istry, K. S. Birdi, Ed. (CRC Press Inc., Boca Raton, FL, 1997), chap. 9.
18. ———, G. McHale, M. I. Newton, *Langmuir* **18**, 2636 (2002).
19. Materials and methods are available as supporting material on *Science* Online.
20. R. N. Wenzel, *Ind. Eng. Chem*. **28**, 988 (1936).
21. A. B. D. Cassie, S. Baxter, *Trans. Faraday Soc*. **3**, 16 (1944).
22. R. A. Veselovsky, V. N. Kestelman, *Adhesion of Polymers* (McGraw-Hill, New York, 2002), chap. 2.
23. L. H. Sperling, *Polymeric Multicomponent Materials* (Wiley-Interscience, New York, 1997), chap. 6.
24. J. Varga, in *Polypropylene Structure, Blends and Composites*, J. Karger-Kocsis, Ed. (Chapman and Hall, London, 1995), vol. 1, chap. 3.
25. We thank A. Altay, M. A. Gülgün of Sabancı University, and A. Alkan of Brisa for their help with SEM measurements. A.L.D. acknowledges the financial support of the Turkish Academy of Sciences in the framework of the Young Scientist Award Program (grant EA/TÜBA-GEBİP/2001-1-1) and the Koç University Fiat Fund.

Supporting Online Material
www.sciencemag.org/cgi/content/full/299/5611/1377/DC1
Materials and Methods
Figs. S1 and S2
References

11 September 2002; accepted 22 January 2003

A New Species of Yunnanozoan with Implications for Deuterostome Evolution

Degan Shu,[1]* Simon Conway Morris,[2] Z. F. Zhang,[1] J. N. Liu,[1] Jian Han,[1] Ling Chen,[1] X. L. Zhang,[1] K. Yasui,[3] Yong Li[4]

Yunnanozoans are a distinctive clade of Lower Cambrian metazoans. Although widely accepted as deuterostomes, their exact placement within this superphylum is controversial. Here we describe a new species of *Haikouella* (*H. jianshanensis*) from the Chengjiang Lagerstätte (Yunnan, China) with exceptional preservation of a number of features. These include external gills, which suggest that the origin of the pharyngeal clefts was independent of the gills. The diagnostic branchial arches of chordates may, therefore, be composite structures. No evidence was found for the chordate-like structures that have been described in other yunnanozoans. We propose that yunnanozoans are stem-group deuterostomes, allied to the vetulicolians.

Yunnanozoans are a distinctive group of metazoans, occurring only in the Chengjiang fossil-Lagerstätte located near Kunming, in southwestern China (*1*, *2*). They are known from the type species *Yunnanozoon lividum* (*3*), *Haikouella lanceolata* (*4*), and *H. jianshanensis*, a new species described here. The body plan of yunnanozoans is defined by a relatively slender anterior bearing metamerically arranged gills and an expanded posterior section that dorsally bears a prominent segmented unit with a cuticular covering. Yunnanozoans have been described as deuterostomes but, alternatively, as some sort of stem group (*5*), hemichordates (*6*), cephalochordates (*7*), or craniates (*4*, *8*). These divergences of opinion have arisen on account of the distinctiveness of the yunnanozoan body plan and because postmortem crushing makes crucial details at the anterior difficult to discern (*3*, *4*, *6*, *8*). Here, on the basis of more than 1420 specimens of *Haikouella jianshanensis* (520 are well preserved), which predate the other two yunnanozoan species (*3*, *4*, *7*, *8*), we report a number of previously unidentified features.

The anatomy of *H. jianshanensis* differs from that of the other two known species in the size of the gills. Unlike other yunnanozoans (*3*, *4*, *5–8*), in which the dorsal segmented unit is well preserved, this region is only occasionally preserved (Fig. 1, A and B). Possibly, in *H. jianshanensis*, the cuticle was thinner, thereby decreasing the preservation potential of the posterior region. The anterior of the main body consists of two discrete units, dorsal and ventral, each in the approximate form of a compressed half cylinder (Fig. 1, G to J). These units are separated by a median zone (Fig. 1, A to F and K). The ventral unit is relatively robust and broadly canoelike, with a straight upper margin and recurved lower side. The dorsal unit has a more arcuate outline and is generally less well preserved, especially toward its posterior.

