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THE PROTHORAX OF COLEOPTERA: ORIGIN, MAJOR FEATURES OF VARIATION¹

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INTRODUCTION

The unique evolutionary success of the order Coleoptera is a result of great size combined with enormous biological diversity. The huge number of species (ca. 280,000) is arrayed across a broader ecological spectrum than that of any other group of terrestrial arthropods. Four adaptive zones have been extensively occupied: surface, substrate, aquatic, aerial. Higher categories of beetles are, with exceptions, very broad, overlapping adaptive radiations. This evolutionary complexity is associated with great structural variation and a small number of basic adaptations, particularly in the locomotory system.

Because the Coleoptera are a series of replicated experiments in ecological differentiation, the group may be used for studying a suite of problems in the evolution of adaptation. And, because beetles are such a large, diverse and ubiquitous group of insects, they should have a place as subjects for developing and refining modern systematic methodologies. Work at these two superficially different levels has been hindered or made unfeasible (q. v. Brundin 1972: 72) by the lack of a firm foundation of comparative morphology.

Most work on comparative structure of beetles suffers from one

¹A preliminary version of this work was submitted as part of a Ph.D. thesis to the Biology Department, Harvard University.

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notum is low (N_1/Th_3 ca. 35%), the most ventral point of the sternum is far above the coxal apex, and the coxa is quite elongate so that Th_1/Th_3 is ca. 70% (figs. 30, 34, 35, 39, 40, 45, 49). Large changes in gross prothoracic size are associated with great modification in relative sizes of structural units due to the geometry of prothoracic musculature.

Major locomotory muscles are housed within the notum (Larsen 1966, fig. 64). Sharp increase in muscle mass, then, implies increased notal volume. And notal enlargement effects other prothoracic structures. There appears to be a distinct upper limit to prothoracic height in most taxa; Th_1/Th_3 rarely exceeds 90%. Given this boundary to vertical growth, large notal increase is accompanied by sternal reduction and coxal modification. The complementarity of notal and sternal heights effects coxal structure.

In generalized forms, the most dorsal point of the coxa is level or nearly so with the noto-sternal joint (fig. 6). As notal height increases, the coxa is either reduced with the sternum, maintaining initial geometry (fig. 27) or the coxa is elongate and enclosed deeply within the notum (figs. 42, 45, 47). Each strategy has been adopted numerous times in the Polyphaga, while only the former occurs in the Adephaga (figs. 8, 61, 65).

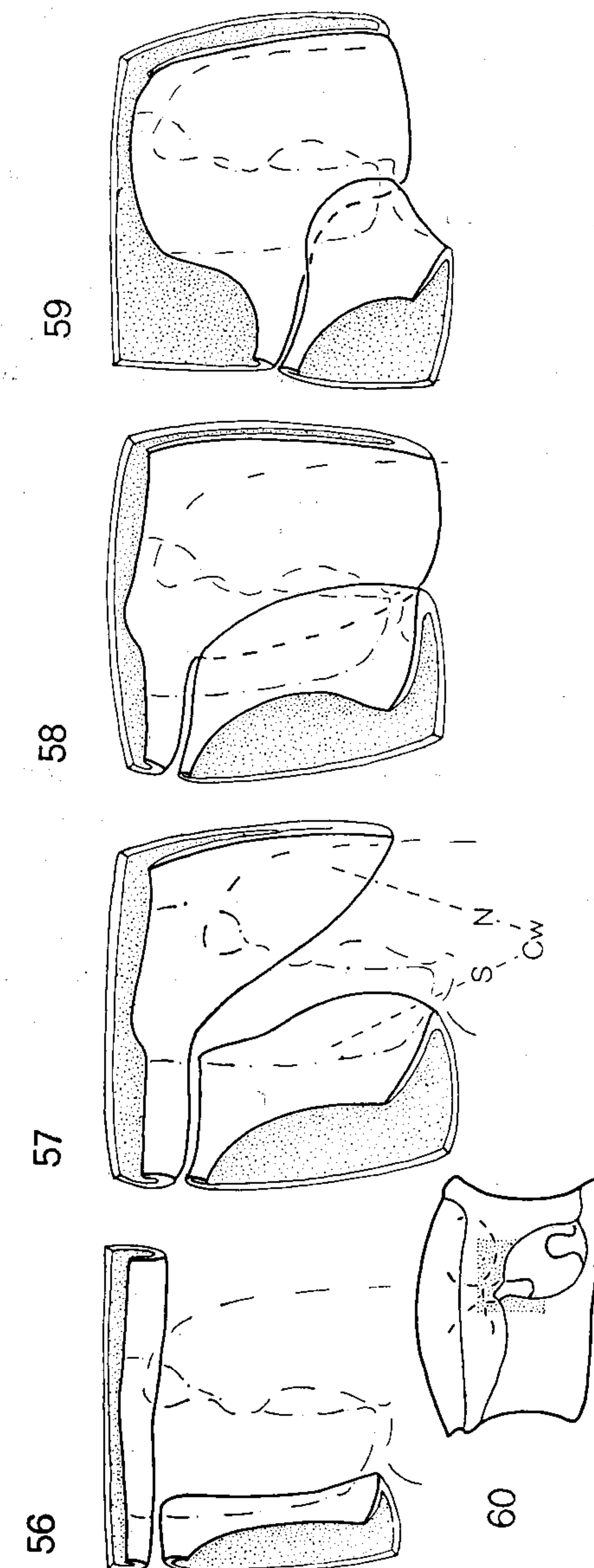
Variation in prothoracic length and width are correlated with height. The width of a prothorax is rarely greater than that of the metathorax (figs. 29, 34, 39, 44, 49). Prothoracic height and width are then usually limited by the corresponding dimensions of the largest segment of the body.

Structure of substrate grade configurations can be explained as an optimization of muscle volume given geometric limiting factors. However, prothoracic structure of extreme surface grade inhabitants represents not only reduced muscle volume but also a mechanism for increasing coxal flexation, see below.

Pleuro-coxal Mechanism. This complex and highly variable system divides naturally into two subunits involving: housing and function of pleuron, trochantin and coxa.

Housing. Concealment of moving parts and surrounding membrane produces improved structural integrity. Enclosure can occur around the entire coxal perimeter, dorsally by notal and sternal cowlings, anteriorly and ventrally by the sternum and sternal projection, and posteriorly by the notal projection. Dorsal and ventral enclosure are particularly variable.

Enlargement of rim folds, which originally protect only membrane around the coxa and trochantin, forms cowlings that partially to



Figs. 56-60; modes of coxal enclosure in Polyphaga, diagrammatic; sclerites disarticulated. Figs. 58-60, internal views of stippled region in fig. 60. See text for explanation.

wholly enclose these structures as well as surrounding membrane (figs. 56-60). Enclosure is accomplished through ventral development (below the noto-sternal joint), overlap, or fusion of notal and sternal cowlings (figs. 27, 57, 58, 60); through dorsal development of the notal cowlings (figs. 5, 45, 47, 59); or through a combination of these two methods (figs. 40, 44, 59).

Ventrally, the sternal projection may be developed below the coxa, thereby protecting the most ventral section of pericoxal membrane. A sterno-coxal articulation is frequently present in high volume forms and prevents the coxa and trochantin from being deflected (figs. 27, 32, 42).

Structures which increase structural integrity by enclosing the coxa, trochantin and surrounding membrane are common in the Polyphaga and are most prevalent in but not restricted to substrate dwelling forms.

Function. Coxal movement, the end product of the pleuro-coxal mechanism, consists, in the Polyphaga, of rotation and sometimes flexation as well. Rotation is simply circular movement about the coxal long axis. Flexation results in antero-posterior motion of the coxal apex and is generated only through movement of the pleuron against its notal attachment (fig. 35). The coxa rotates but does not flex against the pleuro-trochantinal joint. Each type of coxal movement is most suited for locomotion in one adaptive zone.

Flexation is greatly emphasized in many low notal volume, extreme surface grade forms and in a few cursorial interstitial space inhabitants (figs. 30, 35, 40). In both sites, locomotory requirements for power are minimal, so that the quantity of forward motion generated per stroke is a valid measure of coxal performance, which is maximized by employing a combination of rotation and flexation. The effectiveness of flexation is a function of the radius and swing angle. The radius is increased by lengthening the coxa. Anterior and posterior clearances are necessary for a long coxa to traverse a broad arc. Anterior clearance is achieved by sternal reduction so that in extreme cases, its ventral plane lies just below the trochantinal apex permitting the coxa to slide under the sternal rim (fig. 35). Posterior clearance is obtained by reducing and/or flattening the notal projection thereby decreasing the amount of intersegmental overlap and exposing membrane. Modifications permitting extensive flexation also allow a large coxa to rotate extensively. A flexing coxa then imposes strict design limitations on surrounding structures.

Rotation is the sole coxal movement in almost all substrate forms

and is compatible with high muscle volume and structural integrity particularly of the pro-mesothoracic joint (see below). In many substrate dwellers, the coxal rotation axis is distinctly inclined away from the vertical, so that the force generated by coxal movement has a vertical component and can, for example, be used in substrate compression (figs. 33, 38, 48).

