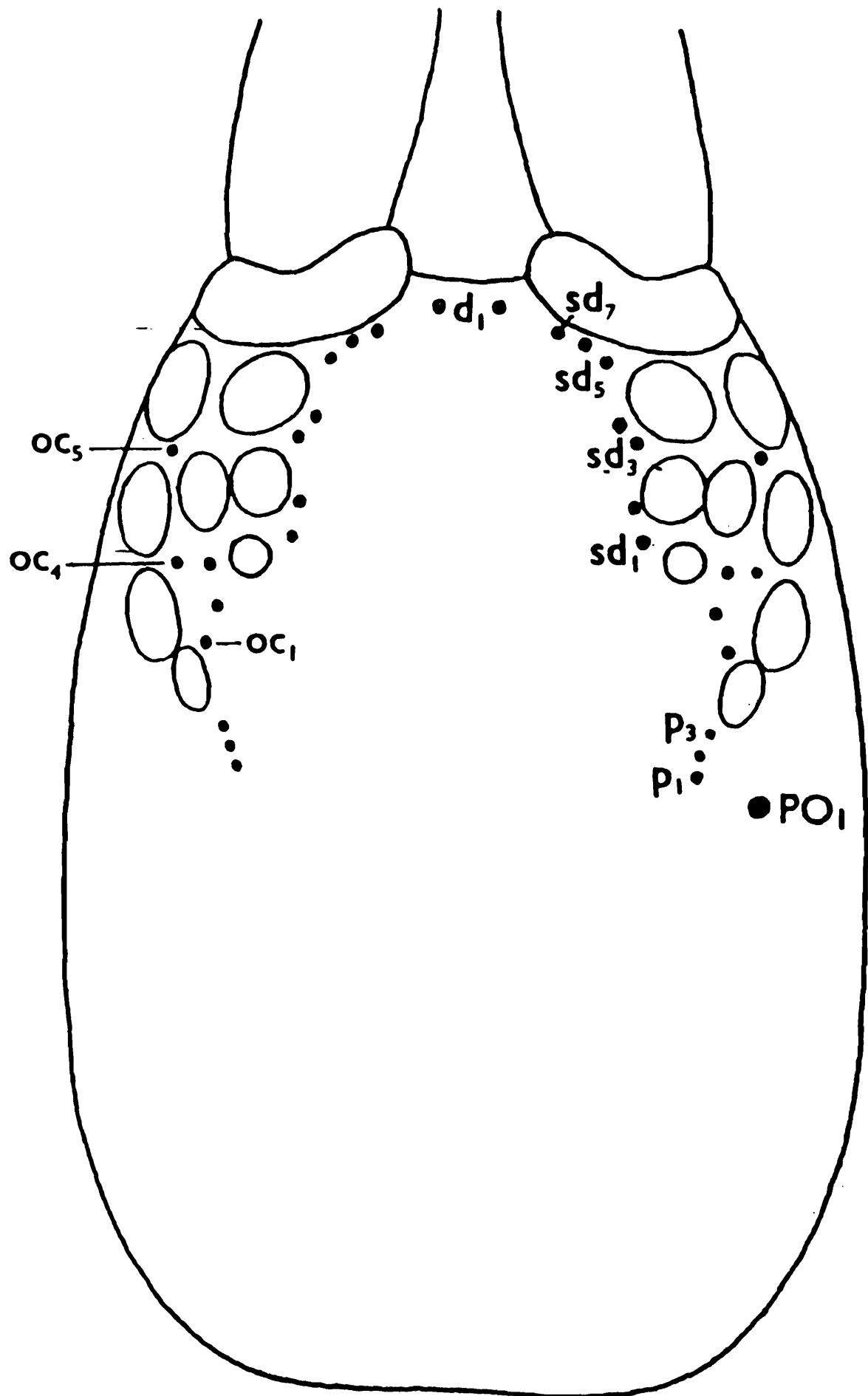


Fig. 35 : Cephalic Chaetotaxy of *Bromacanthus*

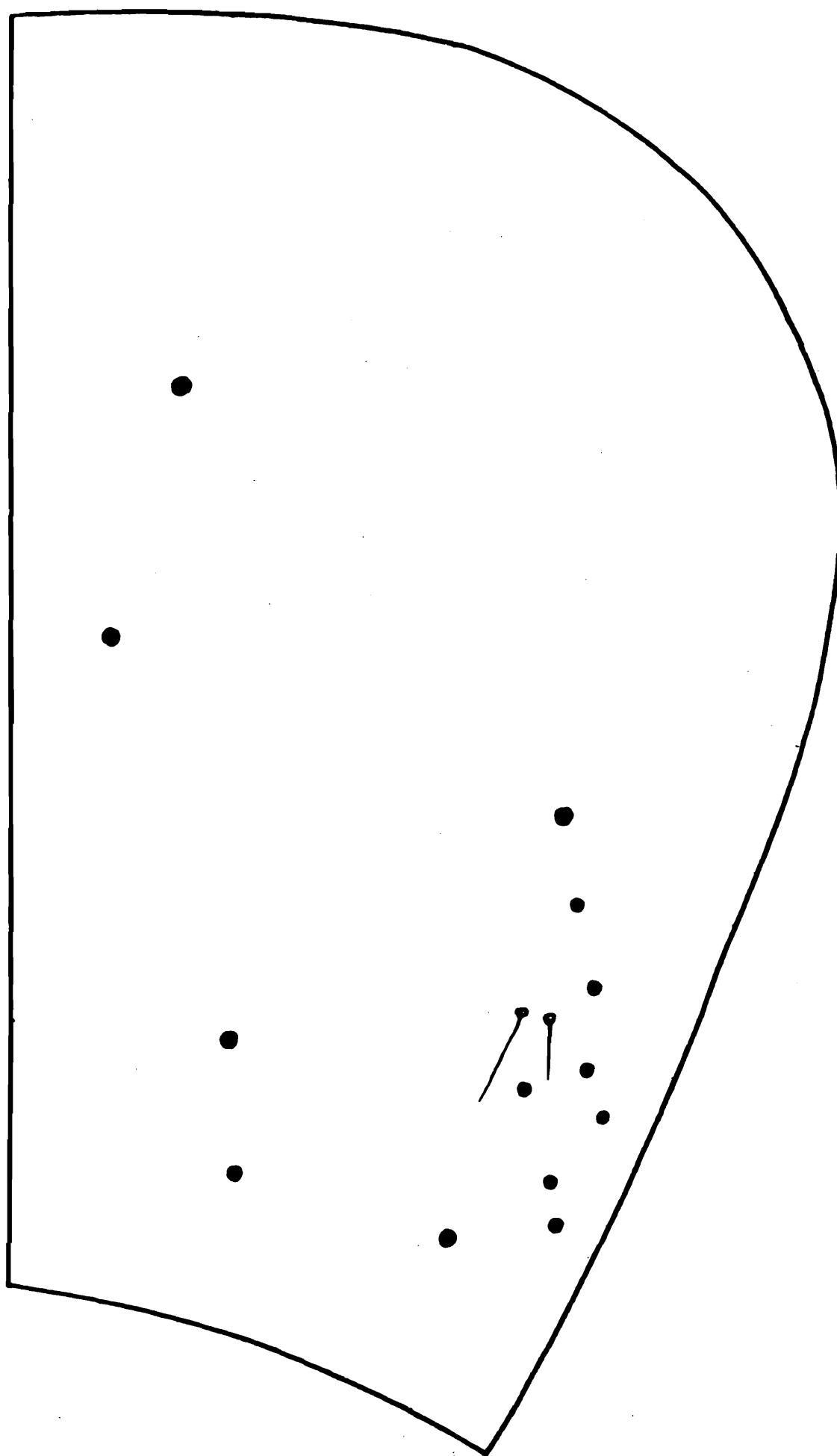


Fig. 36 : Chaetotaxy of Abd. IV of *Bromacanthus*

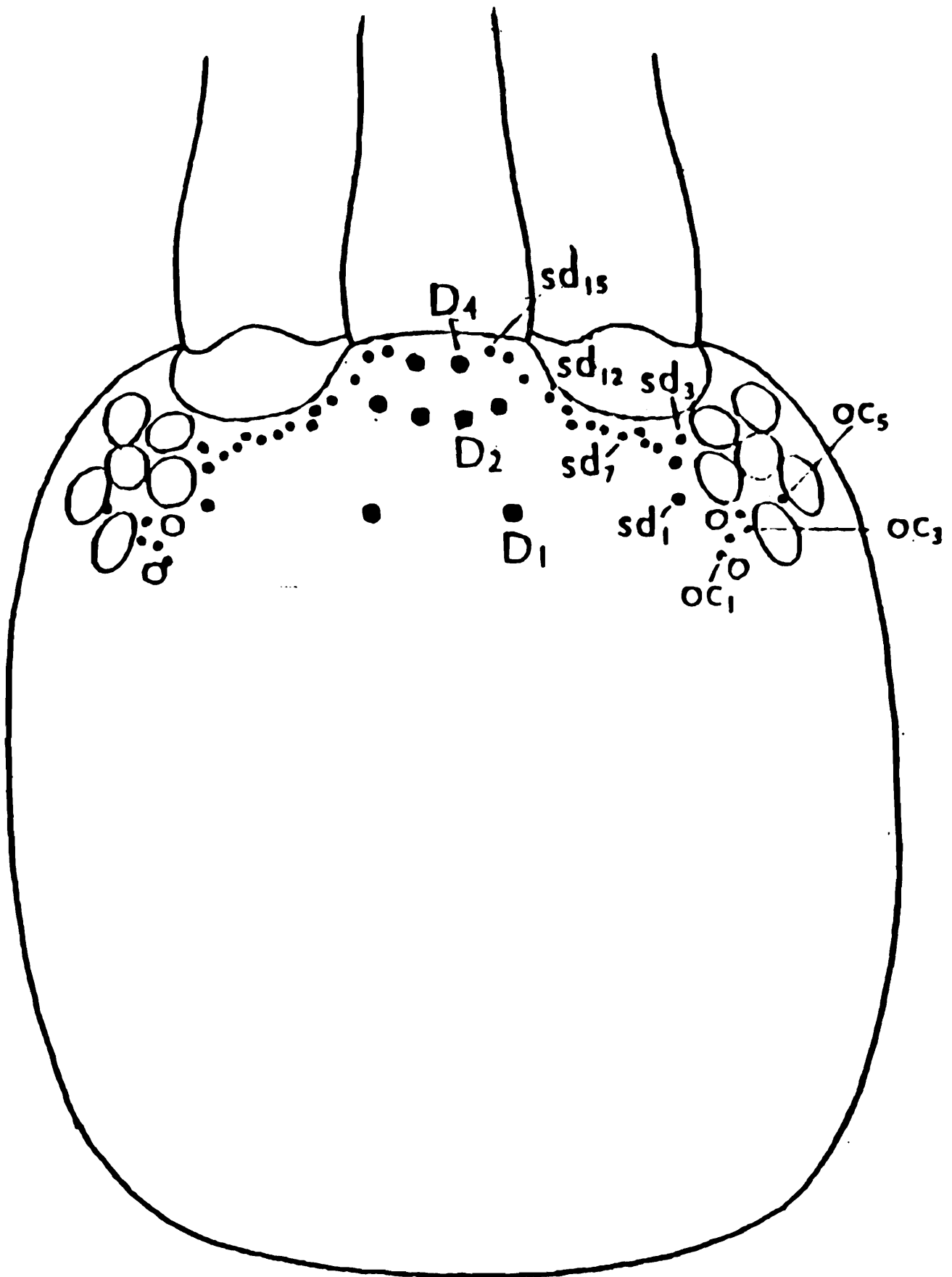


Fig. 37 : Cephalic Chaetotaxy of *Lepidonella*

**Body** : Achaetotic body in the total absence of setae at least on Ths II, III and Abds. I-III ; Abd. IV medially and laterally with setae, medial ones may be absent in some species, anteromedial transverse row of setae absent (Fig. 38) ; each lasiotrichia at its base on each segment with some specialised accessory scales, number and arrangement of such specialised scales constant for each segment (as in *Bromacanthus*) [Pl. 1, F].

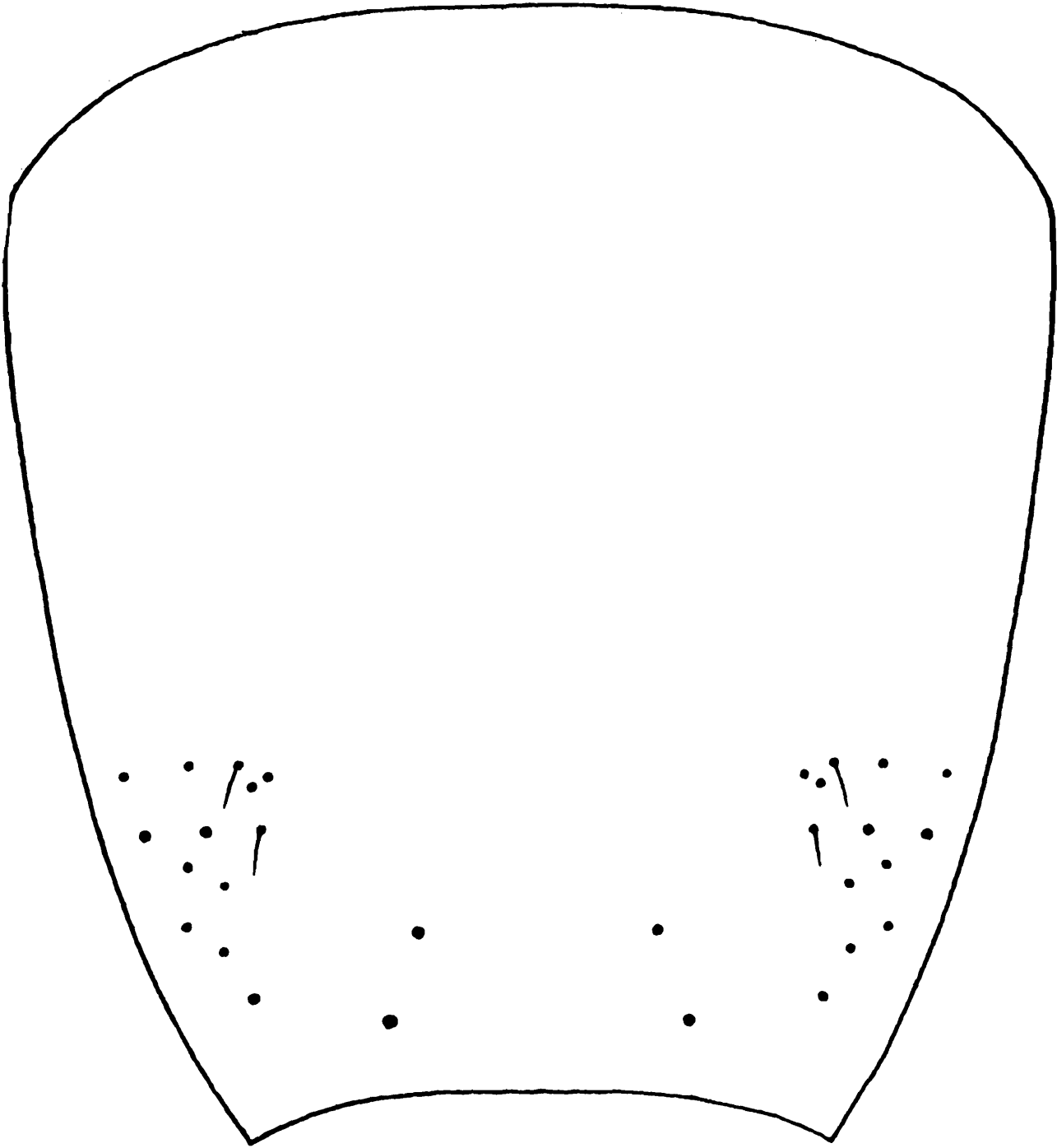


Fig. 38 : Chaetotaxy of Abd. IV of *Lepidonella*

***Trichorypha* Schött, 1893**

1893. *Trichorypha* Schött, *Bih. K. Svenska Vet. Akad. Handl.*, **19** (2) : 1-28

**Head** : Vertex, postocular, parietal, occipital and cervical regions without setae ; dorsal and subdorsal regions with setae ; ocular region represented by 7-8 microchaetae (oc<sub>1-8</sub>) ; genal region represented by 1 macrochaeta (G<sub>1</sub>) on each side ; postocular region on each side with 2 macrochaetae (PO<sub>1</sub>, PO<sub>2</sub>).

**Body** : Short, stiff, monflexed and localised setae found on Th. II (3), Abds. II (4), III (10) ; Abd. IV without a distinct medial transverse row of setae but with 9 setae on each side distributed on its general surface ; other segments devoid of setae (Fig. 39).

***Microparonella* Carpenter, 1916**

1916. *Microparonella* Carpenter, *Proc. Roy. Irish Acad.*, **33** (B) : 1-70.

The material which is available to the present investigator for study involves 1 syntype of *Microparonella caerulea* and lactotype and 1 paraloctotype of *Microparonella doveri*, all of which are mounted on slides. The nature of preservation of these specimens did not permit the author to make a thorough study on the cephalic and body chaetotaxy of these species. Following details, however, could be noted from these specimens : Vertex, parietal and occipital regions without setae ; dorsal region anteriorly with a few macrochaetae ; subdorsal setae near bases of the antennae represented by macrochaetae ; setae on cervical region appear to be absent. In general, chaetotaxy of the head of the genus agrees to some extent with that of *Pseudosinella*. Body, in general, achaetotic ; Th. III, Abds. II, III and IV only with a few localised actae.

