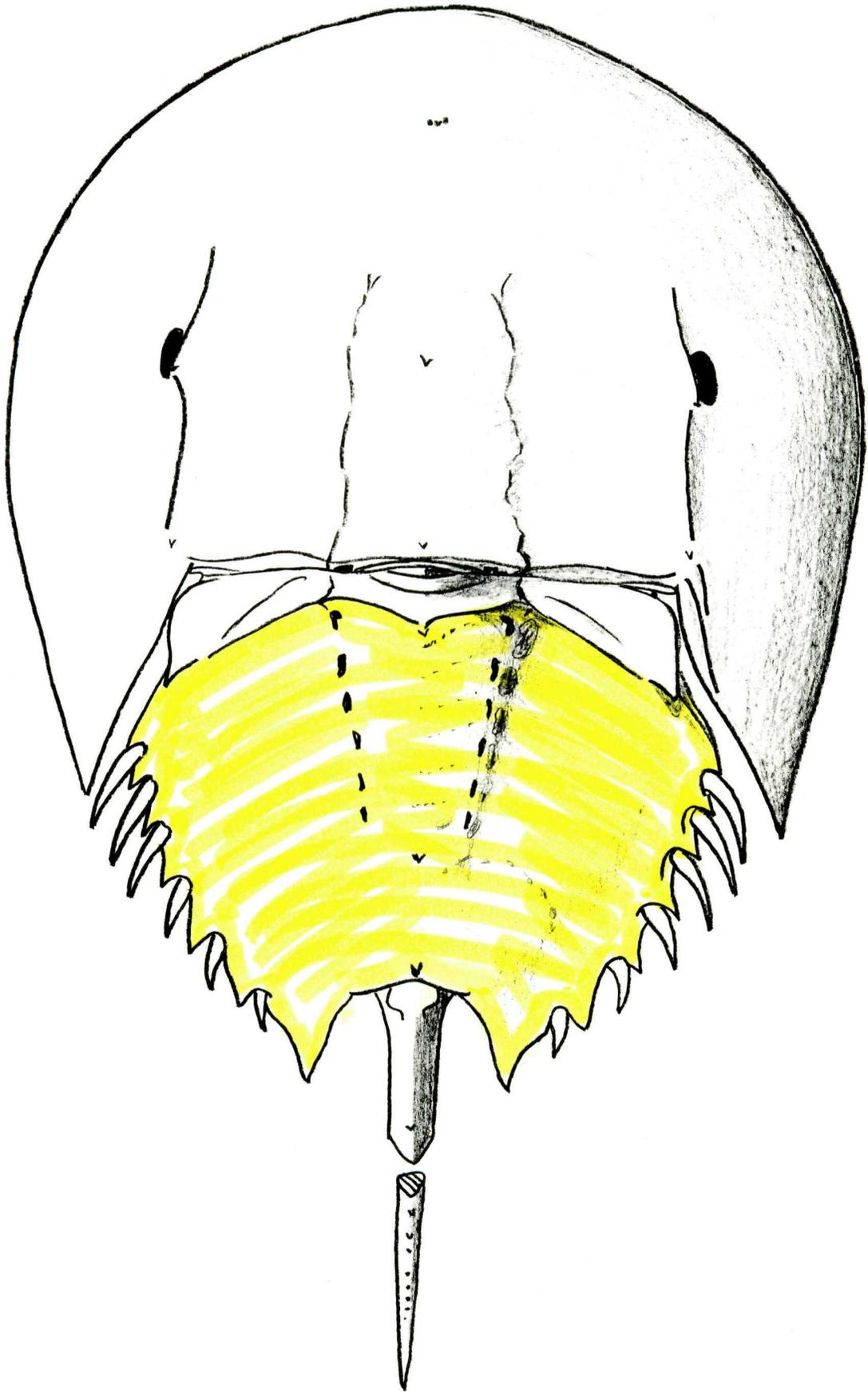


1

Character 1 (thoracetron). – Fusion of opisthosomal tergites IX–XVII, posterior to the opercular tergite (VIII), produces a thoracetron, an apomorphy of Xiphosurida. In *Bellinuroopsis*, the fused nature of the opisthosoma is evidenced by the presence of transverse ridge nodes (character 6) and the modified appearance of the opercular tergite (VIII) from the following tergites. The opercular tergite remains unfused in *Rolfeia* (Fig. 2N) and *Bellinuroopsis* (Fig. 2M) and separate from the thoracetron.

1



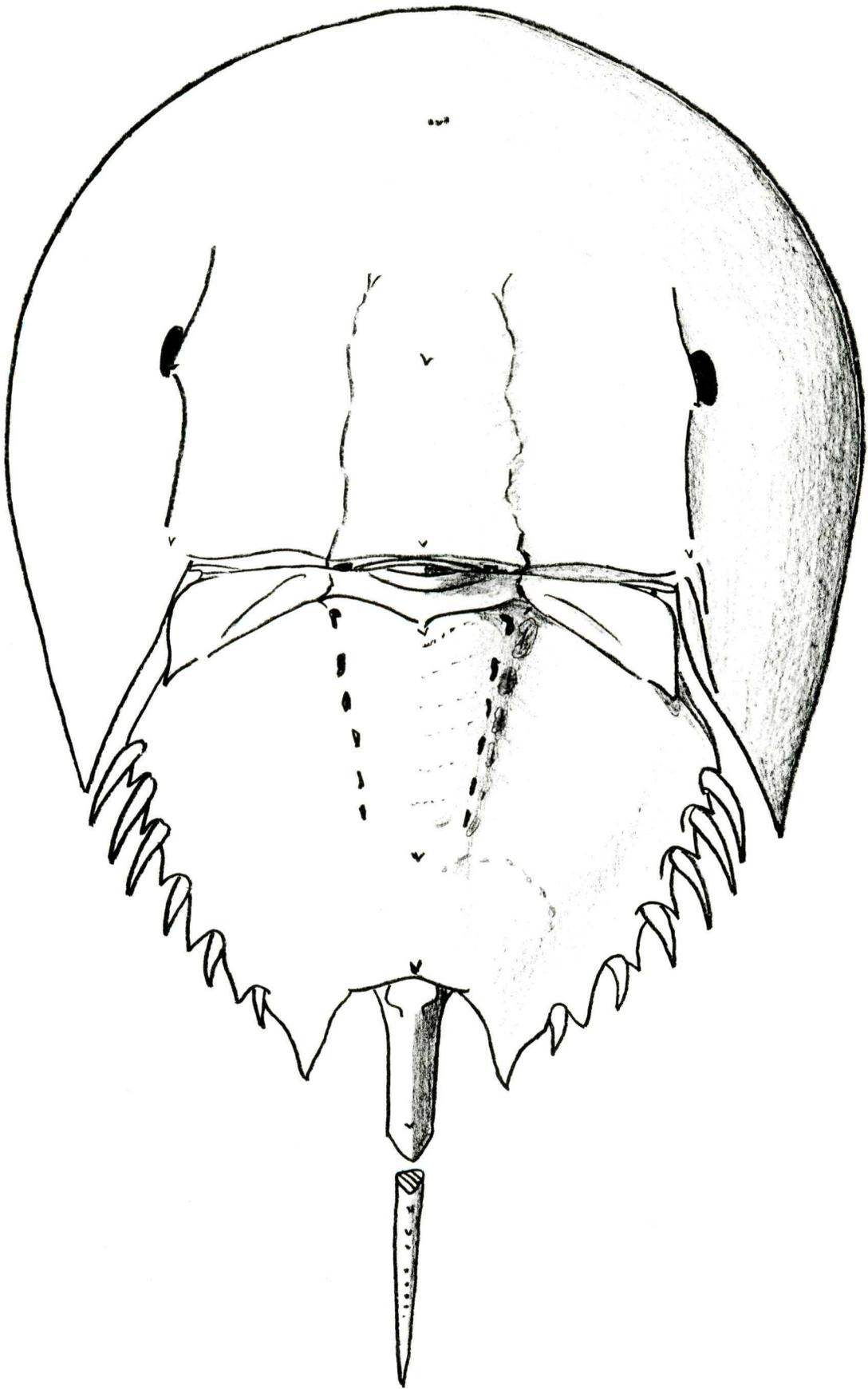
Character 2 (metasoma). – Pseudotagmata may be recognized in the opisthosoma of some early Xiphosura. A metasoma may be formed from the three most posterior opisthosomal segments, the sternites and tergites of which are fused into cylindrical sclerites, clearly distinct from the anterior mesosoma. Where epimera are absent, this character is readily visible, but if epimera are present, as in *Pseudoniscus*, *Pasternakevia* and *Cyamocephalus* (Fig. 2F, G, H) for example, the distinction between mesosoma and metasoma is obscure. The converging axial furrows of the opisthosoma become parallel just anterior to the last three tergites in some of these forms, but the distinction between mesosoma and metasoma is not obvious, as it is in *Lemoneites*, for example. Since the underside of the animal cannot be seen, it is uncertain whether appendages or a fused sternite is present. This character is, to some extent, linked with character 5.