Because the locomotory needs of the two zones are met not only by varying muscle volume but frequently by differences in coxal motility as well, there is great variation in internal mechanism in the prothorax of Polyphaga. In flexing forms, the endopleuron is rather small and does not extend far above the coxal apex (figs. 30, 35). This arrangement increases the distance between the dorsal surface of the endopleuron and notal wall and reflects an increase in the major generator of coxal flexation — the *noto-pleuralis* muscle. And, of course the noto-pleural joint is membranous and highly motile.

Some of the important coxal rotator muscles and part of the femoral depressor, a major vertical force generator, originate on the undersurface of the endopleuron (Larsen 1966: 143, fig. 64). Increase in volume of these muscles is correlated with gross notal development and is diagnosed by a lengthened, frequently stalk-like, endopleural base with an expanded apex. Such modifications increase both attachment surface area and the distance between origin and insertion (figs. 23, 34, 37, 44). In many forms where coxal movement is mechanically restricted to rotation by the notal projection, the pleuron is motile and the *noto-pleuralis* functions as an indirect coxal rotator. But in many substrate dwellers, and others as well, noto-pleural joint is solidly sclerotized so that pleural motility is lost. In some of these cases, the endopleuron lies against and may be solidly fused to the dorsal notal wall, thereby maximizing the length of several important muscles. Loss of a moving part — the pleuron — could also be an improvement in structural integrity in these "heavy duty" systems.

Pro-Mesothoracic Joint. Based on criteria of locomotory function, as well as those of static and dynamic structural integrity, three heterogenous classes of intersegmental attachment can be distinguished: motile, rigid, defensive. In many substrate inhabitants, prothoracic motility is employed to push and compress substrate; the prothorax, as a whole, then, is part of the locomotory system. In such forms, a complete collar formed from the union of notal and sternal projections, plus a mesothoracic clearance, permits the prothorax to move through a wide arc with all intersegmental mem-

brane enclosed (figs. 32, 33, 41, 43, 45-48). A complete collar (sometimes called closed coxal cavities in the taxonomic literature) then increases the structural integrity of a major body joint during movement and can be our adaptation for substrate locomotion.

The posterior collar is only partially developed in many Polyphaga. Commonly, the notal projection extends to the level of the trochantal apex, and mechanically restricts the coxa to rotation and the sternal projection extends behind the coxa. When the prothorax is in its most ventral position, latero-ventral intersegmental membrane is enclosed but will be exposed if the prothorax moves dorsally (figs. 8, 26). The collar is least developed, providing posterior clearance in forms capable of extensive flexation (figs. 30, 35, 40). In these extreme surface grade beetles, prothoracic movement does not contribute directly to locomotion but may aid in leg placement in a multi-planar environment.

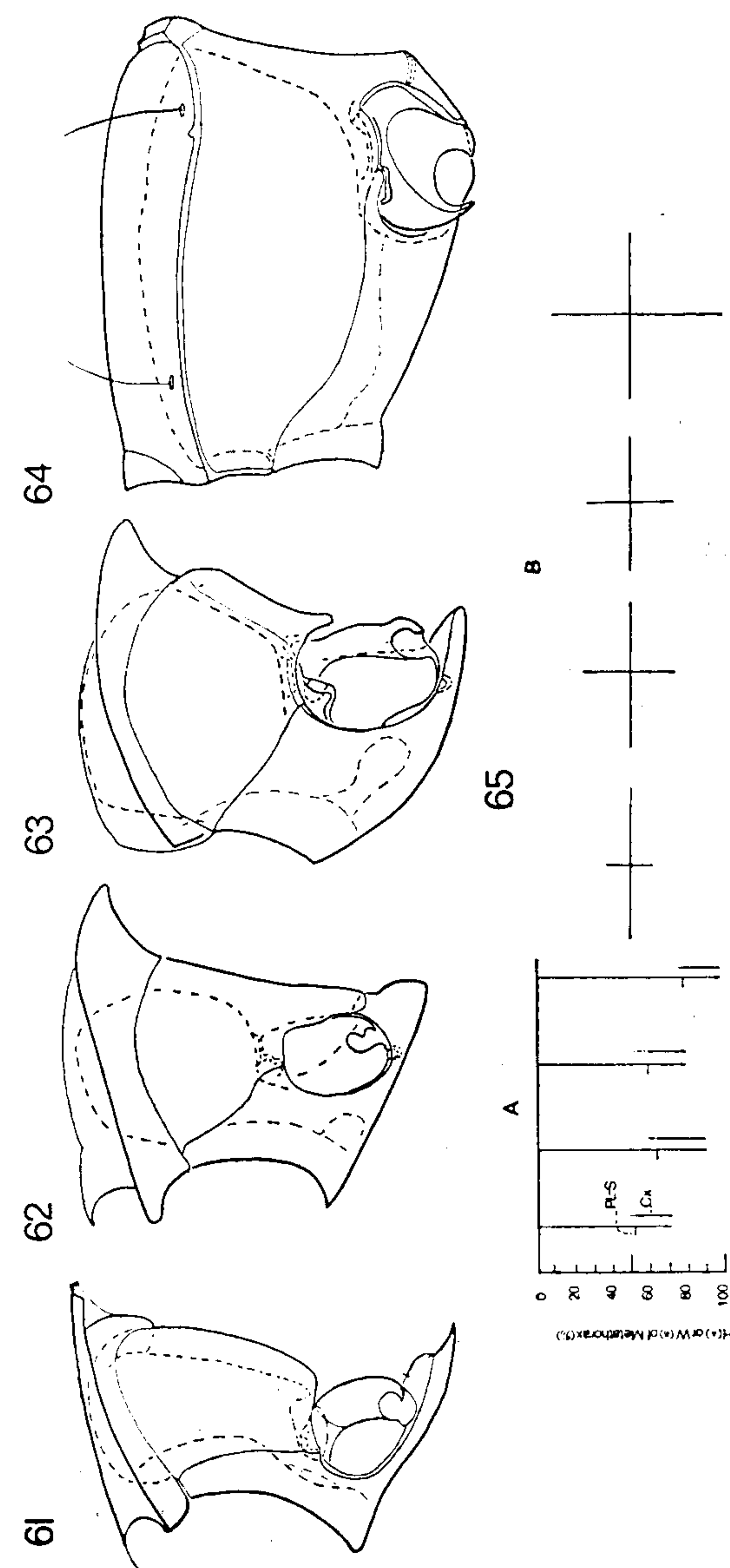
In a few substrate dwellers (e.g., Histeridae), the prothorax is rigidly held against the mesothorax during locomotion and the entire dorsal surface of the squat body is employed to compress material. In some streamlined aquatic groups, the pro- and mesothorax are tightly joined, sometimes by complex interlocking mechanisms, thereby avoiding potential turbulence during swimming. In these two cases, a non-motile joint plays a role in locomotion. Frequently, a potentially rigid joint is an important part of an anti-predator defense system.

As pointed out above, structures increasing structural integrity can be adaptations for substrate locomotion, defense against predators, or both. However, several specializations of the pro-mesothoracic joint and peripheral structures function exclusively as part of an anti-predator system.

Given a thick uncrackable cuticle and widespread enclosed membrane, the remaining vulnerable sites are the appendages and the major body joints, i.e., connections between head-prothorax, prothorax-mesothorax, metathorax-abdomen, elytra-body.

The strength of the pro-mesothoracic joint is increased in some beetles (esp. Elateriformia) by a complex series of interlocking mechanisms involving ball-socket and groove-ridge devices (figs. 25-28, 53-55). Interlocking occurs apparently only after attack or disturbance; during walking the segments are widely separated exposing much intersegmental membrane.

Appendages can be protected via two strategies: compaction and enclosure. In each case, a smooth continuous surface is formed that offers neither purchase for crushing mandibles nor a pathway to



Figs. 61-65; Prothoracic variation within the Adephaga. Fig. 61, *Agabus striatus*; fig. 62, *Methius contractus*; fig. 63, *Carabus nemoralis*; fig. 64, *Clivina impressifrons*. Fig. 65, height and length, width of these forms relative to the height and width of the metathorax plus elytra, see caption for figs. 25-49.

membrane for probing beaks. In compacted forms, elements of the proleg and sometimes the mesoleg as well are drawn tightly together and lie in thoracic cavities, so that exposed leg surfaces are flush with one another and with surrounding sclerites (figs. 53-55). Frequently the antennae are concealed in pronotal grooves and the mouthparts by the prosternum.

In a few groups of Polyphaga, the antennae, mouthparts, front, and sometimes middle legs are enclosed, in defense position, within a complex cavity formed from elements of the head, pro- and prothorax (figs. 50-52). A "roll up in a ball" strategy requires extensive structural and mechanical modifications which result in great reduction of prothoracic volume.

The pro-mesothoracic joint, then, varies greatly in structural integrity and may contain locomotory and defense adaptations.

