

which strand is being copied, so that a rejection of the null hypothesis is expected, yielding an asymmetry in $[A]=[T]$ or $[C]=[G]$ equifrequencies. This asymmetry is expected to switch polarity at the origin and terminus of replication of the chromosome and does switch polarity at the origin and terminus of replication in *Escherichia coli*, *Bacillus subtilis*, and *Haemophilus influenzae*, splitting the circular chromosome into two chirochores (4).

In *Mycoplasma genitalium*, the new method clearly confirms the suggested origin of replication (Fig. 1). The asymmetry in base com-

position, A-T, is $-2.0\% \pm 0.4$ before the origin of replication and $+4.5\% \pm 0.4$ thereafter; and the asymmetry in base composition, C-G, is $+4.0\% \pm 0.7$ before the origin of replication and $-4.5\% \pm 0.6$ thereafter. The switch of the polarity of base composition asymmetries is then significant. This method for the detection of replication origins is useful for the analysis of a new genome when the consensus pattern approach fails.

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6 November 1995; accepted 27 February 1996

Classification of the Arthropod *Fuxianhuia*

Jun-yuan Chen *et al.* (1) provided an invaluable description of *Fuxianhuia*, a problematic arthropod from the celebrated Chinese Chengjiang fauna (2). Pointing to the apparently rudimentary nature of the procephalon and the unspecialized morphology of the trunk appendages, they classified *Fuxianhuia* as a basal euarthropod, a primitive and generalized representative of the phylum. They did not, however, test their assertion with the necessary cladistic analysis. Such an analysis reveals that *Fuxianhuia* is an arachnomorph (3–5), specifically grouping with the chelicerates (arachnids and merostomes). This result establishes *Fuxianhuia* as the earliest known chelicerate by as much as 60 million years.

I coded the new information from Chen *et al.* into a growing database that has been found effective for investigating higher order relationships among Cambrian and Recent arthropods (3, 4). A reduced set of taxa were analyzed using the program PAUP 3.1.1 (Smithsonian Institution, Washington, DC), which produced gross topology consistent with that derived from previous analyses (3, 6). *Fuxianhuia* consistently grouped with the chelicerates (despite the absence of chelicerae and minimal cephalization) in the larger clade of arachnomorphs. To investigate this relationship more fully, a further run was made, reinstating the entire arachnomorph clade (3) and incorporating data from the Silurian eurypterid *Baltoeurypterus* (7), the Devonian xiphosuran *Weinbergina* (8), and the problematic *Cheloniellon* (9, 10) (Fig. 1). *Fuxianhuia* consistently fell within the chelicerates, with *Cheloniellon* and *Aglaspis* basal to them. The arrangement of several arachnomorphs was modified over some previous analyses (3), demonstrating the potentially pivotal role of fossils exemplifying new character state combinations (11).

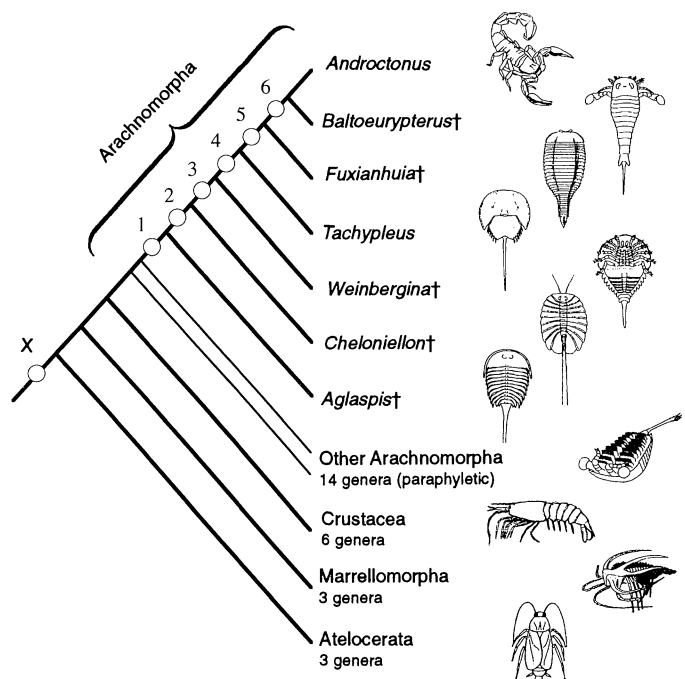
As noted by Chen *et al.* (1), *Fuxianhuia*

