INTRODUCTION

Neurological sciences in the nineteenth and early part of the twentieth century were dominated by researches on vertebrates, particularly on mammalian brain and very little scientific consideration was given to the structure of the brain in insects. A few investigations, carried out prior to 1885, dealt with overt brain structures, and hardly considered behaviour pattern that might be evoked by neural architecture. To be fair, the size of the insect brain did not lend itself to the kinds of lesion experiments that were practised on cephalopods or until much later on vertebrates, and the apparently simple structure of the intact insect brain led to the simplistic statements about its probable mode of action.

In the later part of this century, the various organs
of the insect brain have been brought to light and investigated upon, but the structural variations encountered during the detailed microscopic studies need viable explanations. Even the nomenclature of the various parts of the brain used by the various investigators in their respective works differs. As such, the subject encompasses the problems of nomenclature, structural homologies and structural and functional variations.

The apterygote insects, though small and difficult to analyse structurally and functionally, are of particular interest to the students of neuroanatomy because of the primitive features of their central nervous system. In spite of the fact that this group is very important from the evolutionary point of view, the information about their central nervous system is limited mainly to the papers of Hesse (1901), Hanström (1940, 1943), Marlier (1941), Denis (1949), Satija (1957) and Sumal (1973). The differences between the nervous systems of apterygotes, worked out so far, suggest their polyphyletic origin. The collemboles, that have been studied comparatively in detail, possess a very simple brain but are notable in having different types of ocelli, distributed to different species.

The histological studies of the brain of pterygote insects have been undertaken by many workers but the data collected from these studies throw little light on the
detailed organisation of the various neuropiles of the brain. In recent years, the neuroarchitecture of some of the common pterygote insects has been investigated in detail, but these reports are insufficient to correlate the organisational variations with the behaviour patterns of insects and to draw homologies of the various organs of the insect brain with those of the related invertebrates.

Amongst pterygotes, the structure of the orthopteran brain was first studied in 1876 by Dietl, followed by Newton (1879) and Packard (1880). Their description was neither complete nor detailed, but that gave the information about the names of the major areas and cell groups which formed the basis of the studies of the insect brain. Much later, the orthopteran brain was studied by Satija and Sharma (1965), Satija and Tangri (1968b), Schürmann (1973) and Williams (1975). Schürmann (1973) laid emphasis on the corpora pedunculata in the brain of Acheta domesticus, while Williams (1975) did so on the central complex of Locusta gregaria. The information about the anatomy and histology of the dermapteran brain is fragmentary and is limited to the account of Kühne (1913). He investigated the brain of Forficula auricularia and listed many neuropile areas and commissures. The hemipteran brain has been described by Pflugfelder (1937), Johansson (1957), Parson (1960), Guthrie (1961), Satija and Sohal (1962), Satija and Dhindsa (1967, 1968) and Satija et al. (1971). Johansson (1957) has
laid stress on the varying degree of the concentration of the central nervous system. Parson (1960) studied the nervous system of *Gelastocoris* and compared its structures with those of aquatic, semiaquatic and terrestrial bugs. Satija and Sohal (1962) and Satija and Dhindsa (1967 and 1968) tried to analyse the striking dissimilarities in the homopteran and heteropteran brains.

The structure of the hymenopteran brain is known chiefly from the works of Brandt (1879), Kenyon (1896), Jonescu (1909), Pietschker (1911), Thompson (1913), Vowles (1955), Satija (1958c), Jawlowski (1958), Shaumar (1966), Goll (1967), Mason (1972) and Singh (1975). The studies of these workers revealed that in most of the hymenopterans the cerebral and suboesophageal ganglia are connected intimately and thus appear as one mass. Brandt (1879) reported that the pedunculate bodies are of immense size in the workers of the common honey-bee, while they are slightly developed in the queens and the males.

Our knowledge regarding the histology of the coleopteran brain is due to the studies of Rabl-Ruckard (1875), Holste (1923), Bugnion (1933), Dönges (1954), Satija and Dass (1963a), Agee (1967), Satija and Tangri (1968b) and Singh (1976). The lepidopteran brain has been investigated by Buxton (1917), Bretschneider (1921),
The detailed knowledge of the dipteran brain comes mainly from the studies of Lowne (1890-1892), Power (1943), Satija (1958d), Nayer (1964), Tung and Lee (1969) and Mantaka (1974).