Adephaga. This group consists of a broad adaptive array of substrate and surface inhabitants as well as several exclusively aquatic families. A uniform pleuro-coxal mechanism and high degree of structural integrity are maintained throughout (see subordinal diagnoses above). Structural variation occurs primarily in the completeness and quality of the posterior articulation collar, which is incomplete only in a few apparently primitive taxa. In all major groups of ground and arboreal carabids the collar is complete; reversal following shift in zone seems unlikely (Hlavac 1971). Prothoracic size is quite variable and is, of course, strictly correlated with ecology, as in Polyphaga. In the Adephaga, prothoracic elongation is particularly important and is graphically seen in the increased ventral inclination of the pleuro-sternal joint (figs. 61-65). The pattern of prothoracic evolution in the Adephaga is similar to that found in several biologically diverse higher taxa of Polyphaga with specialized pleuro-coxal mechanisms and relatively little structural variation, e.g., Scarabaeidae (figs. 45-49).

DISCUSSION

As seen above, similar prothoracic configurations and characters occur in members of unrelated taxa which share a common band on a broad ecological spectrum. Reasons why convergence and parallelism are an important aspect of prothoracic differentiation can be seen from a consideration of the relative breadth of adaptive pathway within each functional variable—structural integrity and power. The plasticity of structures varying morphological strength and enclosure of membrane is sharply limited by geometry, i.e., the adaptive pathway is narrow. For example, there are just two modes of pos-

terior collar completion. Either a medial sternal projection or lateral edges of the cryptosternum is/are joined to notal projections, e.g., figs. 42, 43 vs. 50, 51. The presence of similar collars, differing in minor details, in numerous groups of beetles reflects a broad selection pressure acting through a narrow gap-like pathway. And, of course the probability of multiple origin, and convergent improvement is quite high in this and other structural integrity improving adaptations.

Variability of structures increasing prothoracic power generation is limited by the geometry of muscle origins and insertions. Several distinct pathways are possible. For example, figs. 27, 42, 47 depict a trio of high volume prothoraces with three different, specialized pleuro-coxal mechanisms (as compared with that of configurations differing slightly from the generalized reference standard, figs. 25, 32, 37). In two cases, the endopleuron is fused to the notal wall, but two different strategies of coxal reaction to notal increase have been employed (figs. 27, 44). In figs. 45, 47, deep coxal internalization is also employed but the pleuro-coxal mechanism is completely different. The pleuron is reduced and attached to the coxa; both rotate about a notal condyle. In each of these cases, a specialized pleuro-coxal mechanism is uniform throughout a large, biologically diverse higher taxon—i.e., superfamily. And each type of mechanism is present in, at least, several unrelated taxa. The observed diversity of internal mechanics in high volume forms is consistent with a relatively specific selection pressures having acted through a broad, multi-solution pathway, followed by canalization.

The prothoraces of some surface dwelling forms are simply low in volume and have the same pleuro-coxal mechanism as do substrate inhabitants of the same taxon, e.g., Adephaga, Scarabaeoidea (figs. 45, 47). On the other hand, the design limitations of a flexing procoxa have resulted in similar configurations in the several groups of surface grade beasts that have adopted this locomotory mode (figs. 30, 35, 40).

Prothoracic structure is then sensitive to changes in locomotory biology in but a limited number of ways. And, the broad adaptive radiations of Coleoptera may be documented through the study of prothoracic morphology. But since adaptive pathways are so narrow, convergence so common, and putatively unique paradaptive features so infrequent, only limited evolutionary conclusions can be drawn solely from prothorax morphology. The obvious historical questions on ecological differentiation of individual higher taxa circumscribe a major poorly explored area of beetle systematics. Useful ideas on

such problems as the ancestral zone and factors responsible for shift will arise however from integration of pro-and pterothoracic variation. Limited evidence suggests that the predominant direction of shift, in extant forms, has been from substrate to surface, coincident with the evolution of flowering plants and peripheral communities. Thus, characters increasing power and improving structural integrity are likely to be primitive, in a statistical sense, within the Coleoptera.

In summary, adaptive responses to ecological differentiation, including initial exploitation of the substrate zone and shifts back to the ancestral surface locomotory zone, account for diagnostic features of the coleopterous prothorax and also for major features of variation.

ABBREVIATIONS USED IN THE FIGURES

AF — anterior fold	Lb — lobe
AFL — anterior flange	N — notum
ANFL — anterior notal flange	N pj — notal projection
APLFL — anterior pleural flange	Pl — pleuron
ASFL — anterior sternal flange	PlAph — pleural apophysis
Cnd — condyle	PNFL — posterior notal flange
CrS — cryptosternum	Pl-S — pleuro-sternal joint
CS — cervicle sclerite	RFM — rim fold margin
Cw — cowling	S — sternum
CxBr — coxal bridge	S Aph — sternal apophysis
EndPl — endopleuron	SL pj — sternellar projection
Epm — epimeron	S pj — sternal projection
Eps — episternum	Tn — trochantin
Is Mb — intersegmental membrane	Zf — zone of fusion

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or more of the following limitations: small and/or poorly chosen sample; superficial analysis of raw data, or none at all; impoverished treatment of adaptive phenomena. There are few even moderately comprehensive studies of structural variation; see Arnett (1967) for list and brief descriptions. And, many glaring problems have not been dealt with. For example, prothoracic characters have long been used in subordinal diagnoses, yet detailed comparisons of representatives of each taxon have not been made.

Since ecological differentiation and thoracic adaptation are so intimately related, understanding the locomotory system is particularly important for the future development of beetle systematics. Due to size and diversity of the group, work on this functional complex is neither easy nor quickly accomplished. The only feasible compromise is to select a natural subunit of this system for detailed study. The prothorax is the obvious, initial choice.

Prothoracic structure and mechanics are simple as compared to those of the two pterothoracic segments where both ambulatory and flight functions are combined. Differences in size, structure and function in the prothorax are readily perceived and correlated with physical demands of various environments. Furthermore, details of prothoracic mechanisms are commonly diagnostic of higher categories. The interplay between adaptive phenomena and historical development in the prothorax is considered below at 2 levels: origin of the coleopterous prothorax and variation within the two biologically diverse suborders.

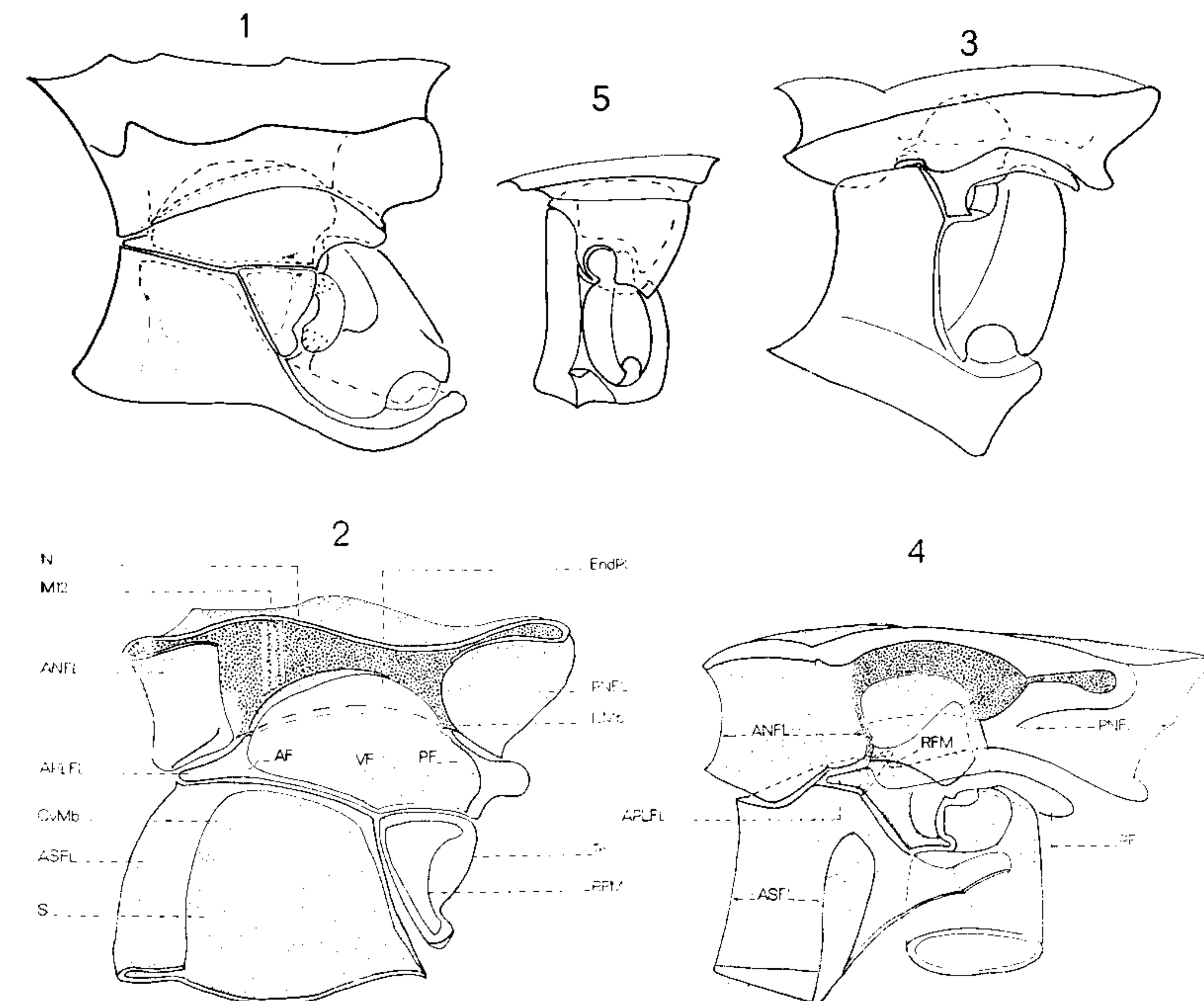
The generalizations and evolutionary hypotheses presented here are based on dissection of over 600 selected genera, and external examination of many others. Raw data, primarily drawings, group diagnoses, and discussions of variation within major taxa, will be presented elsewhere as will results of a current study of pterothoracic structure.

