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STRUCTURAL MODIFICATIONS LEADING TO THE FORMATION OF THE HYPOSTOMAL BRIDGE IN ORDER HYMENOPTERA (INSECTA)

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ABSTRACT

In the lower symphytans (Insecta: Hymenoptera) represented by the family Xyelidae, the hypostomal bridge is absent. In the families Argidae, Diprionidae and Tenthredinidae, though the bridge is absent, the hypostomal sclerites extend mesally in a form indicating a tendency toward the formation of a bridge. This tendency of bridge formation by the hypostomal sclerites is clearly evident in the families Pamphiliidae, Cimbicidae, Cephidae and Xiphydriidae, where a conspicuous bridge is formed, however, it is only moderately sclerotized. In the Siricidae the hypostomal bridge is present, clearly retaining the line of fusion of hypostomal sclerites, a condition which is present in almost all the apocritan families. However, in the bees (Apoidea) even this line of fusion is missing and the bridge is represented by a clear cross bar. Thus, all of the forms studied reveal a distinct chain of modifications which indicate to be an evolutionary trend.

INTRODUCTION

The presence of the hypostomal bridge, termed genaponta by Ross (1937), that separates the foramen magnum from the oral fossa, is a characteristic feature of all the higher hymenopterans. In the formation of this bridge the two mesal ends of the hypostomal sclerites fuse proximally with each other or the membranous area lying between them becomes sclerotized. However, according to Bigelow (1954) the bridge was formed due to the ventral closure of the occipital foramen by the extensions of the post-genal areas.

A survey of the literature brings out the fact that no work is available concerning the phylogenetic history of the hypostomal bridge, which forms an important topographical landmark of the head capsule in the Apocrita (Hymenoptera). Comments on the nature of the hypostomal bridge were made by Wheeler (1910), Snodgrass (1925, 1935, 1941), Bird (1926), Ross (1937), Duncan (1939), Arora (1953), Rivard (1955), Matsuda (1957, 1965), Bracken (1961), Wong (1963), Dhillon (1966) and Khalil & Habib (1969). Many others have also referred to this specialized zone of the head, but only in terms of its ontological nature. Hence, in view of the importance of this distinct and quite prominent area of the head capsule and lack of information on its phylogeny, an attempt was made to present an account of the modifications which led to the formation and consolidation of the hypostomal bridge. The present study also identifies the cranial areas which contribute to the formation of the hypostomal bridge. Furthermore, it reveals and establishes phylogenetic relationships among various families in the order Hymenoptera.

MATERIAL AND METHODS

To carry out the present study, most of the specimens of Apocrita were collected from the Punjab and Himachal Pradesh in India, during September and October, 1975 and preserved in 80% alcohol. Symphyta, with the exception of Megalodontidae and Orussidae, were supplied by the Biosystematic Research Institute, Canada, and the Zoological Survey of India. Since the specimens provided by the latter were dry, they were softened by immersion in 2% KOH for about six days. Diagrams were drawn with the help of a binocular fitted with a graph eye-piece.