The complicated internal organisation of the insect brain was studied first of all by Dujardin (1850). He described the presence of convoluted disc-like structures in the brain of certain hymenopteran and orthopteran insects and termed them as 'Lobesa convolutions'. He observed that these structures are highly developed in ants, bees and wasps. Because of the marked intelligence of these insects, he compared them with the convolutions of the mammalian brain. Leydig (1864) called these convoluted discs as 'Gestielter Korper'. The structure of the corpora pedunculata as closed rings in the brain of Componotus lignipedus, Gryllus italicus, and Locusta verrucornis was described by Rabl Ruckard (1875). Dietl (1876) made extensive studies on the brain of bee, mole cricket and grasshopper and reported the presence of two mushroom-shaped bodies on either side of the brain. He adopted the term 'Pilzhut formiger korper' for them. Kenyon (1896) discussed in detail the structure of these mushroom-shaped bodies in Apis mellifera. Hanström (1928), while describing the structure of the corpora pedunculata in invertebrates
said, "The body of the brain in its primitive form is present in the family Hesionidae (Phylum Annelida) where it is represented by two groups of globuli cells and a stalk". Satija (1957 and 1958d), in his histological studies on the brain of Petrobius brevistylis and Calliphora erythrocephala, stated that corpora pedunculata in its typical form is absent in the former, whereas the calyx cups of the corpora pedunculata are very much reduced in the latter, Satija and Dhindsa (1967, 1968) found it feebly developed in Rhopalosiphum pseudobrassicae and Aphis gossypii. On the other hand, Satija and Sud (1967) in Anopheles stephensi, Satija and Aulakh (1971), in Dacus cucurbitae, Singh and Srivastava (1974) in Philosamia ricini and Singh (1976) in Chilocorus nigritus have reported the presence of a well developed corpora pedunculata.

The marked difference between the appearance of the corpora pedunculata is indeed a very interesting feature. The development of corpora pedunculata is related generally to the optic activity and psychic development of the insect. This deduction, however, does not hold good for all the insects. In Typhlopone (Rabl Ruckard, 1875), an African blind ant, there is a well developed corpora pedunculata which indicates that the optic activity does not govern the development of this structure. In Onthophagus catta (Satija and Dass, 1963b) the corpora pedunculata is found
to be well developed, but the psychic development is at a low ebb. In Diptera, the optic activity, in general, is of a high order but the corpora pedunculata is feebly developed (Flögel, 1878; Newton, 1879 and Power, 1943). In bees and ants, Vowles (1955) believes that the well developed corpora pedunculata is closely associated with the psychic development. In *Monomorium indicum*, where the psychic development is of a high order, Satija and Walia (1967a) observed a well developed corpora pedunculata with all parts having a complex organisation. Investigations carried out by Jawlowski (1963) support the hypothesis put forth originally by Hanström (1940) that the origin of the highest association centres from the sensory areas, both in invertebrates and vertebrates, is related to smell and not to sight.

The development of the corpora pedunculata varies in different insects. In some, it is well developed, while in others, it is feebly developed. Between the two extremes, there also occur transitional stages. A typical pedunculate body has a calyx, a stalk and roots. The use of the term 'root' for the terminal ends of the corpora pedunculata has been objected by Vowel (1955) while studying the brain of hymenopterans. According to him, the term root implies an origin or source of attachment. By degeneration experiments, he proved that the fibres of the corpora pedunculata
originate from the globuli cells of the calyx cups and they end within the body of the corpora pedunculata. No fibres coming out of the root to give it an appearance of a source of attachment for the pedunculate body could be observed. In some insects e.g., \textit{Micropteryx} (Buxton, 1917) there are three roots while in others there are only two; in insects where there are only two roots, it is believed that the third one is lost secondarily.

