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THE EXTERNAL ANATOMY OF THE HEAD AND ABDOMEN OF THE ROACH, *PERIPLANETA* *AMERICANA*¹

BY G. C. CRAMPTON, PH. D.

Massachusetts Agricultural College, Amherst, Mass.

Despite the fact that the very sight of a roach engenders in the minds of many people a feeling of repugnance and disgust, while others consider that roaches are too insignificant to be worthy of one's serious attention, roaches are nevertheless extremely "ancient and honorable" creatures in the sight of the great mother Nature. In fact they were her favorite children some hundreds of millions of years ago when the coal measures were being laid down in Carboniferous times, and their fossil remains are so characteristic of the Carboniferous strata that the Carboniferous period is frequently referred to as the "age of cockroaches," just as the much later Jurassic period is referred to as the "age of reptiles," etc., from the dominant fauna of the periods in question.

We are accustomed to look upon the hills as "eternal," while the occurrence of so frail a creature as a roach is regarded as merely one of Nature's passing incidents; but, frail as roaches are, the roach type has persisted but little changed from the remote Carboniferous period, while in the meantime, mountain ranges have risen and been leveled again, and the whole face of the landscape has changed, and changed again. During the time in which the roach type has been in existence, the great dinosaurs have come and gone, and birds, mammals, and flowering plants have arisen and developed their myriad profusion; but amid these ceaseless comings and goings, the roach type has pursued the even tenor of its way practically unaffected by the passing of the ages. It is therefore of some interest to study the makeup of an organism

¹Contribution from the Entomological Laboratory of the Massachusetts Agricultural College, Amherst, Mass.

so perfectly constructed that it has been able to defy the ravages of time and changing conditions, and the fact that the "changeless conservatism" of roaches has resulted in their retaining many features characteristic of the types ancestral to higher insects, makes their study doubly interesting.

In carrying out this study, I had hoped to include all of the main features of the gross external anatomy of the roach in a single paper; but as the work progressed, it soon became apparent that roaches present so many features of morphological interest that it would require too many figures and plates to illustrate the structure of the entire body adequately in a single article. I would therefore present herewith the principal features of the head and abdomen alone, leaving for a subsequent paper the discussion of the thorax and its appendages. The American roach, *Periplanet americana*, was chosen to illustrate the anatomy of a typical roach because of its large size and relative abundance which render it exceptionally suitable for such a study. Specimens preserved in alcohol may be readily obtained from Southern supply houses for approximately five dollars a hundred, and the study of the external anatomy of these insects is well suited to serve as an introduction to the study of the external anatomy of insects in general for students beginning the study of Entomology. A binocular dissecting microscope is absolutely essential for examining the external anatomy of the specimens, which should be studied immersed under alcohol or water, and the field should be illuminated by means of a powerful lamp provided with a bulls-eye condenser.

Seen under the binocular, the head of the roach (Fig. 5) is a beautiful object, "clean-cut," and smoothly polished. The upper lip or labrum *lr* is emarginate anteriorly (i. e. there is a "nick" or emargination *em* in its anterior margin). Behind the labrum is a non-pigmented area *ac* or anteclypeus followed by a more heavily chitinized and pigmented area *eps* called the post-clypeus or epistoma. The areas *ac* and *eps* comprise the clypeus, which extends from the labral, or clypeolabral, suture (along which the labrum is hinged the clypeus) to the frontal pits *fp*, which are the external manifestations of certain invaginations forming the anterior arms of the tentorium presently to be

described. In some insects a clypeal (or clypeofrontal) suture extends from one frontal pit across to the other to demark the posterior limits of the clypeus, but this suture is absent in many Orthopteroid insects. Each postero-lateral angle of the clypeus bears a cup-like depression, the clypeotheca or "precoila" *cth* of Figs. 5 and 4, into which is received an articulatory process of the mandible labelled *g* in Figs. 5 and 4. I formerly (Crampton, 1921) used these points of articulation of the mandibles with the clypeus, as landmarks for demarking the posterior limits of the clypeus; but it is preferable to use the frontal pits *fp* for this purpose, as suggested by Yuasa, 1920.

If we remove the labrum and clypeus and examine their inner or pharyngeal surfaces, the membranous lining is seen to form an area called the epipharynx bearing the labels *pre* and *poe* in Fig. 8. The anterior portion of the epipharynx or preepipharynx *pre* is slightly more pigmented in the median region, and on each side it bears a lateral series of sense organs (only the left hand ones are shown in Fig. 8). The posterior portion of the epipharynx, or postepipharynx *poe* is located in the clypeal region and contains two epipharyngeal sclerites which are somewhat more deeply pigmented than the rest of the membrane of this region. Between the anterior epipharyngeal region in the labium, and the posterior epipharyngeal region in the clypeus, are the tormæ *tor* or thickenings (one on each side) which serve to demark the labium from the clypeus "internally," and are therefore useful land-marks.

Behind the clypeal region *eps* of Fig. 5 is the frontal region or frons *fr*, which is limited anteriorly by the suture (or by an imaginary line when the suture is absent) extending from one frontal pit *fp* across to the other. The frontogenal (suborbital) sutures *fgs* demark the frons from the genæ *ge* postero-laterally, and the anterior arms of the epicranial suture *frs* demark the frons posteriorly. The epicranial suture is very faint in adult *Periplaneta*, and is therefore represented by a dotted Y-shaped line in Fig. 5. The arms of the epicranial suture which form the frontal suture *frs* (demarking the frons posteriorly) extend to the clear spaces *ofn* or ocellar fenestræ which contain the lateral ocelli and usually remain clear or colorless when the lateral ocelli become atrophied. The scar-like area or frontal myocatrix *mc*, near the

base of each antenna, is a muscle scar—i. e. it marks the attachment of muscles inserted upon the frons.

Behind the frons *fr* is an area designated as the epicranium, or parietals *pa*, into which the epicranium is divided by the coronal suture *cs* formed by the basal portion of the Y-shaped epicranial suture bearing the labels *cs* and *frs*. The upper (apical) or dorsalmost portion of the head is the vertex—a region not clearly demarked in most insects. The postero-dorsal portion of the head in the region of the occipital foramen *ocf* of Fig. 11 (i. e. the region bearing the label *oc*) is called the occiput.