**TROGLOPEDETINI Börner, 1913**

Salmon (1964) placed this tribe under Cyphoderinae on the basis of eyeless conditions in both Cyphoderini and Troglopedetini. Eyeless condition, in Collembola in most cases, is a secondary acquisition and in fact reduction of ocelli is of frequent occurrence in many species belonging to the same genus. Judging from the absence of large, foliate scale-like setae, presence of short, broad mucrones in the genera of Troglopedetini, particularly, in *Troglopedetes* Absolon, 1907, *Cyphoderopsis* Carpenter, 1917, *Trogolaphysa* Mills, 1938, members of this tribe are closer to Paronellini than Cyphoderini. However, the relationship of *Cyphoderopsis* and *Trogolaphysa*, which were synonymised by Salmon (1964) with *Troglopedetes*, is to be ascertained on the basis of examination of their cephalic chaetotaxy.

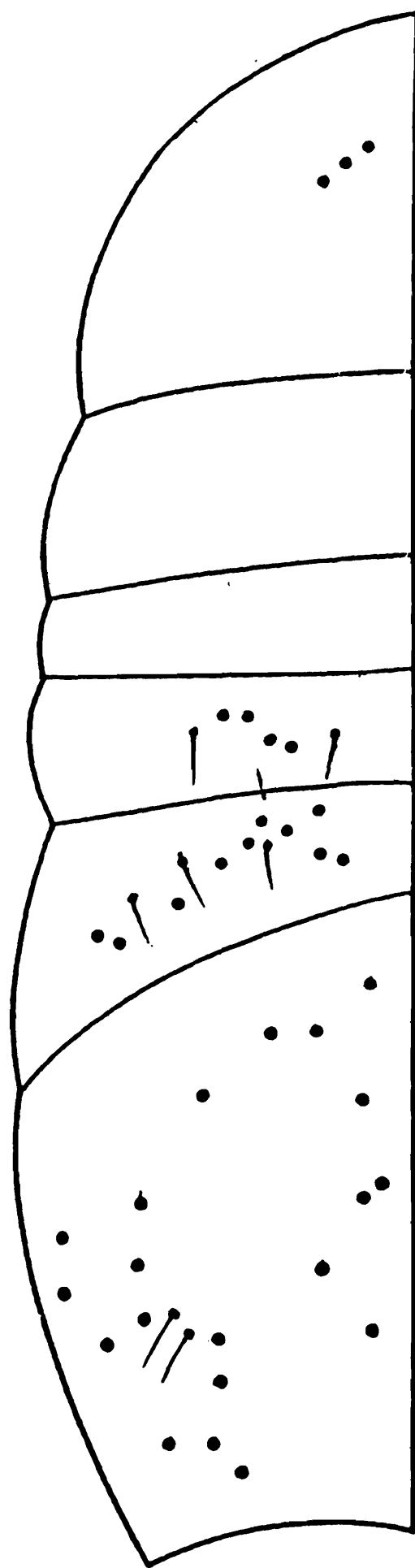


Fig. 39 : Chaetotaxy of Ths. II, III and Abds. I-IV of *Trichorypha*

Examination of some species of *Trogolophysa*, received through the courtesy of Prof. K. Christiansen, Grinnell, Iowa, U.S.A., collected from Mexican Caves, reveal the general pattern of chaetotaxy of the genus as follows :

*Head* : Vertex without any macrochaetae, arrangement of  $V_0, V_1, V_2$  on central vertex characteristic ; dorsal region anteriorly with 2+2 macrochaetae ( $D_1, D_2$ ) ; subdorsal region with *c.* 17 microchaetae ; postoccipital region with single macrochaeta ( $PO_1$ ) on each side ; occipital region with 1+1 macrochaetae ( $O_1 + O_1$ ); ocular region with 3 microchaetae ( $oc_{1-3}$ ); cervical, parietal, genal regions without any setae (Fig. 40).

*Body* : Short, stiff, nonflexed and localised setae present on Th. II (3) ; Abds. I and II devoid of any setae ; Abd. III with 10 setae on each side ; Abd. IV without a transverse medial row of setae but with 18 setae distributed on its general surface (figs. 41, 42).

## DISCUSSION

### (A) Cephalic Chaetotaxy :

Cephalic Chaetotaxy is an important feature in the genera under Paronellinae which not only aids in species-discrimination in certain genera but also reflects on the phylogeny and affinities of the genera from diverse regions of the world. Every genus, as the present study reveals, possesses a principal pattern of cephalic chaetotaxy and in certain genera differentiation takes place at species level by addition or deletion in the number of setae in some regions of head capsule. Such addition or deletion of setae, however, does not cause appreciable change in the principal pattern of orientation of setae which is characteristic at generic level. In certain genera like *Callyntrura*, *Dicranocentroides*, *Salina* and *Pseudosalina*, not much differentiation in cephalic chaetotaxy occurs in individual species. In these genera the species can be subdivided into different species-groups having the similar cephalic Chaetotaxy. Morphological differences which exist in *celebensis* and *indica* species-groups of *Salina* are reflected specially in the chaetotaxy of head. Such differentiation occurs in areas occipitalis and cervicalis. Thus the occipital region in the species of *celebensis*-group is represented by 1+1 setae ( $O_1 + O_1$ ) in contrast to the *indica* species-group which possess at least 3+3 setae ( $O_1, O_2, O_3$ ); *indica* and *celebensis* species-groups further differ from each other in the following points: (a) area cervicalis: 3 in *indica*-group vs. 2 in *celebensis*-group, (b) area parietalis : 0 in *indica*-group vs. 1 in *celebensis*-group (microchaetae in the parietal region of *celebensis*-group are not taken into consideration). Cephalic chaetal index of the two groups, as mentioned above, corresponds well to the number and arrangement of setae on each tergite. The number, nature and orientation of setae on vertex and ocular regions are the characters which are shared by both the species-groups of *Salina*.

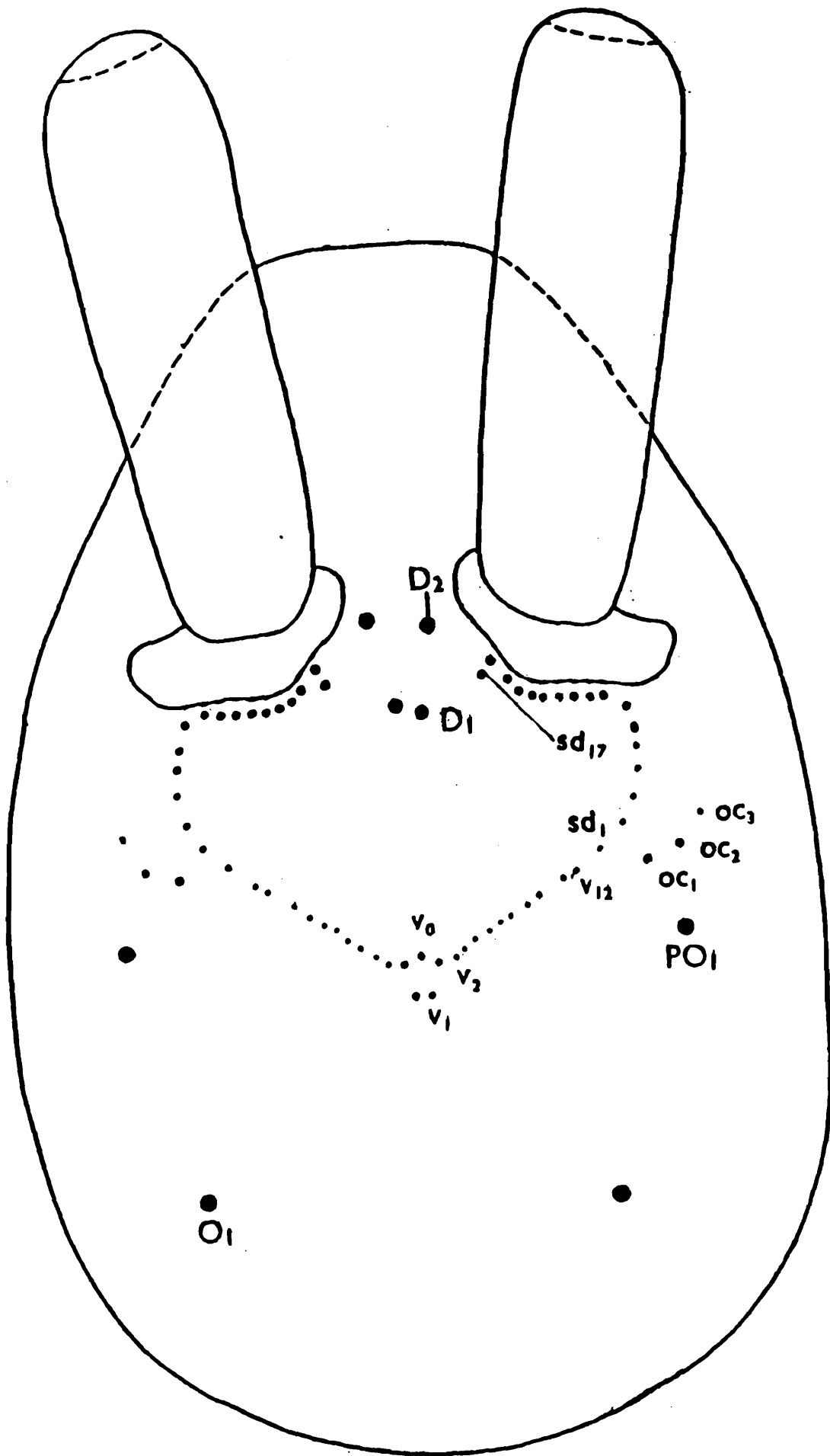


Fig. 40 : Cephalic Chaetotaxy of *Trogolaphysa*

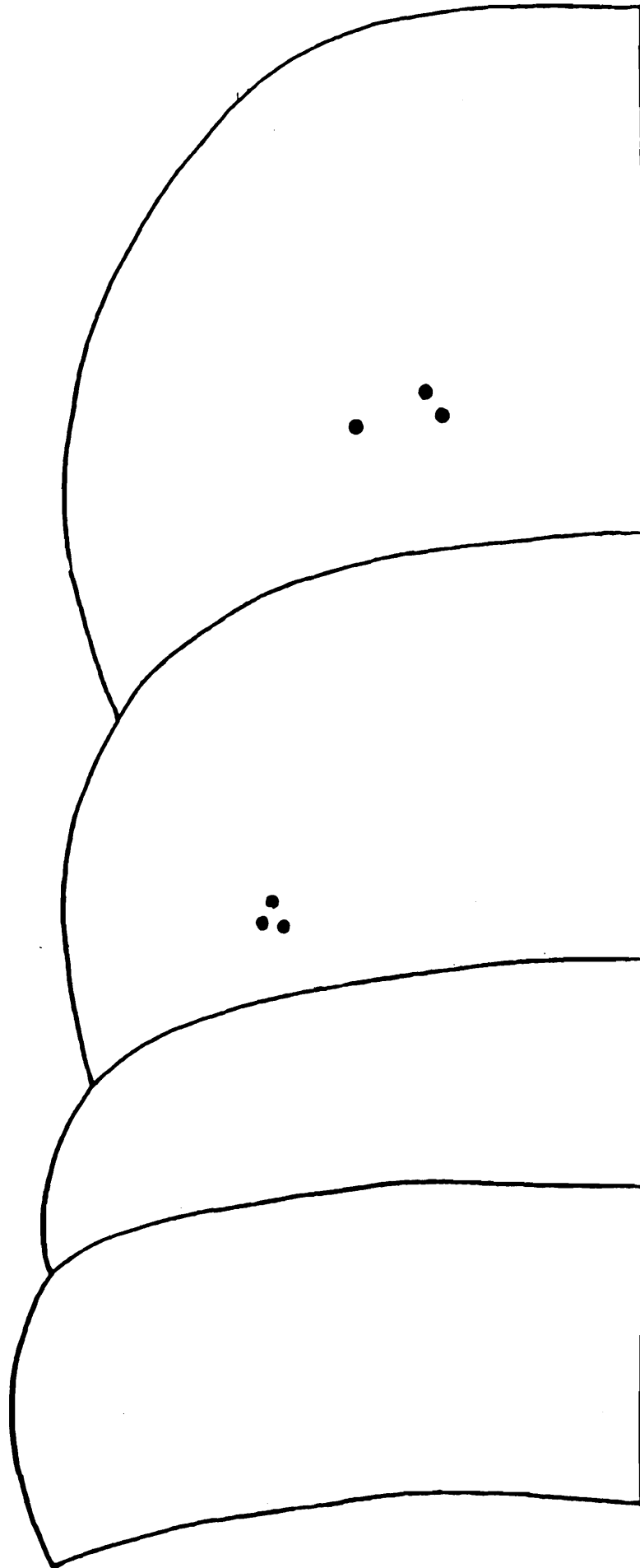


Fig. 41 : Chaetotaxy of Ths. II, III and Abds. I, II of *Trogolaphysa*

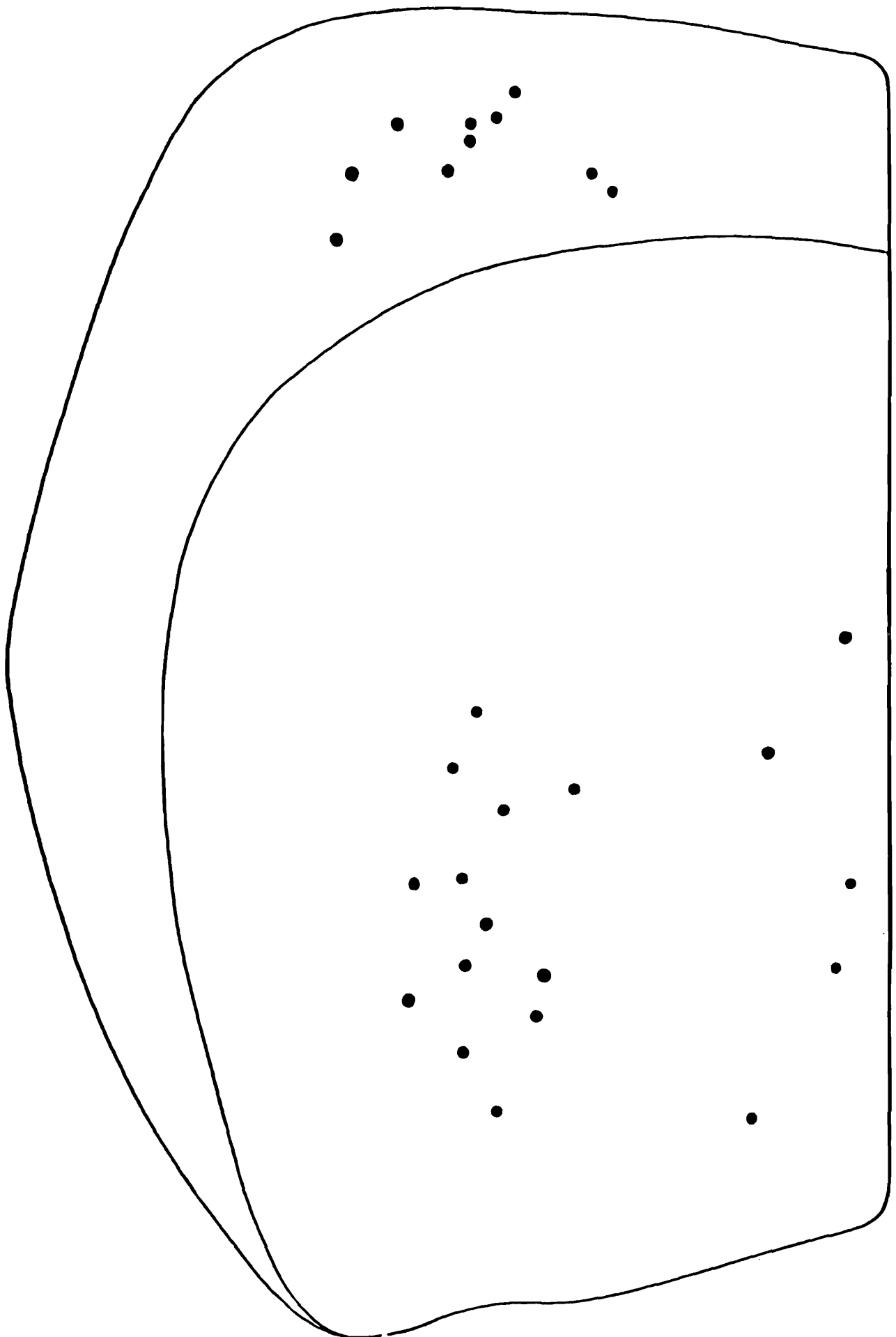


Fig. 42 : Chaetotaxy of Abds. III, IV of *Trogolaphysa*

Chaetotaxic pattern of cephalic region in *Yosiia* is quite characteristic and different from the above genus. Its specialisation has resulted from the reduction of macrochaetae on vertex which is only 1+1 ( $V_1 + V_1$ ) and also in the presence of a number of dorsal macrochaetae ( $D_{1-3}$ ). The number, nature and orientation of ocular setae in *Yosiia*, however, correspond to that of *Salina* and *Pseudosalina* and thus indicate its close affinity with those genera. Presence and nature of insertion of 1+1 parietal ( $P_2 + P_2$ ) and 1+1 occipital ( $O_1 + O_1$ ) macrochaetae indicate its further affinity with the *celebensis* species-group of *Salina*. Number of macrochaetae in cervical region of the genus corresponds to the *indica*-group of species.

*Akabosia*, although possesses many specialised morphological characters which separate it from the closely related genera like *Salina*, *Yosiia* and *Pseudosalina*, it is not so much specialised in its cephalic chaetotaxy as *Yosiia*. The presence of 2+2 macrochaetae ( $V_1, V_2$ ) on vertex in a trapezoid arrangement, absence of macrochaetae in area dorsalis are the major characters *Akabosia* shares with both the species-groups of *Salina*. Presence of 3 ocular setae further indicates its phylogenetic relationship with *Salina*, *Yosiia* and *Pseudosalina*. However, representation of  $oc_2$  by a microchaeta, a specialisation in *Akabosia*, indicates its affinity with the pseudoscaled genera *viz.*, *Callyntrura* and *Dicranocentroides*.