Satija (1958a) has described two calyx cups in each hemisphere of the brain of \textit{Locusta migratoria}. Satija \textit{et al.} (1964a) reported the presence of one calyx cup in \textit{Poecilocerus pictus} and they speculated that it may be formed by the fusion of two calyces. The shape and topographic position of the calyces vary in different insects. The calyx cups are filled up with globuli cells and the latter may lie in groups. For example, the globuli cells lie in one group in \textit{Poecilocerus pictus} and \textit{Mantis religiosa} (Satija \textit{et al.}, 1964a), in two groups in \textit{Locusta migratoria} (Satija, 1958a), and in three groups in \textit{pytiscus marginalis} (Holste, 1923) and \textit{Calliphora erythrocephala} (Satija, 1958d). Thompson (1913) has reported the extreme case in ants where he observed globuli cells in four groups.

On the contrary, Flögel (1878) did not observe the globuli cells of calyx cups in the insects belonging to
Diptera, Hemiptera and Odonata. Hilton (1939), in a review on coleopteran brain, pointed out that the non differentiation of the globuli cells and the poor development of the calyx cups constitute the most primitive stage in the evolution of the corpora pedunculata.

Jarnicka (1959) stated that the corpora pedunculata is not well developed in Calliphora, Sarcophaga, Tubifera and Eristalis but the peduncle is divided into two stalks, one directed anteriorly and the other centrally. On the other hand, Abraham (1967) described a large mushroom-shaped body with a stalk made up of parallel running nerve fibres in the water beetle, Dytiscus marginalis. Schürmann (1970) observed a well developed corpora pedunculata in Acheta domesticus. He noted that the stalk is composed of the axons of globuli cells that are arranged in four groups.

It was Dietl (1876) who, for the first time, working on the mole cricket and grasshopper, reported the presence of a centrally situated mass of peculiar laminated arrangement and labelled it as 'median commissural system, now called the central complex. Berger (1878) and Flögel (1878) named the organs of central complex as the central body only. Packard (1880) described sixteen divisions in the superior medullary mass of the corpus centrale (central body) in Locusta. Buxton (1917) compared the structure of the
the glomerular bodies of the antennal lobes. Power (1943) raised an objection to the use of the term central body for this set of medullary mass because it is not a single structure and very often it is a composite structure, and may consist of two or more medullary masses. He preferred to call it as the central complex for the central body, ellipsoid body, and ventral tubercles.

There has been a little controversy about the structural organisation of the central body, ellipsoid body and their fibrous connections but opinions differ about the presence of the ventral tubercles and their fibrous relations with the other parts of the brain. In Drosophila melanogaster (Power, 1943), Gelas tocoris oculatus (Parson, 1960), poecilocerus pictus and Mantis religiosa (Satija et al., 1964b), Anopheles stephensi (Satija and Sud, 1967) Mylabris phalerata (Satija and Tangri 1968a), Chrotogonus trachypterus (Satija and Tangri, 1968b), Drosophila jambulina (Satija and Sumal, 1970), Cimex lectularius (Satija et al., 1971), Dacus cucurbitae (Satija and Aulakh, 1971), Bruchocida orientalis (Satija et al., 1972), Dacus (Mantaka, 1974) and Pieris brassicae (Ali, 1974), all the three components take part in the formation of the central complex. But in case of Tribolium castaneum (Satija and Luthra, 1969), Philosamia ricini (Singh and Srivastava, 1974), Polistes hebraeus and
Chilocorus nigritus (Singh, 1975 and 1976), only central body and ellipsoid body take part in the formation of the central complex, and the ventral tubercles are lacking. The absence of ventral tubercles has also been reported by Newton (1879) in cockroach, Packard (1880) in Locusta, Wu (1929) in Osmoderma socialis, Satija (1958a,b) in Locusta migratoria and Aeshna nymph, Satija and Walia (1967b) in Odontotermes horni, Satija and Dhindsa (1967 and 1968) in Rhopalosiphum pseudobrassicae and Aphis gossypii, but Viallanes (1887) in Oedipoda, Cuccati (1888) in Somomya erythrocephala, Lowne (1890–1892) in blowfly, Kenyon (1896) and Jonescu (1909) in bee, Buxton (1917) in Micropteryx, Pflugfelder (1937) in some hemipterans, Johansson (1957) in Oncopeltus fasciatus and Satija (1957, 1958c,d) in Petrobius brevistylis, Apis mellifera and Calliphora erythrocephala have reported their presence.