The cuticle of the median zone is thin and normally decomposed (Fig. 1, A to F, and Fig. 2, A to F), but occasionally, it survives as a smooth membrane (Fig. 2, G and H). The median zone generally decreases in height toward the posterior, which brings the dorsal and ventral units into juxtaposition; however, in different specimens, the overall width of this region is variable. The dorsal and ventral units are rarely touching (Fig. 1, G and H), suggesting that the entire anterior region could expand and contract in height. The expansion would occur by an accommodation along the median zone and about an axis of rotation near the posterior of the units.

A skirtlike structure runs around the entire anterior (Fig. 3, A to J) and is deflected outward and, to some extent, ventrally (*9*). The skirt consists of an upper barlike unit (Fig. 3, A and B), whereas the more ventral area is thinner but bears prominent dark lineations (Fig. 3, A, B, and G to J). The skirt is attached to the anterior ends of the ventral unit (on its mid-area), and the upper margin runs around the front end of the dorsal unit to which it may have been joined (Fig. 3, A and B). The lower part of the skirt hangs free (Fig. 3, G to J). In this configuration, the skirt defines a space between itself and the rest of the anterior body (Fig. 3, A, B, and E to H).

As in *H. lanceolata* (*4*), the gills of *H. jianshanensis* consist of six bilaterally symmetrical pairs, with each gill being inclined forward from its ventral insertion. In *H. jianshanensis*, the gills were robust structures, but the cuticle of the individual triangular leaves was thin enough for effective respiration (Fig. 2, C and D). At the anterior, they have an approximately sigmoidal configuration, but at the posterior, they tend to be more elongate. The gills were attached to the ventral unit, just dorsal to circular structures that may represent the proximal part of the gill or, alternatively, pharyngeal openings (Fig. 1, A to F; Fig. 2, A to F; and Fig. 3, K to N). Observations (*4*) on *H. lanceolata* were used to argue that the dorsal end of each gill was free and unattached, and in dorsoventrally compressed fossils of *H. jianshanensis*, the gills also bow outward; however, because of the angle at which such material was buried, it is not possible to determine the nature of the dorsal termination (Fig. 1, I and J, and Fig. 3, I and J). Evidence from laterally preserved specimens of *H. jianshanensis* for a dorsal attachment of the gills includes a consistent alignment with respect to the dorsal unit, and in specimens with an expanded median zone, the more widely separated dorsal and ventral units show straighter gills, especially in the anterior region (Fig. 1, A to F; Fig. 2, A to D; and Fig. 3, K to N). Each gill has a broad axis with transverse markings

---

[1]Early Life Institute and Department of Geology, Northwest University, Xi'an 710069, China, and School of Earth Sciences and Resources, China University of Geosciences, Beijing 100083, China. [2]Department of Earth Sciences, University of Cambridge, Downing Street, Cambridge CB2 3EQ, UK. [3]Institute of Molecular Embryology and Genetics, Division of Development and Biohistory, Kumamoto University, 2-2-1 Honjo, Kumamoto 860-0811, Japan. [4]College of Earth Science and Land Resources, Chang'an University, Xi'an 710054, China.

*To whom correspondence should be addressed. E-mail: elidgshu@nwu.edu.cn and dgshu@sein.sxgb.com.cn

and is bipectinate, with flattened triangular leaflike structures arising on either side (Fig. 1, E to J; Fig. 2, A to H; and Fig. 3, C to J). In laterally preserved specimens, the gills occupy the highest and lowest films of the fossil (*10*), with the rest of the body situated at intervening levels (Fig. 2, G and H). We interpret this configuration as indicating that the gills were external.