The most outstanding specialisation in cephalic chaetotaxy of *Pseudosalina* is an increase in the number of macrochaetae in vertex, which clearly distinguishes it from the genus *Salina*. The presence of  $O_1$  and a general increase in the number of macrochaetae in other regions of head along with their orientation are also the significant specialisations of the species of this genus. The number, nature and orientation of ocular setae ( $oc_1-OC_2-oc_3$ ) signify its relationship with the genus *Salina* and other related genera. Further, presence of more than 1+1 macrochaetae in the occipital region indicates its affinity with *indica*-group of *Salina*.

*Dicranocentroides* and *Callyntrura* exhibit close affinities not only through their morphological characters but also through cephalic chaetotaxy. Thus the number and arrangement of macrochaetae on vertex and ocular region, absence of macrochaetae on parietal and cervical regions and also the presence of single macrochaeta in the postocular region indicate their close relationship. In *Dicranocentroides*, the presence of 2 macrochaetae on area genalis ( $G_{1-2}$ ) and 1 macrochaeta on area occipitalia are its specialised characters. In a few examples of *Dicranocentroides flavescens*, certain variable macrochaetae are noted on vertex, dorsal and parietal regions. Such setae are of rare occurrence and it may be considered as insignificant. However, this variation in cephalic chaetotaxy has not been encountered in the species of any other genus. In *Callyntrura*, no difference has been observed so far in the general pattern of chaetotaxy in the species belonging to two sub-genera. Such absence of specialisation in cephalic chaetotaxy indicates perhaps the little importance of dental scale appendage as a morphological character. It is interesting to note that although *Dicranocentroides* and *Callyntrura* are members of the tribe Callyntrurini, yet they

possess the same number of ocular macrochaetae with almost identical orientation as that of *Salina*, *Pseudosalina*, *Yosiia* and *Akabosia*. However,  $oc_2$  in *Dicranocentroides* and *Callyntrura* is a microchaeta in contrast to the first three genera, where it is represented by a macrochaeta. *Idiomerus* is unique in its cephalic chaetotaxy, specially that of vertex (by reduction of macrochaetae)—the only character which remains linked with its most specialised humped mesothorax including its characteristic mucronal pattern and body chaetotaxy. The genus has a mosaic of characters common to *Campylothorax*, *Callyntrura* and *Dicranocentroides*. Barring the mesothoracic hump and e.o.s., common characters which it shares with *Dicranocentroides* and *Callyntrura* are the presence of pseudoscales, polychaetotic condition and 3 ocular setae. Presence of 4+4 frontal spines in *Idiomerus* makes it closer to *Callyntrura*.

In general, the genera under the tribe Paronellini appear close to the genera *viz.*, *Dicranocentroides* and *Callyntrura* in the paucity of macrochaetae in the parietal, occipital, cervical and genal regions. *Campylothorax*, although is a member of the tribe Paronellini, exhibits affinity with *Callyntrura* and *Dicranocentroides* in the presence and nature of orientation of macrochaetae on vertex. Presence of 4 dorsal setae ( $D_{1-4}$ ) and 6 ocular microchaetae ( $oc_{1-6}$ ) are the specialised characters of *Campylothorax*. It is worthwhile to note that in some characters such as the structures of mucrones and foot-complex, *Campylothorax* is akin to *Callyntrura* and *Dicranocentroides*.

Cephalic chaetotaxy of *Paronella* resembles *Dicranocentruga* in the nature of distribution of setae on head and body. Thus insertion of  $D_1$ ,  $D_2$  in both genera is fundamentally alike i.e., joining of  $D_1-D_1$  and  $D_2-D_2$  forms a rectangle in both the genera. But the nature of rectangle formed in *Paronella* is entirely different from the species of *Dicranocentruga* (Fig.31; P1.II,B). Further, the number of dorsal setae in *Dicranocentruga* varies from  $D_0 + D_{3-5}$  while in *Paronella*, it is strictly 3. *Paronella*, however, differs from *Dicranocentruga* in the presence of  $G_1$  on each side (*vs.* absent in *Dicranocentruga*) and in the constancy of ocular microchaetae. Constancy of  $PO_1$  in both further points out their relationship.

Cephalic chaetotaxy of *Trichorypha* shows its affinity with the above 2 genera (*viz.*, *Paronella* and *Dicranocentruga*). This affinity is reflected through the absence of macrochaetae on vertex, parietal, occipital and cervical regions. Presence of  $PO_1$ ,  $PO_2$ ,  $G_1$  and the nature of dorsal setae, however, appear to be the significant specialisations of this genus.

*Bromacanthus* is related to *Paronella*, *Dicranocentruga* and *Microparonella* in the absence of macrochaetae on vertex, parietal, occipital and cervical regions. Absence of macrochaetae in the postocular region in *Lepidonella* and in the dorsal region in *Bromacanthus* may be considered as specialisation of these two genera. Although macrochaetae occur in the dorsal region of *Lepidonella* and are lacking in

*Bromacanthus*, their distribution pattern is altogether different from *Paronella* and *Dicranocentruga*. General chaetal pattern of *Lepidonella* and *Bromacanthus* comes close to some genera under Lepidocyrtini.

In general, the rest of the genera, represented in the islands of the Oriental and Australian Regions and also in Australia and New Zealand, appear related to one another on the basis of cephalic chaetotaxy. Genera like *Paronellides*, *Pseudoparonella* and *Paronana* exhibit greater number of macrochaetae in the dorsal, occipital, cervical and genal regions with an increase in the number of ocular microchaetae. *Paronellides* is close to *Metacoelura* in (1) 4 ocular microchaetae on each side, (2) number and orientation of macrochaetae on vertex, postocular, parietal and genal regions. In *Paronellides*, however, the number of macrochaetae on dorsal, occipital and cervical regions is larger than *Metacoelura* and their nature of orientation is also characteristic. *Paronellides* and *Metacoelura* are distinct from the scaleless genera from India (both cosmopolitan and endemic ones) in the presence of larger number of macrochaetae in all the regions of head capsule and specially in vertex, dorsal and ocular regions. *Pseudosalina* from India is somewhat close to the above-mentioned Australian genera in the presence of a fairly large number of macrochaetae, specially on vertex and occipital regions. Presence of 1+1 parietal macrochaetae ( $P_1 + P_1$ ) and their nature of insertion also reflect on the affinity of *Pseudosalina* with the above mentioned genera.

*Paronana* is characterised by the number and arrangement of macrochaetae in vertex. It is related to *Pseudoparonella* and *Parachaetoceras*, members of the tribe Callyntrurini, in the identical number and orientation of setae in ocular, parietal and cervical regions. *Parachaetoceras*, *Glacialoca* and *Pseudosalina* also appear to be related to *Paronana* in the presence of macrochaetae on areas dorsalis, parietalis, postocularis and cervicalis. Number of macrochaetae on area genalis of those genera and their orientation are also similar to *Paronana*. Further studies on cephalic chaetotaxy of *Glacialoca* and *Parachaetoceras* on the basis of fresh topotypes are needed to establish their exact affinities.

Above discussion attempts to reveal the relationships of the various genera on the basis of cephalic chaetotaxy. In general, it appears to represent a plesiomorphic character and is useful to ascertain the phylogenetic connections that exist between the genera under Paronellinae.

#### B) *Chaetotaxy of Tergites* :

Chaetotaxy of tergites appears to be of significance if considered in a broad sense (Table-IV). However, chaetotaxy of the medial or anteromedial region of Abd. IV exhibits specialisation in a group of genera. Thus in both the species groups of *Salina*, Abd. IV anteromedially is always with 2+2 macrochaetae which may orient themselves either in a trapezoid fashion or in a straight line. Such number of macrochaetae is although observed in *Pseudosalina*, their arrangement is, however,

distinctly different from *Salina*. In certain genera, the median region of Abd. IV has a distinct transverse row of macrochaetae in all the species examined (e.g., *Callyntrura*, *Dicranocentroides*, *Paronana*, *Paronellides*, *Pseudoparonella*, etc.). This is possibly an indication of the relationship that exists among these genera belonging to two different tribes (i.e., Cremastocephalini and Callyntrurini). In *Paronella* and *Dicranocentruga*, the presence of 6 setae on either side of Th.II in most of the species together with their nature of localisation indicate their close affinity.

The genera under Paronellinae can be distinctly subdivided into two broad categories in the presence and absence of flexed macrochaetae specially on thoracic segments and first two addominal segments together with the nature of scales clothing body (Table-IV): (A) True or typical scaled genera without well developed macrochaetal clothing i.e., achaetoic and (B) Scaleless or pseudoscaled genera with a clothing of well developed flexed macrochaetae i.e., chaetoic. The first category (i.e., "A") represents two distinct types :

(a) *Lepidose* (Yosii, 1961a): Similar to the chaetotaxy found in the genera under Lepidocyrtini in which the thoracic segments and first three abdominal segments at least are totally devoid of any type of setae dorsally; Abdomen IV in these genera exhibit some longer and shorter acuminate setae while Abds. V and VI some pubescent setae; each lasiotrichium at its base has some specialised scales and setae in fixed number and arrangement (P1.I,F). The lepidose condition is a characteristic for the species belonging to *Lepidonella* and *Bromacanthus*.

(b) *Parachaetose* (New term): This condition of chaetotaxy is somewhat intermediate between lepidose of category "A" and oligochaetose of category "B" It is characterised by the reduction of setae on most of the segments and their total absence at least on a few segments. Thus the species belonging to the genera viz., *Paronella*, *Dicranocentruga*, *Campylothorax*, *Microparonella*, *Trichorypha* and *Trogolophysa* although lack well developed macrochaetae on thoracic and first two abdominal segments, some localised, short and stiff setae occur on a few of such segments. This type of chaetotaxic condition can neither be designated as lepidose nor oligochaetose from the point of view of the nature of setae and their nature of localisation. The new term parachaetose is, hence, proposed to indicate the specialised nature of chaetotaxy of these genera, which is close to "lepidose" than "oligochaetose" condition.

The category "B" includes the genera with well developed flexed macrochaetal clothing on all segments and with pseudoscales or scaleless. According to the abundance of setae on each segment, this category can be broadly subdivided into two groups :

(a) *Oligochaetose* : This type is characterised by the reduction in the number of flexed macrochaetae on all segments, specially on Ths. II, III and Abds. I, II. The

species, belonging to genera *viz.*, *Yosiia*, *Akabosia* and *Salina* (*celebensis* group), usually represent the oligochaetotic type of chaetotaxy.

(b) *Polychaetose* : The genera with profuse clothing of macrochaetae on all segments. Most of the genera under Cremastoeophalini and Callyntrurini exhibit the polychaetotic condition. It deserves mentioning that the subdivision of category "B" into two types (*viz.*, oligochaetotic and polychaetotic) is an arbitrary one in the sense that a sharp demarcation line can not be drawn between these two types. For examples, a few species of *Callyntrura* exhibit oligochaetotic condition. The above classification is, however, derived on the basis of majority of species studied for each genus and this chaetotaxic classification, in general, is proposed for Paronellinae.

*A key to the Genera of Paronellinae on the Basis  
of Cephalic Chaetotaxy*

A key to the genera of Paronellinae is given below on the basis of cephalic chaetotaxy. While the basic plan of chaetotaxy is likely to remain constant, the key may need little modification in future in view of further additions of species to any genus, having greater or fewer chaetal number in any particular subregion. This chaetotaxic key reflects the taxonomically important morphological differences that exist between different genera of Paronellinae.

- 1 Vertex without macrochaetae.....13
  - Vertex with macrochaetae .....2
2. Vertex medially only with 1+1 ( $V_1 + V_1$ ) macrochaetae inserted in a straight line; dorsal macrochaetae 3+3 ( $D_1, D_2, D_3$ ); macrochaetae present on areas parietalis, occipitalis, cervicalis; ocular setae 3 on each side,  $oc_2$  a macrochaeta (Fig. 8) .....*Yosiia*
  - Vertex with more than 1+1 macrochaetae .....3
3. Vertex with 2+2 macrochaetae, inserted in a trapezoid fashion; macrochaetae absent on areas dorsalis and genalis; ocular setae 3 on each side,  $oc_2$  may be macro- or a microchaeta .....4
  - Vertex at least with 6+6 macrochaetae inserted in a rectangle or in the form of a "V"; macrochaetae present or absent on areas dorsalis and genalis; ocular setae 3 or more on each side.....5
4.  $oc_2$  always represented by a macrochaeta.....*Salina*
  - a. Parietal region with 1+1 macrochaetae ( $P_4+P_4$ ); occipital region with  $O_1+O_1$  macrochaetae (Fig.2).....*celebensis* group

- b. Parietal region without macrochaetae; occipital region with at least 3 macrochaetae ( $O_1$ ,  $O_2$ ,  $O_3$ ) [Fig. 4].....*indica* group  
 oc<sub>2</sub> represented by a microchaeta (Fig. 10).....*Akabasia*
5. Ocular setae not more than 3, oc<sub>2</sub> always a macrochaeta.....6  
 Ocular setae 3 or more, all microchaetae.....7
6. Macrochaetae on vertex represented by  $V_0+V_{1-6}$ , inserted in the form of “V”; macrochaetae absent on area dorsalis; macrochaetae present on areas genalis, parietalis, occipitalis, cervicalis (Fig. 6).....*Pseudosalina*  
 Macrochaetae on vertex 6+6,  $V_1$ ,  $V_1$  when joined forms a straight line; post ocular region with one macrochaeta ( $PO_1$ ) on each side; other regions devoid of macrochaetae (Fig. 27).....*Idiomerus*
7. Ocular setae not more than 3.....8  
 Ocular setae always more than 3.....9
8. Areas genalis and occipitalis always with 2 and 1 macrochaetae respectively ( $G_1$ ,  $G_2$ ;  $O_1$ ) [Fig. 21].....*Dicranocentroides*  
 Area genalis with  $G_1$  only (which may be absent in some species), area occipitalis always without macrochaetae (Fig. 19).....*Callyntrura*
9. Macrochaetae absent on areas parietalis, genalis, occipitalis, and cervicalis;  $V_0$  absent, macrochaetae on vertex represented by  $V_{1-6}$ ,  $V_1-V_1$  and  $V_2-V_2$  inserted in a trapezoid fashion; ocular setae 5 (oc<sub>1-5</sub>) [Fig. 33].....*Campylothorx*  
 Macrochaetae present on areas parietalis, genalis, occipitalis and cervicalis;  $V_0$  present or absent, vertex with at least 6 macrochaetae on each side, macrochaetae on mid-vertex inserted either in a trapezoid or rectangular fashion; ocular setae either 4 or 5.....10
10. Ocular setae 4,  $V_0$  present.....11  
 Ocular setae 5,  $V_0$  present or absent.....12
11.  $V_1-V_1$  and  $V_2-V_2$  inserted in a trapezoid fashion; dorsal setae represented by  $D_1$ ,  $D_2$ ,  $D_3$  (Fig. 17).....*Metacoelura*  
 $V_1-V_1$  and  $V_2-V_2$  inserted in a trapezoid fashion; dorsal macrochaetae represented by  $D_0+D_{1-9}$  (Fig. 12).....*Paronellides*
12.  $V_0$  absent, vertex medially with  $V_1-V_1$ ,  $V_2-V_2$ ,  $V_3-V_3$ , inserted in a rectangular fashion; area genalis with 3 macrochaetae ( $G_{1-3}$ ) [Fig.14].....*Paronana*

- $V_0$  present, vertex medially with  $V_1-V_1$ ,  $V_2-V_2$  macrochaetae inserted in a trapezoid fashion, area genalis with 2 macrochaetae ( $G_{1-2}$ ) [Fig.23].....*Pseudoparonella*
13. Ocular setae 3 ( $oc_{1-3}$ ); areas dorsalis away from vertex with 2 macrochaetae ( $D_1, D_2$ ), post ocularis and occipitalis each with one macrochaeta ( $PO_1, O_1$ ) [Fig.40].....*Trogolaphyusa*
- Ocular setae more than 3; dorsal macrochaetae towards vertex present or absent.....14
14. Ocular setae 5 ( $oc_{1-5}$ ); dorsal macrochaetae towards vertex absent.....15
- Ocular setae more than 5; dorsal macrochaetae towards vertex present.....16
15. Dorsal macrochaetae 3 ( $D_{1-3}$ ), located anteriorly in between antennal bases and ocellar fields; postocular macrochaetae ( $PO_1$ ) absent (Fig.37).....*Lepidonella*
- Dorsal setae 1+1, represented by microchaetae, located anteriorly; postocular macrochaeta ( $PO_1$ ) present (Fig.35).....*Bromacanthus*
16. Dorsal macrochaetae ( $D_1, D_2$ ) located towards vertex, joining of which forms a broad rectangle;  $PO_1$  present;  $G_1$  absent (Fig.31).....*Dicraanocentruga*
- Dorsal setae, ( $D_1, D_2$ ) located towards vertex, forms a narrow rectangle on joining; both  $PO_1$  and  $G_1$  present (Fig.29).....*Paronella*

**TABLE—I**

**\* Maximum Number of setae Occurring in the Cephalic Regions in the Genera under Paronellinae**

GENERA	Regions of the Headcapsule									Remarks
	Area verticalis (V)	Area dorsalis (D)	Area sub-dorsals (Sd)	Area ocellaris (Oc)	Area post-ocellaris (Po)	Area parietalis (P)	Area occipitalis (O)	Area cervicalis (C)	Area genalis (G)	
<b>CREMASTOCEPHALINI</b>										
<i>Yosita</i>	5	3	4	3	2	2	1	3	—	—
<i>Akbosia</i>	9	—	6	3	2	1	3	3	—	—
<i>Salina</i> ( <i>indica</i> group)	5	4	6	3	2	—	6	3	—	O <sub>1</sub> , O <sub>4</sub> , O <sub>6</sub> exhibit asymmetry and variation.
<i>Salina</i> ( <i>celebensis</i> group)	2	d <sub>0</sub> + 4	4	3	2	4	1	2	—	—
<i>Pseudosalina</i>	V <sub>0</sub> + 6	4	6	3	2	2	5	6	1	—
<i>Paronellides</i>	V <sub>0</sub> + 6	D <sub>0</sub> + 9	8	4	1	1	10	5	3	—
<i>Paronana</i>	8	D <sub>0</sub> + 9	9	5	1	1	10	6	3	—
<i>Matacoelura</i>	V <sub>0</sub> + 6	3	Not noted	4	1	1	7	4	3	—
<b>CALLYNTRURINI</b>										
<i>Pseudoparonella</i>	V <sub>0</sub> + 6	7	8	5	1	1	5	6	2	—
<i>Lawrenceana</i>	V <sub>0</sub> + 7	5	17	5	1	—	6	4	2	—
<i>Callyntrura</i>	V <sub>0</sub> + 7	6	14	3	1	—	—	—	1	V <sub>0</sub> and G <sub>1</sub> present in all the species examined except in one.