The area situated below and behind the compound eye, bearing the label *ge* in Figs. 5 and 11, is called the gena. Its anterior limits are demarked by the frontogenal or suborbital suture *fgs* on each side of the frons, and its posterior limits are demarked by a suture or ridge, the postgenal ridge *por* (Fig. 11) which separates it from the postgena. The basimandibular suture *bms* of Fig. 5 demarks the gena from the sclerite below it called the basimandibula, mandibulare, or the trochantin of the mandible—i. e. the area bearing the label *bm* in Fig. 5. Comstock suggests that the region *bm* represents the trochantin of the limb forming the mandible, but the region in question was probably formed by a chitinization of the mandibular membrane between the base of the mandible and the head capsule.

Behind the genæ *ge* of Fig. 11, and separated from the genæ by the postenal ridges *por* are the postgenæ *pge*, which form the greater portion of the posterior region of the head. A cup-like depression of the postgena, the postgenotheca *pgt* of Figs. 11 and 12, receives a condyle of the mandible labelled *h*. A narrow median area labelled *pes* in Figs. 11, and 12, extends along the vento-median portion of the postgena, in the neighborhood of the mandibles and maxillæ, and the cardo of the maxilla (*cc* of Fig. 2) articulates with its postero-dorsal region. An area called the hypostoma becomes demarked in this region in certain Coleopterous larvæ, etc., but this area is not shown in the roach, nor is there a well defined gular region along which the postgenæ usually extend in Coleoptera and Neuroptera etc.

The chitinized fold-like area labelled *tf* in Figs. 13 and 11 was termed the trophifer by Crampton, 1917, because the labium is

borne by it, and the maxillæ are closely associated with it. Yuasa, 1920, calls it the "maxillaria." Holmgren considers that it represents the labial segment in embryonic termites. It bears the occipital condyles labeled *x* in Fig. 13, and the cephaligers (*z* of Fig. 13) or head-bearing processes of the lateral cervical sclerites articulate with these condyles. Two occipital tendons *oct* furnish attachment for muscles, as also do the small cervical tendons *y*. The Cushion-like prominences labelled *tpn* in Fig. 13 lie near the gular pits which are the external manifestations of the invaginations forming the posterior arms of the tentorium.

When the mandibles, maxillæ and underlip are removed, and the head capsule is boiled in 10% caustic potash to remove the muscles and other soft parts (which are removed by washing them out with a pipette, or by plucking them away with a fine forceps) one may observe the inner beam-like structures called the tentorium. These structures serve as supports for muscle attachment, for buttressing and strengthening the head capsule, and for holding in place the brain and other delicate structures within the head.

As shown in Fig. 13, the tentorium consists of the following parts. The posterior arms *pot* (called the postentoria, or the "metatentoria" by Yuasa—though the prefix "meta" should be restricted to structures belonging to the metathorax) arise as invaginations of the gular pits *gp* (Fig. 11) situated just beneath the pad-like tentorial prominences labelled *tpn* in Fig. 13; and these invaginations forming the posterior arms of the tentorium unite to form the tentorium proper, or body of the tentorium *etn*, called the eutentorium, or "corpotentorium." An invagination from each of the frontal pits *fp* of Fig. 5 forms one of the anterior arms of the tentorium labelled *ptn* in Fig. 13, and these anterior arms of the tentorium are called the pretentoria. They unite to form a transverse plate labelled *itin*, which is called the intertentorium, laminatentorium, or frontal plate of the tentorium (Comstock & Kochi). Backward prolongations of the structure *itin* extend on each side of the neuroforamen *nf* to connect the plate *itin* with the body of the tentorium *etn*; and the dorsal arms *stn* or surtentoria (supratentoria) extend upward to the region of the antennal sclerite *ban* of Fig. 5. There are thus

three pairs of tentorial arms, the anterior arms, *ptn*, the dorsal arms, *stn*, and the posterior arms *pot* shown in Fig. 13; and in the embryo (according to Riley) the posterior arms unite to form the body of the tentorium *etn*, while the anterior arms unite to form the plate *itn*, and they also give off the dorsal arms *stn*, and later become connected with the body of the tentorium *etn*.

The neuroforamen *nf* forms a circular opening through which the crura cerebri pass, and within it may be seen the tentorial tendons by means of which the oesophageal muscles are attached to the tentorium. The plate *itn* is situated between the crura cerebri and the mouth, and upon it are inserted certain muscles, the median tentorial carina which it bears being apparently developed in connection with this purpose. The body of the tentorium serves to protect the suboesophageal ganglion to some extent, and the nervous system passes below it (i. e. the body of the tentorium) while the gullet passes above it in passing backward into the thorax through the large foramen magnum or occipital foramen *ocf*.

The mouth cavity or pharynx, contains the hypopharynx or lingua, *hph* a tongue-like organ composed of a basal portion, or basilingua labelled *bl* in Fig. 10, and a distal portion of distilingua *dl*. The basal portion is strengthened by the basilingual sclerites, from which a lingualora *ll* or slender lora-like sclerite extends backward to the oesophagus *oes* on each side of the base of the tongue (hypopharynx), while a lingual tendon *lt* serves for the attachment of muscles to the base of the tongue. The distal portion of the tongue is strengthened by the distilingual sclerites which send down ventro-mesal arms from each side, meeting at the opening of the salivary duct or salivadiet *sd*. The salivary glands are paired, and their paired ducts unite to form the common salivadiet *sd* opening at the salivapore which is located below the tongue, in the median line, at its base. The tongue or hypopharynx is provided with taste organs, as are also the epipharyngeal areas in the roof of the pharyngeal cavity and the regions adjacent to the oesophageal opening, etc. The pharyngeal cavity is closed by the labrum and clypeus in front, by the labium in the rear, and by the maxillæ and mandibles on the sides, and it leads into the oesophagus *oes* of Fig. 10 which

passes above the tentorial plates *itn* and *etn* of Fig. 13, and out of the head into the neck through the occipital foramen *ocf*.