The mouth was housed at the back of the recess that is encompassed by the anterior skirt. The mouth is associated with a recurved (in lateral view) or semicircular (in dorsoventral view) dark area (Fig. 3, C to F). This is probably a cuticular bar. The anterior gut was probably relatively voluminous, but in the posterior, it extends as a narrow intestine. This latter region often has a scalloped and

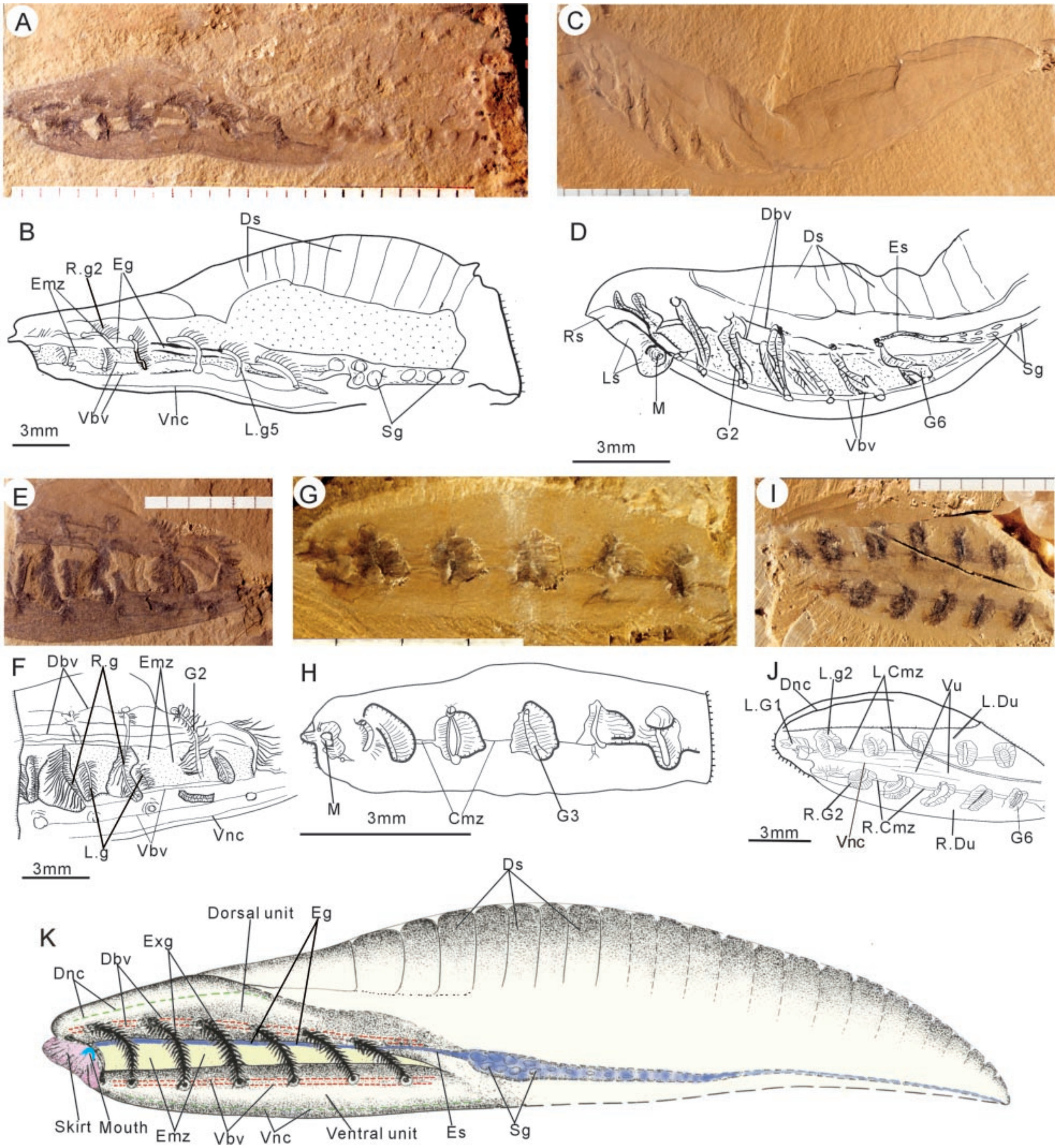

Fig. 1. Examples of *Haikouella* and a reconstruction of *H. jianshanensis*. (**A**, **B**, and **E** to **J**) *H. jianshanensis*; (**C** and **D**) *H. lanceolata*. All are lateral views, except for (I) and (J). In (A)and (B), the dorsal posterior segments are faintly visible [specimen (226)]. The complete specimen with well-preserved dorsal segments (totaling 10) is shown in (C). A drawing of the anterior of (C) is shown in (D). The anterior with an expanded median zone [specimen (010)] is shown in (E) and (F), and the anterior with a closed median zone [specimen (358)] is shown in (G) and (H). An oblique view [specimen (238)] is given in (I) and (J). (**K**) A reconstruction of *H. jianshanensis*. Abbreviations are as follows: Cmz, closed median zone; Dbv, dorsal blood vessels; Dnc, ?dorsal nerve cord; Ds, dorsal segments; Du, dorsal unit; Eg, ?epipharyngeal structure; Emz, expanded median zone; Es, esophagus; Exg, external gills; G1 to G6, gill arch 1 to 6; L.Cmz, left closed median zone; L.Du, left dorsal unit; L.g1 to L.g6, left gill arch 1 to left gill arch 6; Ls, left skirt; M, mouth; R.Cmz, right closed median zone; R.Du, right dorsal unit; R.g1 to R.g6, right gill arch 1 to right gill arch 6; Rs, right skirt; S, skirt; Sb, bar of skirt; Sbsb, space between skirt and body; Sg, ?spiral gut; Tmmz, thin membrane covering median zone; Vbv, ventral blood vessels; Vnc, ?ventral nerve cord; and Vu, ventral unit. Scale intervals are in millimeters.