TABLE—I (continued)

GENERA	Regions of the Headcapsule									Remarks
	Area verticalis (V)	Area dorsalis (D)	Area sub-dorsals (Sd)	Area ocularis (Oc)	Area post-ocularis (Po)	Area parietalis (P)	Area occipitalis (O)	Area cervicalis (C)	Area genalis (G)	
<i>Idiomerus</i>	4	4	25	3	1	3	—	—	—	—
<i>Dicranocentroides</i>	V <sub>0</sub> +7	6	14	3	1	1	2	1	2	1-2 variable macrochaetae seldom occur in vertex ; d <sub>6</sub> , c <sub>1</sub> , o <sub>1</sub> , p <sub>1</sub> variable.
PARONELLINI										
<i>Campylothorax</i>	5	4	10	6	1	3	—	—	—	—
<i>Paronella</i>	—	3	22	5	1	—	—	—	1	—
<i>Dicranocentruga</i>	—	D <sub>0</sub> +5	20	11	1	1	—	—	—	D <sub>3</sub> of specific significance; D <sub>0</sub> , D <sub>4</sub> and P <sub>1</sub> variable.
BROMACANTHINI										
<i>Bromacanthus</i>	—	—	8	5	1	3	—	—	—	—
<i>Lepidonella</i>	—	4	9	5	—	—	—	—	—	—
<i>Trichorypha</i>	—	Present <sup>+</sup>	Present <sup>+</sup>	7-8	2	—	—	—	1	+Actual number of D and Sd could not be determined as the specimens are mounted on slides.
TROGLOPEDETINI										
<i>Trogolaphysa</i>	V <sub>0</sub> +V <sub>1-12</sub>	2	17	3	1	—	1	—	—	—

\* From the species dealt with in this investigation.

**TABLE—II IN THE CAPHALIC REGIONS**

**\*Maximum Number of Macrochaetae Occurring in the Genera under Paronellinae**

GENERA	Regions of the Headcapsule									Remarks
	Area verticalis (V)	Area dorsalis (D)	Area sub-dorsals (Sd)	Area ocularis (Oc)	Area post-ocularis (Po)	Area parietalis (P)	Area occipitalis (O)	Area cervicalis (C)	Area genalis (G)	
<b>CREMASTOCEPHALINI</b>										
<i>Yosiia</i>	V <sub>1</sub>	D <sub>1-3</sub>	SD <sub>2-4</sub>	OC <sub>2</sub>	PO <sub>1-2</sub>	P <sub>2</sub>	O <sub>1</sub>	C <sub>1-3</sub>	—	—
<i>Akabosia</i>	V <sub>1-2</sub>	—	SD <sub>1,2,5,6</sub>	—	PO <sub>1-2</sub>	P <sub>1</sub>	O <sub>1-3</sub>	C <sub>1-3</sub>	—	—
<i>Salina</i> ( <i>celebensis</i> group)	V <sub>1-2</sub>	—	SD <sub>1-4</sub>	OC <sub>2</sub>	PO <sub>1-2</sub>	P <sub>4</sub>	O <sub>1</sub>	C <sub>1-2</sub>	—	—
<i>Salina</i> ( <i>indica</i> group)	V <sub>1-2</sub>	—	SD <sub>3,5,6</sub>	OC <sub>2</sub>	PO <sub>1-2</sub>	—	O <sub>1-6</sub>	C <sub>1-3</sub>	—	—
<i>Pseudosalina</i>	V <sub>0</sub> + V <sub>1-6</sub>	—	SD <sub>3-6</sub>	OC <sub>2</sub>	PO <sub>1-2</sub>	P <sub>2</sub>	O <sub>1-5</sub>	C <sub>1-6</sub>	G <sub>1</sub>	—
<i>Paronellides</i>	V <sub>0</sub> + V <sub>1-6</sub>	D <sub>0</sub> + D <sub>1-9</sub>	SD <sub>5-8</sub>	—	PO <sub>1</sub>	P <sub>1</sub>	O <sub>1-10</sub>	C <sub>1-5</sub>	G <sub>1-3</sub>	—
<i>Paronana</i>	V <sub>1-8</sub>	D <sub>0</sub> + D <sub>1-9</sub>	—	—	PO <sub>1</sub>	P <sub>1</sub>	O <sub>1-10</sub>	C <sub>1-6</sub>	G <sub>1-3</sub>	—
<i>Metacoelura</i>	V <sub>0</sub> + V <sub>1-6</sub>	D <sub>1-3</sub>	not noted	—	PO <sub>1</sub>	P <sub>1</sub>	O <sub>1-7</sub>	C <sub>1-4</sub>	G <sub>1-3</sub>	—
<b>CALLYNTRURINI</b>										
<i>Idiomerus</i>	V <sub>1-4</sub>	D <sub>4</sub>	—	OC <sub>2</sub>	PO <sub>1</sub>	P <sub>3</sub>	—	—	—	—
<i>Pseudoparonella</i>	V <sub>0</sub> + V <sub>1-6</sub>	D <sub>1-7</sub>	SD <sub>4,6,7,8</sub>	—	PO <sub>1</sub>	P <sub>1</sub>	O <sub>1-5</sub>	C <sub>1-6</sub>	G <sub>1-2</sub>	—
<i>Lawrenceana</i>	V <sub>0</sub> + V <sub>1-7</sub>	D <sub>1-5</sub>	SD <sub>4,5,10-17</sub>	—	PO <sub>1</sub>	—	O <sub>1-6</sub>	C <sub>1-4</sub>	G <sub>1-2</sub>	—
<i>Parachaetoceras</i>	+V <sub>0</sub> + V <sub>1-3</sub>	+D <sub>1-3</sub>	+Present	—	PO <sub>1</sub>	P <sub>1</sub>	+O <sub>1-4</sub>	+C <sub>1-3</sub>	G <sub>1-3</sub>	—
<i>Callyntrura</i>	V <sub>0</sub> + V <sub>1-7</sub>	D <sub>5-6</sub>	SD <sub>1,5,9-14</sub>	—	PO <sub>1</sub>	—	—	—	G <sub>1</sub>	—

TABLE—II (continued)

GENERA	Regions of the Headcapsule									Remarks
	Area verticalis (V)	Area dorsalis (D)	Area sub-dorsals (Sd)	Area ocularis (Oc)	Area post-ocularis (Po)	Area parietalis (P)	Area occipitalis (O)	Area cervicalis (C)	Area genalis (G)	
<i>Dicranox entroides</i>	V <sub>0</sub> + V <sub>1-7</sub>	D <sub>6</sub>	SD <sub>9-12</sub>	—	PO <sub>1</sub>	—	O <sub>1</sub>	—	G <sub>1-2</sub>	Inparietal region seldom an asymmetrical macrochaeta occurs.
PARONELLINI										
<i>Campytothorax</i>	V <sub>1-5</sub>	D <sub>1-4</sub>	SD <sub>1</sub>	—	PO <sub>1</sub>	—	—	—	—	—
<i>Paronella</i>	—	D <sub>1-3</sub>	—	—	PO <sub>1</sub>	—	—	—	G <sub>1</sub>	G <sub>1</sub> may be represented by a microchaeta.
<i>Dicranocentruga</i>	—	D <sub>0</sub> + D <sub>1-5</sub>	SD <sub>1-7,10,17</sub>	—	PO <sub>1</sub>	—	—	—	—	—
BROMACANTHINI										
<i>Bromacanthus</i>	—	—	—	—	PO <sub>1</sub>	—	—	—	—	—
<i>Lepidonella</i>	—	D <sub>1-4</sub>	—	—	—	—	—	—	—	—
<i>Trichorypha</i>	—	+Present	—	—	PO <sub>1-2</sub>	—	—	—	G <sub>1</sub>	—
TROGLOPEDETINI										
<i>Trogolaphysa</i>	—	D <sub>1-2</sub>	—	—	PO <sub>1</sub>	—	O <sub>1</sub>	—	—	—

\*From the species dealt with in this investigation.

+ Exact number could not be ascertained as the study is based on specimens mounted on slides.

TABLE—III

\*Range of the Number of Macrochaetae found on Each Side of Thorax and Abdomen in the Genera under Paronellinae

GENERA	Segments						Remarks
	Th. II	Th. III	Abd. I	Abd. II	Abd. III	Abd. IV	
CREMASTOCEPHALINI							
<i>Yosiia</i>	1	3	3	3	4	1	Anteromedially on Abd. IV
<i>Akabosia</i>	11	5	3	3	13	2	Do
<i>Salina</i> ( <i>celebensis</i> group)	15-25	6-12	4-5	2-4	+1	2	Do
<i>Salina</i> ( <i>Indica</i> group)	28-40	17-26	9-17	4-6	+1	2	Do
<i>Pseudosalina</i>	43-58	30-40	17-23	13-18	5-6	2	Do
<i>Paronellides</i>	68-69	46-47	23-26	10-11	9-10	7	Do
<i>Paromana</i>	52	42	20	8	7	19-20	Do
<i>Metacoelura</i>	38	30	18	7	3	10	Do
<i>Glacialoca</i>	16	23	3	8	8	+	Figures indicate the minimum number of macrochaetae
CALLYNTRURINI							
<i>Idiomerus</i>	20	13	3	4	1	13	Anteromedially on Abd. IV in a transverse row
<i>Pseudoparonella</i>	17	12-20	3-5	4-5	10	8	Do
<i>Lawrenceana</i>	17	15-21	5-12	4-8	4-7	13-16	Do

TABLE—II (continued)

GENERA	Segments						Remarks
	Th. II	Th. III	Abd. I	Abd. II	Abd. III	Abd. IV	
<i>Callyntrura</i>	8-26	11-23	5-15	5-12	4-11	9-16	Anteromedially on Abd. IV in a transverse row
<i>Dicranocentroides</i>	35-55	33-49	18-31	12-20	+2	10-14	Do
PARONELLINI							
<i>Campylothorax</i>	4	7	0	0	8	6	Do
<i>Paronella</i>	6	0	0	2	8	6	On general surface of Abd. IV
<i>Dicranocentruga</i>	6	0	0	0	7	5	Do
BROMACANTHINI							
<i>Bromacanthus</i>	0	0	0	0	0	13	Do
<i>Lepidonella</i>	0	0	0	0	0	13	Do
<i>Trichorypha</i>	3	0	0	4	10	8	Do
TROGLOPEDETINI							
<i>Trogolaphysa</i>	3	3	0	0	10	18	Do

\*From the species dealt with in this investigation.

+ Medially on Abd. III.

++ Present in the form of a transverse row but exact number could not be noted.

TABLE-IV

## Chaetotaxic classification of the Genera under Paronellinae

Category "A" Typical Scaled Genera without Flexed Macrochaetae (Achaetoic)		Category "B" Scaleless or Psuedo-Scaled Genera with Flexed Macrochaetae (Chaetoic)	
Lepidose	Parachaetose	Oligochaetose	Polychaetose
<i>Lepidonella</i>	<i>Paronella</i>	<i>Salina (celebensis group)</i>	<i>Salina (indica group)</i>
<i>Bromacanthus</i>	<i>Dicranocentruga</i> <i>Campylothorax</i> <i>Microparonella</i> <i>Trichorypha</i> <i>Trogolaphysa</i>	<i>Yosia</i> <i>Akabosia</i>	<i>Pseudosalina</i> <i>Paronana</i> <i>Parasalina</i> <i>Peronellides</i> <i>Metacoelura</i> <i>Glacialoca</i> <i>Pseudoparonella</i> <i>Lawrenceana</i> <i>Dicranocentroides</i> <i>Callynrura</i> <i>Idiomerus</i>

## ULTRASTRUCTURES

Examination of the cuticle of Collembola through the Scanning Electron Microscope proves that it is granulate which in fact appears as smooth under light microscope. Massoud (1969) recognised that collembolan cuticle is composed of two types of granules : primary or single basic granules, triangular in form and secondary granules formed by the association or fusion of certain primary granules. These granules, developed variously, remain linked by linear connections and appear as hexagonal network. Dallai and Ferrarī (1970) and also Lawrence and Massoud (1973) observed a common hexagonal pattern composed of triangular primary granules of identical shape and dimension in the entomobryomorphs, viz., *Seira*, *Entomobrya*, *Heteromurus*, *Lepidocyrtus*, *Orchesella*, *Pseudosinella*, *Tomocerus*, *Cyphoderus*, *Oncopodura*, *Troglopedetes* and *Salina*. In the present investigation cuticular configuration, characteristic for entomobryomorpha, has also been observed in *Callyntrura* ( Pls. VI, VII ). Similar cuticular pattern also occurs in *Idiomerus* ( Fig. 43 A ). In *Compylothorax*, where the granules are alternately larger and smaller in hexagonal network ( Fig. 43 B ), is an extremely apomorphic feature, not seen as yet in any other genus of entomobryomorpha ( Mitra and Dallai, 1980 ).

These studies further reveal the presence of thick ciliations on the general surface of pseudoscales similar to the microchaetae which appear branched in view of coarse ciliations ( P1. IV, 1, 2 ). The setae of legs in *Callyntrura* appear coarsely plumose, that of dentes finely plumose; flattened apex of tenent hair coarsely and sparsely ciliated with thick cilia while, apex of Ant. IV with feathered microchaetae and adjacent smooth sensory roads ( P1. V ).

## PHYLOGENY AND BIOGEOGRAPHY

Biologists interested in the phylogeny of soft bodied animals like Collembola are greatly handicapped because of the absence of fossil records furnishing direct evidence of the origin, evolution and distribution of organisms during the geological epochs. Of necessity, one has to rely on the data available from other groups of animals, whose geological history can be traced through fossils, and which furnish the necessary background information about configuration of land and water masses through ages well as the possible climatic conditions that might have prevailed at different epochs in the geologic history of the earth. The present day distribution of organisms also indirectly provides us with at least some clues about their possible origin and dispersal in the past. The author has attempted to discuss here the evolution of the sub-family Paronellinae from the data furnished by pattern of distribution of its recent forms, thier ecology and morphological affinities and by correlating these informations with the various hypotheses regarding the configuration of land masses in past geological areas as revealed by palaeontological and geomagnetic evidences.

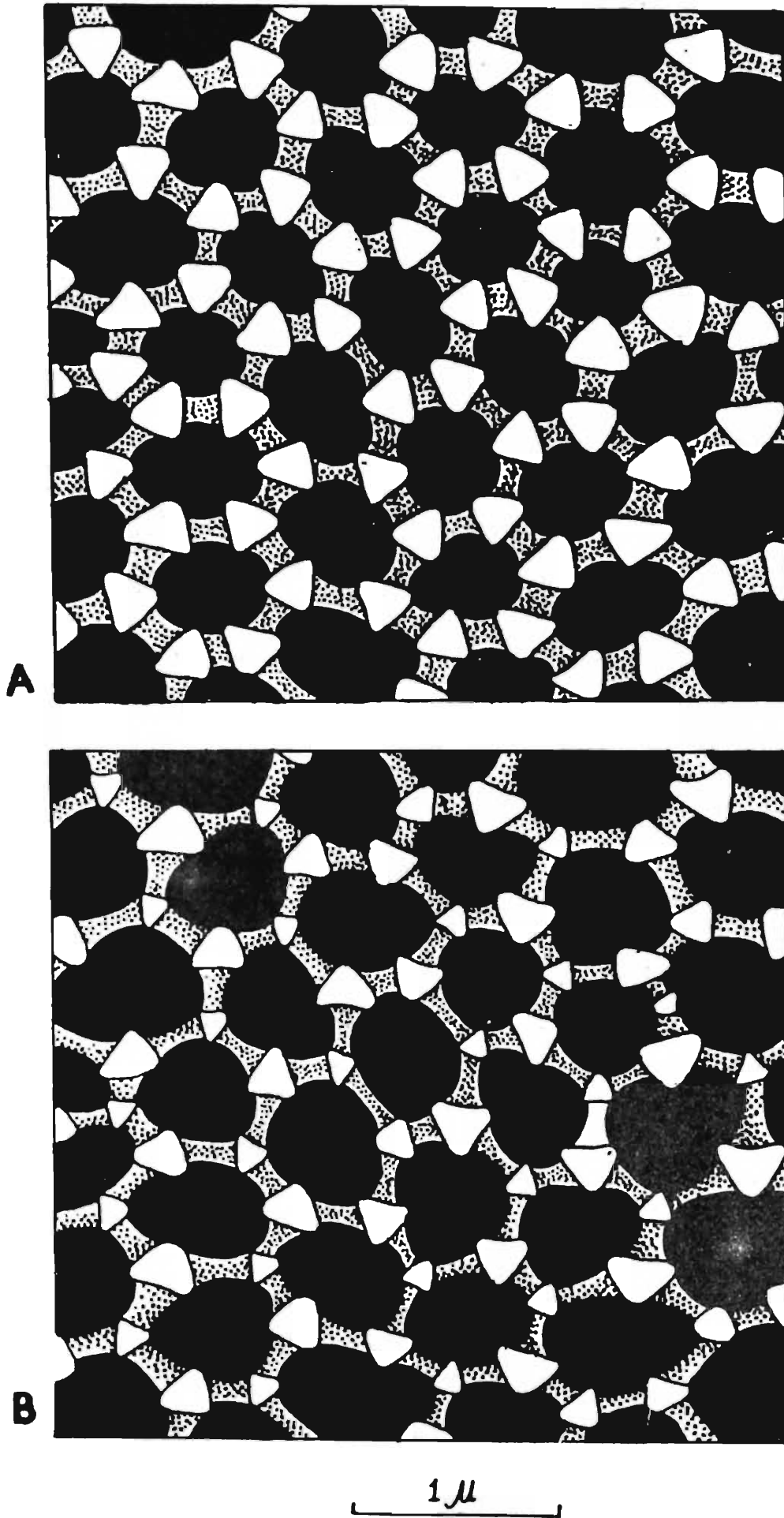


Fig. 43 : Cuticular ornamentation (adopted from S.E.M. photomicrographs), A, *Idiomerus pallidus* Imms ; B, *Campylothorax logicornis* Schott.