displays a number of characters typical of more basal arthropods. However, caution is required when constructing a model solely on the purportedly directional evolution of small numbers of characters (12). The presence of numerous trunk somites bearing relatively undifferentiated appendages is traditionally considered a plesiomorphic feature, but recent work on homeobox genes indicates that this may be an unwarranted assumption (13). Multiarticulate endopods are often regarded as primitive but are also known from derived (3, 4) groups of atelocerates (14), crustaceans (15), and other

arachnomorphs (16). The significance of diplosegmentation is as yet unclear (17, 18). Thus, these characters do not oppose a chelicerate affinity.

Fuxianhuia also exhibits several features, however, that make it unique among chelicerates. Given the early plasticity of arthropod bodyplans (3, 19, 20), these differences may be expected, but their occurrence in a taxon in this location is worthy of comment. The anteriormost appendages are multiarticulate antennae rather than chelicerae. The absence of chelicerae was used to exclude the aglaspids from the chelicerates *sensu stricto* (21), but the two groups show many derived similarities (Fig. 1) and are probably closely related (22). Similar considerations apply to *Fuxianhuia*. Al-

Fig. 1. Simplified cladogram of Recent and fossil euarthropod taxa (strict consensus). Detailed topology illustrated for chelicerates and allied genera. †, Fossil genus. X, Location of *Fuxianhuia* proposed by Chen *et al.* (1). Shared, derived characters are (DELTRAN optimization): (i) Dorsal cuticle trilobed. Cuticle strongly tuberculate. Fourteen somites in cephalon and trunk. Exopod of second appendage absent. Inner rami of trunk appendages composed of four podomeres and lacking spines. (ii) Six appendages in the cephalon. Labrum detached. Gnathobases absent from trunk appendages. (iii) First appendages chelicerae. Cephalic shield with marginal ecdysial sutures. Cardiac lobe present. Trunk tergites with straight posterior margin in dorsal aspect. (iv) Cephalic shield with marginal rim. Postcephalic articulation without overlapping pleurae. Two median eyes. Outer rami of trunk appendages lacking fine filaments (rounded and lamellate). Cuticle smooth. (v) Trunk tagmatized (mesosoma and metasoma in eurypterids and arachnids). (vi) Dorsal cuticle not trilobed. Inner and outer rami of trunk appendages absent. Eighteen somites in the cephalon and trunk.



though its second appendages were not coded as chelicerae, they are uniramous, subchelate, and reminiscent of the range of morphology displayed by this appendage (23). Moreover, some schemes equate the cheliceral somite with the antennal somite of crustaceans [for example, (24)], so that chelicerae derive from the second somite after the acron. Thus, the possession of a pair of antennae, as in *Fuxianhuia* (9), may represent the primitive chelicerate condition.

The cephalon in *Fuxianhuia* apparently incorporates just two pairs of appendages rather than six or seven as in other chelicerates (8). The number of cephalic limbs has proved to be one of the most labile characters in previous cladistic analyses of the arthropods (6). Its low consistency index is largely attributable to the inclusion of Cambrian forms. The implications of this finding for possible post-Cambrian developmental entrenchment and canalization have already been discussed (3, 20). The cephalon has proved difficult to define for a number of taxa [for example, euthycarcinoids (25) and *Sidneyia* (17, 26)], and it may be an oversimplification to regard *Fuxianhuia* as possessing only two pairs of limbs in the "head" (27).

Statements that other Cambrian arthropods should be drawn into the chelicerate fold seem based on scant evidence. The Lower Cambrian *Eolimulus* is known only from carapaces and cannot be assigned to the group with confidence (28). *Sanctacaris* from the Middle Cambrian Mount Stephen Formation has chelicerate-like tagmosis (29) but has consistently failed to resolve with the group cladistically (3, 4, 6). The earliest, undisputed chelicerates therefore date from the Arenigian (22).

Unweighted cladistic analysis places *Fuxianhuia* within the arachnomorphs (3). Only by making premature assumptions about the sequence in which characters are acquired (for example, recruitment of appendages into the cephalon) or by attributing overriding weight to these features can *Fuxianhuia* be interpreted as basal to the other euarthropods (1), a status more probably afforded to the tardigrades (4, 30). Rooting a phylogeny with a relatively apomorphic taxon could seriously mislead our understanding of arthropod evolution.