nodular appearance, suggesting a complex internal structure. Immediately above the median zone in the anterior section, a longitudinal tubelike structure is posteriorly connected to the intestine via an esophagus. The tube may be flattened (Fig. 1, A and B, and Fig. 3, K and L) or three-dimensional (Fig. 3, M and N). Its shape and location suggest that it may be some sort of epipharyngeal structure.

On the ventral unit, a prominent longitudinal strand running parallel to the gill bases on either side may represent a pair of ventral blood vessels (*11*) (Fig. 1, A to F, and Fig. 2, A and B). A dark line along the ventral margin could represent a ventral nerve cord (Fig. 1, A, B, E, and F; Fig. 2, E and F; and Fig. 3, M and N). On the dorsal unit, there is a similar set of dark narrow lines, usually connected with the upper ends of gill arches. They may represent a pair of dorsal blood vessels (Fig. 1, E and F, and Fig. 2, A and B). A dark line, occasionally visible in both oblique (Fig. 1, I and J) and lateral views (Fig. 2, G and H), is possibly a dorsal nerve cord. In addition, narrow strands observed within the main axis of the gills may represent vascular tissue.

Neither a lateral eye (*12*) nor a tripartite brain was identified in *H. jianshanensis* or in the material of *Y. lividum* and *H. lanceolata* available to us. No structure in *H. jianshanensis* can be identified as a notochord, although on the basis of taphonomic evidence, this organ would be expected to be robust (*13*). In addition, although only occasionally preserved in *H. jianshanensis*, the dorsal posterior segmentation has no similarity to the myomeres that are unequivocally expressed in the Chengjiang fish (*14*, *15*). We find no evidence for tentacles in the buccal cavity or pharyngeal teeth (*4*). The cuticular bar that defines the mouth has been illustrated in *H. lanceolata* (*4*), but has not been previ-