Kenyon (1896), Jonescu (1909) and Buxton (1917) believe that the ventral tubercles are actually the ocellar centres. The termination of the ocellar nerve in the ventral tubercles has been reported by Kenyon (1896), and Jonescu (1909) in bees, Holmgren (1916), Hanström (1940) and Satija (1957) in Thysanurans, and by Johansson (1957) in Oncopeltus fasciatus. Buxton (1917), in Micropteryx, also observed the ocellar fibres entering the tubercles of the corpus centrale. On the contrary, the termination of
the ocellar fibres in the ventral tubercles could not be observed by Power (1943) in Drosophila, Satija (1958d) in Calliphora erythrocephala, Satija et al. (1964b) in Mantis religiosa, and by Satija and Tangri (1968b) in Chrotoponus trachypterus. Satija and Dass (1963a) reported that the ventral tubercles are well developed and the ocelli are completely lacking in Onthophagus catta and thus concluded that these two structures are not related to each other.

The pons cerebralis was described by Viallanes (1887) in Oedipoda as a small association centre of the ocellar fibres. Cuccati (1888) reported an undivided medullary mass of pons cerebralis in Sarcophaga. The observations of Cuccati were confirmed later on by Satija (1958b,c,d) for Aeshna nymph, Apis mellifera, Calliphora erythrocephala and by Jarnicka (1959) for Calliphora sp. On the contrary, Holste (1923) found that the pons cerebralis is a divided mass in Dytiscus. Power (1943), in Drosophila melanogaster, also observed it as a divided mass joined by fibres, which corresponds to the median line of the brain. Viallanes (1887) in Oedipoda, Jonescu (1909) in honey-bee and Buxton (1917) in Micropteryx have observed a connection between the pons cerebralis and ocelli. The presence of such a connection in bee and Drosophila has been refuted by Kenyon (1896) and Power (1943).

The deutocerebrum is the second largest division of
the brain, but it has not attracted as much attention of the neuroanatomists as it demands. Conspicuous variations exist in the antennal lobes and the antennal glomeruli. Presswala and George (1936) have encountered a single deutocerebral lobe in each hemisphere of the brain in Sphaerodema rusticum. Satija and Dhindsa (1967 and 1968) reported that the deutocerebral lobe is one in each hemisphere in Rhopalosiphum pseudobrassicae and Aphis gossypii, but appears to be divided into two by a faint line. Singh (1976) stated that in Chilocus nigiritus, the deutocerebral lobe is a simple structure without any differentiation of cortical and medullary areas. On the contrary, in Poecilocerus pictus (Satija and Sharma 1966), Periplaneta americana (Satija and Singla, 1967) and Polistes hebraeus (Singh, 1975), the deutocerebrum consists of an outer glomerular and an inner fibrous region.

In Odontotermes horni, Satija and Walia (1967b) observed that the fibrous region of the antennal lobe has irregularly scattered masses of glia cells, the so-called glomeruli. Johansson (1957) in Oncopeltus fasciatus, Parson (1960) in Gelastocoris oculatus, Satija and Sohal (1962) in Dysderous cingulatus and Satija et al. (1971) in Cimex lectularius reported a physiological division in the deutocerebrum as they noted the presence of a sensory and motor lobe in each half of the deutocerebrum.
The previous investigators seem to be in agreement with regard to the structural organization of the tritocerebrum but there appears to be a little contradiction with regard to the number of commissural connections in Hemiptera. Leinard (1880), while studying the commissural connections between the tritocerebral lobes in Hemiptera, concluded that there are two commissures, one situated within the neurilemmar wall and the other outside it. The latter, he labelled as free commissure. He further suggested that in Hemiptera where free commissure is absent they still have two commissures, but both of them lie within the neurilemmar wall. Malouf (1933) in *Nasara*, Johansson (1957) in *Oncopeltus fasciatus*, Satija and Dhindsa (1967 and 1968) in *Rhopalosiphum pseudobrassicae* and *Aphis gossypii* also observed a free commissure but Satija and Sohal (1962) in *Dysdercus cingulatus* and Satija et al. (1971) in *Cimex lectularius* stated that the free commissure is conspicuous by its absence.