The mouthparts, as was pointed out a century ago by Savigny, are modified limbs. The mandibles represent the basal segment of a mouth-part-limb (see Crampton, 1921), and their "cutting" or masticatory surface bears the incisors distally—i. e. the tooth-like projections *in* of Figs. 12 and 4, while in the middle of the median or masticatory surface is the mola *mo* or grinding area. Basal to this is the submola or "accia" *smo*, an area lacking in pigment, and clothed with fine hairs in certain insects. The mandible has two "rocking points" or fulcrum used as points of support when the muscles attached to the gnathotendons or mandibular tendons *ft* and *et* of Fig. 12 open and shut the mandibles which work with a "sidewise" or "horizontal" movement as they meet under the upper lip *lr* of Fig. 5. Thus, when the muscle attached to the flexor tendon *ft* of Fig. 12 contracts, the mandible rocking on the pivotal point *h* (Fig. 12) on one side, and on the pivotal point *g* (Fig. 4) of the other side is flexed or closed. On the other hand, when the flexing or closing muscles relax, and the opening or extensor muscles attached to the tendon *et* contract, the mandible pivoting upon the same two rocking points, is opened, or extended. The flexor tendon *ft* is borne by a small plate *gn* (Fig. 12) in the medio-basal region of the mandible, and the flexor tendon is usually hugely developed to furnish points of attachment for the powerful muscles which close the mandibles in the movements of chewing. Since the opening muscles need not be very powerful, their tendon *et*, which is attached to the protuberance *gpr*, is not very large. Of the two rocking or pivoting points, the posterior or ventral one *h* of Fig. 12 consists of a condyle which is received in a cup or theca *pgt 9* (Fig. 12) at the anterior (ventral) end of the postgena *pge* (compare also Fig. 11). The anterior or dorsal pivoting point of the mandible is a projection labelled *g* in Fig. 4, which is received in a theca *cth* at the postero-lateral angle of the clypeus (compare also Fig. 5). The process *g* of Fig. 4 bears a groove which fits over a ridge or projection of the clypeal angle, and is thus a kind of condyle and cup combined.

The maxilla (Fig. 2) represents a modified mouth part-limb,

in which the second and third segments of the limb give off lobe-like processes (or "endites") to form the lacinia and galea, while the so-called endopodite of the limb becomes modified to form the maxillary palpus, as was discussed by Crampton, 1922, and 1923. When the extensor muscles of the maxilla, which are attached to the cardotendon *ct* of Fig. 2. contract, the point *cc* acts as a fulcrum and the maxilla is opened or extended; and when the muscles attached along the sclerite *pas* and to other portions of the maxilla contract, the maxilla is flexed or closed. The basal sclerite *bc* bears a process *cp* to which the tendon *ct* is attached, and from the point *cc* (where the sclerite *bc* of Fig. 2 articulates with the head in the region of the area bearing the label *pge* in Fig. 11) there extends a groove fitting over a ridge on the under side of the head in the neighborhood of the region bearing the label *pge* in Fig. 11. The maxilla, however, has been removed from the left hand side of Fig. 11, and the right hand maxilla dips beneath the region *sm* of the labium, so that the articulating point of the base of the maxilla with the head region is not seen in Fig. 11.

The cardo or basal region of the maxilla is divided into a basiscardo *bc* and a distiscardo *dc*, as is shown in Fig. 2. The stipes is divided into a true stipes *st* and a narrow median marginal region *pas*, and the muscles attached to this sclerite may have been responsible for its demarcation. Internally, there is a parastipital ridge extending along the parastipital suture demarking the sclerite *pas* and there is likewise an internal cardine ridge demarking the sclerite *bc* from the sclerite *dc* in the cardo. A basimaxillary membrane *bm* connects the maxilla with the region in the basal region of the underlip.

The stipes *st* bears a lacinia *la* provided with a fringe of bristles *lf* for sweeping the food into the mouth, or for preventing it from falling out of the mouth during the movements of lacinia. The lacinia dentes *ld* (Fig. 2) or tooth-like processes at the apex of the lacinia *la* are probably used in aiding to comminute the food—or to hold the food when it is comminuted ("chewed") by the mandibles. A peculiar appendage *ma* is called the midappendix lacinula, or hamadens, and is present even in such primitive arthropods as the Crustacea. The palpifer *pf* is bent around on

the other side of the maxilla, and is therefore not well shown in the view of the maxilla drawn in Fig. 2. The palpifer *pf* is a distinct sclerite in lower insects and bears the galea *ga*, but in the roach the palpifer becomes rather closely united with the stipes *st*, and the stipes appears to bear the galea, although if one examines the other surface of the maxilla, the connection of the basal portion of the galea *bg* with the palpifer *pf* is more readily apparent. The galea *ga* is composed of two segments, the basigalea *bg* and the distigalea *dg*, and the distal segment *dg* forms a sort of hood into which the tip of the lacinia is received. A strengthening rod *gb* (Fig. 3) stiffens the galea on its mesal surface (the one which fits around the tip of the lacinia) and a marginal region *pga* (Figs. 2 and 3) of the galea is clothed with fine hairs. The maxillary palpus *mp* is borne by the palpifer *pf* and is composed of five segments. The terminal segment is membranous at the tip and is provided with sense organs.

The labium or underlip of the roach articulates posteriorly with the sclerite labelled *tf* in Fig. 11, and the sclerite in question probably represents the dorso-lateral portions of the labial segment, according to the investigations of Holgren, 1909. The basal sclerite *sm* of the labium (Fig. 11) is made up chiefly of the submentum, although its posterior portion may contain the gular region of other insects such as soldier termites, Coleoptera, etc. On the other hand, the gular region may form behind the submentum, and the origin of the gular region is still a matter of doubt. The gular pits *gp* of Fig. 11, which are usually situated on the gular sutures demarking the gular region laterally, are hidden by the postero-lateral edges of the submentum *sm* in Fig. 11. These gular pits are the external manifestations of the invaginations forming the posterior arms of the tentorium (Fig. 13 *pot*) as was mentioned above.