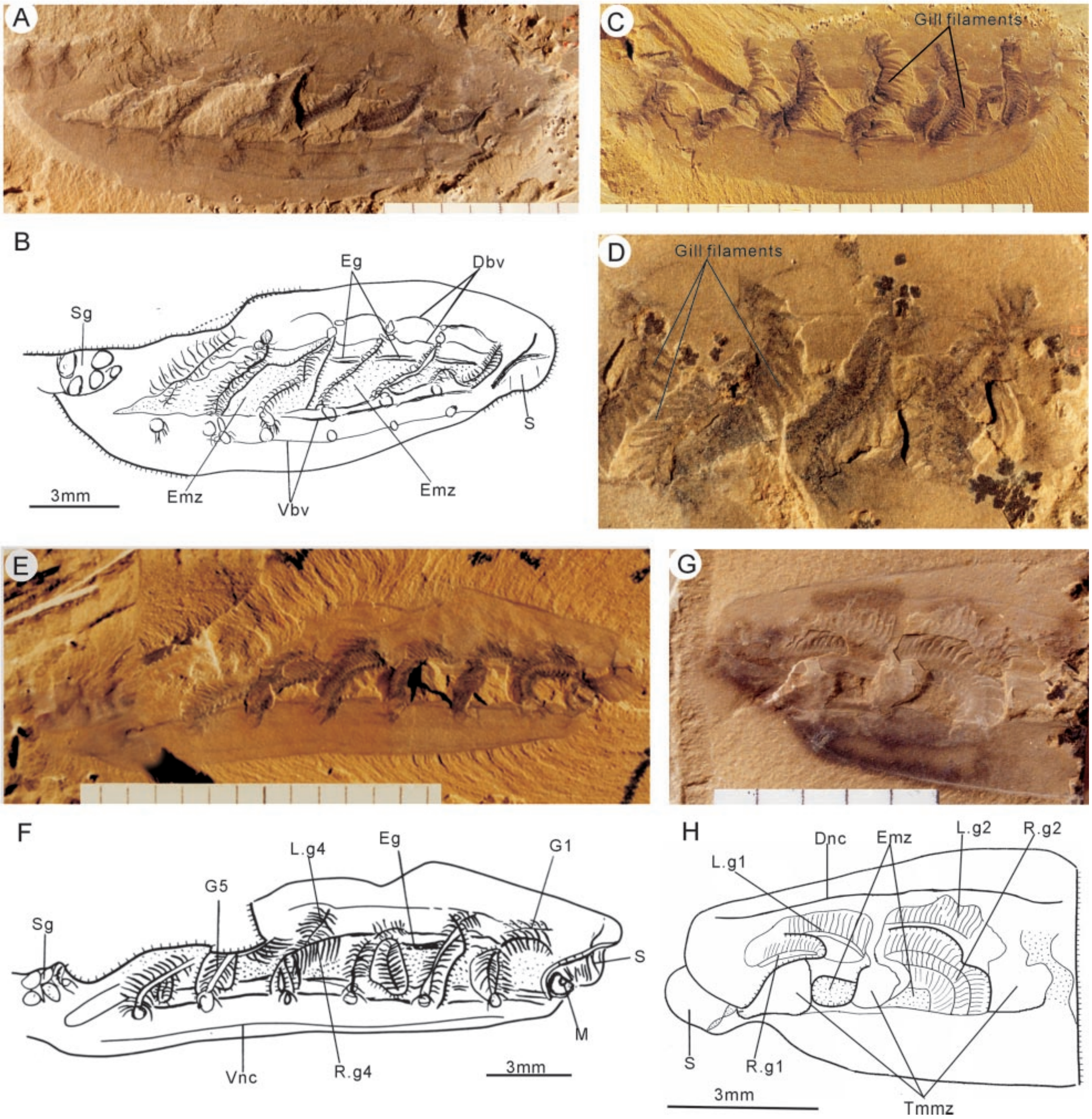

Fig. 2. Details of *H. jianshanensis*, showing paired dorsal and ventral blood vessels (**A** and **B**), ?dorsal nerve cord (**G** and **H**), ?ventral nerve cord (**E** and **F**), thin membrane covering the median zone (G and H), and gill filaments (**C** and **D**). All are lateral views. Specimens are as follows: (A) and (B), (131); (C), (146); (D), (099); (E) and (F), (299); and (G) and (H), (088). Abbreviations are as in Fig. 1; scale intervals are in millimeters.