The metasoma, where present, always consists of three segments, but which somites are involved in its formation is not clear. In the most plesiomorphic forms with a metasoma, such as *Lemoneites*, *Legrandella* and *Weinbergina* (Fig. 2A, B, C), it is formed from the ninth to eleventh opisthosomal segments (presumed somites XV–XVII). In *Bunodes* and *Limuloides* (Fig. 2D, E) it is the eighth to tenth opisthosomal segments. These would represent somites XIV–XVI if a segment had been lost posterior to the metasoma but XV–XVII if a segment had been lost anterior to the metasoma. If the latter, then the metasomas of *Lemoneites*, *Legrandella* and *Weinbergina* would be homologous with those of *Bunodes* and *Limuloides*. This would also suggest that either the hypertrophied tergite VIII or the supposed double tergite XIII was indeed formed by fusion of two tergites (Eldredge 1974; Selden & Siveter 1987). *Cyamocephalus* clearly shows two fused tergites (XII and XIII) which could be a further advancement of this trend, but looking at Fig. 2A of Eldredge & Plotnick (1974), there is an alternative possibility. These authors suggested that the tail spine lying to one side of the specimen was broken, its base remaining with the rest of the body. It seems strange that the rigid tail spine should break at its thickest point, yet the rest of the exoskeleton remain fully articulated. If the spine base were actually the posteriormost tergite, then *Cyamocephalus* would represent a more primitive stage in which fusion of tergites was still clearly visible. We have coded the metasoma as absent (0) in *Paleomerus*, present (1) only where it is distinct, and lost (2) elsewhere, thus assuming homology.

3

Character 3 (*tergite VII*). – The first opisthosomal segment, expressing tergite VII, is reduced to a microtergite and lacks lateral tergal fields in the apomorphic condition (1). The plesiomorphic state (0) for this character is shown by *Lemoneites*, which has a fully expressed tergite with lateral fields. Eldredge (1974) reported that *Legrandella* had reduced epimera associated with the microtergite. *Cyamocephalus* also has short epimera on this segment (Eldredge & Plotnick 1974). The microtergite is lost (2) in forms possessing a free lobe.