BASIC STRUCTURE

The walls of the rigid, cylinder-like prothorax of Coleoptera are always formed by the notum dorsally, by the sternum ventrally, and, in some forms, the pleuron forms distinct lateral walls (figs. 1-9). The trochantin, a small, sometimes movable sclerite, is attached to the sternum and pleuron and along with the latter articulates with the coxa, the basal leg segment (figs. 2, 7 Tn). The coxa also rests on and sometimes mechanically articulates with the posterior section of the sternum — the cryptosternum (fig. 7 CrS).

Almost without exception, the pleuron is divided into an external section and an internal, invaginated region, the endopleuron, that is concealed by the notum (figs. 2, 7, 9, Pl, EndPl). The rim of the external portion may be completely folded over, broadly so anteriorly and posteriorly to form flanges, parts of paired articulation-collars and quite narrowly so ventrally forming half of membranous sternal and trochantinal attachments and part of the coxal articulation (figs. 2, 4, 9 ANFL, APLFL, PNFL, PPLFL, RFM, AF, VF, PF).

These anterior notal, sternal, and sometimes pleural flanges produce a complete articulation-collar or socket which encloses the posterior aspect of the head, cervical membrane, and, if present, cervical sclerites. Likewise, the posterior notal flange, and sometimes a pleural



Figs. 1-5. Prothoraces of Archostemata and Myxophaga.

Figs. 1, 2. Lateral external and internal views of *Priacma serrata* (Archostemata, Cupedidae).

Figs. 3, 4. Same of *Ptyopteryx britskii* (Myxophaga, Torridinicolidae).

Fig. 5. Lateral view of *Hydroscaapha natans* (Myxophaga, Hydroscaaphidae).

Margins of enclosed structures indicated by dashed lines.

flange as well, form an incomplete collar enclosing part of the mesothoracic rim and some intersegmental membrane (fig. 8).

The fold forming the anterior sternal flange may continue dorsally to join with a pleural or notal rim fold and then extend ventrally to form a membrane enclosing joint with the trochantin. Below the trochantin, the sternum generally bears a shelf-like, poorly pigmented, concave region, the cryptosternum, which supports and is concealed by the coxa (figs. 7, 9 CrS). The cryptosternum also bears a pair of invaginations or apophyses close to the posterior margin. Frequently, the sternum is evaginated medially, forming a projection which may extend between, behind, and sometimes above the coxa. Sometimes a second, smaller sternallar projection is present as well (fig. 7 Spj, SLpj). A complete posterior collar is commonly formed from union of either of these projections with notal or pleural projections (figs. 33, 43, 46, 48, 62, 64).

SUBORDINAL DIFFERENCES AND THE HYPOTHETICAL STEM CONFIGURATION

There are major differences in pleural size, structure, motility and in its trochantinal attachment among the four suborders of Coleoptera. Subordinal configurations can be diagnosed as follows.

ARCHOSTEMATA. Pleuron large, rigid, forming lateral wall of segment. Trochantin motile, external. Anterior pleural flange external, small and enclosed, or absent with internal anterior fold. Sternal joint membranous to solidly fused (figs. 1, 2, 11, 12, 14).

MYXOPHAGA. Pleuron variable in size (figs. 3-5), rigid, fused to trochantin. Anterior pleural flange external or enclosed (figs. 3-5). Sternal joint membranous.

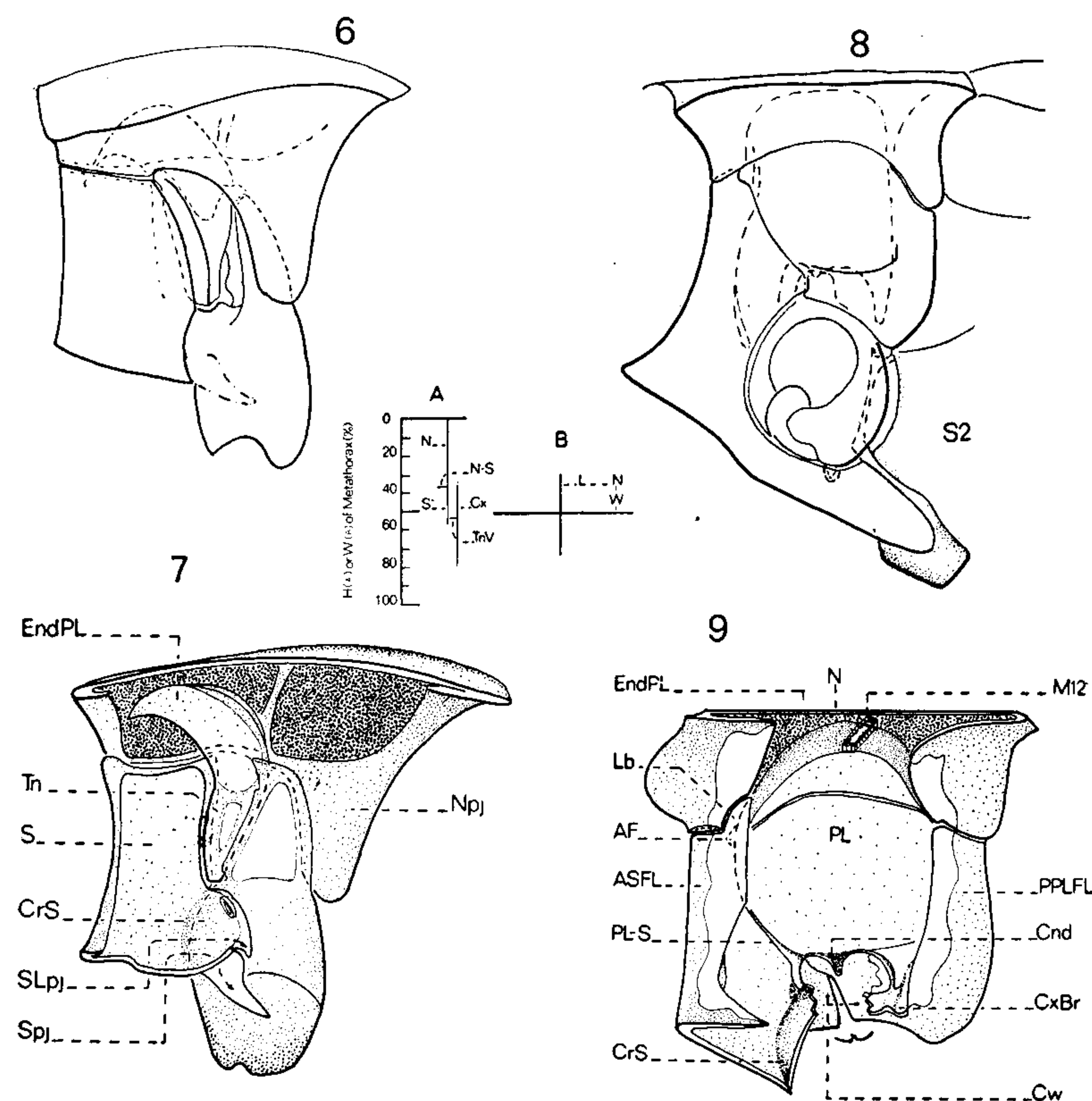
ADEPHAGA. Pleuron, a prominent part of body wall, rigid. Trochantin, small, motile, enclosed along with coxal articular region by pleural and sternal cowlings. Anterior pleural flange absent, anterior fold internalized by union of notal and sternal flanges (figs. 8, 9, 13, 61-65). Sternal joint fused.

POLYPHAGA. Pleuron greatly reduced in size and fused to trochantin; this highly variable compound structure may be motile and contribute to coxal movement, and may be completely enclosed. Notum and sternum attached anterior to pleuron to form body wall. Anterior pleural fold and zone of fusion between pleuron and trochantin present in a few primitive groups. Sternal joint membranous to solidly fused (figs. 6, 7, 15-17, 23-55).