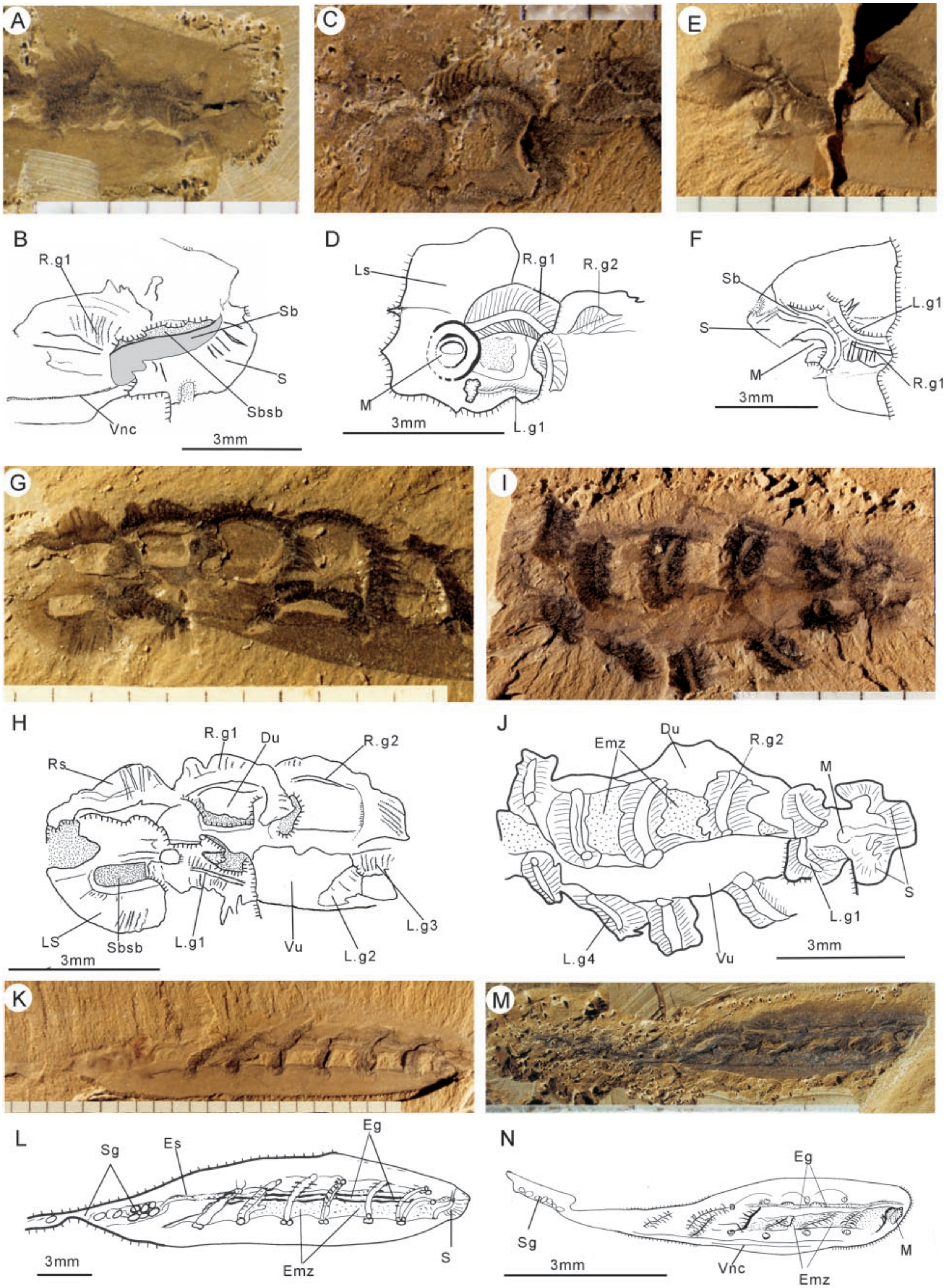

Fig. 3. (**A** to **N**) Details of *H. jianshanensis*, showing a skirtlike structure, the skirt bar (A, B, E, and F), mouth (C to F, I, and J), ?epipharyngeal groove (K to N), and esophagus and spiral gut (K and L). All are lateral views except (C), (D), (I), and (J). Specimens are as follows: (A) and (B), (158); (C) and (D), (332); (E) and (F), (142); (G) and (H), (214); (I) and (J), (294); (K) and (L), (266); and (M) and (N), (360). Abbreviations are as in Fig. 1; scale intervals are in millimeters.

ously identified. The structure identified here as the anterior skirt has been illustrated previously but identified as an anterior branchial vessel, an anterior projection, or lobated structures (*4*). Other structures, such as the heart and copulatory organ (*4*, *7*, *8*), find no counterpart in our yunnanozoan material.