Fuxianhuia therefore joins the growing ranks of fossils that, despite their outwardly perplexing array of features, fit decisively into a small number of large and increasingly densely occupied clades (4).

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22 June 1995; accepted 13 October 1995; revised 12 March 1996

Response: We welcome Wills's test of our hypothesis (1) that *Fuxianhuia* is a basal euarthropod. However, his conclusion that *Fuxianhuia* is a chelicerate conflicts with better quality data than those marshalled in its support. The exercise he has undertaken serves to illustrate some analytical problems

that may be producing spurious results in parsimony analyses of arthropod phylogeny.

The cladogram derived by Wills is consistent with the traditional interpretation of chelicerate tagmosis: No more than 19 somites are divided into a prosoma and opisthosoma. The former bears six pairs of appendages, or the appendage of a seventh, opisthosomally derived somite may be incorporated into the prosoma (2). Fossil arachnomorphs reveal that the precursors of chelicerates had biramous head and trunk appendages (3), but crown group chelicerates provide clear evidence that one ramus was suppressed on each tagma. Evidence for a relict exopod on the prosomal walking legs of chelicerates may be provided (4) by the flabellum on the sixth leg of xiphosurids or by transient rudiments on the embryonic prosomal limbs (5). On other prosomal appendages of xiphosurids and all other chelicerates, there is meager evidence for an exopod, leading to the general conclusion that this ramus was lost in the course of chelicerate evolution. Where present, opisthosomal appendages of chelicerates have been interpreted as predominantly exopodal. A relict endopod is represented by the small segmented median branch on the platelike appendages of xiphosurids (4). Wills's interpretation of *Fuxianhuia* within Chelicerata forces the removal of prosomal-opisthosomal tagmosis, despite the fact that these body regions may be identified with precision in all other chelicerates, living or fossil. Furthermore, his hypothesis forces the reevolution of exopods on all prosomal limbs except the chelicerae, as well as the reevolution of opisthosomal endopods. Given the extreme modification of the vestigial rami (when present at all) in all other chelicerates, it is most implausible that reevolved prosomal exopods and opisthosomal endopods would be completely undifferentiated from those on the other tagma. Wills states that antennae in *Fuxianhuia* provide support for their existence in chelicerate ancestors, a hypothesis already supported by Palaeozoic fossils (6). Yet if *Fuxianhuia* is an ingroup chelicerate as he argues, the presence of antennae must be interpreted as reevolving after a prior loss at node 3 of his cladogram.

We will not argue that structures lost in phylogenesis can never be reacquired—an atavistic scenario can always be evoked. But it must be asked if such transformations can be defended in the name of parsimony. The low phylogenetic cost (as measured by number of steps) that Wills affords to such major transformations as the reevolution of lost limb rami may be an artifact of his method of coding inapplicable characters. The database used in his prior studies (7) often does not distinguish between inapplicable characters, such as prosomal exopods and opis-

thosomal endopods (and exopods in arachnids), and missing data, both being scored identically. This may have the effect of optimizing a nodal state based on other characters that conflict with the observed absence (or inapplicability) of a state (8). By allowing several appendage characters for the scorpion and eurypterid to be spuriously optimized as missing data, real differences from *Fuxianhuia* are not being acknowledged in tree construction.

We observe that many of the putative synapomorphies used by Wills to defend his interpretation (his nodes 1 through 5) are characters that are absent in *Fuxianhuia* (9); his topology forces their interpretation as reversals. Compelling chelicerate synapomorphies, such as genital modifications of the eighth (first opisthosomal) somite, are lacking in *Fuxianhuia*.

Wills dismisses the value of diplosegmentation as too ambiguous for comment and endorses a phylogeny in which the obliteration of basic chelicerate tagmosis is associated with the evolution of diplosegments de novo. That such a profound structural innovation would occur within the crown group of Chelicerata opposes notions that arthropod morphology was canalized after the Cambrian explosion (10). Wills alludes to this canalization being a post-Cambrian phenomenon, an assertion contradicted by his cladogram. Were *Fuxianhuia* a chelicerate as he suggests, its eurypterid-arachnid sister group must be as old (11), and xiphosurids even older. Again, we concede that this is a possibility. This scenario contradicts the known evidence concerning the age of these groups as well as widely held views on chelicerate evolution.