In front of the submentum *sm* is the mentum *mn* (Fig. 11); and the entire region in front of the mentum *mn* is referred to as the eulabium, because it is the only part of the underlip formed by the union of the labial appendages in termites, according to Holmgren, who maintains that the mentum and submentum are formed behind the labial segment in the embryo. In front of the mentum *mn* is a small median triangular region *il* or in-

terlabium, and on each side of it are the palpigers *pgr*, which bear the labial palpi *lp*. The palpigers are larger and better developed on the other side of the labium (see Fig. 10, *pgr*). The labiostipes *ls* bear the glossa *gl* and paraglossa *pgl*. When the glossæ and para-glossæ unite to form a single median structure, they are termed the ligula. The labial palpi have a membranous region at the tip of the terminal segment which is supplied with sense organs.

It has long been known that the labium is made up of the union of two appendages like the maxillæ, which are distinct in the embryo; but it is not known what parts of the maxilla correspond to the parts of the labium in every case.. The earlier investigators thought that the cardines (pleural of cardo) unite to form the mentum, while the palpifers form the palpigers, the stipites, (pleural of stipes) form the labio-stipites, the lacinix form the glossæ, the galeæ form the paraglossæ, and the maxillary palpi form the labial palpi, when the maxilla-like appendages unite to form the labium. The only matter which seems to be in doubt is whether the united cardines form the mentum *mm*, or whether they form the small median region *il* of Fig. 11. I am inclined to think that the small region *il*, rather than the mentum *mn*, represents the united cardines, since Holmgren states the mentum is formed in the embryo *behind* the labial segment, so that the basal segments of the maxilla-like appendages of the labium, which unite to form the underlip can have nothing to do with the mentum, if the latter is formed behind the labial segment. The whole matter is still very puzzling, and should be re-investigated with a view to determining exactly what structures represent the united cardines of the appendages which form the underlip.

Of the other external features of the head which are of any great interest, there remain to be considered only the antennæ. In the roach these are long, slender, delicate, filiform or flagellate structures composed of a great number of segments. At the base of each antenna is a narrow ring-like sclerite *ban* of Figs. 5 and 7, surrounding the antennal membrane at the base of the antenna. This ring-like antennal sclerite is called the bas-antenna, or antennale. (Yuasa, 1920, uses the form "anten-

naria," instead of the original form antennale). The basal segment or scape *sc* of Figs. 5 and 7 is borne on a process *af* originally called the antennifer, for which designation Yuasa substitutes the term "antacoila." On each side of the antennifer *af* of Fig. 7 is a small basantennal plate to which is attached a basantennal tendon labelled *tn* in Fig. 9. When the muscles attached to these tendons contract, they move the antennæ, using the tip of the antennifer *af* as a fulcrum, as shown in Fig. 9. Above the base of the antenna is a surantennifer *saf* which connects the base of the antenna above, with the antennal sclerite *ban*, and assists in the complicated movements of the antenna, which is capable of great freedom of movement, as is necessary in a structure bearing the delicate chemical-sense organs and tactile organs of the "feelers." As is shown in Fig. 7, the scape *sc* articulates with the pedicel *pd* at a point indicated in the drawing, and a similar articulating point is located on the other surface of the antenna. Between these two "rocking points" are small chitinous pedicellar plates embedded in the connecting membrane, furnishing points of attachment for certain of the muscles operating the antennæ. Beyond or distal to the pedicel *pd* is the postpedicel *ppd*, and distal to this are the segments of the flagellum or filament, as the remainder of the antenna is called. The relative sizes of the pedicel, postpedicel etc., vary with the sex of the individual, but these slight sexual differences have not been dealt with in this paper. The flagellum is composed of four principal types of segments. Those in the proximal portion of the antenna are the brachymeres or shorter segments (i. e. *a* and *b* of Fig. 6), while those in the distal portion of the antenna are the dolichomeres or longer segments (i. e. *c* and *d* of Fig. 6). We may further distinguish the short or annular brachymeres *a* from the long brachymeres *b*, and the stout dolichomeres *c* from the slender dolichomeres *d*, though the types merge, and are rather difficult to describe.

Turning next to the consideration of the abdomen: as shown in Fig. 14, there are eight spiracle-bearing segments followed by what appear to be three non-spiracle-bearing segments (the terminal ones) best seen in the dorsal region of the abdomen. The typical segments (in the middle of the abdomen) consist of a dor-

sal plate of tergite *t* with a lateral subtergite or pleurite *pl* on each side (probably a demarked portion of the tergite proper), and a sternite or ventral plate *s* separated from the subtergites by a lateral membrane. The spiracles *sp* are borne at the anterior ends of the subtergites *pl*, and if the first segment can be taken as the criterion, the spiracles apparently belong to the antero-lateral area of the tergite which becomes detached to form the subtergite. The membranes connecting successive segments are called conjunctiva, and this term is also applied to the membrane connecting the sclerites of the abdominal segments. It is preferable to distinguish the lateral membranes, however, and they are here referred to as the lateral or pleural membranes.

The spiracles are extremely interesting structures, and the first may be taken as an illustration of the way in which a closing appliance was developed to prevent the entrance of deleterious substances. If the first spiracle *sp* (counting from the base of the abdomen) of Fig. 14 is removed with its surrounding body wall, and is examined from within, after removing the soft parts, it may readily be seen that within the atrium or entrance chamber there is a triangular sclerite of suboperculum *sop* of Fig. 19, which was located ventrally when the spiracle was *in situ*, as in Fig. 14, but is apparently dorsal in Fig. 18, which depicts the inner surface when the fragment containing the spiracle is turned over and viewed from within. Certain ocluser muscles such as the one labelled *m* in Fig. 18 are attached to the suboperculum *sop* and extend to the arch or bow *sar* called the spirarcus. When these ocluser muscles contract, the bow *sar*, which pivots at the point *p*, is drawn up against the suboperculum *sop* and effectively closes the entrance to the trachea by pinching the tube together. When the ocluser muscles relax, the elasticity of the parts cause them to spring back, and the trachea is opened again. This is but one more of the marvellous little mechanical devices developed by these interesting creatures, and as one studies their anatomy one's wonder increases that Nature has endowed them with such cleverly efficient mechanisms for carrying on the commonplaces of a cockroach's existence—though I suppose we should naturally expect to find some pretty efficient devices in an organism which has successfully maintained itself for so many

million of years despite the vicissitudes of time and changing environment!