Hitherto the yunnanozoan gills have been regarded as internal structures (*16*), integral to the perforated pharynx and comparable to those of the lamprey ammocoete larva (*4*). In *H. jianshanensis*, the gills formed external arches, attached to the outer surfaces of the dorsal and ventral units. An external position of the gills makes the location of any pharyngeal openings more problematic. No evidence exists for openings in the cuticle of the median zone. However, well-defined circular structures [also seen in *Y. lividum* (*7*, *8*)] adjacent to the ventral terminations of the gills, each consisting of an outer annulus and central zone (Fig. 2, A and B), could represent individual openings, each defined by a narrow rim. An alternative possibility is that these circular structures represent attachment discs for the gills.

Earlier suggestions for a phylogenetic connection to the vetulicolians, interpreted as stem-group deuterostomes (*17*), can be supported by our observations of *H. jianshanensis*. In particular, the prominent dorsal and ventral units are similar to the carapace-like anterior of *Vetulicola*, although in yunnanozoans, the intervening cuticular median zone is expanded. Provisionally, we identify the circular structures on the lower unit as pharyngeal openings, ventral to the equivalent structures in the vetulicolians. The yunnanozoans, therefore, are interpreted as a deuterostome stem group, but the possession of gills suggests that phylogenetically they are more crownward than the vetulicolians. If the dorsal and ventral nerve cords are correctly identified, this would find a counterpart in enteropneust hemichordates; in other respects, the yunnanozoan body plan is markedly divergent.

Deuterostome phylogeny is problematic, both because of the disparate nature of the extant phyla and the seemingly bizarre nature of the candidate stem taxa. Although molecular data on deuterostomes (*18*, *19*) offer new insights into previously unexpected relationships, the fossil records of groups such as calcichordates (*20*), vetulicolians (*17*), and yunnanozoans are of central importance. In particular, it is possible that the diagnostic pharyngeal arches are effectively composite structures, being derived from a pharyngeal opening that evolved [in the vetulicolians (*17*)] before the appearance of prominent gill arches. In this scenario, only subsequently did these gills migrate to an internal (and more protected) position.

Systematic Paleontology is as follows:
?Phylum Vetulicolia
Class Yunnanozoa Dzik 1995 (*5*)
Family Yunnanozoonidae Dzik 1995 (*5*)
Genus *Haikouella* Chen *et al.* 1999 (*4*)
Haikouella jianshanensis n. sp.

Etymology: Specific name refers to Jianshan (peaked hill), where the material was collected.

Holotype: ELI-0010001(226)

Other material: More than 1420 specimens.

Stratigraphy and locality: Qiongzhusi (Chiongchussu) Formation, near base of Yu'anshan Member (*Eoredlichia* Zone), Lower Cambrian. Specimens collected from Jianshan, about 2 km east of Ercai village, Haikou, near Kunming, Yunnan.

Diagnosis: Anterior of main body consisting of dorsal and ventral units, connected by membrane; six pairs of external gills, attached to both units; gills robust, bipectinate; skirtlike extension, attached to anterior end of either unit. Posterior section segmented, lightly cuticularized. Mouth large, anterior gastric cavity probably voluminous, posterior with narrow intestine.