OBSERVATIONS AND DISCUSSION

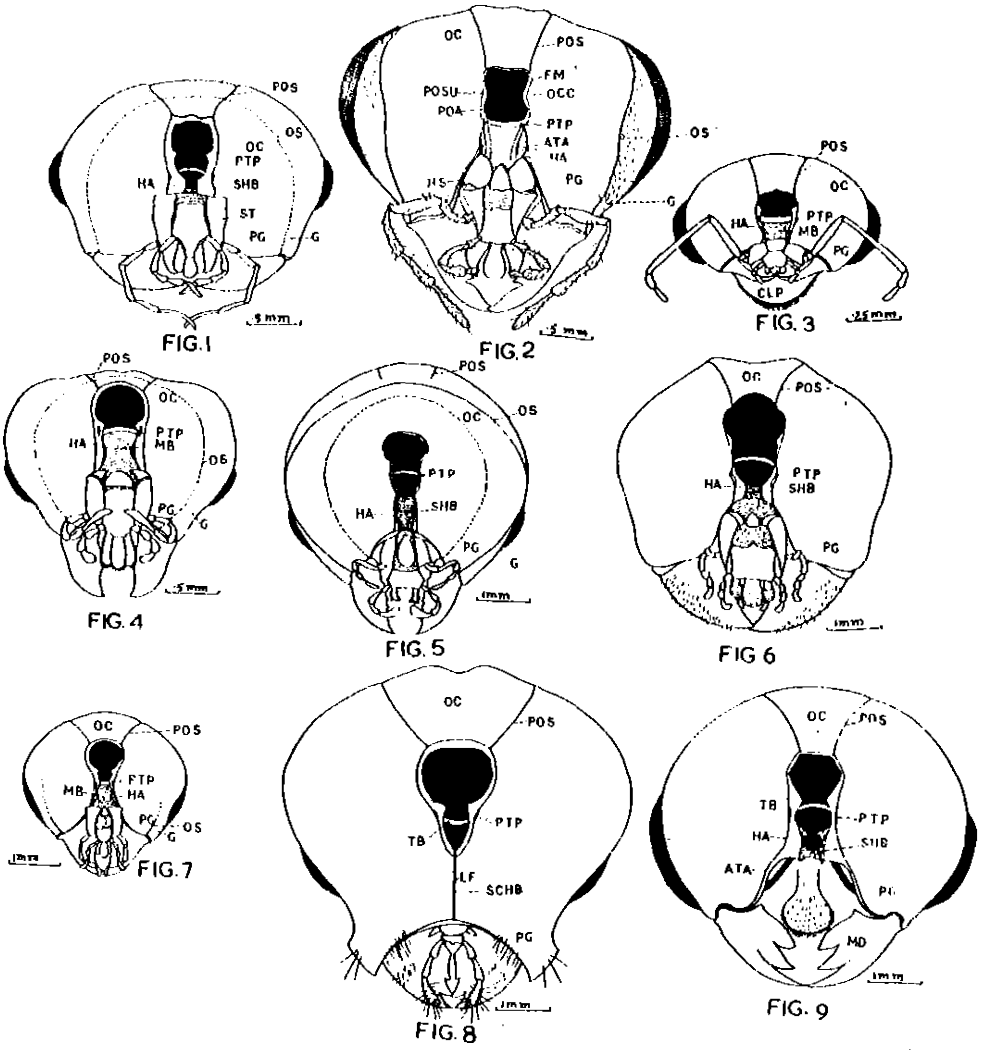
Comparative studies reveal that in the lower symphytans the hypostomal bridge is absent. In higher representatives of the group, though the bridge is not present, the mesal ends of the hypostomal sclerites are extended in a manner indicating a tendency towards the formation of a bridge. In more higher symphytans a conspicuous bridge is present but it is only moderately sclerotized. Ultimately in members of the family Siricidae the hypostomal bridge is prominent, but the line of fusion of the two mesal hypostomal extensions is still retained. This condition in a modified form is present in the apocritans generally, while in the bees even the line of fusion is missing. All the studied forms

thus reveal distinct chain of modifications which indicate an evolving structural pattern, a detailed account of which is given below.

The series of modifications begin with the members of the family Xyelidae. In *Xyela bakeri* Konow (Fig. 3) the hypostomal sclerites occur under the post-occipital areas but have no mesal extensions. These precursors, though, can be clearly observed in *Arge clavicornis* (Fabricius) (Fig. 4) (Argidae), *Neodiprion abietis* (Harris) (Fig. 7) (Diprionidae) and *Tenthredo verticalis* Say (Fig. 2) (Tenthredinidae). In all these representatives the mesal margins of the hypostomal areas slightly below the tentorial bridge, show conspicuous triangular extensions with which articulate the proximal tips of the cardines. Similar observations have also been made on *Pristiphora cincta* Newman, *Pachyprotasis versicolor* Cameron *Pachyprotasis brunetti* Rohw and *Tomostethus (Eutomostethus) assomensis* Rohw (Tenthredinidae). A similar condition has also been reported by Bird (1926), Snodgrass (1935), Ross (1937), Arora (1953), Matsuda (1957), Bracken (1961), Wong (1963) and Dhillon (1966). However, Bracken (1961) and Wong (1963) have shown these extensions in the form of separate sclerites, and named them as maxillaria.