The typical tergites and sternites are composed of two principal areas. In the tergite the anterior area (demarcated by a transtergal suture or ridge) is the antetergite *at* (Fig. 14) and the posterior region is the tergite proper or eutergite *etg*. Similarly, in the sternal plate there is an antesternite *as* and a sternite proper or eusternite *eus* separated by a transternal suture or ridge. The antetergite and antesternite are apparently demarcated by the friction of the overlapping edges of the telescoping segments, or at any rate, the antetergite and antesternite are usually over-lapped by the posterior portions of the preceding segments and are usually less deeply pigmented than the rest of the tergal and sternal sclerites. The telescoping of the segments of the abdomen allows for distention with eggs, etc., and in its normal state the abdomen of the female is more flattened than is the case with the egg-distended abdomen shown in Fig. 14; and the anterior portions of the sternal and terga are usually hidden in non-distend individuals.

Following the generally accepted usage of systematists, I have restricted the use of the terms tergite, pleurite and sternite to the dorsal, lateral and sternal plates of the abdomen alone, and I would use the designations notum, pleurum and sternum for the parts of the thoracic segments. The segments of the abdomen may be referred to as the uromeres, for the sake of brevity, and counting from the base of the abdomen, I would refer to them as uromere 1, uromere 2, etc., instead of using the longer designation "first abdominal segment, second abdominal segment," etc. The terminal abdominal segments and their various structures are referred to as the terminalia (Crampton, 1918) but Freeborn, 1924, includes in the designation "terminalia" the genital structures as well in higher insects, and the latter usage is preferable in the higher forms where the genitalia and terminal structures are compactly grouped by the shortening and telescoping of the terminal segments of the abdomen. When there is a reduction in the number of the abdominal segments, it is usually the terminal ones which fuse or unite, as is indicated by the fact that the spiracles remain distinct (for the most part)

in the basal segments even when the latter become greatly reduced in size.

In Fig. 19, the terminal segments of the abdomen of the female roach are shown more enlarged than in Fig. 14, and uromeres 8, 9, and 10 are shown more in detail, while in Fig. 21 the terminalia of the male are shown more in detail.

The tenth abdominal segment is essentially the same in both sexes, and its sternite is usually reduced or atrophied, while its tergite forms the huge epiproct *ep* or supraanal plate of Figs. 14, 19 and 21. I suspect that the tergite of the eleventh segment unites with that of the tenth to form this large supraanal plate, but the embryologists claim that the eleventh abdominal segment lies behind the plate in question. The epiproct *ep* is divided into a basepiproct or basal region and a postepiproct or terminal region which becomes divided into two lobes or epiproctal lobes by a deep emargination or epiproctal cleft in its posterior margin. The membranous structure bearing the anal opening posteriorly is the protiger *pro* of Figs. 14, 19 and 21.

In may flies and other primitive insects, the parapodial plates or paraprocts form the basal segment of the cerci; and as was pointed out in a former paper (Crampton, 1921) the paraprocts apparently represent the protopodite of a crustacean limb, in which the endopodite forms the cercus in insects. In the roach, the paraprocts or parapodial plates *par* of Figs. 14, 19 and 21, are large plates situated on each side of the anal opening, and they are divided by a lateral flange, or paracarina, into an upper and lower region. When the gynoalvular membrane, which forms a pouch for carrying the oötheca, becomes distended, as is shown in Fig. 16, it extends dorsalward under the lateral flange of the paraprocts of the female, and this flange thus has an especial use in the female.

At the base of and below the cercus *cē* of Figs. 19, etc., is the basicercus *bce*, which may represent a basal segment of the cercus.

The cercus itself (*ce* of Figs. 14, 21, 24, etc.) is a multi-articulate structure serving as a pair of hinder "antennæ", and is said to bear olfactory organs as well as the tactile organs usually present in the cerci of insects in general. As is shown in Fig. 14, the cercus may be divided by a lateral ridge (cercocarina)

into an upper and lower region. The basal segments of the cercus are usually more annular, while the terminal ones are more cylindrical (Fig. 24). In the roach, the cercus migrates from the paraproct *par* (Fig. 19) which originally bore it, and becomes secondarily associated with the epiproct *ep*. The cerciger *cg* or process of the epiproct *ep* bears the cercus in such cases, and the surcerciger *scg* forms a second pivotal point in certain of the movements of the cercus.

In handling living roaches, one is made painfully aware of a most nauseating odor which clings to one's fingers even after repeated washing with soap and water. The fluid which produces this odor is probably secreted by the repugnatoria or scent glands labelled *rep* in Fig. 14. These repugnatoria are eversible glands located in the membrane between the fifth and sixth abdominal tergites, and are slightly nearer to the sixth than to the fifth tergite, so that they may possibly belong to the sixth abdominal segment.

The gynomeres, or abdominal segments of the female which become modified to form the secondary sexual characters of the abdominal region, are the seventh, eighth and ninth uromeres. The sternite of the seventh abdominal segment is produced posteriorly to form the hypogynium *hg* of Fig. 14, which hides the oviositor, and forms the sides and floor of the gynatrium or genital chamber of the female, which receives the parts of the male in copula, and also forms a genital pouch for carrying the ootheca or egg-case which is carried protruding from the end of the abdomen, for a time, before it is deposited. Like the other abdominal sternites, the hypogynium *hg* of Fig. 14, has an anterior region *as* and a posterior region *eus* demarked by a transternal suture or ridge; but in addition to these typical divisions of the sternum, the seventh sternite has a backward projecting structure *gv*, which is divided into two gynovalvæ or pseudo-valves *gv* of Figs. 14, 15, and 16 in the American roach and certain of its allies. The gynovalvular membrane, as shown in Fig. 16, extends between these pseudovalves and upward on each side to the flanges of the paraprocts, to form a pouch for carrying and protecting the ootheca or egg-case, as was mentioned above. When not distended for this purpose, the membrane in question

becomes folded between the valves, as in Fig. 26. The endogynal plates *eng* shown in Fig. 26 are probably involved in the stretching of the membrane in question, though it apparently becomes distended and turgid by intanal pressure also. At the base of the seventh sternite is the saccopore, or external opening of a ventral bilobed sac, the ventrosacculus *sac*, which apparently serves as a glandular reservoir; and a repellent substance is secreted in it.