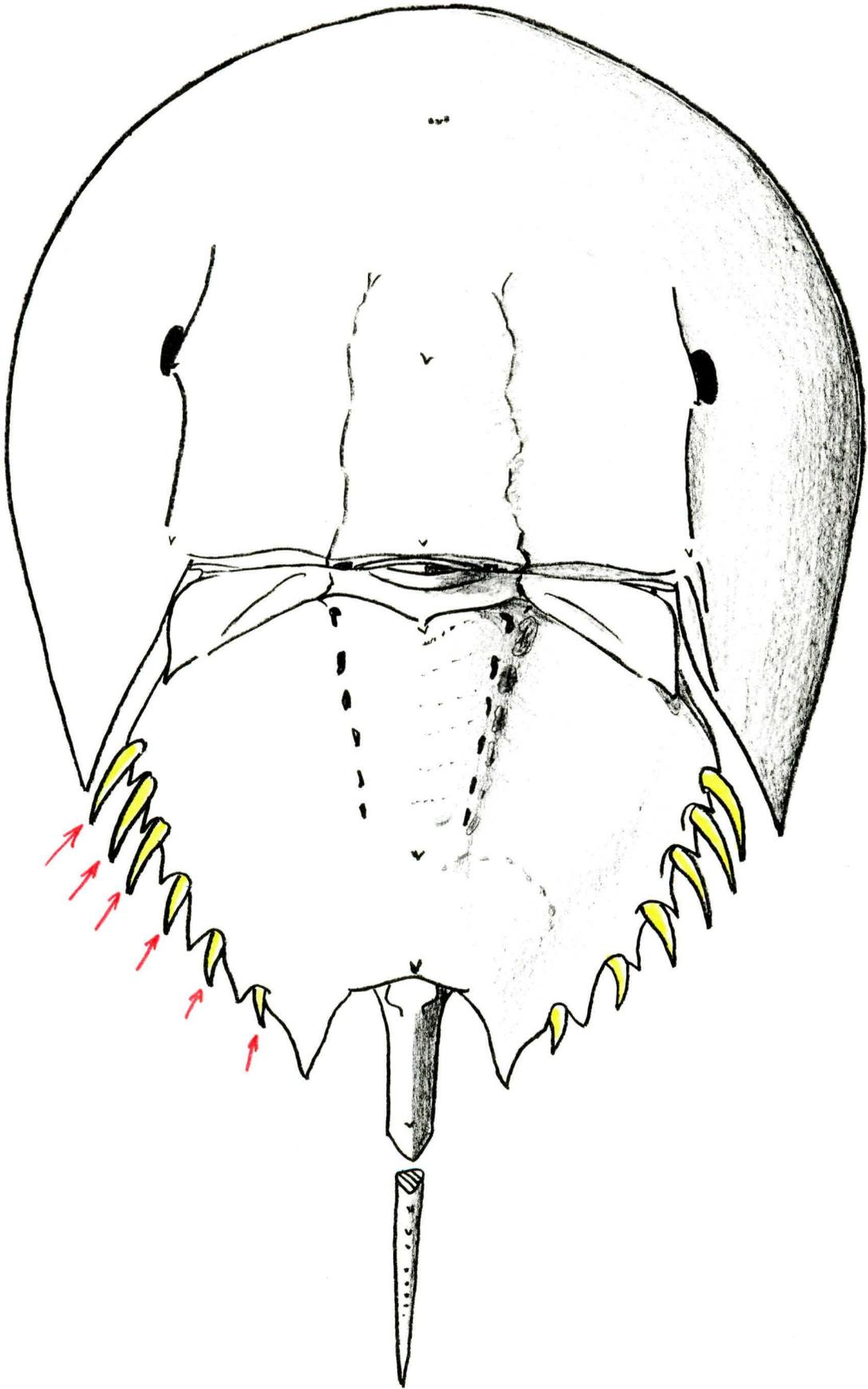
3



4

Character 4 (*movable opisthosomal spines*). – The presence of movable opisthosomal spines is an autapomorphy of suborder Limulina. Movable opisthosomal spines are absent in all other genera, including *Bellinuroopsis*. *Dubbolimulus* Pickett (1984) lacks movable spines, which is interpreted here as an autapomorphy for this genus, though it is possible that movable spines were present but lost by disarticulation during biostratinomy. Interestingly, *Rolfeia* lacks both fixed and movable spines on the second opisthosomal tergite (IX) though they occur on all more posterior tergites, and our preliminary observations of *Paleolimulus longispinus* Schram, 1979, show that this animal has the same pattern of fixed and movable spines (*contra* Schram 1979, Fig. 2, but as hinted at by Waterston 1985). Possibly, *P. longispinus* is actually a *Rolfeia*, and the lack of spines on tergite IX is autapomorphic for the genus.

4



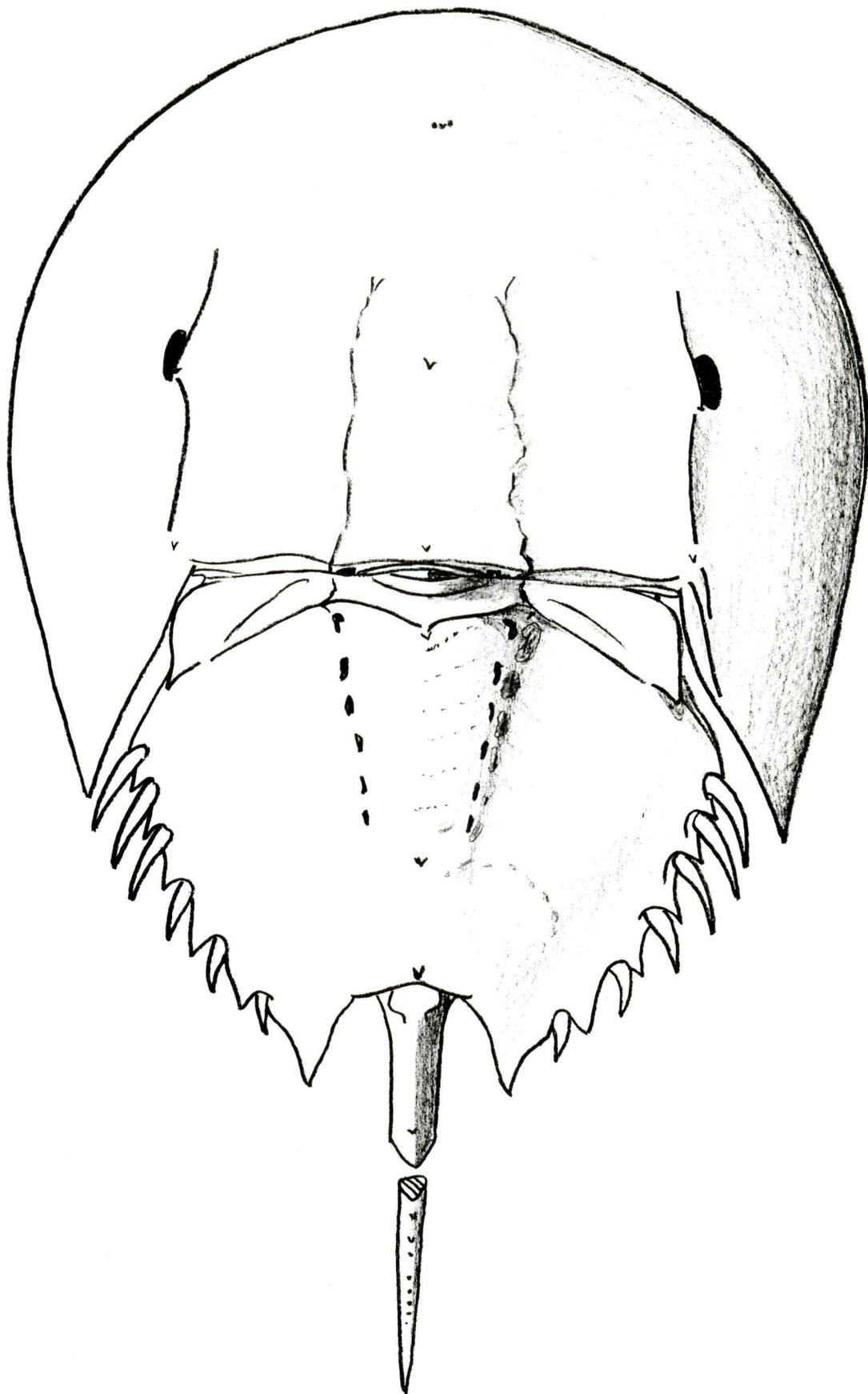
5

Character 5 (*fixed lateral opisthosomal spines*). – Opisthosomal tergites in the outgroups of Xiphosura (e.g., *Paleomerus*) show no or very short epimera (0). Synziphosurines show short and broad (sag.) or longer, curved epimera (1), depending on the width of the opisthosomal axis (character 20). True lateral spines (2) are reinforced by the continuation of the corresponding transverse ridge of the thoracetron. Fixed lateral spines on the opisthosoma occur in *Bellinuroopsis*, *Rolfeia*, *Bellinurus* and *Euproops*. Loss of lateral spines (3) may be derived relative to their presence; this occurs in *Liomesaspis* and some later limuloids.

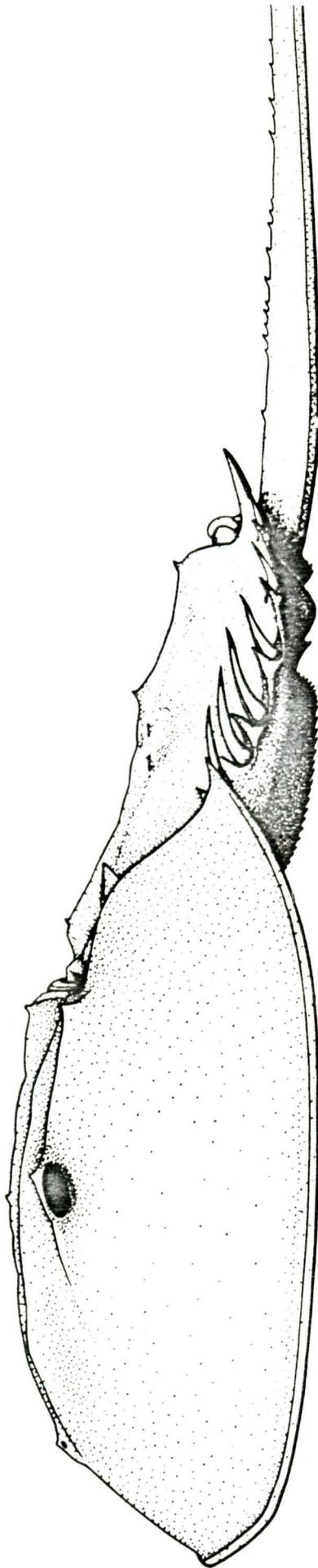
6

Character 6 (*transverse ridge nodes*). – Swollen nodes on the transverse ridges of the opisthosoma occur in *Bellinuroopsis*, *Xaniopyramis* and *Paleolimulus*. Undescribed specimens of *Rolfeia* (BMNH In 34941 and I 889) show evidence of transverse nodes as well as longitudinal ridges (see character 7). Presence of nodes is coded as 1, absence as 0, though the absence of these nodes in limuloids probably reflects a secondary loss.