Present geological opinion tends to prove that before the end of the Cretaceous, the world was a single land mass, or a series of interconnected land masses. The manner in which changes leading to present day topographical conditions took place is a matter of controversy between different hypotheses based on postulates of subsidence and uplift caused by large scale orogenic movements following the Cretaceous, or on the hypothesis of Continental Drift which envisages physical separation and drifting apart of Continental land masses once in intimate contact. Wegner's hypothesis, enunciated in the last century, has received considerable support from recent geomagnetic data which show the way rocks were facing when first formed and indicated the rocks all over the world were differently oriented—in a pattern that seems to fit in with the theory of Continental Drift. The former postulate, based on subsidence of vast portions of land masses as a result of large scale tectonic movements and uplift of land surface in other areas, envisages presence of land-bridges to explain the distribution of such groups of animals which evolved latter ( after the separation of continental land masses ) and could not be dispersed through the agency of sea, but only through overland routes.

It, however, appears reasonably certain that there was direct contact between different continental land masses and that the separation occurred gradually and between differential time intervals. It is also a reasonable belief that Australia was already separate from the remaining Asian land mass through the Cenozoic and that New Zeland also became a separate entity almost simultaneously ( de Beaufort, 1951; Darlington, 1957 ). The biogeography and phylogeny of the sub-family Paronellinae apparently reflect the historical events, that occurred through various geological epochs and are amply substantiated by evidences obtained through other groups of land dwelling animals, adequately represented by fossils.

Through deficient in fossil records, the Collembola is an ancient group of insects which became differentiated at a fairly early period in the geologic history. Among the oldest known fossil insects is a collembolan fossil, *Rhyniella praecursor* Hirst and Maulik ( 1926 ), from the middle Devonian Rhynie Chert of Scotland. This fossil Collembola does not differ significantly in morphological features from its modern representatives, a fact which indicates the morphological stability achieved by this Order early in its phylogenetic history. Another find of a fossil Collembola in the Cretaceous amber deposits of Saskatchewan River, *Protentomobrya walkeri* Folsom ( 1937 ), confirms the great antiquity of the group and also of its rather wide distribution in space during those times when the present day temperate areas enjoyed a warmer and milder climate conducive to the spread of these minute insects which are, today, mostly restricted to the tropical and subtropical belts, chiefly of the Oriental Region.

Nothing much is known as yet about the exact mode of dispersal of Collembola. Salmon ( 1949 ) suggested that collembolan living on foliage of trees and shrubs are probably dispersed by wind. It, however, appears doubtful whether the

cosmopolitan genera inhabiting foliage of trees and shrubs could be solely dispersed through this agency traversing wide stretches of oceans. The possibility of chance dispersal of Collembola from one island to another through driftwood transported across seas can also not explain perhaps satisfactorily the presence of the same genera in the widely separated areas like Africa and South America. A more definite agency like contiguous habitats connecting these areas biogeographically appears to be more probable.

Against this background are considered, as in below, some of the wide aspects of the phylogeny and biogeography of the sub-family Paronellinae.

*Phylogeny* : Fig. 45 presents a diagrammatic representation of the phyletic connections that exist between the different tribes, genera and sub-genera of Paronellinae based on the results of the present study. The sequences of branching and their mode of connections are now discussed:

It is difficult to conceive a common prototype or archetype of the genera under Paronellinae. It appears, however, that (a) Stock, that gave rise to the tribes Cremastocophalini and Callyntrurini, was probably hyperadaphic and used to live on the surface of litter or on herbs and shrubs. This stock might have possessed a well developed clothing of flexed macrochaetae and was without scales. (b) Stock, that gave rise to the tribes Bromacanthini, Paronellini and Troglopedetini as precursor of the forms, was perhaps true soil-type Collembola possessing typical or true scales and achaetotic body.

Characterisation of the first stock, *i.e.*, for Cremastocephalini and Callyntrurini, as a scaleless one and with a clothing of flexed macrochaetae, is derived from the fact that these characters are common to majority of the genera now known under Cremastocephalini and Callyntrurini. The possession of 'scales' by members of Callyntrurini does not invalidate this characterisation as is explained below.

(a) Though all genera of Callyntrurini possess a distinct clothing of scales, these are, as has already been mentioned earlier, not true or typical scales. Scales in the genera of this tribe have been termed as "pseudoscales", as they exhibit gradations between the setiform scale-primordia to such 'scales' ( Pls. I, D; IV ).

True scales are mostly round or oval in shape with the apices always round. In contrast, the pseudoscales are mostly lanceolate in shape with sharp apices, though in many forms these may have secondarily rounded apices, at least on the throacic and first two abdominal segments.

The differentiation of scales in Callyntrurini varies according to the nature of habitat of the species. Forms living on herbs and shrubs or on a relatively dry surface have less differentiated scales, mostly narrow and lanceolate; those, that inhabit surface of moist litter, have a thick investment of variously shaped scales and scale-primordia. The secondary development of scales in this tribe has apparently

widened the range of its adaptation to ecological niches from very dry to moist habitats. Gisin ( 1967c ) has discussed the functional aspects of scale structures. An important point, in this connection, is the similarity between the early stage scale-primodia of Callyntrurini and the microchaetae of the genera under Cremastocephalini, that not only serves to emphasise the affinities between the two tribes but also throws light on the nature of 'scales' in Callyntrurini. Ultrastructural studies further substantiate this morphological homology.

(b) A well-developed clothing of flexed macrochaetae, found in the genera under Cremastocephalini and Callyntrurini, are primarily sensory in function and thus helping them to avoid predators which they encounter in the various ecological niches on free surface.

(c) It follows from the present studies that the number and nature of setae in each ocellar field ( ocular setae ) are extremely stable and probably represent plesiomorphic characters. This character is common to a group of genera which may have descended from the same ancestral stock. All the species so far studied under *Callyntrura* and *Dicranocentroides* ( the genera chiefly represented in the Oriental Region ) including monotypic *Idiomerus* have the same number of ocular setae as that of the four scaleless genera under Cremastocephalini viz., *Yosiia*, *Akabosia*, *Salina* and *Pseudosalina*. Further, the species of the scaled-genera viz., *Pseudoparonella* ( including its sub-genera ) and *Parachaetoceras* of the Australian Region have number of ocular microchaetae identical with that of the scaleless genus *Paronana* from New Zeland. Such similarity in the number of ocular setae in the group of genera, belonging to two widely different tribes and from two widely different zoogeographical regions, indicates possibly the origin of such genus-groups of both the tribes from two stock patterns each of which possessed a specific number of ocular setae. The points, discussed above, explain the real nature of scales found in the genera under Callyntrurini and hints at their probable origin from a scaleless ancestral stock. Since the number of genera and sub-genera under Cremastocephalini outnumbers that of Callyntrurini, it is reasonable to presume that the genera of Callyntrurini might have originated from the scaleless ancestral forms. The genera of both the tribes primarily originated from a common scaleless ancestral stock and the pseudoscales of the tribe Callyntrurini are later acquisitions.

The genera under Cremastocephalini, as we see them today, might have arisen from more than one specialised stocks. One of these represents the form which had 3 ocular setae and frontal spines and this possibly has given rise to the genera like *Salina*, *Pseudosalina*, *Akabosia* and *Yosiia*. Australian genera seem to have been derived from a stock which had more than 3 ocular setae and was devoid of frontal spines. *Yosiia* and *Akabosia* represent a distinct line of specialisation from that of the other two genera in the reduction of the number of prelabral setae. Characteristic mucrone and dental scale appendage of both the genera are to be considered as their apomorphic features. Cephalic chaetotaxy of *Akabosia* conforms to the pattern

which is of primitive type like *Salina*, while *Yosiia* appears to have advanced one step further than *Akabosia* in the specialisation of its cephalic chaetotaxy. *Salina*, as mentioned before, is a very old genus and appears closest to the ancestral form in the presence of 4 prelabral setae, a feature common to all the genera under Paronellinae except *Akabosia* and *Yosiia*. *Pseudosalina* exhibits specialisation from its nearest ally *Salina* in the reduction of a mucronal tooth ( probably the one which represents apical tooth in *Salina* ) and increase in the number of macrochaetae anteriorly on the anterior face of ventral tube. It exhibits extreme specialisation in cephalic chaetotaxy, which is different from the primitive pattern of *Salina*. However, the general morphological features and the number of ocular microchaetae indicate their probable origin from a common stock. *Salina*, as mentioned before, is the oldest genus and might be very close to the primary ancestral form which gave rise to the modern genera of Cremastocephalini and Callyntrurini.

*Glacialoca* and *Paronana* are new in the scale of evolution than *Paronellides*. *Paronellides* and *Metacoelura* have identical number of ocular setae and do not possess dental spines. Such common characters of both the genera indicate their closest relationship and their primitive nature. *Metacoelura* appears more primitive than *Paronellides* in its mucronal feature. Sub-genus *Pseudoparonellides* probably represents an off-shoot from the stock which gave rise to *Paronellides* and *Metacoelura* and it shows specialisation in the structure of mucrones which appears to be its only apomorphic character. In *Glacialoca* and *Paronana* presence of dental spines is an apomorphic character and indicates their close relationship. *Paronana* is less specialised than other genera under this sub-family as is evident from some of the species of this genus which still retain narrow dentes and mucrones of the entomobryid pattern. Further, the general body facies of a species viz., *Paronana (Paronana) pilosa* Salmon (1941), appears close to entomobryid genus *Homidia*. Christiansen's (1958) arguments about *Homidia* having a distinct phyletic connection with Paronellinae find further confirmation from this fact.

Like Cremastocephalini, the genera under Callyntrurini also have been derived from two distinct ancestral stocks, one representing a line which gave rise to the genera like *Callyntrura*, *Dicranocentroides* and *Idiomerus*, characterised by the presence of 3 ocular microchaetae. Umbonate or humped mesothorax of *Idiomerus* is an apomorphic character, while in *Dicranocentroides* dental spines and the cluster of outstanding macrochaetae on antennal segments I and II represent its apomorphic characters. *Callyntrura* appears to be less specialised than these two genera. It is of interest to note that both *Dicranocentroides* and *Callyntrura* retain a common general plan of cephalic chaetotaxy, at least that of vertex. This appears to be a plesiomorphic character retained by them. *Callyntrura*, at any rate, appears closest to the ancestral form which has given rise to the genera of Callyntrurini and is chiefly represented in the Oriental Region. Further, it is worth mentioning that some of the species of *Callyntrura* represent a primitive chaetal architecture of mid-vertex

close to that of *Salina*. Further, the presence of 4+4 frontal apines in the species of *Callyntrura* and in *Idiomerus* indicates their primitiveness and also hints at the phyletic connection that exists between Callyntrurini and Cremastocephalini.

Presence of e.o.s. in *Idiomerus*, found only in the ethiopian and neotropical genera of Paronellinae like *Campylothorax*, *Paronella* and *Dicranocentruga* (Mitra, 1972; Mitra and Dallai, 1980), poses a question if the Indian genus is a primitive one having originated from the same precursor of the forms that gave rise to those genera. If it is so, then the precursor that gave rise *Campylothorax*, *Paronella* and *Dicranocentruga* might have existed in the Gondwanaland Continents. Conversely, if e.o.s. is an apomorphic character, developed independently as a consequence of parallel evolution in response to similar changes at a later period, then the genus is a specialised off-shoot from a common ancestral stock that gave rise to *Callyntrura* and *Dicranocentroides*. In fact, large number of characters shared by *Idiomerus* with *Dicranocentroides* and *Callyntrura*, mentioned above, leans heavily on the last possibility. Further cuticular configurations at ultrastructural level of *Idiomerus* (Fig.43 A) is widely different from *Campylothorax* but similar to *Salina* and *Callyntrura* of Paronellinae and other entomobryomorph genera (Dallai and Ferrai, 1970; Lawrence and Massoud, 1973; Mitra and Dallai, 1980).

*Pseudoparonella* (including *Lawrenceana*) and *Parachaetoceras* appear to have arisen from an ancestral stock which had more than 3 ocular setae. *Parachaetoceras* is of more recent origin than *Pseudoparonella* as it possesses many apomorphic characters like the presence of dental spines and long outstanding macrochaetae on antennae and appendages. Further, the presence of less specialised pseudoscales clothing the body (Pl 1,D) points out to its later evolution as a genus under Callyntrurini. It appears reasonably certain that Callyntrurini is a specialised off-shoot from the stock which gave rise to the genera of Cremastocephalini and the members of the tribe can be termed as "specialised Cremastocephalini"

The tribes Bromacanthini, Paronellini and Troglopedetini appear to have arisen from true soil-type forms. This is evident from the fact that all the genera under these tribes are clothed with typical or true scales and are devoid of a well-developed clothing of flexed macrochaetae on body.

In the tribe Bromacanthini, which appears to be polyphyletic in origin, all the genera lack the extraordinary extra ocular structure (e.o.s.). *Bromacanthus* and *Lepidonella* probably arose from a common ancestral stock which is indicated by some primary and common plesiomorphic features like the number and nature of arrangement of the ocelli, fundamental similarity in footcomplex and general body-facies which is often lepidocyriform in the species of both the genera. Furthermore, the number of ocular microchaetae is identical in both the genera. *Bromacanthus* is more specialised than its nearest ally *Lepidonella* in the mucronal structure which lack the inner basal tooth and in the presence of femoral organ representing

apomorphic features of the genus. Contrary to *Bromacanthus*, *Lepidonella* retains the primitive type of mucronal pattern, the general plan of which conforms to the mucrone of an entomobryid genus; the inner basal spiniform tooth appears to be the homologue of the basal spine of the entomobryid genus. Presence of dental spines is an apomorphic character common to both the genera. General features of both the genera suggest their probable origin from a lepidocyrtriform ancestor.

The genus *Microparonella* is still a very plastic one as is revealed by its semi-cavernicolous as well as normal edaphic life. Thus the known species of this genus show adaptations of both the types of life which is reflected through certain characteristics like the nature of ocellar fields and footcomplex. The genus in general has affinity with the members of Troglopedetini.

*Trichorypha* is an extremely specialised genus and at present it is difficult to comment on its phylogeny. It is neither close to any Ethiopian and Neotropical genus nor to any under other tribes.

The genera under Paronellini apparently have originated from a common ancestor as evidenced by the presence of e.o.s. in all of them. Presence of normal inner paired basal and distal unpaired teeth on unguis in *Campylothorax*, a feature found in most of the genera of Paronellinae, indicates that the enlarged paired basal unguis teeth of *Paronella* and *Dicranocentruga* might be the later acquisitions in response to similar adaptations. Humped metathorax of *Campylothorax* is an apomorphic character like *Idiomerus* from India. Manubrial spines of *Paronella* is also of derived nature representing an apomorphic character. Though in the presence of e.o.s., *Campylothorax*, *Paronella* and *Dicranocentruga* apparently appear to have been derived from a common ancestral stock (as mentioned above), the principal morphological differences existing among these genera cast some doubt about their probable origin and phylogenetic relationship. Large size of the species of *Campylothorax*, the nature of its mucrones and general plan of cephalic chaetotaxy are no doubt close to *Callyntrura* and *Dicranocentroides* (members of the tribe Callyntrurini) and widely different from other genera under Paronellini. *Paronella fusca*, on the other hand, has a distinctly large, entomobryiform body facies which is strikingly different from the species of *Dicranocentruga*. Species of *Dicranocentruga* are smaller than *P. fusca* and their body-facies, nature of footcomplex and other features indicate their apparent similarity to the species of *Pseudosinella*. Such gross morphological differences, that exist between these genera of Paronellini, lead to the possibility that these genera are initially polyphyletic in origin and the e.o.s. is an apomorphic character developed independently in each genus owing to similar mode of living. Further researches on *Pseudosinella* and its related genera and also on *Entomobrya* along this line may elucidate this point in future. *Paronella*, however, is phylogenetically closer to *Dicranocentruga* than to *Campylothorax* in the basic pattern of its cephalic chaetotaxy.

It is possible that most of the genera under Paronellinae are polyphyletic in origin. Each genus or a group of genera originated from independent generic units which were initially close to some genera of Entomobryinae. Stout dentes and plump mucrones which mainly characterise the sub-family might have been acquired independently by each generic unit and this probably represents an extreme example of adaptive convergence.