The next stage in the series of these modifications is represented by *Acantholyda maculiventris* (Norton) (Fig. 1) (Pamphiliidae), *Cimbex americana americana* Leach (Fig. 6) (Cimbicidae), *Cephus (Cepus) cinctus* Norton (Fig. 9) (Cephidae) and *Xiphydria mellipes* Harris (Fig. 5) (Xiphydridae), where a complete hypostomal bridge occurs. This bridge is not completely sclerotized and it consists of three distinct portions, one median and two lateral. The lateral portions are the mesal extensions of the hypostomal sclerites and are still differentiated as such; they are connected with each other at the median portion of the bridge, which appears as a different sclerotized region and replaces what earlier used to be membranous.

These observations clearly indicate that besides the lobes of the hypostomal sclerites which fuse directly with each other to form the bridge, the latter is also reinforced due to the sclerotization of the membrane lying between these lobes. A similar form of the bridge has also been observed in *Cephalcia provancheri* (Huard) and *Pamphilius luteicornis* (Norton) (Pamphiliidae) and in *Zarea inflata* Norton (Cimbicidae). Presence of a similar hypostomal bridge has also been reported by Snodgrass (1941) in the members of the families Megalondontidae, Pamphiliidae, Syntectidae, Xiphydridae and Siricidae and by Rivard (1955) in *Cephalcia marginata* (Pamphiliidae).



The next stage in the series can be observed in *Sirex cyaneus* Fabricius (Fig. 8) (Siricidae), where the two hypostomal sclerites instead of producing extensions are directly fused with each other underneath the foramen magnum. On this account, the hypostomal bridge is quite wide. The line along which the two sclerites have fused is distinctly visible in the form of a suture.

This condition is not confined only to *Sirex*. It also occurs in all the Hymenoptera Apocrita such as *Sycoscapter stabilis* (Walker) (Fig. 10) (Chalcidoidea: Torymidae), *Netelia kashmirensis* Cameron (Fig. 11) (Ichneumonidae), *Chrysis indogotea* Duf. et Perr.

(Fig. 13) (Chysididae), *Scolia quadripustulata* Fabricius (Fig. 12) (Scoliidae), *Scelephron intrudens* Smith (Fig. 14) (Sphecidae), *Vespa orientalis* Linnaeus (Fig. 15) (Vespidae), *Calicurgus* sp. (Fig. 16) (Pompilidae), *Camponotus camelinus* Smith (Fig. 17) (Formicidae) and *Mutilla* sp. (Fig. 18) (Mutillidae). In all these species a distinct hypostomal bridge is present. The breadth of this bridge varies from species to species, but in all these representatives the line of fusion is clearly indicated. These observations are further substantiated by the studies of Wheeler (1910), Snodgrass (1935, 1960), Duncan (1939), Khalil and Habib (1969) and Chapman (1972).

In *Xylocopa lemuiscapa* Westwood (Fig. 19) a member of the super-family Apoidea, the fusion of the two hypostomal sclerites forming the bridge is complete to the extent that the suture is completely missing. Thus below the foramen magnum, the post-genal area forms a complete uninterrupted sheet, which is interpreted here as being the hypostomal bridge. A similar type of hypostomal bridge has also been reported by Berthol (1925), Snodgrass (1925, 1942, 1960), Metcalf and Flint (1928), Fox and Fox (1964) and Delong and Borror (1970). This condition represents the final stage in the serialized modifications.

Figs. 1-9. Hymenoptera species, posterior views of heads of: 1 - *Acantholyda maculiventris* (Pamphiliidae); 2 - *Tenthredo verticalis* (Tenthredinidae); 3 - *Xyela bakeri* (Xyelidae); 4 - *Arge clavicornis* (Argidae); 5 - *Xiphydria mellipes* (Xiphydridae); 6 - *Cimbex americana americana* (Cimbicidae); 7 - *Neodiprion abietis* (Diprionidae); 8 - *Sirex cyaneus* (Siricidae); 9 - *Cephus (Cephus) cinctus* (Cephidae). ATA - Anterior tentorial arm; F.M. - Foramen magnum; G - Gena; HA - Hypostomal area; HS - Hypostomal suture; LF - Line of fusion; MB - Membrane; MD - Mandible; OC - Occuput; OCC - Occipital condyle; OS - Occipital suture; PG - Postgena; POS - Par occipital suture; POSU - Post occipital suture; PTP - Posterior tentorial pit; R - Ridge; SCHB - Sclerotized hypostomal bridge; SHB - Semisclerotized hypostomal bridge; ST - Stipes; TB - Tentorial bridge.