6



6



7

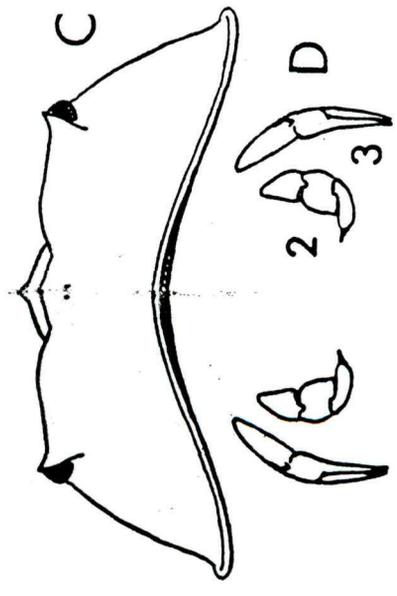
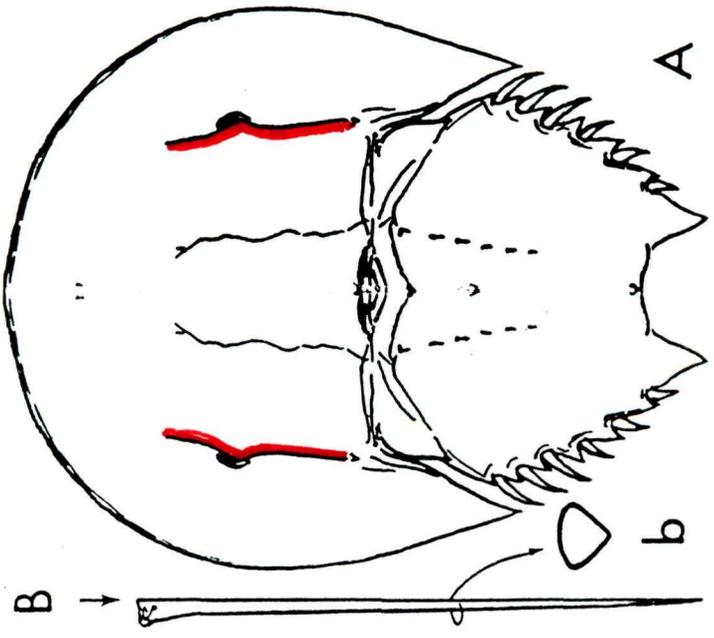
Character 7 (*longitudinal opisthosomal ridges*). – Longitudinal ridges which link the transverse ridge nodes (forming quadriradiate nodes) occur in *Paleolimulus*, *Xaniopyramis* and *Rolfeia*. They are also useful as indicators of full fusion of the opisthosomal tergites. Their presence in *Bellinuroopsis* is not confirmed from study of the single holotype specimen. Siveter & Selden (1987) reported that ‘probable homologues of the longitudinal pleural ridges and associated nodes’ were present in *Paleolimulus*; our re-examination of the holotype and new, additional material has shown the presence of well defined longitudinal ridges in this genus.

8

Character 8 (*pyramidal cheek node*). – Siveter & Selden (1987) cited the presence of a cheek node with an associated anteriorly running ridge in the Lower Carboniferous *Xaniopyramis* as a possible autapomorphy for the genus. Investigation of new specimens of *Paleolimulus* show that this character is also present in this form. The node appears to be absent in *Rolfeia*.

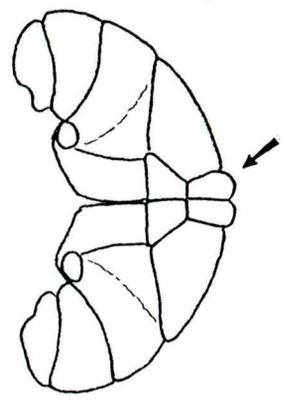
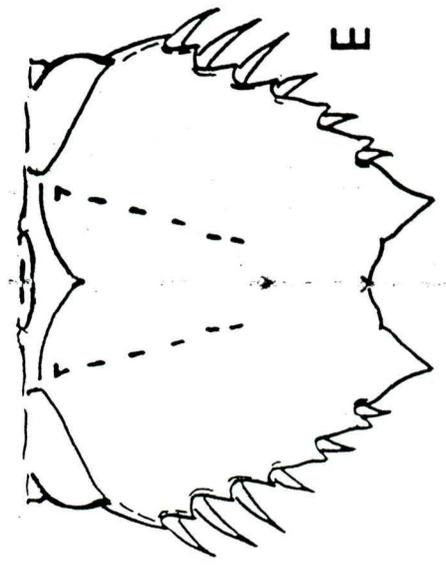
9

Character 9 (*course of ophthalmic ridges*). – Ophthalmic ridges are absent in *Paleomerus* and *Lemoneites* (0). In synziphosurines, the ophthalmic ridges bearing the compound eyes are bowed outwards laterally (convex, 1). In *Euproops* and *Liomesaspis* the ophthalmic ridges follow a concave course to the cardiac lobe (2); this state is presumed to be synapomorphic for these two taxa.



6

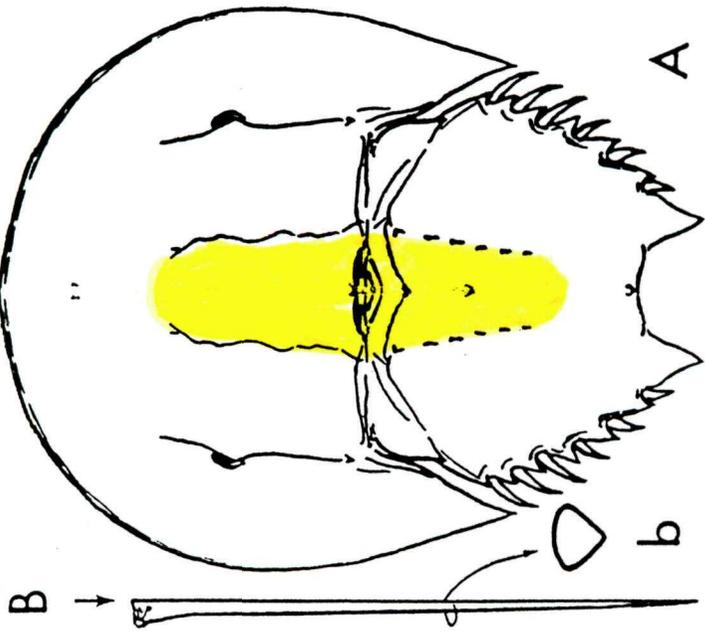
Limulus polyphemus



(Shuster, 1982 [modified])