Paronellinae is closest to Cyphoderinae in the possession of stout dentes and plump mucrones. One of the principal characters by which Cyphoderinae is distinguished from Paronellinae is the presence of fringed, foliate scales of dentes which do not occur in the genera under Paronellinae. Troglopedetini, a tribe placed under Cyphoderinae (Salmon, 1964), does not possess such fringed, foliate scales on dentes and its armature of dentes is similar to those of the genera under Paronellini (in the present sense) and Bromacanthini. Reduced ocelli which is considered as one of the characteristics of this sub-family (i.e., Cyphoderinae) is also exhibited by the species of *Microparonella* Carpenter, a genus under Bromacanthini of Paronellinae. Thus the existing differences which one can observe between Troglopedetini and Paronellinae are the highly enlarged inner paired basal unguis teeth and elongate mucrones in some species of Troglopedetini. Womersley (1939), justifiably included *Trogolaphysa* Mills under sub-family Paronellinae. Delamare Deboutteville (1951b) described *Trogonella* from Ivory Coast having highly enlarged (winglike) inner paired basal unguis teeth and elongate mucrones but devoid of large, foliate scales on dentes and treated it under Paronellinae. The two genera viz., *Trogolaphysa* and *Trogonella*, are placed in Troglopedetini were included under Cyphoderinae (Salmon, 1964). Present investigator had an opportunity to examine a few species of *Cyphoderopsis* Carpenter, a member of the tribe Troglopedetini. This genus also does not differ significantly in gross salient features from members of Paronellinae other than the two characters cited above. Further, *Cyphoderopsis kempfi* (type-species) possesses a distinct scale appendage, a characteristic structure restricted only to some genera of Paronellinae. Further, enlargement of inner paired basal teeth of unguis in this species of *Cyphoderopsis* is similar to some species of *Dicranocentruga*. A tendency of enlargement of inner paired basal teeth of unguis is also observed in the species of *Dicranocentruga* and *Paronella fusca* and *Microparonella*. Further, genera under Paronellini (in the present sense) and Bromacanthini are also devoid of flexed macrochaetae (achaetoid body) like the genera under Troglopedetini. Troglopedetini, however, presents major features which justify its placement under Paronellinae. According to Delamare Deboutteville (1951b), *Trogonella* reduces the gap which exists between the primitive groups of Paronellinae and Troglopedetini.

It is possibly that the genera of Troglopedetini had evolved from the precursors which were more close to those of Paronellini and Bromacanthini than those of Cyphoderini. Troglopedetini most probably represents a specialised off-shoot from the stalk which gave rise to Paronellini and lost their ocelli secondarily for their

troglophilic adaptation in caves and other dark microhabitats like coniferous forests within semi-humified needle litter (*Cyphoderopsis* sp.).

**Biogeography** : Collembolans in general have some limitations in their mode of dispersal owing to their small size, apterous condition and their susceptibility to changes of temperature and humidity. Stretches of flowing water and bodies of saline water, in most cases, further create insurmountable natural barriers for their dispersal. Paronellinae is a small group of Collembola which is primarily tropicopolitan in distribution. They are scarce in the temperate regions except New Zealand which has a few endemic and specialised genera and sub-genera (Fig.44). Fig.45 provides at a glance the main features of the connection between geographical distribution and probable phyletic relationships of the genera and sub-genera under Paronellinae. New Zealand has been shown as a separate biogeographic entity from the Australian Region as most of the genera represented there are endemic and specialised and not found in any other parts of the Australian and other zoogeographical regions.

Table-V shows the distribution of the genera and sub-genera under the tribe Cremastocephalini. Most of the genera under this tribe are endemic in distribution. Thus, out of the six genera, five are endemic to particular zoogeographical regions. Further, such endemic genera represent a very restricted distribution, being confined to a particular continent or sub-continent of each zoogeographical region. Thus, *Metacoelura* is restricted to the main territory of Australia, *Yosia* and *Pseudosalina* to India and *Akabosia* to Japan and its adjacent Tokara Island. Endemism of these genera suggests that they are probably of very recent origin, presumably after the close of Cretaceous which closed the direct physical links connecting different continental land masses. *Paronana* with its two sub-genera and the sub-genus *Pseudoparonellides* are restricted to New Zealand. These possibly originated sometime in the Tertiary i.e., after close of the Cretaceous when Australia and New Zealand were completely isolated from other continents. Sub-genus *Paronellides* is common to both Australia and New Zealand including Tasmania. This sub-genus has not so far been reported from the islands of the Australian Region. *Paronellides* probably originated before the isolation of New Zealand from Australia i.e., before the close of the Cretaceous and it is also indicative of the faunal similarity that exists between these two countries. *Salina*, the oldest genus under Cremastocephalini, exists in all the zoogeographical regions except New Zealand which is a temperate country. *Salina maculata* Folsom (1932), endemic to Hawaii and the Society Islands of the South Pacific, indicates the limited tolerance of this genus to sea water like other terrestrial organisms. The genus appears certainly to have evolved before the close of Cretaceous somewhere in the Northern Hemisphere which at that time as evidence suggests, had a uniformly tropical climate. Pleistocene glaciation and the advent of acute temperate climate perhaps have exterminated them from the regions where they are now absent.

The tribe Callyntrurini appears to be a newly evolved one as most of the genera and sub-genera are endemic either to the Oriental or Australian Regions. The only genus under this tribe which appears to have a moderately wide distribution is *Callyntrura*. It is chiefly a genus of the Oriental Region, outside which it is represented by one species each in the Palaeartic and Australian Regions. The abundance of the species of *Callyntrura* in the Oriental Region apparently indicates its probable origin and proliferation in this Region. It also appears likely that it might have originated in the late Cretaceous somewhere in the Northern Asia which at that time had a tropical climate. Chilling of climate in the early Tertiary and subsequently the Pleistocene glaciations might have compelled its representatives to migrate to the tropical Southern Oriental Asia and later they had spread to the islands of the Oriental Region. Next to *Callyntrura*, *Dicranocentroides* exhibits relatively wide distribution in comparison to the other genera under Callyntrurini. Though restricted to the Oriental Region, it is abundant in the tropical Southern Asia as well as in the islands of the Oriental Region. Like *Callyntrura*, *Dicranocentroides* also may be a migrant to the tropical Oriental Region from the Northern Asia. Its total absence in the Palaeartic Region indicates its low range of adaptation as compared to *Callyntrura*. Other genera of this tribe, viz., *Idiomerus* is restricted to India and *Pseudoparonella* and its sub-genus *Lawrenceana* to Australia and in the islands of the Australian Region. Distribution of the genera under Callyntrurini (Table-VI) suggests in general their probable origin not before the Tertiary.

Table-VII shows the general distribution of the genera under Paronellini. *Paronella*, in the broad sense, was recorded from almost all the zoogeographical regions by various workers who tried to justify the comopolitan distribution of this genus by many hypotheses. Denis (1925) considered the genus as a very old one which had spread in various parts of the Gondwanaland and extended upto Japan and thus justified its presence in the South America. Present investigation proved that *Paronella* is extremely specialised and is endemic to the African continent. Besides the presence of extra ocular structure, a character which *Paronella* shares with the other two genera under this tribe, double rows of non-transiting manubrial and dental spines and strikingly large entomobryiform body facies in the type-species (*P. fusca*), not only make it distinct from other species, now known under this genus from Ethiopian Region but also from other Zoogeographical regions of the world. *Paronella*, as its present distribution indicates, appears to have originated sometime in the Tertiary after isolation of Africa and South America. *Dicranocentruga* and *Campylothorax* are distributed both in the Ethiopian and Neotropical Regions. Such distribution apparently indicates that they have originated before *Paronella*. In terrestrial organisms, such distribution could be explained from two stand points: (1) if these existed before the Cretaceous and (2) the use of land bridges between Africa and South America spanning the Atlantic Ocean. Further, if these genera or units from which they have evolved existed before the close of Cretaceous, it may be

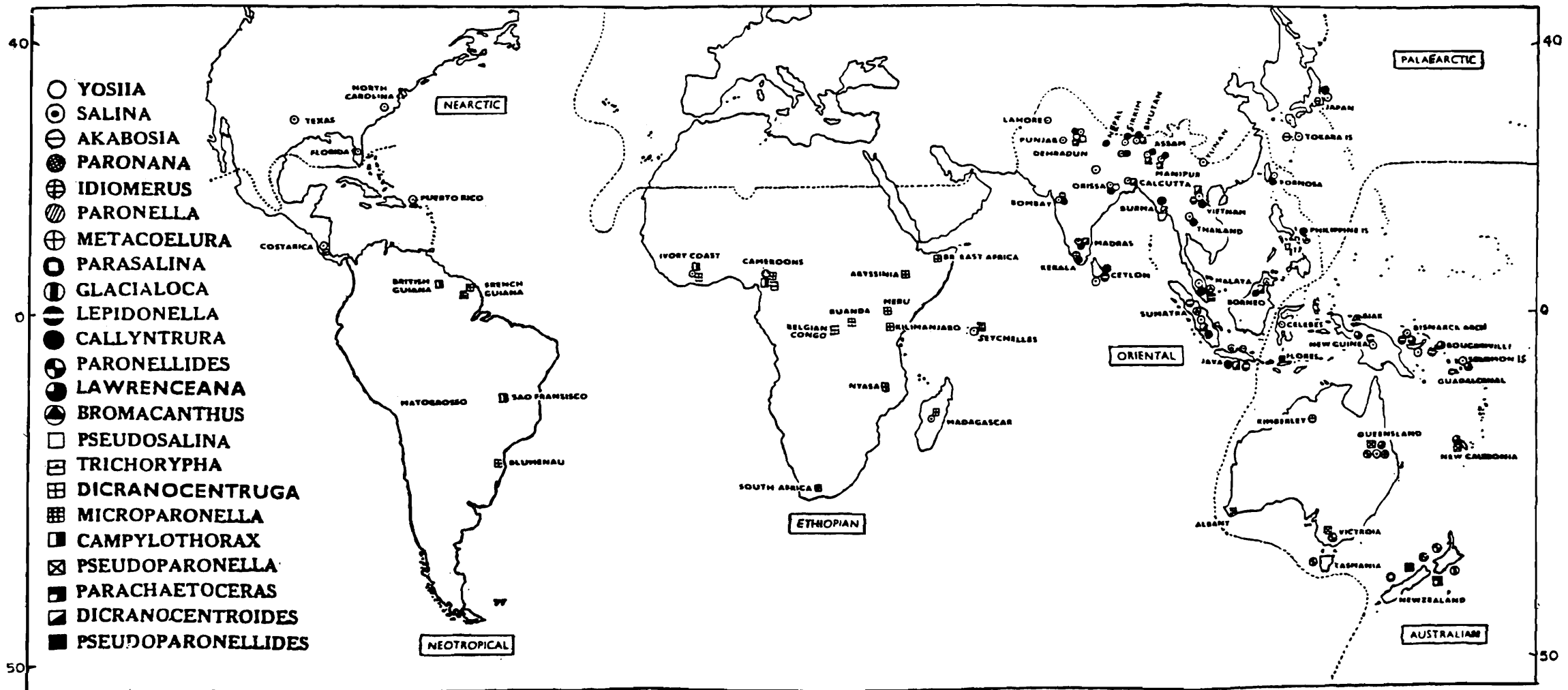


Fig. 44. Distribution of The World Genera Under Paronellinae

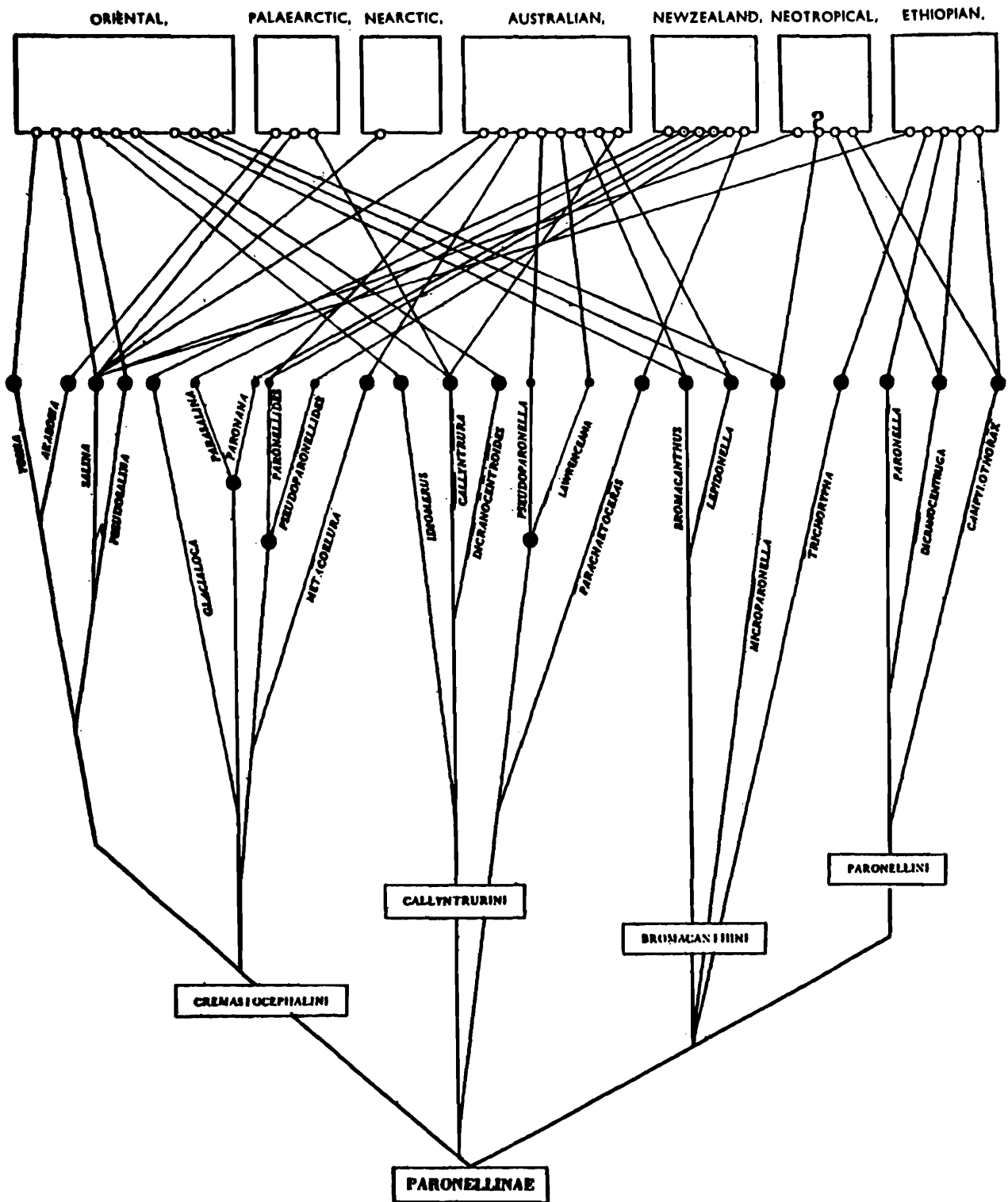


Fig. 45 : Main Features Of The Connection Between Geographic Distribution And Probable Phyletic Relationships Of The Genera Under Paronellinae

possible they originated somewhere in the Northern Eurasia and dispersed to South America and Africa before the onset of the Pleistocene glaciation when temperature of that region started falling down. Moreover, as mentioned before, there is evidence of the existence of tropical climate during the Cretaceous in the Northern Hemisphere.

Table-VIII provides an account of the distribution of the genera under Bromacanthini. The genus *Bromacanthus* is restricted to the islands of the Oriental Region. Present investigation proves it to exist in a small island of the Australian Region viz., Biak, adjacent to the east of New Guinea. Its absence in the other regions of the world indicates its recent origin, sometime in the Tertiary. Its probable place of origin appears to be somewhere in the islands of the Oriental Region as the three species which are recognised in this genus are chiefly distributed to and were originally described from this region. Further, the species viz., *Bromacanthus handschini* Schott (1925), which occurs in Biak, was originally described from Sarawak, an island in the Oriental Region; its presence in Biak may be incidental. *Lepidonella* is represented in the Oriental Region and in the islands of the Australian Region. In the Oriental Region also, it is chiefly represented in the islands. Such pattern of distribution suggests that it is relatively a newly evolved genus and originated possibly in the Tertiary; somewhere in the islands of the Oriental or Australian Regions. In contrast to *Bromacanthus*, *Lepidonella* has a relatively wide distribution and it is represented by one species viz., *Lepidonella ceylonica* (Yosii, 1966a), which is common to both Ceylon and India. Further, some species like *Lepidonella annulicornis* (Oudemans, 1890) and *Lepidonella subcarpenteri* (Denis, 1948) occur in both Oriental main land [Indochina (Denis, 1948)] and Oriental and Australian islands (Java and Solomon Islands). *Lepidonella*, therefore, appears to have evolved in the same geological era as that of *Bromacanthus*. *Trichorypa* is a specialised genus from Africa and so far is not known from any other part of the world. Its endemism in Africa indicates its probable recent origin sometime in the Tertiary. *Microparonella* exhibits striking discontinuous distribution. The species *Paronella berlandi* Denis (1925) from South America, as its features suggest, is most probably a *Microparonella*. The genus, as the current records show, is restricted to the Oriental (Malaya and Seychelles) and Neotropical Regions. Such discontinuous distribution of the genus possibly indicates that it is old and presumably had originated before the Cretaceous and spread all over the world which had at that time almost uniform climatic conditions. Later, the advent of unfavourable climatic conditions in the Tertiary (Pleistocene) might have wiped or modified it in other parts of the world. Consequently, its representatives are today localised in a few pockets of the Oriental and Neotropical Regions. Such discontinuous distribution of *Microparonella* can be compared with the distribution of Tapirs which are now localised in the tropics of South and Central America and Malayan Region.

The salient points, which emerge from the above discussion, can be summarised as follows: (a) Strong endemism exists in the genera under Paronellinae, (b) Almost each zoogeographical region has at least one or more endemic genera and sub-genera, (c) Most of the genera, as are seen in the present form today, do not appear to have originated before Tertiary, (d) New Zealand has the most specialised and endemic genera. It appears to be the result of its long isolation and the temperate climatic conditions, (e) New Zealand and Australia exhibit the faunal similarity, (f) Islands of the Australian Region represent specialised genera, some of which, though common in the main territory of Australia, are not represented in New Zealand. *Lepidonella* is the genus which is frequently found in both the Oriental and Australian Island but does not occur in the main territory of Australia and New Zealand, (g) Oriental Region has its own specialised genera, except *Callyntrura* which is represented sporadically in the Palearctic (Japan) and in an oceanic island (Flores) of the Australian Regions, (h) *Salina* appears to be the oldest genus of Paronellinae which occurs in almost all the zoogeographical regions of the world including small isolated oceanic islands. It is, however, absent in New Zealand, (i) Ethiopian Region has the strongest faunal similarity with the Neotropical Region, (j) *Paronella* is an endemic genus of the African Continent, (k) *Microparonella* exhibits discontinuous distribution.