When the hypogyium or modified seventh abdominal sternite is removed, as in Fig. 19, the ovipositor or oviscapt with its basal plates etc., is exposed. As may be seen in Fig. 19, the eighth tergite is the dorsal portion of the eighth segment whose ventral parts form the structures labelled *pvu* etc. The sclerites *pvu* normally project backward under the sclerites *vs* and conceal the latter, but in Fig. 19 the structures labelled *pvu* are represented as though forced back and upward in order to show the relation of the parts to one another. Similarly, in Fig. 20 the sclerites *pvu* are represented as though laid back from the sclerite *vs* which they would normally cover and hide from view. The large cavity within the opening labelled *vul* in Fig. 20, is the uterus and vagina, or common passage of the two oviducts through which the eggs are conducted to the exterior from the ovaries where they are formed. The elongated opening of the vagina, labelled *vul* is the vulva, and the sclerites surrounding it are the perivulva *pvu*. Each half of the perivulva gives off an arm *vbr*, and the two halves are joined by an arch *var*. The walls of the vaginal cavity are membranous, and are thrown into folds in specimens treated with caustic potash. If this condition is normal, it would indicate that the vaginal cavity is capable of considerable dilation at the time of egg-laying, and the character of the perivaginal sclerites would indicate that the vulva might readily be widened considerably to permit the extrusion of a batch of eggs (the eggs apparently are formed at about the same time). If one observes the relation of the sclerite *pvu* to the tergite of the eighth uromere in Fig. 19 (in which the plate in question has been forced back and the parts about it have been everted) it would appear as though the perivulva *pvu* is a modified portion of the sternum of the eighth uromere. Paytoureau, 1895, however, and recent in-

vestigators, such as Chopard, consider that the vagina opens between the seventh and eighth sternites, and in a footnote; Peytoureau refers to the observations of Miall and Denny, 1893 on the development of the region in question, in a passage which may be roughly translated as follows: "The delicate indurated membrane which leads out to the vaginal opening is **not** the eighth sternite, but arises as a fold of the intersegmental membrane." If this is true, it would seem to indicate that the perivulva is a thickening of the intersegmental membrane, rather than a sclerite of the eighth abdominal sternum.

The sclerites immediately behind the plates labelled *vs* in Figs. 20, 19, 17, etc., may represent the structures called the basivalvulæ in other Orthopteroid insects by Crampton, 1917, and Walker, 1919. As may be seen in Fig. 19 the plates *vs* are sclerites of the eighth uromere, and they are connected with the bases of the ovipositor valves *vv*. A small transverse ventral sclerite *ms* situated between the sclerites *vs* of Fig. 20, is considered to be the ninth sternite by Miall and Denny, 1886, although it is not quite clear how they arrived at this conclusion. Its posterior portion surrounds the thecapore *tp* of Fig. 20, or opening of the spermatheca, in which spermatozoa are stored up at the time of mating, to fertilize the eggs. Hence the opening of the spermatheca *tp* of Fig. 20 is normally situated immediately above the vulva *vul* (out of which the eggs pass) when the parts are not unnaturally separated as in Fig. 20. Dr. Walker, however, informs me that this supposed spermatheca is really a gland. The sclerite labelled *ms* in Fig. 17 represents the internal view of the sclerite labelled *ms* in Fig. 20, showing the internal projections of the plate in question.

The ovipositor of the roach is composed of three pairs of valvulæ. Of these, the dorsal valvulæ *dv* and inner valvulæ *iv* (Figs. 20, 17, 19, etc.) belong to the ninth uromere, while the ventral valvulæ *vv* belong to the eighth uromere. The dorsal valvulæ *dv* have been variously termed the posterior or third gonapophyses, dorsovalvulæ, survalvulæ, nono-valvulæ, etc. The inner ones *iv* have been called the inner or second gonapophyses, intervalvulæ, etc.; and the ventral valvulæ have been called the anterior or first gonapophyses, octovalvulæ, subvalvulæ, ventrovalvulæ, etc.

The sclerite just behind the plate *vs* of Fig. 19 probably represents a modified coxite or protopodite of a limb (of the eighth uromere) in which the outer branch or exopodite was lost and the endopodite or inner branch became modified to form the ventral valve *vv*. The greatly elongated coxite or protopodite of the ninth uromere apparently formed the dorsal valve *dv* whose external branch or exopodite (represented by the stylus in immature roaches) becomes lost in the adult, while the inner branch, or endopodite, becomes modified to form the inner valve *iv*. This is a very complicated idea of the origin of the parts. A simpler view (though one which is less in accord with the facts of comparative anatomy) is that the ventral valves *vv* are merely outgrowths of the eighth uromere, while the dorsal valves *dv* are outgrowths of the ninth uromere, and the inner valvulæ *iv* are outgrowths of the tenth uromere which become secondarily associated with the ninth segment.

Miall and Denny state that "In the cockroach the ovipositor is used to grasp the egg capsule, while it is being formed, filled with eggs, and hardened: and the notched edge is the imprint of the inner posterior gonapophyses, made while the egg capsule is still soft. The shape of the parts in the male and female indicates that the ovipositor is passive in copulation, and is then raised to allow access to the spermatheca." A richly branched valviglian-dula or valve gland (*vgl* of Fig. 17), which is probably an accessory colleterial gland, pours out its secretion through the valvipore *vpo* (Fig. 20) located between the bases of the inner valvulæ *iv*.