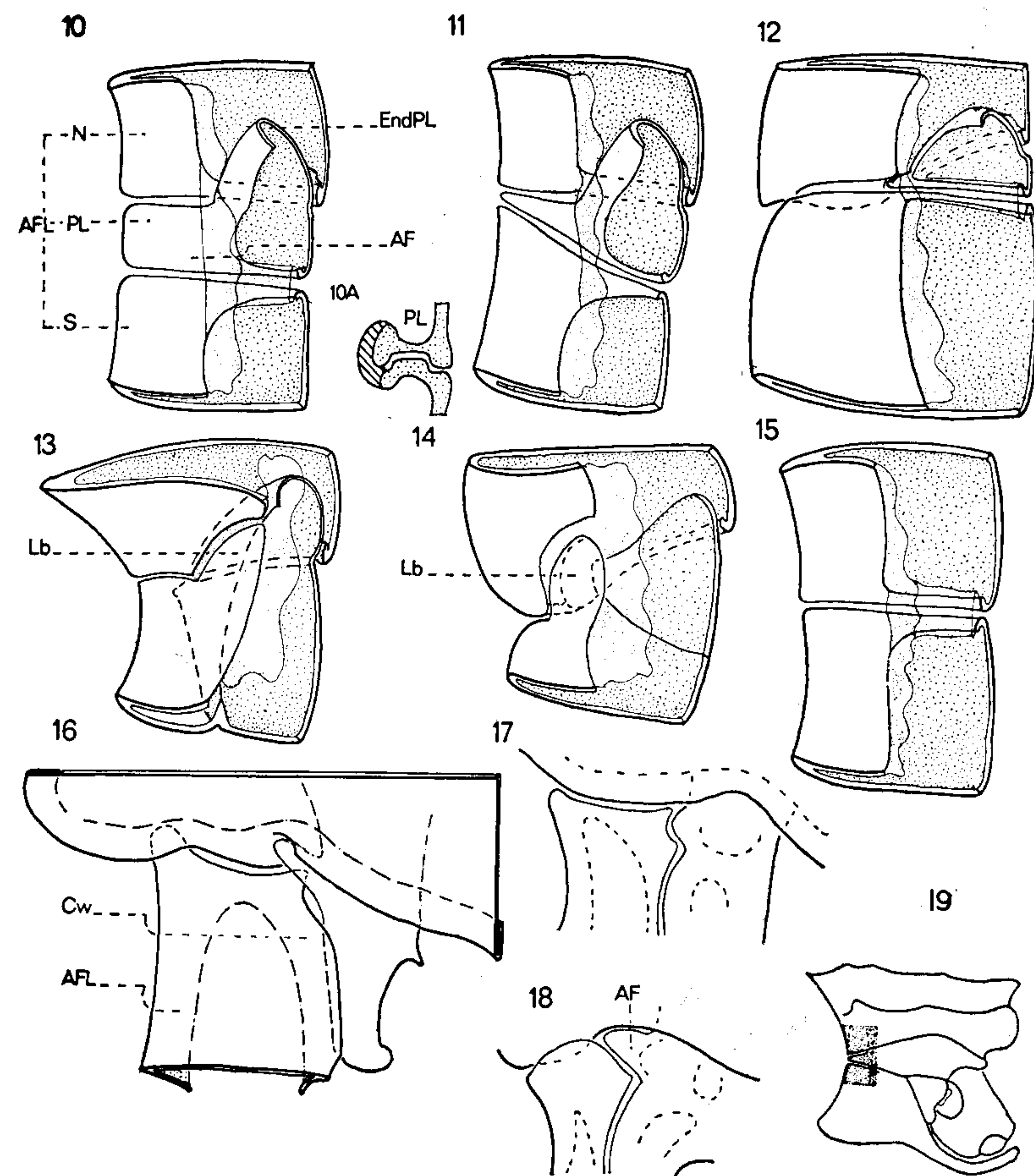
In addition, rim-fold joints between body wall sclerites and moving parts are very widely distributed within the Coleoptera.

Prothoracic configurations of extant forms can be derived from a single hypothetical stem form diagnosed as follows.

HYPOTHETICAL STEM CONFIGURATION: Pleuron large, rigid, forming distinct part of body wall, with broad anterior and posterior flanges; attached by rim-fold joints to notum and sternum. Endopleuron present. Trochantin external, motile. A complete anterior collar and partial posterior collar enclose most of the intersegmental



Figs. 6-9. Prothoraces of Polyphaga and Adepaga.
Figs. 6, 7. Lateral external and internal views of *Omalium marginatum* (Polyphaga, Staphylinidae). [See text and captions of Figs. 25-55 for explanation of Fig. 6A, B].
Figs. 8, 9. Same of *Amphizoa insolens* (Adepaga, Amphizoidae).



membrane. Peri-coxal and trochantinal membrane enclosed by cowlings on pleuron, sternum and trochantin (fig. 24).

Evidence for the primitiveness of individual characters is obtained from both extant and fossil forms.

The tripartite body wall and anterior collar is a major feature of the archtypical coleopterous prothorax. This arrangement is geometrically the simplest way of producing a sclerotized cylinder bearing paired sockets, i.e., through anterior development and folding of dorsal, lateral and ventral elements without shift in relative position. Pleural size and structure of three suborders (Archostemata, Adephaga, Myxophaga) is similar to that of the stem configuration but differ from it in having a reduced or internalized anterior flange.

A relatively small, external, anterior pleural flange is present only in some extant members of the Archostemata and Myxophaga. In other members of both groups, the flange is even further reduced and enclosed by overlap of notal and sternal elements (figs. 1-5, 11, 12). In one group of Archostemata (Cupedidae, Ommadinae) and in all Adephaga, the anterior flange is absent, and a small anterior pleural fold is internalized, frequently by membranous connection of a lobe-like expansion of the sternal flange with the notal flange (figs. 8, 9, 13, 14). In some Adephaga and Myxophaga notal and sternal flange rims may overlap but are not connected (figs. 3, 8). The Myxophaga and Adephaga then overlap the Archostemata at opposite ends of this morphocline.

In many Mesozoic Coleoptera of dubious subordinal position, the notum and sternum are widely separated by the pleuron (e.g., Ponomarenko 1969; figs. 74, 102). No internal evidence is available. However, since the posterior rim of the head is clearly enclosed by

Figs. 10-19. Morphology of anterior section of the pleuron and surrounding structures; sclerites slightly disarticulated.

Figs. 10-15. Internal views.

Fig. 10. Hypothetical stem configuration. Fig. 10A. Section through pleuro-sternal joint.

Fig. 11. *Priacma serrata* (Archostemata, Cupedidae, Cupedinae).

Fig. 12. *Cupes concolor* (Cupedidae, Cupedinae).

Fig. 13. *Amphixoa insolens* (Adephaga, Amphizoidae).

Fig. 14. *Tetraphalerus wagneri* (Cupedidae, Ommadinae).

Fig. 15. Generalized Polyphagon.

Figs. 16-18. External views of Polyphaga.

Fig. 16. *Peltastica turberculata* (Derodontidae).

Fig. 17. *Sarabandus robustus* (Helodidae).

Fig. 18. *Megarthus robustus* (Staphylinidae).

Fig. 19. External view of *Priacma*; sections included above, heavily stippled.

the prothorax in these forms, it is reasonable to infer the existence of a tripartite anterior collar. In other fossil beetles, the notum and sternum extend in front of the pleuron. This could represent either a stage of anterior pleural reduction as in figs, 3, 4, 12, or a distinct noto-sternal joint. The evidence is ambiguous.

Based on the geometry of major sclerites, and structural variation in extant and fossil forms, a three element body wall and anterior collar is taken to be primitive for Coleoptera. The distribution of extant forms evolved though variable, possibly, parallel reduction of the anterior flange.

A separate, motile trochantin occurs in the Archostemata, Adephaga and in other holometabolous orders. The trochantin and pleuron are fused in the Myxophaga and Polyphaga. A separate trochantin is doubtless a primitive trait in Coleoptera.

The almost universal presence of membrane enclosing rim-fold joints between major sclerites, and moving parts within both extant and fossil forms is evidence for the primitiveness of these articulations within the Coleoptera. A rigid rim-fold joint is produced by medially bending the edges of two sclerites to form a pair of flattened, normally horizontal articulation surfaces which may bear tongue-groove devices (fig. 10A). Attachment membrane extends between the margins of the two sclerites and is enclosed. In all extant forms, the body wall elements are connected with membranous rim-fold joints (frequently in primitive members of higher taxa) or are solidly fused together, sometimes with a distinct internal carina and often without the slightest vestige of a suture (figs. 9, 59, 50). Rigid rim-fold joints seem to be universally present in fossil Coleoptera, as well.

Except in extreme surface grade polyphagans, membrane around the coxa and trochantin is enclosed by loose rim-fold joints or both structures may be entirely enclosed by cowlings, see below. There is no obvious membranous band between moving parts in the fossil Coleoptera depicted by Ponomarenko (1969). It is assumed, then, that rigid and loose rim-fold joints are primitive characters in the Coleoptera.

Except for the Polyphaga, Recent suborders and early fossil Coleoptera are similar to the stem configuration in basic organization. The major differences between the Adephaga, Archostemata, and Myxophaga are either simple modifications of structural details (reduction of anterior pleural flange, trochantinal fusion) or adaptations for improving structural integrity (enclosure of coxal articular region and trochantin in the Adephaga). The great differences between

Polyphaga and other Coleoptera are integral parts of a unique pleuro-coxal mechanism.