The known distribution of Troglopedetini (Table-IX) suggests its presence in Palearctic, Ethiopian, Oriental and Neotropical Regions. The genera, known from different zoogeographical regions under this tribe, need a thorough revision to precise their relationships and also to elucidate their biogeography.

The biogeographical picture of Paronellinae, given above, is chiefly based on the study of large collections from different parts of the world as well as on informations available in literature. Further survey and examination of collections from different zoogeographical regions of the world might widen or modify the present perspective of the biogeography of this group of insects.

**TABLE—V**  
**Distribution of the genera and sub-genera of Cremastocephalini**

Genera/Sub-genera	R e g i o n s							
	Nearctic	Palaeartic	Ethiopian	Oriental	Australian	New Zealand	Islands*	Neotropical
<i>Salina</i>	+	+	+	+	+	+	+	+
<i>Pseudosalina</i>	—	—	—	+	—	—	—	—
<i>Yosia</i>	—	—	—	+	—	—	—	—
<i>Akabosia</i>	—	+	—	—	—	—	—	—
<i>Metacoelura</i>	—	—	—	—	+	—	—	—
<i>Paronellides</i>	—	—	—	—	+	+	—	—
<i>Pseudoparonellides</i>	—	—	—	—	—	+	—	—
<i>Paronana</i>	—	—	—	—	—	+	—	—
<i>Parasalina</i>	—	—	—	—	—	+	—	—
<i>Glacialoca</i>	—	—	—	—	—	+	—	—

+ = Present

— = Absent

\* Islands of the respective region or regions, where the genus or sub-genus is represented

**TABLE—VI**  
**Distribution of the genera and sub-genera of Callyntrurini**

Genera/Sub-genera	R e g i o n s							
	Nearctic	Palaeartic	Ethiopian	Oriental	Australian	New Zealand	Islands*	Neotropical
<i>Idiomerus</i>	—	—	—	+	—	—	—	—
<i>Dicranocentroides</i>	—	—	—	+	—	—	+	—
<i>Callyntrura</i>	—	+	—	+	+	—	+	—
<i>Pseudoparonella</i>	—	—	—	—	+	—	+	—
<i>Lawranceana</i>	—	—	—	—	+	—	+	—
<i>Parachaetoceras</i>	—	—	—	—	—	+	—	—

+ = Present

— = Absent

\* Islands of the respective region or regions, where the genus or sub-genus is represented

**TABLE—VII**  
**Distribution of the genera of Paronellini**

Genera/Sub-genera	R e g i o n s							
	Nearctic	Palaeartic	Ethiopian	Oriental	Australian	New Zealand	Islands*	Neotropical
<i>Paronella</i>	—	—	+	—	—	—	—	—
<i>Dicranocentruga</i>	—	—	+	—	—	—	+	+
<i>Campylothorax</i>	—	—	+	—	—	—	—	+

+ = Present

— = Absent

\* Islands of the respective region or regions, where the genus or sub-genus is represented

**TABLE—VIII**  
**Distribution of the genera of Bromacanthini**

Genera/Sub-genera	R e g i o n s							
	Nearctic	Palaeartic	Ethiopian	Oriental	Australian	New Zealand	Islands*	Neotropical
<i>Bromacanthus</i>	—	—	—	+	+	—	+	—
<i>Lepidonella</i>	—	—	—	+	+	—	+	—
<i>Microparonella</i>	—	—	—	+	—	—	+	+
<i>Trichorypha</i>	—	—	+	—	—	—	—	—

+ = Present

— = Absent

\* Islands of the respective region or regions, where the genus or sub-genus is represented

TABLE—IX

## Known Distribution of the genera of Troglopedetini Börner, 1913

Genera/Sub-genera	R e g i o n s							
	Nearctic	Palaeartic	Ethiopian	Oriental	Australian	New Zealand	Islands*	Neotropical
<i>Troglopedetes</i>	—	+	+	—	—	—	—	—
<i>Cyphoderopsis</i>	—	—	—	+	—	—	—	+
<i>Troglaphysa</i>	—	—	—	—	—	—	—	+
<i>Trogonella</i>	—	—	+	—	—	—	—	—
<i>Troglopedetina</i>	—	+	+	—	—	—	—	—

+ = Present

— = Absent

\* Revisional studies in progress.

## SUMMARY

Results of chaetotaxic studies of Paronellinae are presented in this communication. It is seen that cephalic chaetotaxy is characteristic for each genus. According to chaetotaxy and general clothing of body, three new tribes are recognised. The genera can be grouped as "lepidose", "parachaetose", "oligochaetose" and "polychaetose" on the basis of the presence or absence of true scales or pseudoscales coupled with presence or absence of flexed macrochaetae. The pseudoscales are later acquisitions as revealed from seti-form scale primordia as well as their ultrastructures.

Cephalic chaetotaxy, specially of certain regions, is useful for determining the phyletic connections that exist between different genera of Paronellinae (plesiomorphic features). While it is difficult to conceive and characterise a single archaetype that gave rise present day Paronellinae, it is, however, evident that the genera of Paronellinae evolved from two distinct stocks, one giving rise to the genera under Cremastocephalini and Callyntrurini and the other Paronellini, Bromacanthini and Troglopedetini, representing true soil-type Collembola.

Present day distribution of Paronellinae can be explained on the basis of past configuration of land masses because of their primarily wingless conditions and their susceptibility to bodies of saline water. Their present distribution pattern supports the Wengner's Hypothesis.

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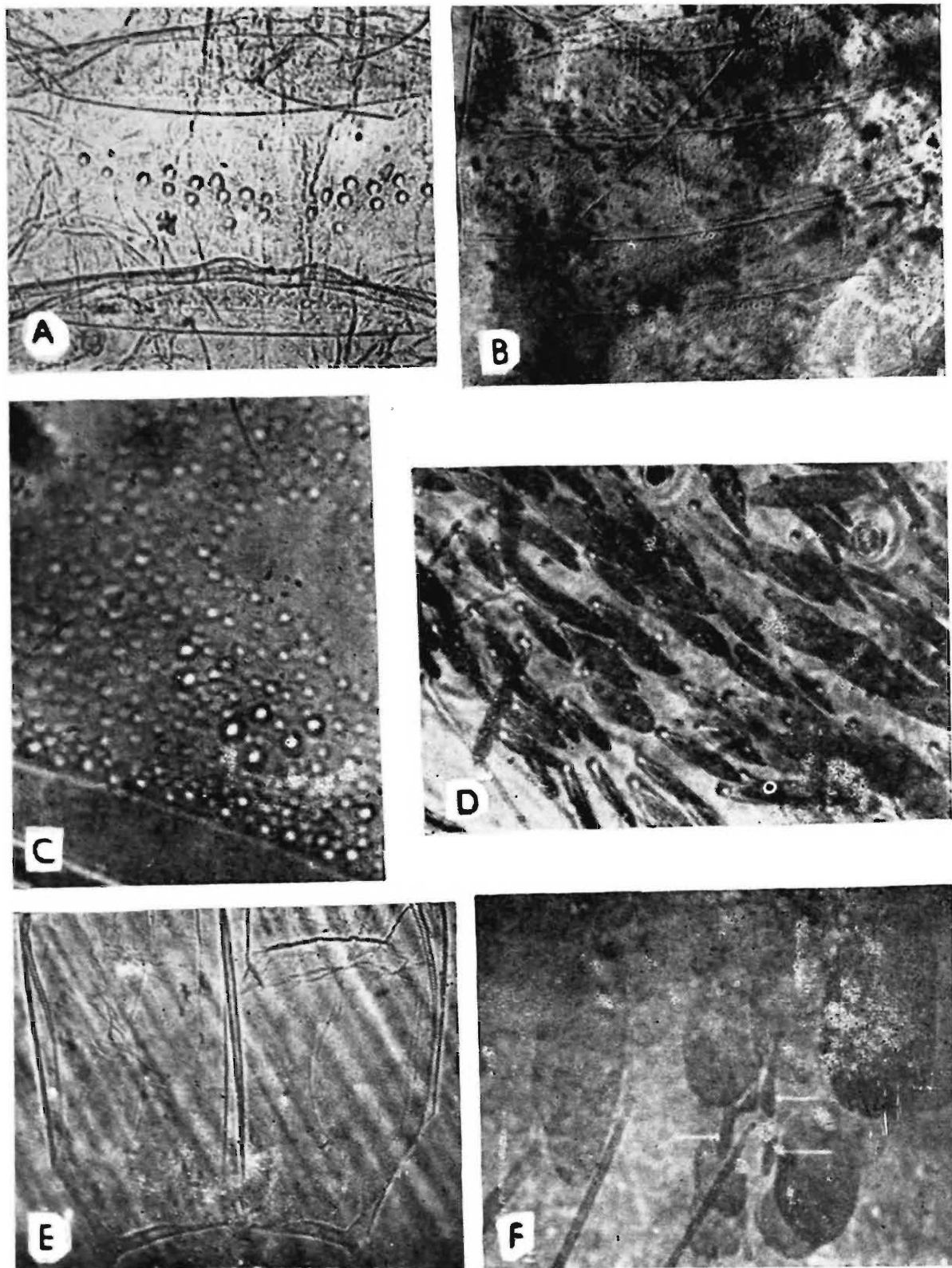
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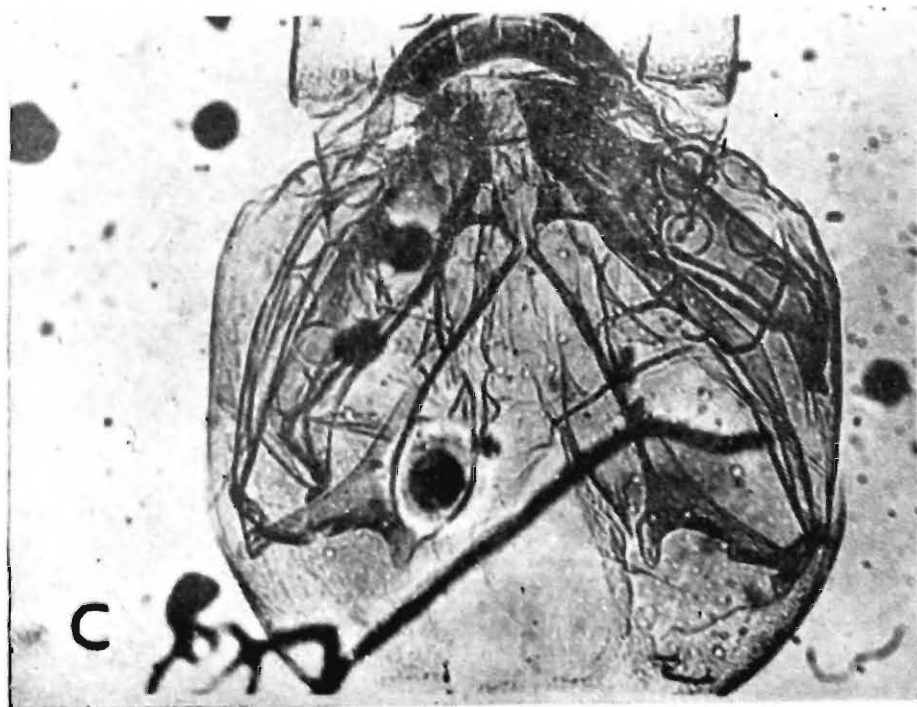
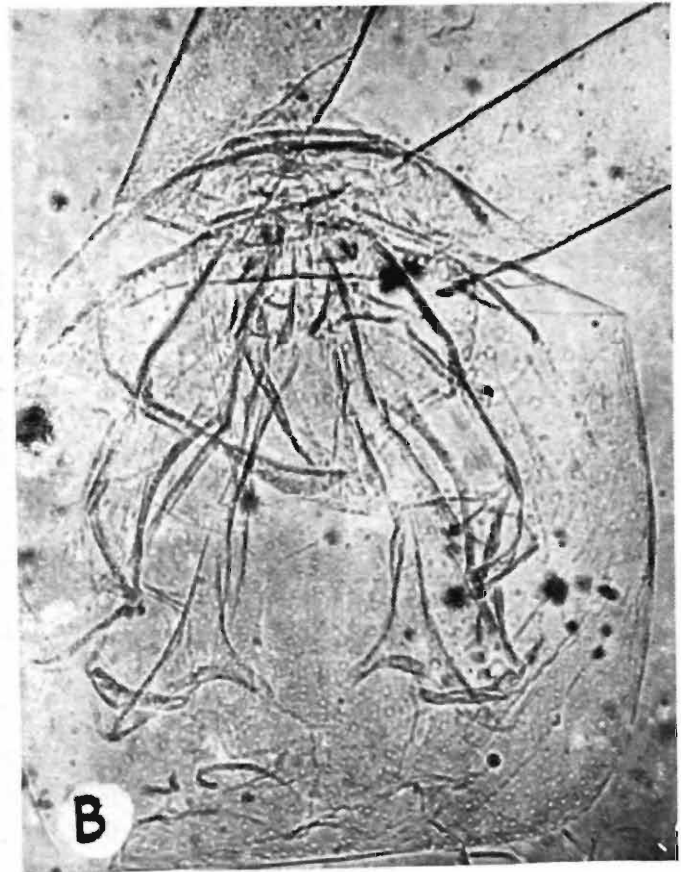
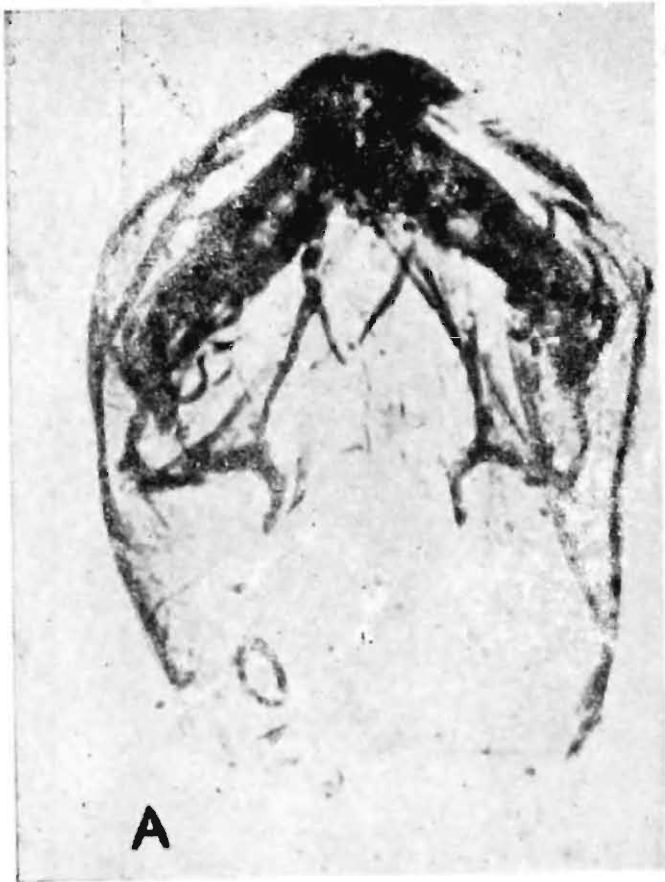
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- A. *Pseudoparonella (Lawrenceana) queenslandica* (Schott)—Th. III with portions of Th. II and Abd. I.
- B. *Dicranocentruga nigromaculata* (Schott)—Ths. II, III and Abds. I, II, III.
- C,E. *Campylothorax longicornis* (Schott)—C. Th. II ; E. Abd. IV.
- D. *Dicranocentroides gisini* Mitra—Pseudoscales and scale primordia from Abd. IV.
- F. *Lepidonella tokiokai* Yosii—Typical scales and accessory scales (marked with arrows) near base of 11.

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PLATE II

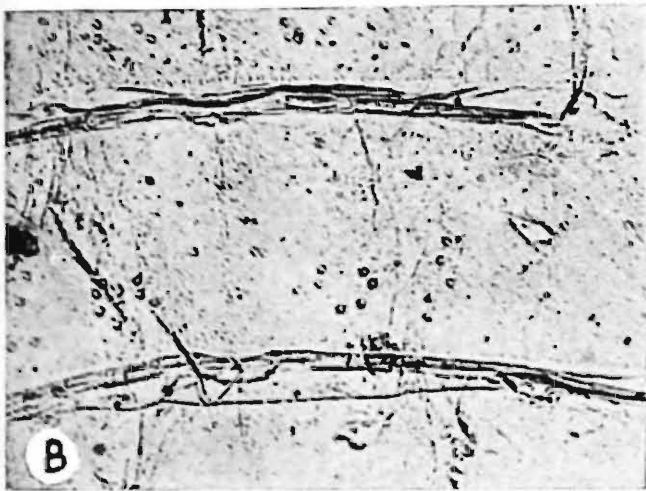
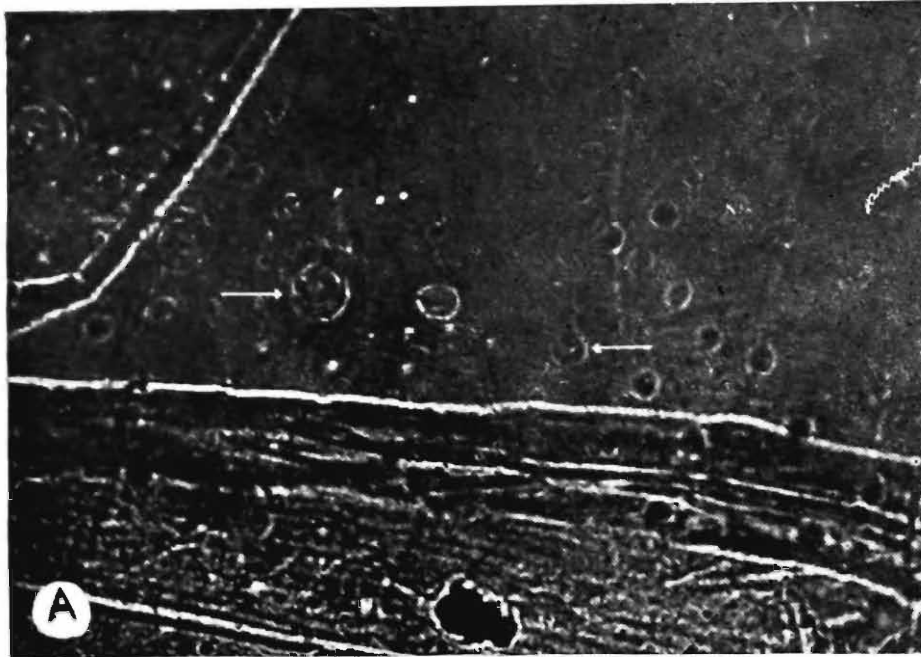


Cephalic Chaetotaxy

A, *Sallna* (*indica* group); B. *Dicranocentruga nigromaculata* (Schott);  
C. *Pseudoparonella (Lawrenceana) queenslandica* (Schott).