According to Snodgrass (1935), fully developed compound eyes are present only in Crustacea and Insecta. Among insects, such eyes occur in Machilidae and in nearly all the pterygotes. In Collembola, Lepismatidae, Strepsiptera, Siphonoptera and holometabolous larvae, the site of the compound eye is occupied by simple lateral eyes. In apterygote and pterygote insects, the lateral
eyes are entirely suppressed.

The number of facets in the larvae varies greatly in different insects depending upon the number of ommatidia in the eye. Usually, they are from a few hundred to several thousands, the maximum has been estimated in Odonata as being close to thirty thousand. According to Melnichenko (1963), the number of facets in Apis mellifera is subjected to geographic variability. However, Yagi (1964), while working on the compound eye of butterfly, Leptidea amurensis, remarked that the size of the facet is uniform in most of the compound eyes of insects with some exceptional cases, such as the eyes of certain tabanid flies and dragon flies and moth, Psilogramma increta.

The retinal part of each ommatidium consists primarily of eight retinal cells, though in rare cases as many as 7, 10 and even 12 retinal cells have been observed. Seven retinal cells in an ommatidium have been observed by Fernández-Mordón (1956) in Musca domestica, Yasuzumi and Deguchi (1958) in Drosophila virilis, Wolken and Gupta (1961) in Periplaneta americana and Blaberus giganteus, and by Eguchi et al. (1962) in Bombyx mori. Johnas (1911) has reported the presence of 10 retinal cells in the ommatidium of Lycaena icarus, Chrysophanus hippothoe and Botis verticalis. During the course of an investigation of the structure of the compound eye of the representative types
from several families of insects of order Hemiptera, a unique type of compound eye having 24 retinal cells was discovered in the male of *Drosicha stebbingii* by Ramachandran (1963).

Krecker (1909) described the presence of three pairs of eyes in *Dactylopius destructor*. A careful examination of his account and a scrutiny of the illustrations furnished by him reveal that this insect possesses only ocelli and no compound eyes. Similarly, Marshall (1935) dealt with paired lateral ocelli of *Saissetia oleae* and Pflugfelder (1936) described the detailed structure of the ocelli of *Lecanium corni*. In the words of Snodgrass (1935) "The dorsal ocelli are the simple eyes of adult insects and of exopterygote larvae and nymphs". The dorsal ocelli have a primitive structure in some of the apterygotes, as is in *Machilis* described by Hesse (1901). In the Siphonoptera, Hanström (1927) considered that the paired ocelli when present occur on the sides of the head, the compound eyes having disappeared completely in this group. Wenk (1953), however, doubted this interpretation. In some Odonata (Snodgrass, 1935), the median ocellus exhibits a bilateral structure which is never found in remaining ocelli. The dorsal ocelli of *Sympetrum rubicundulum*, *Libellula luctuosa*, *Libellula pulchella* were studied with light and electron microscope by Ruck and Edwards (1964). Pipa *et al.* (1964) have
compared the median ocellus of *Tricholepidion gertschi*
and median frontal organ of *Thermobia domestica* with
respect to location, innervation and fine structure. The
data suggest that the two organs are homologous. The
multivesicular bodies are present in both the frontal
organ and ocellus, but elementary neurosecretory granules
were lacking in the median frontal organ.

Thus, a survey of the literature indicates that most
of the previous studies are primarily limited to the
elucidation of the structural variations of the various
medullary masses of the brain of a few common insects; the
study of the commissures and fibrous tracts has received
little attention. Keeping this in mind, the present project
has been undertaken with the principal objective of report-
ing in detail the histological organisation of insect brain
and the commissures and fibrous tracts of the various neuro-
pile masses. Accordingly, the detailed histological investi-
gations of ten species belonging to eight orders of the class
Insecta have been worked out at the level of light micro-
scopic observations of serial sections, and reconstruction
of different medullary masses, fibrous tracts and commissures
from the camera lucida diagrams. The results, thus obtained,
have made it possible to compare their general features in
the light of the past and present findings.