The ninth abdominal segment is the genital segment *par excellence* in the male, and it may be referred to as the andromere. As shown in Fig. 21, its pleurite *pl* is much enlarged and extends downward to the ninth sternite or hypandrium *ha*. The hypandrium *ha* of Fig. 21 consists of a basal portion or hypandrium proper, labelled *eha* and a posterior *scx* formed by the union of the coxites, or stylus-bearing rudimentary abdominal limbs (vestigial protopodites) which unite with a portion of the sternum to form the area labelled *scx* in Figs. 21 and 24, while the styli (vestigial exopodites) remain distinct to form the peg-like appendages *stil* of the ninth sternite in the male. Normally the basal

portion to the ninth sternite *eha* of Fig. 21 is overlapped by the eighth sternite and only the portion labelled *scx* projects as in Fig. 24.

Usually the parts of the male genital apparatus are withdrawn, and are concealed by the hypandrium or ninth sternite. At the time of mating, however, they are protruded, and may remain so to some extent even when the male has been killed, as is shown in Figs. 21 and 24—and in some cases the parts are even more protruded than is indicated in the figures in question. When the genitalia are boiled in caustic potash and spread apart, they are seen to consist of the following parts, shown in Figs. 23 and 25. The penis *pe* (Fig. 25) is membranous-walled and is possibly turgid in mating. It is located on the dorsal surface of the penislobus *pel* of Figs. 25, 24 and 23. The ejaculatory duct *ej* of Fig. 25, or common duct from the testes, utriculi, etc. of the male, conducts the genital products to the exterior through the meatus or opening on the side of the penis *pe* (Fig. 25). The walls of the ejaculatory duct are strengthened by depositions of chitin, and muscles involved in the mating process, are attached to these structures. The glandopore, or opening of the conglobate gland, is indicated by the label *o*, just behind the asperate lobe *asl*, in Fig. 25.

The pseudopenis *psp* of Figs. 21, 23, 24, and 25, serves to introduce the genital products of the male into the parts of the female at the time of mating, and on this account the structure in question has been called the penis by some investigators, but it is not homologue of the true penis (through which the ejaculatory duct empties) of other insects, and on this account it is here designated as the pseudopenis. It bears a lateral papilla labelled *e* in Figs. 25 and 21, and it is possible that a gland may open through this protuberance, although I was unable to find any trace of such a gland in the specimens treated with caustic potash. The process has been called the titillator by Brunner von Wattenwyl, and it has been suggested that it serves to dilate the parts of the female during copula, as may also the bird's-head-shaped, serrate lobe *ser* with its process *fa* (Figs. 25 and 23), although the latter may serve to anchor the parts when the male products are introduced during coitus. The opposing lobes *op* are called claspers by Walker, but nothing definite is known con-

cerning their function, or that of the pointed process *acl* or of the small plate *bu* which bears a short recurved hook-like fold or process. The large supporting arches labelled *ana* and *bar* in Fig. 23 and 25 serve to strengthen the lobes and processes, and also furnish points of attachment for muscles, as do the internal projections and processes labelled *enl* and *epr* in Fig. 25.

The interpretation of the homologies of the above-mentioned parts has not been thoroughly worked out, although Walker, 1922, suggests that the structures labelled *tt*, *ser*, etc., represent the parameres of other insects. Walker, however, applies the designation parameres to entirely different structures in the Apterygota and Pterygota, and different investigators apply the term to so many different structures in different insects, that it is practically impossible to say what is meant by the term parameres. If we restrict the designation parameres to the secondarily-formed outgrowths and chitinizations of the membrane about the intromittent organ, the term parameres might well be applied to the above-mentioned structures in the roach. The lobes *op* etc., of Fig. 25, however, are probably formed in the membrane about the intromittent organ also, and it is necessary to find some other method of differentiating the parameres from the other structures formed in this region. Walker refers to the lobe *pel* as the penis, but I think it is preferable to restrict the designation penis to the structure labelled *pe* in Fig. 25, since I think it very probable that the lobe *pel* corresponds (partly, at any rate) to the chitinized parts about the true penis called the *adeagus* in other insects. It is quite evident, however, that the whole subject of the homologies of the genitalic parts of male insects should be more thoroughly studied from the standpoint of comparative anatomy, development, etc., with a view to determining the true interpretation of the parts in these structures which are so much used in systematic entomology.

In the immature roach shown in Fig. 22, the chitinous projections, etc., of the adult insect are not yet developed, and the membranous lobes shown in Fig. 22 represent the undeveloped condition of the more complicated genitalia shown in Fig. 25. In capturing the specimen shown in Fig. 22, the insect was rather tightly squeezed, and the pressure apparently caused

the rectum to become everted, exposing the rectal lining and the endorectal plates *enp*, which are rather weakly-pigmented chitinous protections of the rectal folds or bands. The rectum protrudes in a similar fashion in specimens of termites, psocids, etc., preserved in alcohol, and it is possible that the insects in question may be able to protrude the parts voluntarily when irritated by the alcohol into which they are thrown when collected.

In the foregoing discussion, only the external parts of the head and abdomen have been taken up. In a second paper, already practically completed, the external features of the thorax and its appendages will be discussed; and I am hoping to take up the gross internal anatomy as well, in subsequent papers dealing with the structure of the roach *Periplaneta americana*. In the present paper, most of the drawings are based upon a study of *P. americana*; but in a few instances drawings were made from specimens of a closely allied form. The parts of the other forms, however, are so similar to those of *P. americana*, that there will be no difficulty in identifying all of the structures figured, in studying *P. americana*, with the figures in question as a guide.