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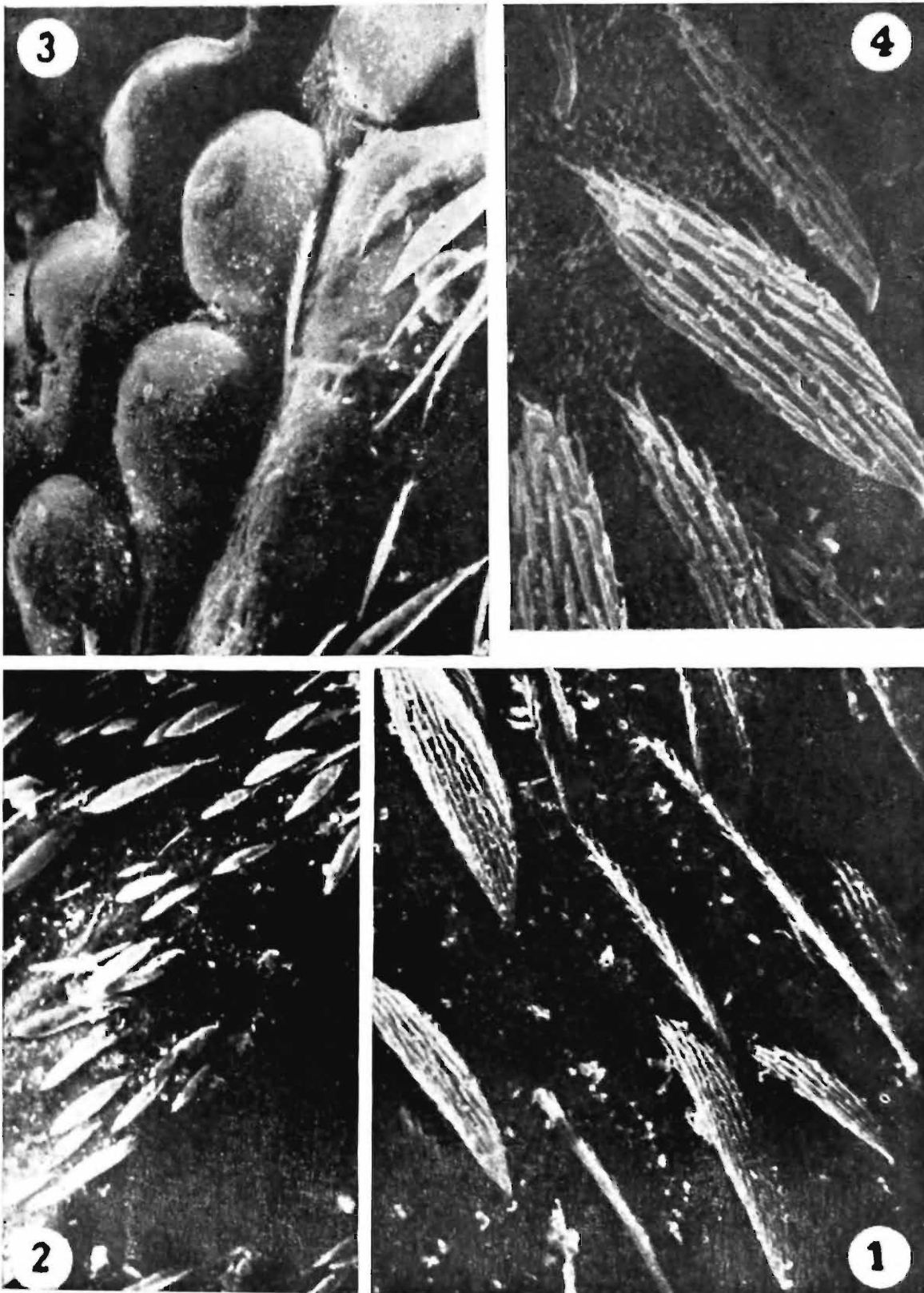
PLATE III



A., *Pseudoparonella (Lawrenceana) queenslandica* (Schott)—A portion of Abd. II (left) showing the socket of a lasinotrichium (11) [soc. 11, indicated by an arrow] and sockets of macrochaetae (set. soc.) after clearing (from a paralectotype). B., *Pseudoparonella (Pseudoparonella) appendiculata* (Schott)—Portions of Ths. II, III and Abd. I showing the presence of flexed macrochaetal sockets and insertions of scales after clearing (from a paralectotype). C., *Callyntrura (Handschinphysa) vestita* (Handschin)—showing the presence of flexed macrochaetal sockets and insertions of scales.

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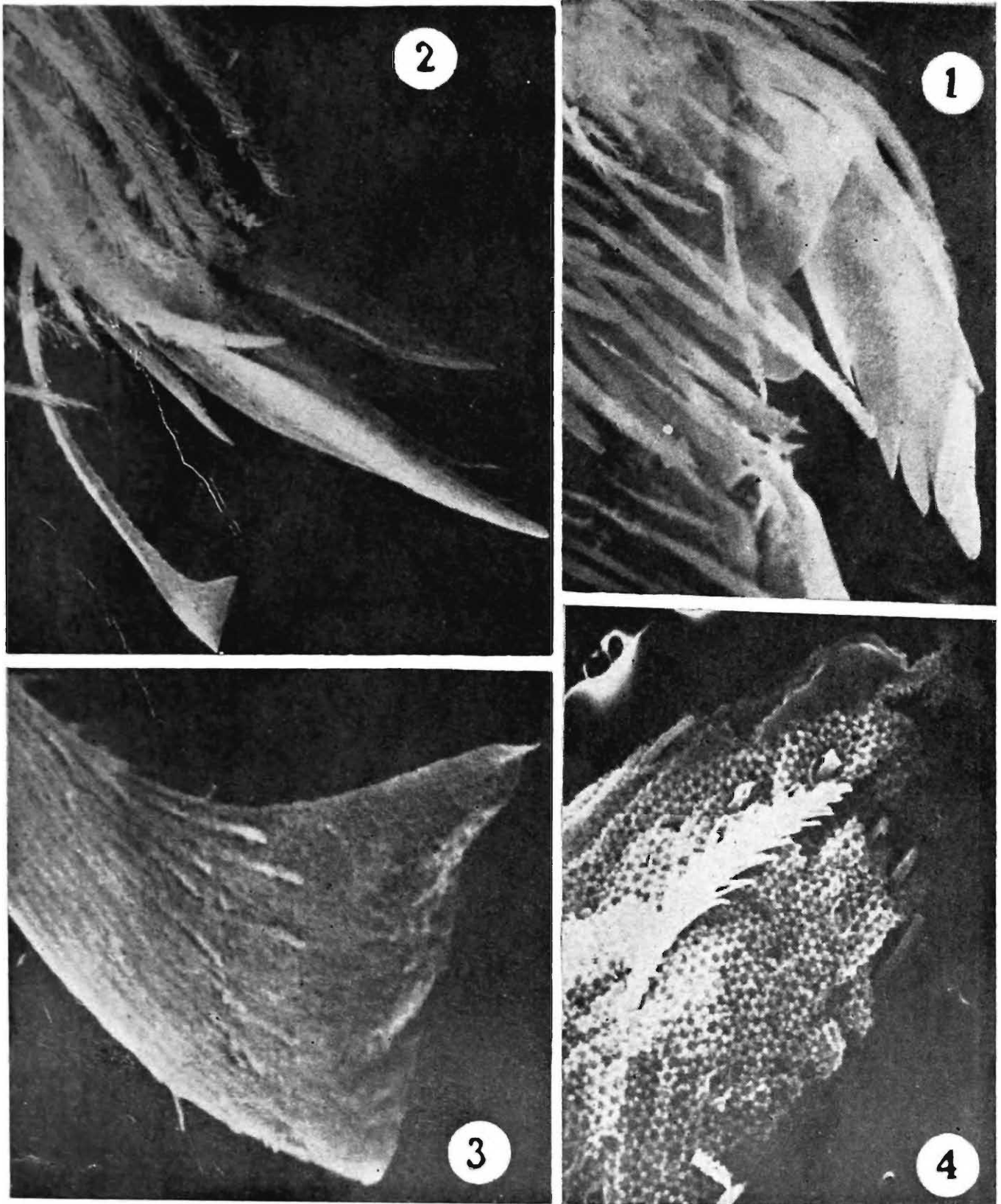
PLATE IV



*Callyntrura (Handschinphysa) lineata* (Parona): 1. Pseudoscales from Abd. IV (X 1,600); 2. Pseudoscales from Abd. IV (X 450); 3. Ocelli (X 1000); 4. Pseudoscales from Th. II (X 4,500) [SEM Photomicrographs]

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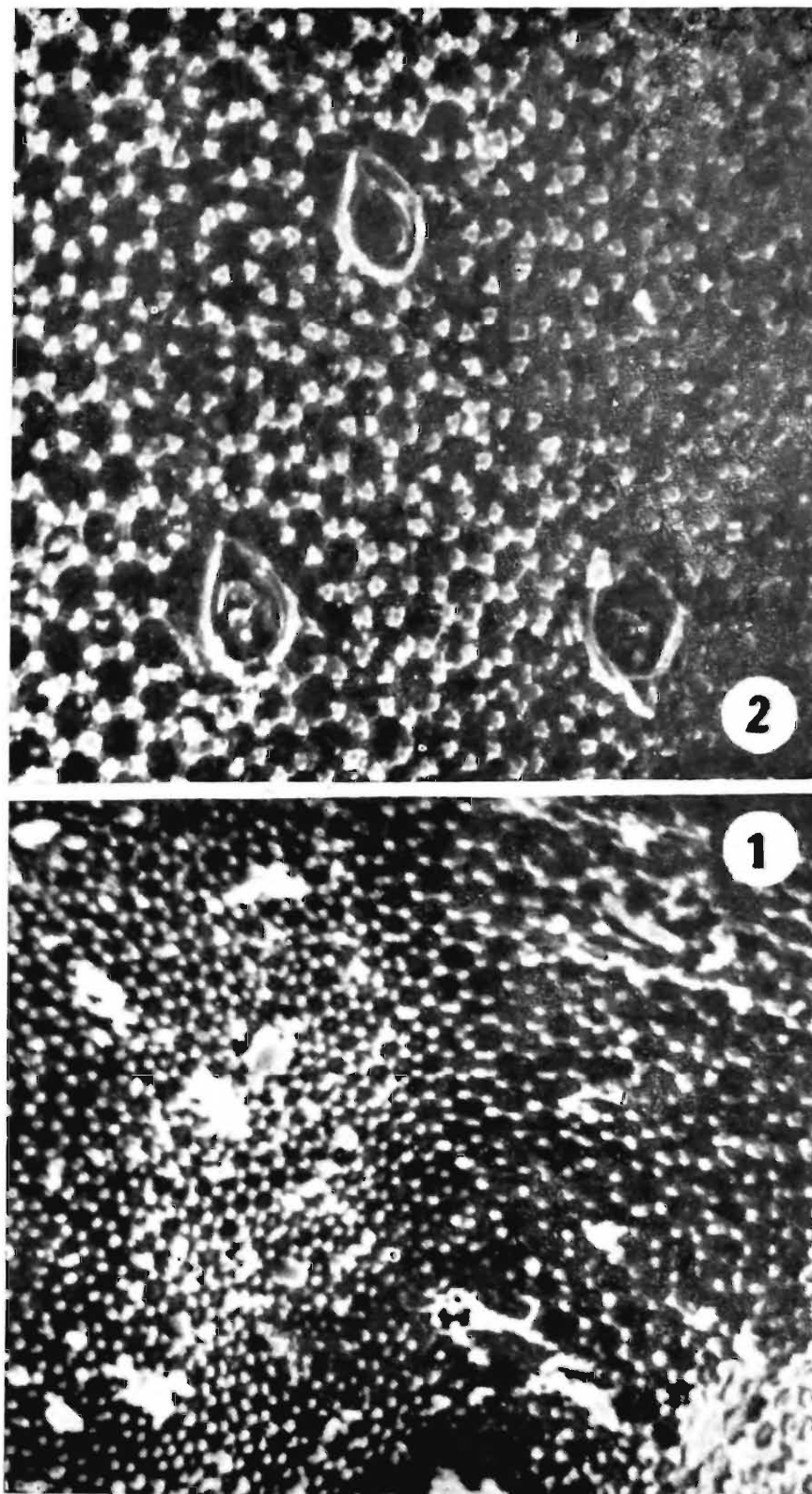
PLATE V



*Callyntrura (Handschirphysa) lineata* (Parona) : 1. Mucrone (X 1000) ; 2. Unguis and unguiculus from leg II (X 1,600) ; 3. Apex of tenant hair (X 4,500) ; 4. Apex of Ant. IV (X 3000) (SEM Photomicrographs).

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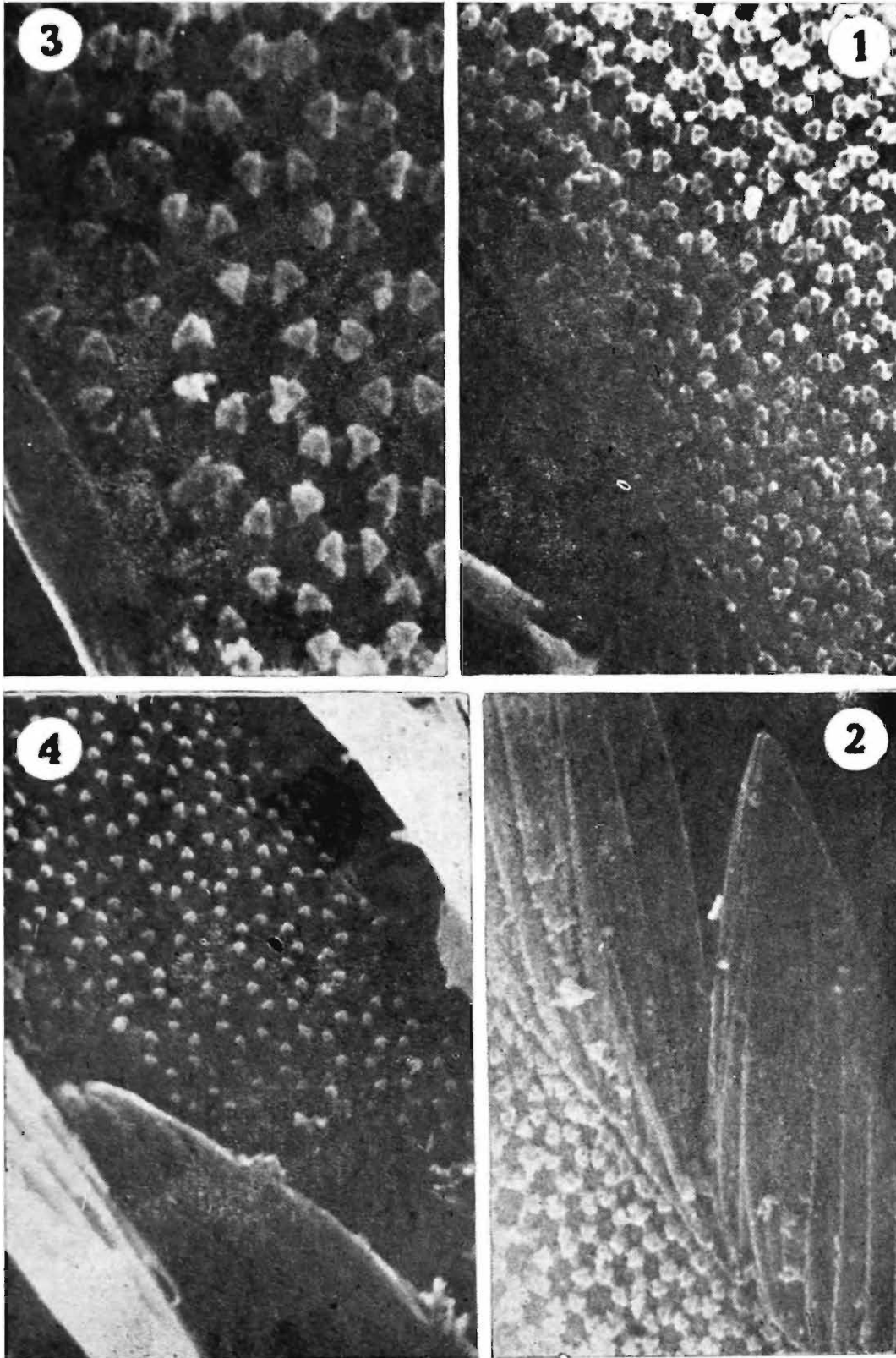
PLATE VI



*Callintra (Handschinphysa) lineata* (Parona) : 1. Cuticular configuration of Ocelli (X 10,000) ; 2. Cuticular configuration of Ant. III (X 10,000) [ Note : 3 setal sockets ] [ SEM Photomicrographs ]

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PLATE VII



*Callvnrura* (*Handschinphysa*) *lineata* : 1. Cuticular configuration of dental-scale appendage (X:10,000); 2. Cuticular configuration of mucrone (X 10,000); 3. Cuticular configuration from mucronal tip (X 30,000); 4. Cuticular configuration of thorax (lateral) (X 10,000).

[ SEM Photomicrographs ]