In all Polyphaga, the trochantin and pleuron are fused together; in a few members of apparently primitive groups (Staphylinoidea, Eucinetoidae) the structure of a distinct internal zone of fusion between the two sclerites indicates union of a pair of rim folds (figs. 7, 24). This compound structure is frequently movable and can contribute to coxal rotation and/or flexation. Since the pleuron is a moving part, it can not contribute to the rigidity of the segmental wall, and is greatly reduced in length and width. In most cases, pleural height is so reduced that the coxal apex is concealed by the notal rim-fold. A rigid segment is obtained by anterior attachment of notum and sternum. Evidence that this specialized mechanism has evolved from a configuration with a tripartite body wall is found in what are probably vestiges of the anterior pleural fold between the notum and sternum in members of these presumed primitive groups of Polyphaga (Eucinetoidae, Staphylinoidea, Derodontidae) (figs. 16-18). The major muscle powering pleural motility in the Polyphaga is also found in other suborders, but its function, in these groups, given rigid external pleural walls, is problematical (figs. 2, 9 M12). The Polyphaga can therefore be derived from the hypothetical configuration through modification of the pleuro-coxal mechanism resulting in the acquisition of pleural motility.

PROTHORACIC STRUCTURE OF THE ANCESTRAL GROUP

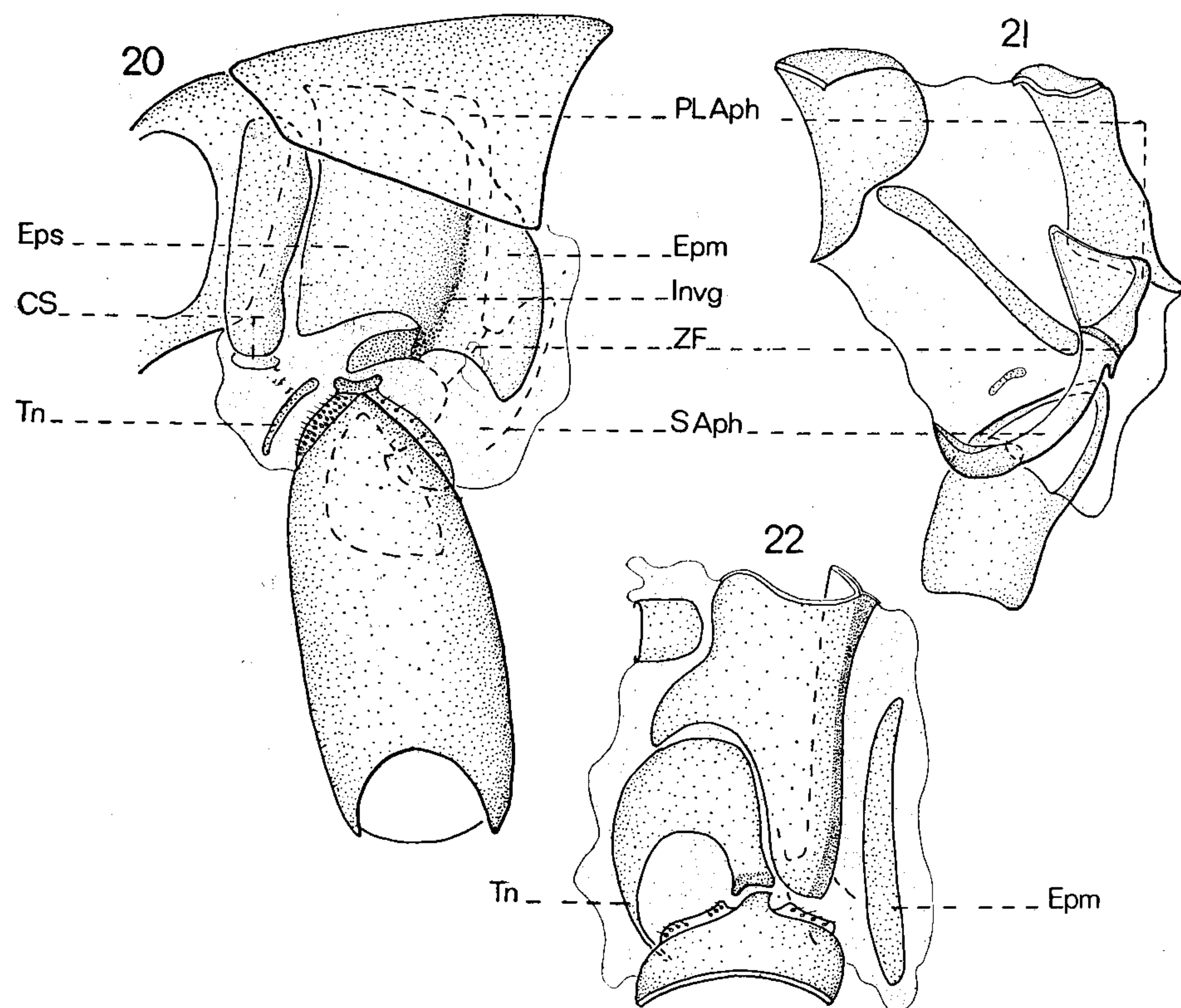
It is generally concluded that the Holometabola is a strictly monophyletic taxon, but see Matsuda (1970: 215). The Coleoptera and the other major orders are believed to have evolved from a generalized stock of lower Holometabola, closest to Neuroptera and Mecoptera (Crowson 1956: 1, 1960: 111).

There are enormous differences in prothoracic structure between the Coleoptera and other Holometabola; and there is only moderate variation within the Lower Holometabola. Based on study of members of all major groups, it is possible to diagnose a presumed primitive configuration as follows:

GENERALIZED HOLOMETABOLUS PROTHORAX: Noto-pleural joint, loose, membranous. Dorsal portion of pleuron enclosed by notum but the pleural rim only narrowly folded over; there is no deep, horizontal, endopleural invagination as in Coleoptera. The pleuron does bear a ventral invagination, or apophysis, which divides it into an episternum, anteriorly and an epimeron, posteriorly. Pleural apophysis fused internally to sternal apophysis. Trochantin motile, closely

attached to pleuron and as heavily sclerotized as the other structures. Sternum joined only internally to pleuron, does not extend in front of the coxa. Anterior and posterior collars absent, coxal articulation external so that considerable cervical, intersegmental, and pericoxal membrane is exposed (fig. 23).

This configuration is most similar to the extant Australian genus *Ithone* (Neuroptera) (fig. 20) but with a large, articulatory trochantin, as in the Trichoptera (fig. 22). Reducing the trochantin while maintaining associated musculature may be a modification for increasing the angle of coxal flexation. Division of the pleuron into



Figs. 20-22. Prothoracic structure of the Lower Holometabola.
 Fig. 20. External lateral view of *Ithone* sp. (Neuroptera).
 Fig. 21. Internal lateral view of *Panorpa virginica* (Mecoptera).
 Fig. 22. External lateral view of coxal articulation of *Ptilostomis ocellifera* (Trichoptera).