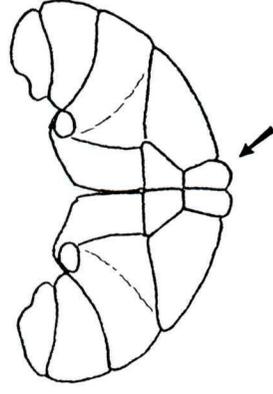
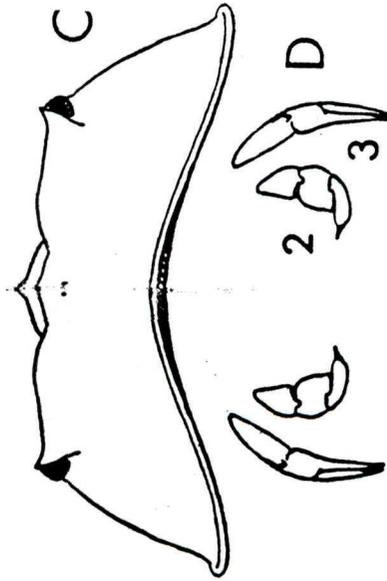
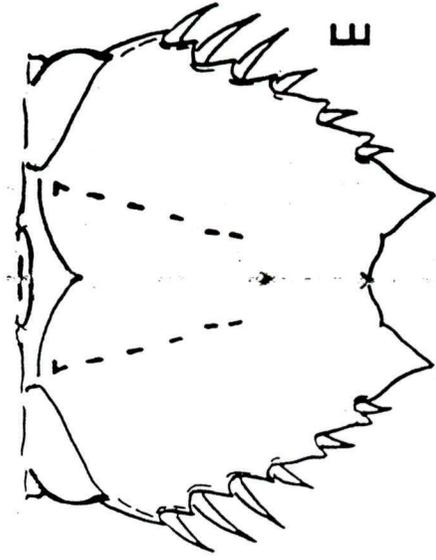
10

Character 10 (*cardiac lobe*). – A cardiac lobe is absent from *Paleomerus* (0) and cannot be confirmed in *Lemonites*. In all other sufficiently well preserved xiphosurans in this analysis a cardiac lobe is present (1).



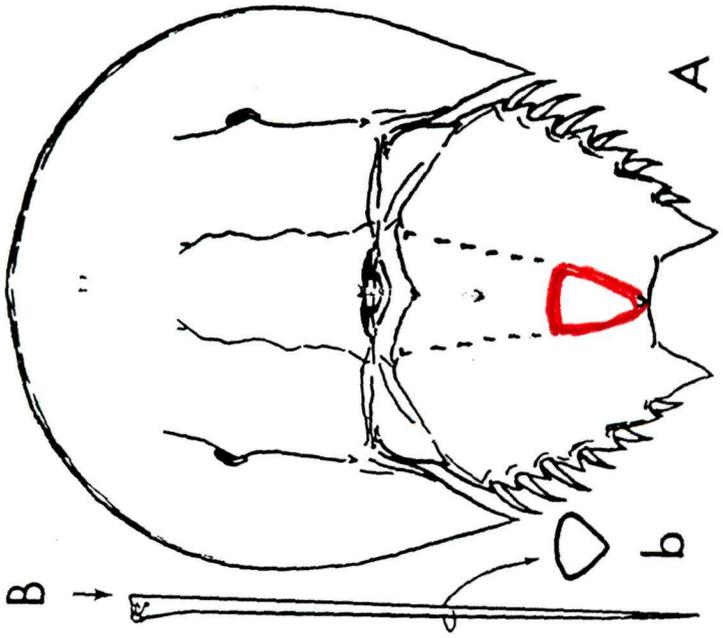
1φ

*Limulus
polyphemus*



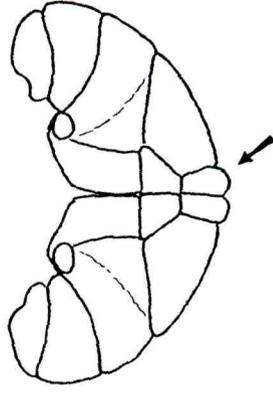
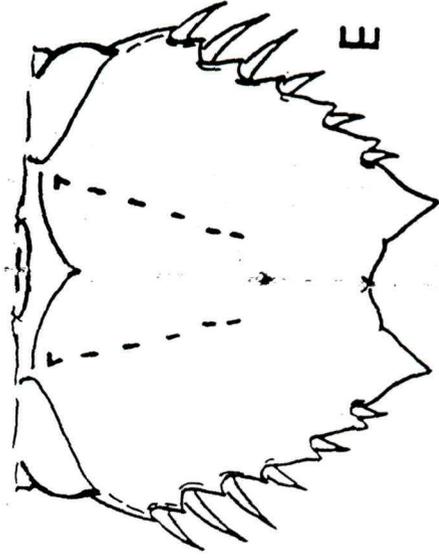
(Shuster, 1982 [modified])

Character 11 (posterior axial lobe). – The posterior three segments (XIII–XV) of the thoracetron of xiphosurids commonly lose their intersegmental divisions to form a distinct triangular or trapezoidal area, here called the posterior axial lobe (Fisher's (1981) O₇–O₉ tagma). In *Bellinurus*, *Euproops* and *Liomesaspis* the axial region of this lobe is triangular and tapers posteriorly. The corresponding region in *Valloisella*, *Paleolimulus* and *Limulus* is broadly trapezoidal in shape.