References and Notes

1. X. Zhang, D. Shu, Y. Li, J. Han, *J. Geol. Soc. London* **158**, 211 (2001).
2. L. E. Babcock, W. Zhang, S. A. Leslie, *GSA Today* **11** (no. 2), 4 (2001).
3. X. Hou, L. Ramsköld, J. Bergström, *Zool. Scr.* **20**, 395 (1991).
4. J. Chen, D. Huang, C. Li, *Nature* **402**, 518 (1999).
5. J. Dzik, *Acta Palaeontol. Pol.* **40**, 341 (1995).
6. D. Shu, X. Zhang, L. Chen, *Nature* **380**, 428 (1996).
7. J. Chen *et al.*, *Nature* **377**, 720 (1995).
8. N. D. Holland, J. Chen, *BioEssays* **23**, 142 (2001).
9. A somewhat similar conclusion was reached by Dzik (*5*), who identified two large ventrolateral lobes in *Y. lividum*. However, he compared this structure with the sclerotic ocular rings of the conodont animal.
10. In Burgess Shale–type preservation, turbulent burial introduces sediment into spaces and cavities of the animal. Subsequent compaction greatly reduces the thickness of this sediment and converts the fossil into a series of thin films. Typically, small scarps (denoted on the interpretative drawings as hachured lines, with the hachures pointing downslope) separate the various parts of the fossil and so allow inferences on their relative position and imbrication.
11. A similar structure is identified in *Y. lividum* [figure 3B in (*7*)], where it is identified as an endostyle. A ventral aorta is identified in figure 1 of (*4*), but as a single structure.
12. The failure to recognize eyes is unlikely to be a result of taphonomic circumstances, because well-developed eyes occur in the agnathan *Haikouichthys* (*15*), as well as in a number of Chengjiang arthropods.
13. D. E. G. Briggs, A. J. Kear, *Lethaia* **26**, 275 (1994).
14. D. Shu *et al.*, *Nature* **402**, 42 (1999).
15. D. Shu *et al.*, *Nature* **421**, 526 (2003).
16. The gill bars of yunnanozoans with spaced discs are described in (*4*) and (*7*), but these are more likely to be cuticular bands, marking in *H. lanceolata* and *H. jianshanensis* the insertion points of the extended filaments and leaves, respectively.
17. D. Shu *et al.*, *Nature* **414**, 419 (2001).
18. C. B. Cameron *et al.*, *Proc. Natl. Acad. Sci. U.S.A.* **97**, 4469 (2000).
19. C. J. Winchell *et al.*, *Mol. Biol. Evol.* **19**, 762 (2002).
20. P. Dominguez, A. G. Jacobsen, R. P. S. Jefferies, *Nature* **417**, 841 (2002).
21. We thank the National Natural Science Foundation of China; the Ministry of Sciences and Technology of China; the National Geographic Society; The Royal Society; and St. John's College, Cambridge. M. Cheng, L. Guo, X. Cheng, J. Zhai, H. Guo, Y. Ji, S. Last, and A. Allen are thanked for technical assistance. M. M. Smith and an anonymous referee are thanked for constructive dialogues.

28 October 2002; accepted 15 January 2003

Homo erectus Calvarium from the Pleistocene of Java

Hisao Baba,[1,2]* Fachroel Aziz,[3] Yousuke Kaifu,[1] Gen Suwa,[4] Reiko T. Kono,[1] Teuku Jacob[5]

A *Homo erectus* calvarium [Sambungmacan 4 (Sm 4)] was recovered from Pleistocene sediments at Sambungmacan in central Java. Micro–computed tomography analysis shows a modern human–like cranial base flexion associated with a low platycephalic vault, implying that the evolution of human cranial globularity was independent of cranial base flexion. The overall morphology of Sm 4 is intermediate between that of earlier and later Javanese *Homo erectus*; apparent morphological specializations are more strongly expressed in the latter. This supports the hypothesis that later Pleistocene Javanese populations were substantially isolated and made minimal contributions to the ancestry of modern humans.

Javanese *Homo erectus* is best represented by the Early and Middle/Late Pleistocene remains found at Trinil, Sangiran, and Ngandong (*1*–*4*). Shared features of these hominids have led to the notion of continuous regional evolution in Java (*5*–*7*) as part of a broader *H. erectus* species distribution (*8*, *9*). However, the actual evolution of Asian *H. erectus* is uncertain (*7*, *8*), and phyletic relationships concerning *H. erectus*, other archaic *Homo*, and modern humans remain unresolved (*6*–*11*). Aside from the widely acknowledged increase of cerebral mass (*12*), the underlying morphogenetic basis of the transition from *H. erectus* to *H. sapiens* has only begun to be explored. Here we describe a new calvarium, Sambungmacan 4 (Sm 4). We analyzed Sm 4 by micro–computed tomography (micro-CT)–based visualization and compared it with other Javanese crania.