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ABBREVIATIONS

a.... Short antennal brachymeres	at... Antetergite
ac... Anteclypeus	b.... Elongate antennal brachymeres
acl... Pointed process (acutolobus)	ban... Basantenna
af... Antennifer	bar... Basarcus
am... Andromembrane	bat... Basantennal tendons
ant... Antenna	bc.... Basicardo
ana... Basal arch (andrarcus)	bce... Basicercus
as... Antesternite	bg.... Basigalea
asl... Asperate lobe (asperolobus)	bl... Basilingua
	bm... Basimandibula
	bms... Basimandibular suture

bse.. . Basiserrata	eus.. . Eusternite
bsl.. . Basilamina	ev... Endovalvula
bu... . Basuncus	fa... . Falx or pointed process
c... . Broad dolichomeres	fgs... Frontogenal suture
ca... . Cardo	fp.. . Fronts pits (frontocavæ)
cc... . Cardocondyle	fr... . Frons or front
ce.. . . Cercus	frs... Frontal suture
cg... . Cerciger	ft... . Flexor gnathotendon
cl... . Clypeus	g.... . Gnathartus (articulatory process)
cm... Basivalvular membrane	ga... . Galea
cp... Cardoprocess	gb... . Galeabacillus
cs... . Coronal suture	ge... . Gena
ct... Cardotendon	gf... . Galea fossa
cth... Clypeotheca	gl... . Glossa
d.... Slender dolichomeres	gn... . Gnathite
dc... . Disticardo	gp... . Gular pits (gularcavæ)
dg... . Distigalea	gpr... Gnathoprocess
dl... . Distilingua	gv... Pseudovalves (gynovalvæ)
dv... Dorsal valvulæ (dorso- valvulæ)	h.... Gnathocondyle or hypo- condyle
e.... . Pseudopenis papilla	ha... Hypandrium (subgenital plate of male)
eha... Euhypandrium	hg... Hypogynium (subgenital plate of female)
ej... . Ejaculatory duct	hph... Hypopharynx or lingua
em... Emargination of labium	hpl... Hypoplica or endohypan- drium
eng... Endogynal plates	hs... . Hypandrial suture
enl... Endolamina	il.... Interlabium
enp... Endorectal plates	in... . Incisors
ent.. . Endotergite	int... Intertentorium
ep... . Epiproct or supraanal plate	iv... Inner valves (intervalvu- læ)
eph... Epipharynx	la... . Lacinia
epr.. . Endoprocessus	ld... . Laciniadentes
eps.. . Epistoma or postclypeus	lf... . Lacinial fringe (laciniafim- brium)
epv... Epivalves	
et... . Extensor gnathotendon	
etg... Eutergite	
etn.. . Body of tentorium (eu- tentorium)	

li....Labium	pl....Pleurite
ll....Lingualora	poe...Postepipharynx
lp....Labial palpus	por...Postgenal ridge
lr...Labrum	pot...Postentorium
ls...Labrostipes	ppd...Postpedicel
lt...Lingatendon	pre...Preepipharynx
m...Occlusor muscle	pro...Proctiger
ma...Midappendix	psp...Pseudopenis
mc...Myociacatrix	pt...Pedicel tendons
md...Mandible	pvu...Perivulva
mn...Mentum	rep...Repugnatoria
mo...Mola	s...Sternite
mp...Maxillary palpus	sac...Ventrosacculus
ms...Medisternite	saf...Surantennifer
mtn...Metanotum	sar...Spiracular bow (spirarcus)
nf...Neuroforamen	sc....Scape
o....Glandopore	seg...Surcerciger
oc...Occiput	sex...United coxites (syncoxite)
ocf...Occipital foramen	sd...Salivaduct
oct...Occipital tendons	ser...Serrate lobe (serrata)
oes...Oesophagus	sm...Submentum
ofn...Ocellar fenestræ	smo...Submola
op....Opponentes	so...Suboperculum
p....Pivot of spiracular bow	sp...Spiracles
pa....Parietals (of epicranium)	spt...“Spermatheca” (probably a gland.)
par...Paraprocts (parapodial plates)	ssa...Subserrata
pas...Parastipes	st...Stipes (eustipes)
pd...Pedicel	stl...Stylus
pe...Penis	stn...Surtentorium (supratentorium)
pel...Penislobus (sublamina)	t....Tergite
pes...Peristome	tf...Trophifer
pf...Palpifer	tor...Tormæ
pga...Perigalea	tn...Basantennal tendons
pge....Postgenæ	tp...Thecapore
pgl...Paraglossæ	tpn...Tentorial prominences
pgr...Palpiger	tt...Titillator
pgt...Postgenatheca	

var... Vulvarcus	vr... Valviramus
vbr... Vulvabrachium	vs... Valvisternite
vf... Valvifer	vul... Vulva
fgl... Valviglandula	vv... Ventral valvulæ (ventro- valvulæ)
vju... Valvijugum	x.... Occipital condyles
vl... Valvifera	y.... Cervical tendons
vm... Vulvar membrane	z... Cephaligers
vpo... Valvipore	

EXPLANATION OF PLATES V, VI, AND VII

- Fig. 1. Tendons at base of pedicel of anténna.
Fig. 2. Posterior (ventral) view of dextral maxilla.
Fig. 3. Mesal view of tip of same.
Fig. 4. Anterior (dorsal) view of sinistral mandible.
Fig. 5. Frontal view of head.
Fig. 6. Types of antennal segments.
Fig. 7. Basal region of antenna.
Fig. 8. Inner view of labrum and clypeus.
Fig. 9. Inner view showing tendons at base of antenna.
Fig. 10. View of hypopharynx in relation to upper and lower lip.
Fig. 11. Posterior view of head.
Fig. 12. Posterior (ventral) view of dextral mandible.
Fig. 13. Posterior view of head with mouthparts removed to show tentorium.
Fig. 14. Lateral view of abdomen of female.
Fig. 15. Ventral view of valves at tip of subgenital plate of female.
Fig. 16. Lateral view of same, showing hypogynal membrane.
Fig. 17. Dorsal view of ovipositor and inner view of its basal plates.
Fig. 18. Inner view of first abdominal spiracle.
Fig. 19. Lateral view of segments 8, 9, and 10 of female.
Fig. 20. Ventral view of ovipositor and basal plates.
Fig. 21. Lateral view of segments 9 and 10 of male.
Fig. 22. Ventral view of terminal structures of immature male.
Fig. 23. Ventral view of male genitalia spread apart.
Fig. 24. Ventral view of terminal structures of adult male.
Fig. 25. Dorsal view of male genitalia and subgenital plate seen partially from within.
Fig. 26. Dorsal view of subgenital plate of female, basal portion seen from within.

Fig. 14

Fig. 17

Fig. 15

Fig. 16

Fig. 18

Fig. 20

Fig. 19