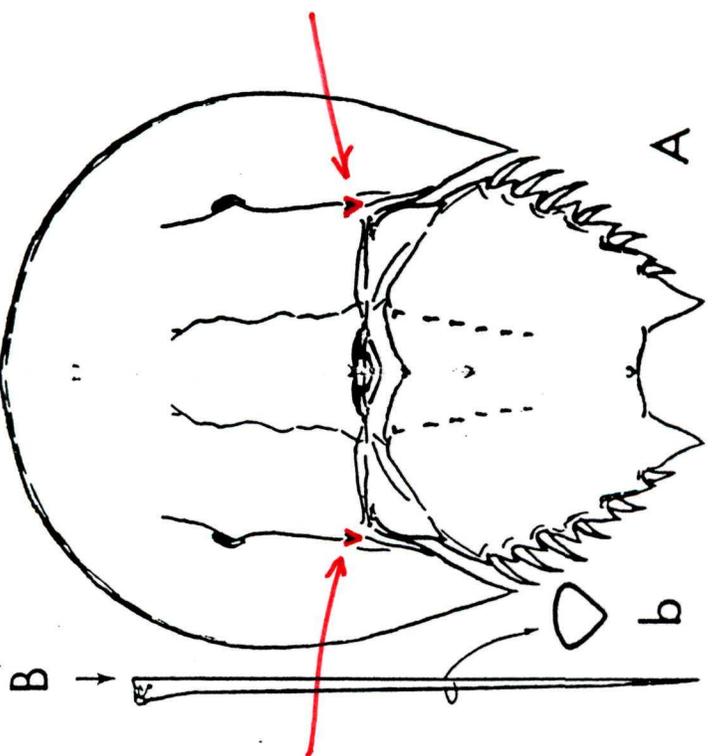
11

*Limulus
polyphemus*



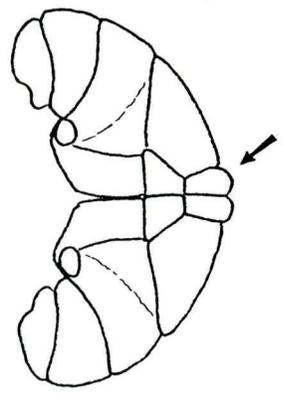
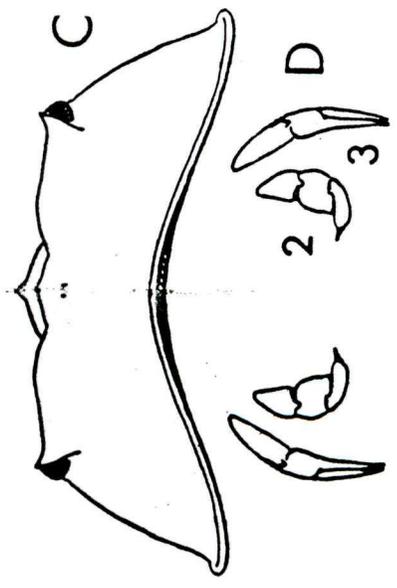
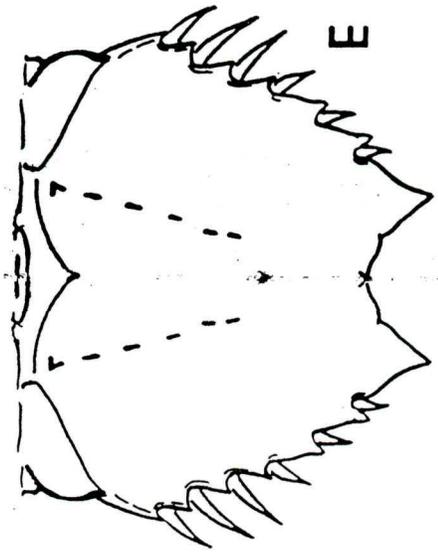
(Shuster, 1982 [modified])

Character 12 (*ophthalmic spines*). – Ophthalmic spines are posterior elongations of the ophthalmic ridges, and we consider their absence to be plesiomorphic, their presence a novelty. Ophthalmic spines occur in *Bellinurus*, *Euproops* and *Liomesaspis*, but they are not always observable (Anderson 1994), so they may yet be shown to occur in other xiphosurids. *Limulus* and *Paleolimulus* bear upwardly pointing thorns at the posterior ends of the ophthalmic ridges; we considered these not to be homologous with true ophthalmic spines.



12

Limulus polyphemus



(Shuster, 1982 [modified])

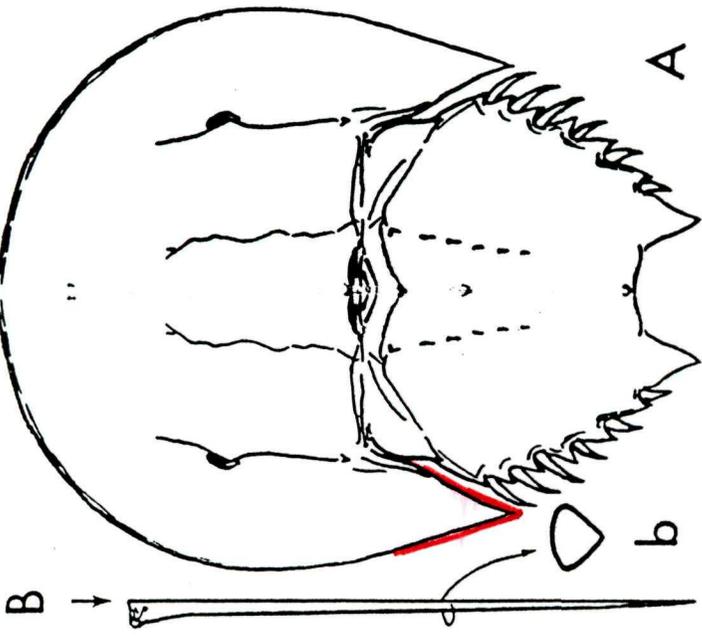
13

Character 13 (*posterior carapace margin*). – The plesiomorphic state (0) for the carapace is a straight posterior margin. Derived states are gently (1) and strongly (2) curved. Character 13 may be linked with character 14.

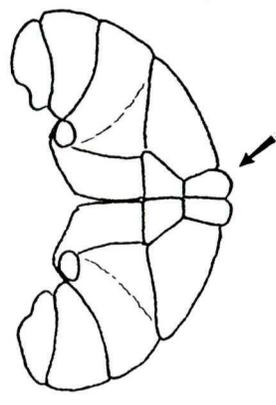
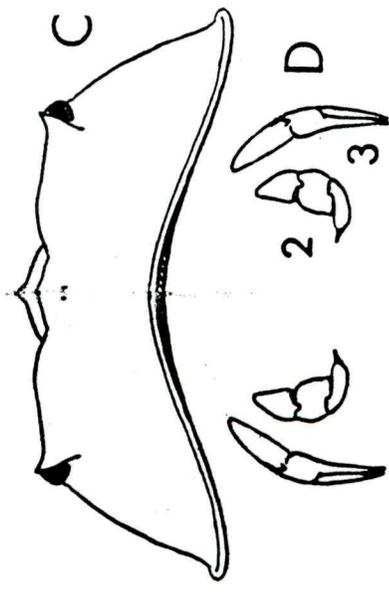
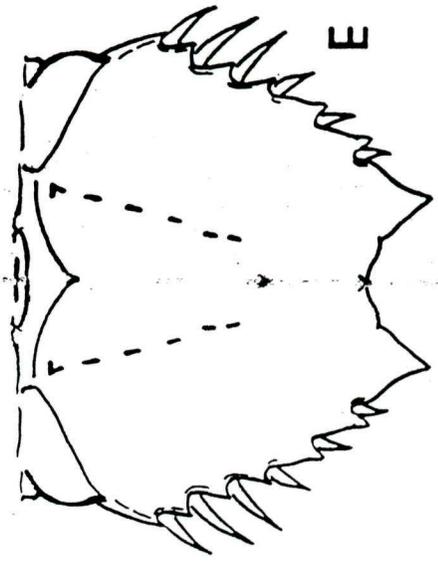
14

Character 14. – The carapace **genal angles** may be rounded (0), pointed (1) or modified into genal spines (2). Genal spines have a dorsal ridge which distinguishes them from pointed genal angles. Character 14 may be linked with character 13.

14



Limulus polyphemus



(Shuster, 1982 [modified])

15

Character 15 (*macrotergites*). – A hypertrophied second opisthosomal tergite (VIII) occurs in *Bunodes*, *Limuloides* and *Pasternakevia* (Eldredge 1974; Selden & Drygant 1987).

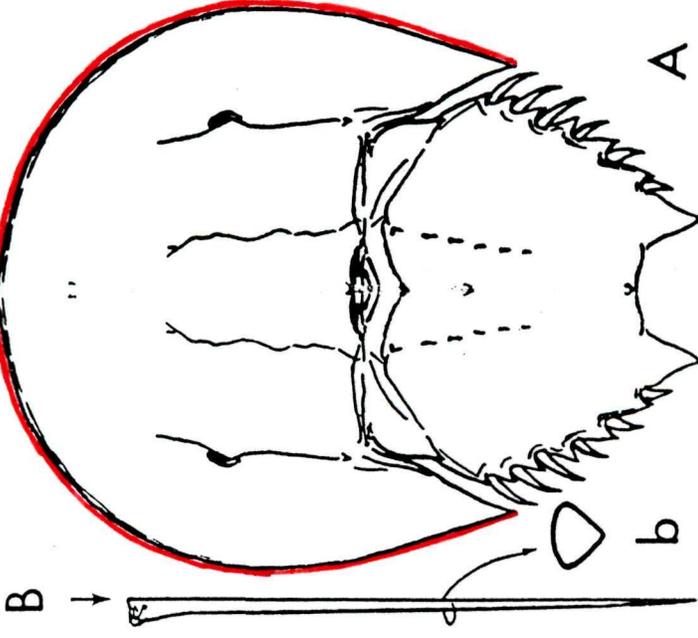
Character 16 (tergites XII–XIII). – *Cyamocephalus* Currie, 1927, has fused sixth and seventh opisthosomal tergites (Eldredge & Plotnick 1974). Størmer (1955), Eldredge (1974), Stürmer & Bergström (1981), and Selden & Siveter (1987) discussed possible fusion of the last mesosomal tergite (XIII and XIV) in *Bunodes* and *Limuloides*, but in all of the material we studied, these tergites appear not to be fused.