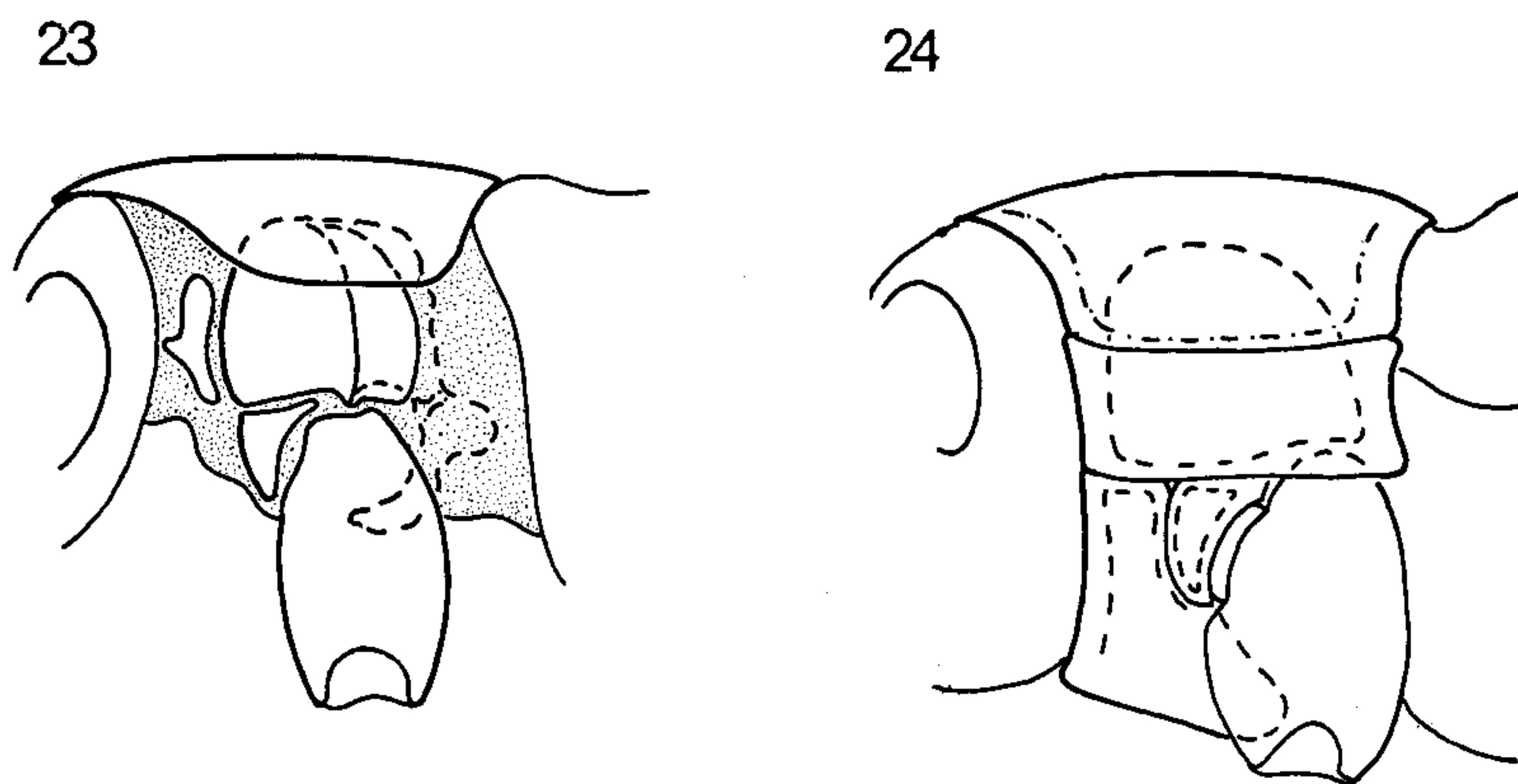


Fig. 23. Generalized Prothorax of the Lower Holometabola; Fig. 24, Hypothetical stem prothorax of Coleoptera. Membranous regions stippled.

two parts by an apophysis, or pleural suture is a common feature of pterothoracic segments. Among Holometabola this arrangement is preserved in the prothorax only in *Ithone* and a few related forms (fig. 20, Eps, Epm, Invg). In the Trichoptera, a detached epimeron is present (fig. 22). In all other Holometabola the posterior rim of the apophysis is membranous. Ventral enlargement, and fusion of sternum, pleuron and even the cervical sclerites of the Corydalidae and Raphidioidea are doubtless specialized features readily derived from a generalized configuration (Kelsey 1954, figs. 1, 7; Ferris and Pennebaker 1939, fig. 61).

COLEOPTERA AND THE ANCESTRAL GROUP DIFFERENCES IN PROTHORACIC STRUCTURE

Comparison of the generalized holometabolous prothorax (GH) with that of the hypothetical stem coleopteran (SC) yields differences in five major categories (figs. 23, 24). The abbreviations (GH and SC) are employed below for simplicity and to emphasize the fact that two abstract assemblages are being considered rather than elements of actual organisms.

A). *Head-Prothoracic Joint*. — In SC an anterior articulation-collar composed of notal, pleural and sternal flanges encloses part of the head and all cervical membrane as well as the cervical sclerites. The sternum is developed anteriorly and joined to the pleuron. An articulation-collar is absent in GH, the head may be slightly en-

closed by the notum, cervical membrane, and sclerites are exposed, and the sternum is not externally joined to the pleuron.

B). *Pro-Mesothoracic Joint*. — In SC a partial posterior articulation-collar is formed from notal and pleural flanges, which rest on the mesothorax and enclose dorsal and lateral intersegmental membrane. Such flanges are absent and intersegmental is exposed in GH.

C). *Noto-Pleural and Pleuro-Sternal Joints*. — In SC these connections are of the rim-fold type and result in a rigid frame prothorax. The horizontal invagination that forms the endopleuron is located close to the notal rim. In GH, the noto-pleural joint is loose and there is neither an external pleuro-sternal connection nor a broad endopleuron.

D). *Trochantinal and Coxal Articulations*. — In SC the coxa and trochantin are connected to one another and to the sternum and pleuron via loose rim-fold joints, which enclose peritrochantinal and pericoxal membrane (fig. 56). Loose rim-fold joints are absent in GH and these membranous regions are exposed.

E.) *Attachment of Sternal and Pleural Invaginations (or Apophyses)*. — There is no vertical pleural apophyseal invagination in any extant coleopteron; the sternal apophyses are always present. In all other Holometabola, both sternal and pleural apophyses are present, and these invaginations are solidly fused together (fig. 21).

These differences are of two major types, those that result in the enclosure of membrane between moving parts (A, B, D) and one that results in a rigid frame prothorax (C).

ORIGIN OF THE COLEOPTEROUS PROTHORAX

Major features of the hypothetical stem prothorax of beetles result in great improvements in structural integrity over the ancestral condition due to development of rigidly attached segmental walls, and widespread enclosure of membrane. Two differences seem to be side effects of an increase in structural stability. An anterior, external sternal attachment provides potentially rigid attachment for this sclerite to the pleuron or notum, and permits the sternum to form the ventral body wall, and part of the anterior collar. An internal attachment can give only rigidity. To have both is redundant. Loss of both the internal sterno-pleural attachment and the pleural apophysis itself may be a structural simplification occurring after development of a multi-purpose anterior sternal attachment. Parenthetically, the line of fusion between the posterior rim fold and the body

wall, is sometimes incorrectly called a pleural suture (= apophysis) in the taxonomic literature especially in the Adephaga.

The endopleuron provides increased surface area for muscle attachment. It is argued below that the key event leading to the unique coleopterous locomotory system was entrance into a substrate adaptive zone. Strength and power are both important in substrate locomotion. The features described above provide increased strength. The endopleuron is part of a mechanism for improving power generation.

All features of the stem prothorax are either direct improvements in structural integrity or ancillary modifications.

The unique structure of the pterothorax and abdomen of Coleoptera also represents a great increase in structural integrity over the ancestral condition.

In Lower holometabolous groups, the pterothoracic segments and wings are quite similar. The two pairs of wings are membranous. There are generally considerable patches of exposed membrane between abdominal segments. In beetles the pterothoracic segments and wings are highly differentiated in structure and function. The mesothoracic wings of beetles are modified into rigid, heavily sclerotized elytra whose rims can be fitted together, via a tongue-groove device, and which also lie on the pleural margins of the pterothoracic and abdominal segments, thereby forming a structurally stable unit protecting abdominal tergites and folded wings. The abdomen is reduced in relative length, does not often extend behind the elytra, and the sternites are connected by rim-fold joints or are solidly fused together.

The membranous metathoracic flight wings are folded lengthwise, as well as widthwise, and are generally completely enclosed at rest, within the cavity formed by union of the body and elytra. The pterothoracic segments themselves are also highly differentiated. The metathorax, which houses all flight muscles, is much larger and highly modified as compared to the mesothorax.

The characters discussed above as improvements in structural integrity or side effects thereof encompass all major adult diagnostic features of the order Coleoptera.

Improvements in structural integrity can be responses to two potentially quite different but blendable selection pressures involving locomotion or defense. In a surface zone (i.e., crawling on a leaf) where environmental geometry does not oppose forward motion, high structural integrity can be the mechanical portion of an anti-predator system. For example, many arthropod predators, even relatively large

ones, are unable to crush, crack, or pierce cuticle but must attack through vulnerable membranous zones. Enclosing membrane hinders such forms. Of course, this argument applies to substrate dwelling forms as well. In addition, a substrate form not dependent on interstitial spaces must generate force against obstacles to make progress. Consequently, features increasing structural integrity can be adaptations which prevent structural deformation as those locomotory forces are generated and also prevent membrane from coming in contact with abrasive materials. Increasing structural integrity can be a defense adaptation in either zone or a locomotory adaptation in a substrate zone.

Extant members of the groups closest to the presumed ancestral stock of Coleoptera are surface dwellers, except possibly *Merope* (Mecoptera). The gross structure of fossil Lower Holometabola is similar to that of extant forms and suggests that these groups have been surface grade forms throughout their long history.

Beetles are the dominant adult insects in substrate environments. Specialized coleopterous faunas occur in: leaf litter, soil, living, dying and decomposing woody plants, dung, carrion, etc. In each habitat many members of at least several families are present. However, a diverse assortment of beetles is also found in the surface zone, particularly on vegetative surfaces.

The major diagnostic features of Coleoptera are adaptations for improved structural integrity. Beetles have entered and radiated in the substrate locomotory zone; and many higher taxa contain surface dwellers clearly derived from substrate grade forms. An increase in structural integrity can either be an adaptation for substrate locomotion or for mechanical defense against predators. These facts and assumptions indicate that penetration of the substrate zone and development of these adaptations are related, and that both occurred rather early in the history of Coleoptera. Within the framework provided by Bock (1965), then, the following historical diagnosis is suggested.