We conclude that the phylogenetic position of *Fuxianhuia* is near the basal node of the euarthropods. A more precise positioning awaits the results of our continued study of the Chengjiang material, promising to yield new data for use in a stringent phylogenetic analysis. Our original comparison with euthycarcinoids has already been taken up in an unorthodox study (12) that, in this respect, may well be closer to the point than the view held by Wills. Wills and his co-workers regard euthycarcinoids as ingroup

taxa for a curiously resolved Hexapoda (13). This position conflicts with our data, which indicate a more basal position (14), and, as significantly, it forces robust apomorphies of hexapods to be radically reversed in euthycarcinoids (for example, detailed homologies of the tripartite thorax, cerci, and caudal filament). A close affinity between *Fuxianhuia* and euthycarcinoids is irreconcilable with their cladogram (13), resulting from a study rooted in the analytical problems (9) repeated in Wills's arguments.

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9. We have examined these putative synapomorphies and below use the character and state numbering as by Wills and his co-workers (7). Massive homoplasy is displayed by many of the listed characters, with frequent use of reversals as synapomorphies. We endorse computerized parsimony methods but stress that in any phylogenetic analysis, strict screening of detailed similarities must be made to increase the likelihood that the characters used are homologous in both ingroup and outgroup taxa [L. Ramsköld, *Lethaia* **25**, 443 (1992)], and we emphasize the need for more than a mechanical computer treatment of data without considering the implications of the resultant trees. • Node 1: None of 3:1, 37:0, or the combined 40:1 and 42:0 are present in *Fuxianhuia*. Character 25:0 shows rampant homoplasy, being present also in Annelida, Lobopoda, Atelocerata, and in several Crustacea and Arachnomorpha. A trilobed dorsal cuticle, 10:1, is almost ubiquitously present also in "Other Arachnomorpha." • Node 2: Neither 21:6 or 16:1 are present in *Fuxianhuia*. Character 43:0 shows rampant homoplasy (distribution as 25:0 above). • Node 3: To code the subchela appendages in *Fuxianhuia* as chelicerae (23:2) is to assume a priori that *Fuxianhuia* is a chelicerate. The lack of such derived states as a movable finger and two or three podomeres indicates a superficial resemblance. There is no evidence of marginal ecdysial sutures (2:1), and *Fuxianhuia* lacks a cardiac lobe (a new character). The straight posterior margin of trunk tergites (a new character) is a questionable synapomorphy at node 3, being present below node 2 in *Aglaspis*, other Arachnomorpha, and Atelocerata. To interpret it as synapomorphic at node 2, it must first be reversed there (because of its absence in *Cheloniellon*), only to be re-reversed at node 3. This extensive homoplasy indicates either a plesiomorphic character or its multiple development as a functional optimum. • Node 4: Neither 9:0 or 20:1 are present in *Fuxianhuia*. Character 12:1 is mis-coded for *Fuxianhuia* (no rim is present, the shield surface slopes evenly before being flexed under). Even so, the character is coded present in numerous taxa below node 4, such as in *Aglaspis* and in other Arachnomorpha, and shows massive homoplasy with several reversals and re-reversals. Character 45:0 occurs also in numerous arachnomorphs and crustaceans. The presence of exopod filaments in *Weinbergina* is used to interpret their absence as synapomorphic at the next higher node, but for a character state with a near random distribution, we consider this to carry little weight. Character 3:0 (smooth cuticle) is coded so for all Atelocerata, Marrellomorpha, Crustacea, and most Arachnomorpha and thus is a poor synapomorphy for node 4. • Node 5 is defined by a single character that is similar to 39:1, trunk abdominalized. This was coded as present in numerous arachnomorphs and crustaceans, and in some atelocerates, showing rampant homoplasy. Trunk tagmosis can be considered a synapomorphy for *Fuxianhuia* plus eurypterids and arachnids only if the tagmata in *Fuxianhuia* were homologous with the mesosoma and metasoma, an unwarranted assertion given their very different numbers of somites. The trunk tagmata in *Fuxianhuia* shows closer similarity with euthycarcinoids than with eurypterids and arachnids.
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21 July 1995; accepted 13 October 1995