17

Character 17 (*metasomal epimera*). – Epimera occur on the metasomal tergites of *Pseudoniscus*, *Weinbergina*, *Cyamocephalus*, *Pasternakevia*, *Bunodes* and *Limuloides* and *Kasibelinurus* (1). (Note that these animals do not necessarily show a clear distinction between mesosoma and metasoma.) Since metasomal epimera are lacking in *Paleomerus* and *Lemoneites* (0), their presence appears as apomorphic within the scope of this analysis.

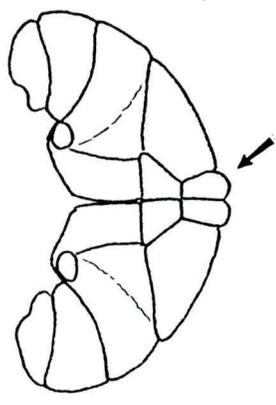
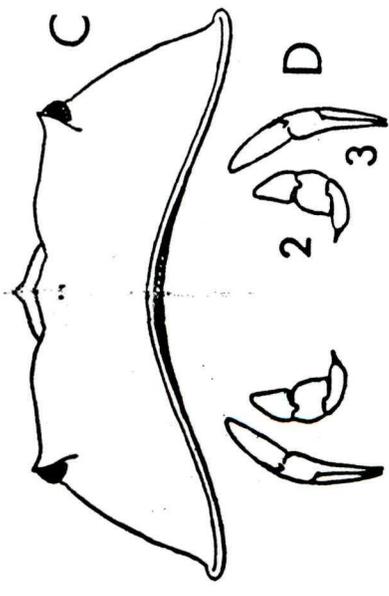
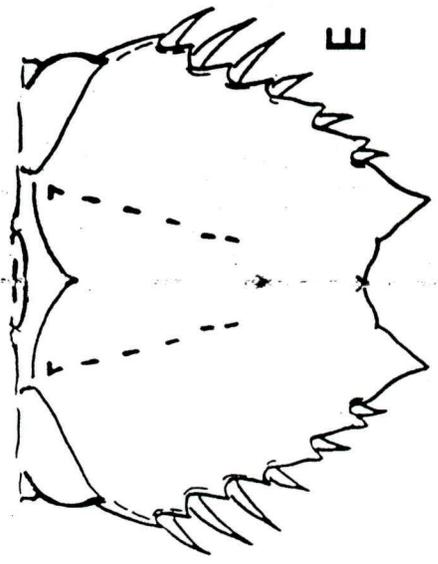
18

Character 18 (*carapace margin*). – The cuticular projections that produce a characteristic serrate anterior and anterolateral margin of the carapace of *Limuloides* are autapomorphic for this taxon. The plesiomorphic state is a smooth carapace rim.



*Limulus
polyphemus*

18



(Shuster, 1982 [modified])

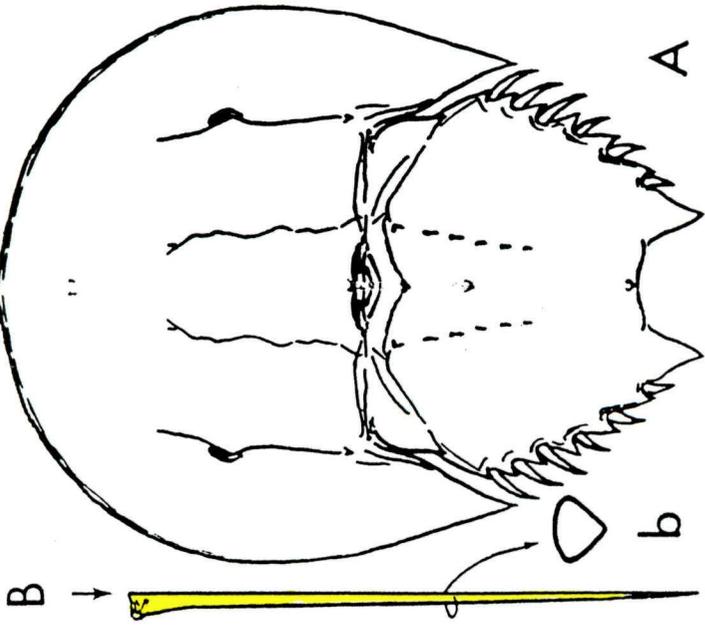
Character 19 (**precardiac lobe**). – In *Bunodes*, *Limuloides*, *Kasibelinurus* and *Pseudoniscus*, the cardiac lobe is divided by a transverse groove forming an H-shaped area. Pickett (1993), in describing *Kasibelinurus*, had access to relatively uncrushed material and named the anterior portion of this H-shaped area the precardiac lobe (1). In *Legrandella* the cardiac lobe is broadly triangular in form and tapers rapidly anteriorly; there is no evidence of a precardiac lobe in this form. The shape of the cardiac lobe was reported to be unknown in *Weinbergina*, however Stürmer & Bergström (1981) reconstructed the cardiac lobe of *Weinbergina* as resembling that of *Legrandella*. The illustration of *Pasternakevia* (Selden & Drygant, 1987, Fig 3a) shows a faint H-shaped medial region on the carapace. Re-examination of the holotype (BMNH I 16251) and an additional specimen (BMNH I 25) of *Cyamocephalus* suggests that it, too, has a precardiac lobe. Xiphosurids possess a much smaller node, bearing ocelli, anterior to the apex of the cardiac lobe (2). *Paleomerus* lacks a cardiac, and hence a precardiac, lobe (0).

20

Character 20 (*opisthosomal axis*). – *Paleomerus* and *Lemoneites* have no discernible axial region, which is thus coded as 0 in this analysis. All other taxa show a vaulted median axis, but the ratio of the width of the axial to the lateral regions varies. *Bunodes*, *Limuloides* and *Paster-nakevia* all have wide opisthosomal axes, with narrow lateral areas (1). *Pseudoniscus*, *Cyamocephalus*, *Kasibelinurus* and all xiphosurids have a narrow axis relative to the lateral areas (2). The axis of *Legrandella* is about half the total width of the opisthosoma, which is here coded as wide.