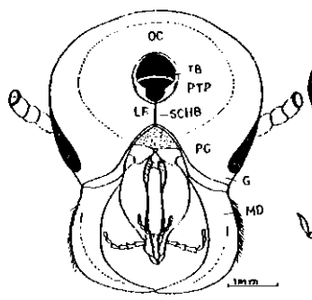


FIG. 12

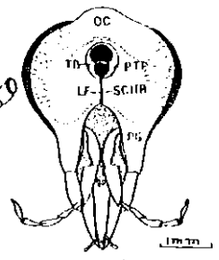


FIG.13

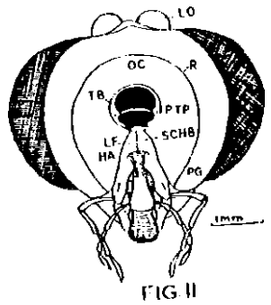
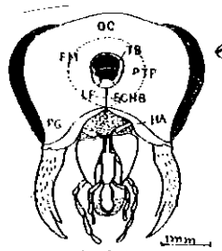


FIG. 11



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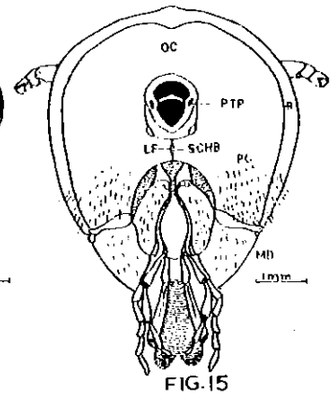


FIG.15

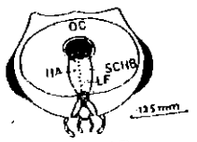
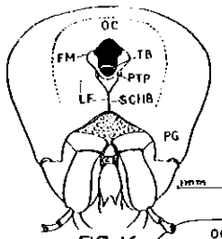


FIG. 10



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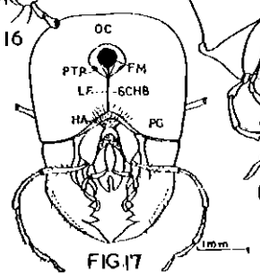

FIG.17

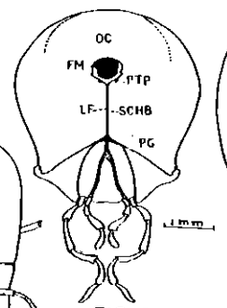

FIG.18

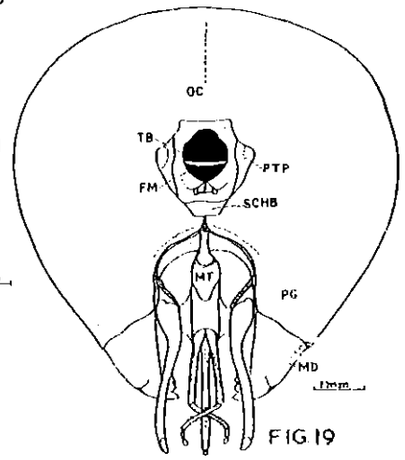

FIG.19

Figs. 10-19. Hymenoptera species, posterior views of heads of: 10 - *Sycoscapter stabilis* (Torymidae); 11 - *Netelia kashmirensis* (Ichneumonidae); 12 - *Scolia quadripustulata* (Scoliidae); 13 - *Chrysis indogotea* (Chrysididae); 14 - *Scelephron intrudens* (Sphecidae); 15 - *Vespa orientalis* (Vespidae); 16 - *Calicurgus* Sp. (Pompilidae); 17 - *Camponotus camelinus* (Formicidae); 18 - *Mutilla* sp. (Mutillidae); 19 - *Xylocopa lemuiscapa* (Xylocopidae). ATA - Anterior tentorial arm; FM - Foramen magnum; G - Gena; HA - Hypostomal area; HS - Hypostomal suture; LF - Line of fusion; MB - Membrane; MD - Mandible; OC - Occiput; OCC - Occipital condyle; OS - Occipital suture; PG - Postgena; POS - Par occipital suture; POSU - Post occipital suture; PTP - Posterior tentorial pit; R - Ridge; SCHB - Sclerotized hypostomal bridge; SHB - Semisclerotized hypostomal bridge; ST - Stipes; TB - Tentorial bridge.

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