The suite of unique diagnostic characters of Coleoptera originated and/or became coordinated as a response to selection pressure for increased structural integrity encountered during initial entrance and radiation in a substrate locomotory zone. Individual characters, which may have originated on a surface zone as a mechanical defense adaptation are preadapted for a change in zone and shift in function. The adaptive transformation of the coleopterous prothorax is but a part of the large scale reorganization of the locomotory system stimulated by a major change in ecology.

The central position of the stem configuration here is an artifact of analysis. Due to the great structural discontinuity and lack of intermediate forms between Coleoptera and Lower Holometabola, several important matters can not be considered. In the preceding analysis, then, no statement is made or implied on: monophyly of the stem form and extant suborders, parallel or convergent development and origination sequences of structural adaptations.

VARIATION

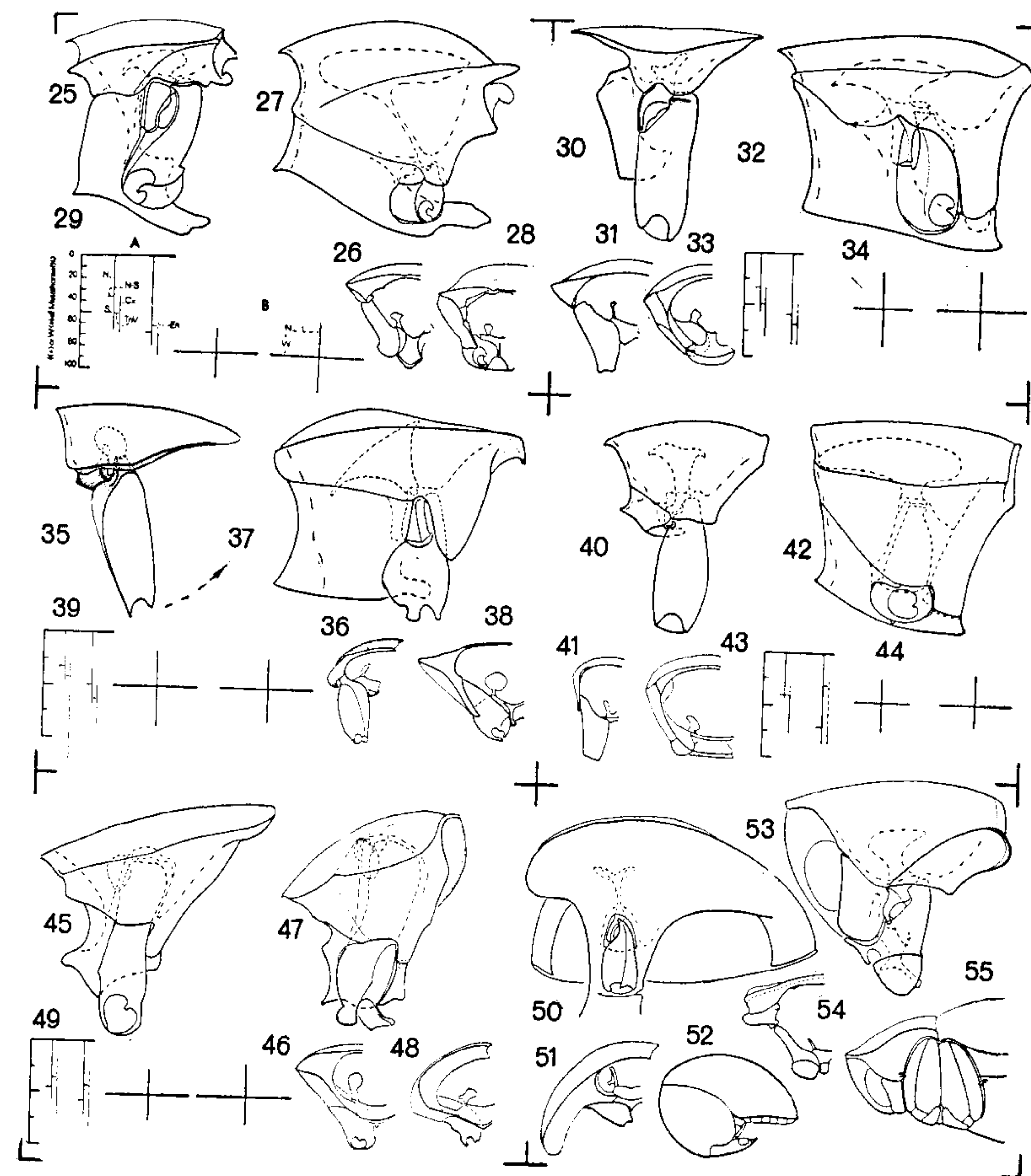
Of the four suborders of Coleoptera, only the Adephaga and Polyphaga are large and biologically diverse.

Polyphaga. The great size (90% of known beetle species) and taxonomic confusion/complexity (20 superfamilies, ca. 155 families) of the Polyphaga makes even a limited discussion of structural variation quite difficult. A sampling technique can be used to facilitate matters. Much of prothoracic diversity consists of interwoven variations on a pair of adaptive themes — power and structural integrity. And, strong relationships exist between biology, structure and prothoracic volume. These variations can be demonstrated by comparing forms from several higher taxa which differ widely in relative prothoracic size (figs. 25-48).

A stem polyphagous prothorax may be diagnosed as follows:

Primitive/Generalized Polyphagous Prothorax: Notal volume low. Noto-sternal joint membranous. Notal projection, if present, may not extend below trochantal apex. Pleuron motile. Endopleuron with short, broad unstricted base and moderately flared apex. Coxal articular region and trochantin large, not completely enclosed. Sternum does not reach coxal apex. Sternal projection does not extend below coxa and is not attached to the notal projection forming complete collar, but may be flattened and extend behind the coxa (figs. 6, 7, 23). Vestiges of the anterior flange and zone of fusion between trochantin (figs. 16-18 AF) may be present.

This sort of configuration is likely to be primitive for Polyphaga, representing a minimal divergence from the hypothetical ancestral condition and it is frequently associated with the two vestigial pleural structures noted above. The adaptations and functional specializations, discussed below, are absent or poorly developed in this prothorax. This could be additional evidence for primitiveness or could represent a generalized, though advanced, configuration at or near the midpoint of an adaptive spectrum. In either case, this assemblage provides a useful reference standard in discussing adaptive extremes.



Since a number of forms are to be compared in some detail, it is convenient to treat variation separately in three functional units:

- 1) Size (volume, muscle housing)
- 2) Pleuro-coxal mechanism (housing, motility of coxa, trochantin, pleuron)
- 3) Intersegmental attachment (pro-mesothoracic joint)

Size. Variation in muscle volume and consequently in gross prothoracic size represents adaptive equilibria to the sharply different power requirements of substrate and surface locomotion. Obviously, compression of substrate requires more power than simply countering the force of gravity on a surface. Changes in prothoracic size are most easily demonstrated through consideration of one dimension height, i.e., prothoracic height and that of component structures/height of metathorax plus elytra ($= Th_1, \text{ etc.}/Th_3$).

In the high volume prothoraces of substrate dwellers, the notum is tall (N_1/Th_3 ca. 60%), the sternum extends to near the coxal apex and the entire assemblage is frequently ca. 85% Th_3 (figs. 27, 29, 32, 34, 37, 39, 42, 44, 47, 49). At the other extreme, in the low volume prothoraces of a surface or interstitial space inhabitants the

Figs. 25-49. Prothoracic variation within five higher taxa of Polyphaga. Each set, bounded by brackets, compares two forms differing widely in prothoracic volume and consists of five figures: a pair of lateral views, drawn parallel to the coxal long axis, a smaller pair of posterior views and a set of graphs comparing the height, length and width of the prothorax with the dimensions of the metathorax. The set on the left, e.g. fig. 29A, contrasts the cumulative heights of prothoracic structures expressed as a percentage of height of metathorax plus elytra, measured at the level of the posterior edge of the noto-sternal joint, and depicted in the same order as the drawings. While the paired, crossed lines on the right, e.g. fig. 29B, contrast the length (vertical line) and width of the pronotum expressed as a percentage of maximum width of metathorax plus elytra; the percentage scale on the right applies here as well.

Figs. 25-29; Elateriformia; figs. 27, 28 *Lutrochus geniculatus* (Limnichidae); figs. 28, 29, *Perothops muscida* (Perothopidae).

Figs. 30-34, Cleroidea; figs. 30, 31 *Malachius aeneus* (Melyridae); figs. 32, 33, *Temnochila chorodia* (Trogositidae).

Figs. 35-39; Staphylinidae; figs. 35, 36, *Philonthus cyannipennis*; figs. 37, 38, *Trigonurus crotchii*.

Figs. 40-44; Cucujoidea; figs. 40, 41, *Epicauta pennsylvanica* (Meloidae); figs. 42, 43 *Alobates pennsylvanica* (Tenebrionidae).

Figs. 45-49; Scarabaeidae; figs. 45, 46, *Euphoria limbalis*; figs. 47, 48, *Copris fricator*.

Figs. 50-55; compaction and enclosure in Polyphaga. Figs. 50-52, lateral, posterior view of prothorax and lateral view of body of *Agathidium* sp. (Anisotomidae). Figs. 53-55, same of *Chelonarium lecontei* (Chelonariidae). See text for explanation.