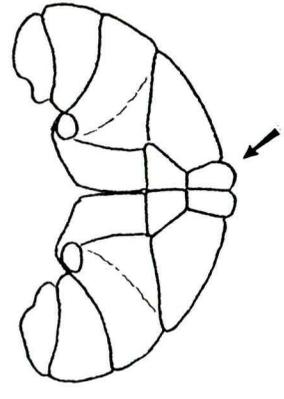
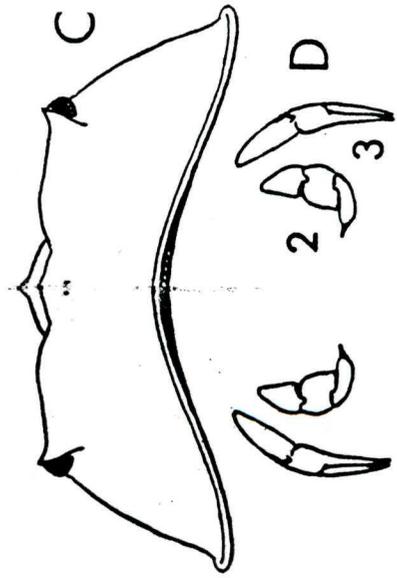
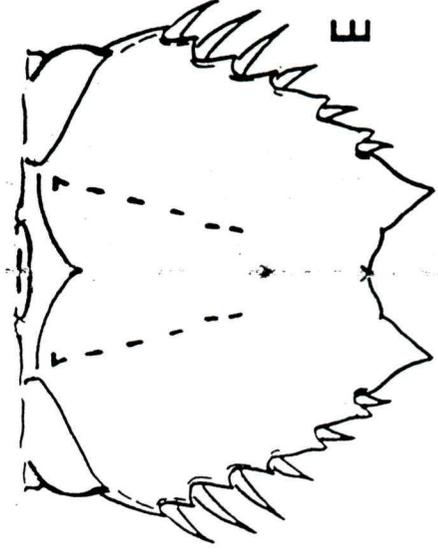
21

Character 21 (tail spine). – A short, basally wide, rapidly tapering, tail spine is considered the plesiomorphic condition because it occurs in *Paleomerus* and all synziphosurines. In xiphosurids, the tail spine is longer and thinner and can be equal to, or slightly longer than, the combined length of the prosoma and opisthosoma.



21

*Limulus
polyphemus*



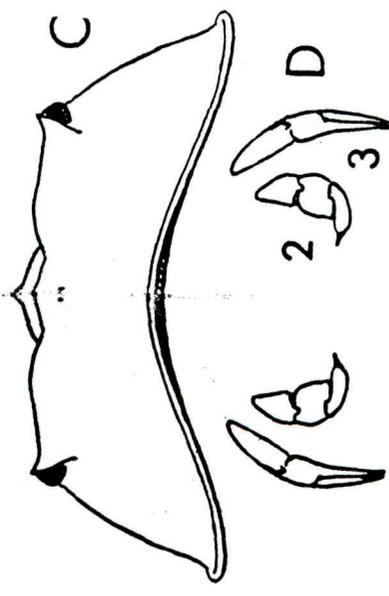
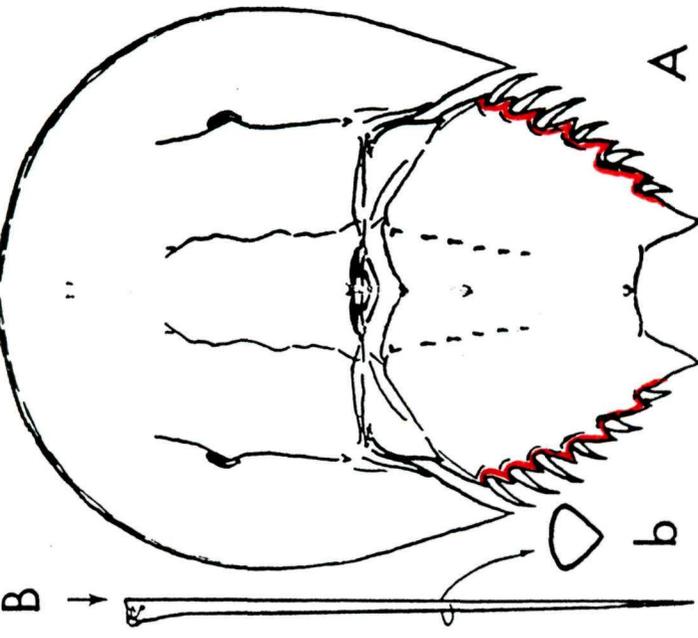
(Shuster, 1982 [modified])

22

Character 22 (*loss of opisthosomal segments*). – *Lemoneites*, *Legrandella* and *Weinbergina* show evidence of eleven segments in the opisthosoma (0). Ten segments are seen in *Pseudoniscus*, *Cyamocephalus*, *Bunodes*, *Limuloides* and *Pasternakevia* (1). Further loss of a segment resulted in a segment count of nine in *Kasibelinurus* and all xiphosurids (2). Since we are uncertain exactly which somites are expressed as tergites, a simple count seems the easiest way of scoring this character. The counting of opisthosomal segments in *Limulina* is a little difficult because of the trend towards loss of transverse ridges demarcating separate segments on the lateral fields of the opisthosoma as well as on the axis. Nevertheless, it is possible to count opisthosomal segments by locating the paired apodemes on either side of the axial ridge.

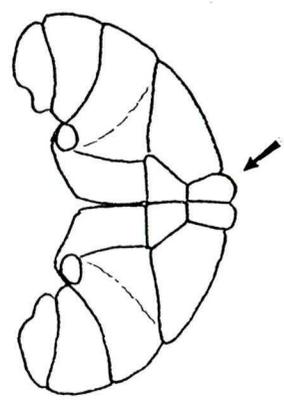
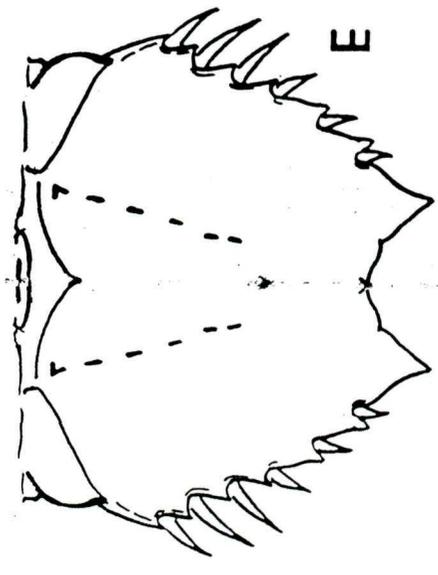
23

Character 23 (*opisthosomal flange*). – Fusion of the bases of the fixed lateral spines to form an opisthosomal flange is a synapomorphy of *Euproops* and *Liomesaspis*.



*Limulus
polyphemus*

23



Character 24 (*tergite VIII*). – The plesiomorphic state for this character is a freely articulating tergite (0). Incorporation of the opercular tergite (VIII) into the thoracetron is a synapomorphy of Bellinuridae and Euproopidae (1). In *Bellinuroopsis* and *Rolfeia* the opercular segment articulates freely with the thoracetron (0). In *Paleolimulus*, *Valloisella*, *Limulus* and *Xaniopyramis*, the opercular tergite has lost the axial part of the tergite and forms the so-called free lobes, which are fused to the thoracetron (2).

25

Character 25 (*anterior medial carapace projection*). – Both *Pseudoniscus* and *Legrandella* possess a small median projection on the anterior edge of the carapace. This structure is not encountered in any other xiphosuran taxon and is therefore considered to be derived in these taxa.

26

Character 26 (*axial carina*). – The plesiomorphic condition for the opisthosomal axis is a series of rounded nodes, one per segment (0). In *Valloisella* and *Limulus*, the axial lobes of individual tergites are barely distinguishable, and a continuous, carinate ridge runs the full length of the opisthosoma (1).
