PALEONTOLOGY

Parsing the Trilobites' Rise and Fall

In Earth's first evolutionary flowering, the Cambrian explosion, the trilobites—hardy, shelled arthropods beloved of fossil hunters everywhere—were big winners, quickly filling many niches on the ocean bottom. But they seemed to miss out on the next evolutionary burst, about 475 million years ago during the Ordovician period. While mollusks, corals, and stationary filter feeders diversified rapidly and laid the foundation for today's seafloor ecosystem, trilobites seemingly slid into a protracted decline. By 250 million years ago, they had disappeared for good.

Now on page 1922 of this issue, paleontologist Jonathan Adrain of London's Natural History Museum and two colleagues report that this widely accepted picture of the trilobites' fate is too simplistic. With a detailed new survey, they show that while one group, or fauna, of trilobites faded precipitously during the Ordovician, the other thrived. A still-mysterious combination of ecology, geographic distribution, and high rates of speciation evidently gave this fauna an evolutionary edge.

Biting the dust? Trilobites from the Ibex Fauna *(bottom)* vanished after the Ordovician period, while those from the Whiterock Fauna *(right)* thrived.

PHOTOS: P. HURST / NATURAL HISTORY MUSEUM

Other paleontologists are impressed. "The contrast between the two faunas is amazing," says David Jablonski of the University of Chicago. "You really get the sense of trilobites as a boom-and-bust group." Adds Arnold Miller of the University of Cincinnati: "This is an unassailable data set." But paleontologist Jack Sepkoski of the University of Chicago notes that even the more rapidly diversifying trilobites were laggards compared with other Ordovician organisms.

The new view of trilobite diversity stems from a reanalysis of the literature, led by Adrain. The team identified 945 genera and grouped them into 56 families that share common features, such as unique shell segments and shapes. They were then able to realize for the first time that the trilobites cluster into two major groups of families. Members of one cluster, the Ibex Fauna, dominated the start of the Ordovician but then grew less diverse and vanished at the end-Ordovician mass extinction 440 million years ago. The other cluster, the Whiterock Fauna, tripled their genera in the Ordovician and skimmed through that extinction virtually unscathed; not until 30 million years later did they start to wane.

These differences in rates of evolution are "the most compelling clue to [the faunas'] strikingly disjunct fates," the authors say. Although the Ibex Fauna did not stray far from the Cambrian forms, the Whiterock Fauna rapidly evolved novel shapes and spread into new niches, which may have insulated them from extinction. "Something different about this extinction allowed the more diverse families to survive," says Adrain, noting that diverse families weren't as protected in most other mass extinctions.

Ecology and geography may also have helped dictate the faunas' fates. Whiterock species preferred middepth environments in the ocean, while their Ibex cousins lived either in shallower or deeper water. And although tropical trilobites, including the Whiterockians, fared well, most high-latitude trilobites perished. No one knows exactly why these differences were important, but the extinction probably involved glaciation—which could have different effects at different latitudes—and the reorganization of ocean currents, adding up to what co-author Richard Fortey of the Natural History Museum calls a "global oceanic crisis."

To disentangle these factors, "we have to get out of the library and back into the field," says co-author Stephen Westrop of the University of Oklahoma, Norman. New fossil finds and studies of ocean conditions may reveal why some trilobites survived while others scuttled into silence on the sea floor.

–Robert Irion

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EVOLUTIONARY BIOLOGY

Females Pick Good Genes in Frogs, Flies

Finicky females have long mystified both suitors and evolutionary biologists, particularly when the female tends to pick the most flamboyant male, even if he doesn't appear to have any other redeeming qualities. Almost 70 years ago, R. A. Fisher threw up his hands and suggested that such preferences as the peahen's yen for a showy tail are arbitrary—whims that set off an evolutionary race won by the most outlandish male. By the mid-1970s, however, some biologists argued that females are not only finicky but wise. The exaggerated traits, they theorized, are a sign of less obvious "good genes" that will lead to fitter offspring. But testing these ideas has been difficult, as many factors can influence the success of offspring. "There's been a dearth of [good] data," says Richard Howard, a behavioral ecologist at Purdue University in West Lafayette, Indiana.

Now, on page 1928, Allison Welch and her colleagues at the University of Missouri, Columbia, present an elegant series of experiments that demonstrate good genes at work. They report that male tree frogs with long calls—known to be favored by females—sire higher quality young than those with short calls. The work fits well with a handful of other studies analyzing good genes, including a study in stalk-eyed flies that links the long stalks preferred by females to an unusual genetic advantage in males.

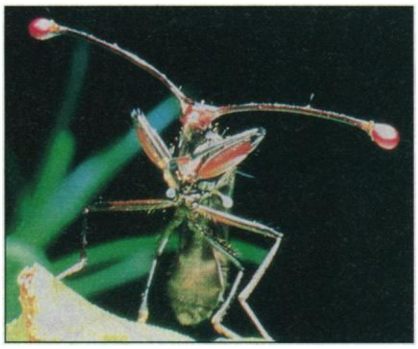
Together, these and other studies have convinced skeptics that finicky females are actually choosing good genes, although researchers disagree on whether the effect accounts for most female preferences. "I think the good-genes theory is coming into its own," says Mike Ritchie, an evolutionary geneticist at the University of St. Andrews in Scotland.

Few female tastes seem more whimsical than that of the gray tree frog (*Hyla versicolor*). Male frogs attract mates with calls that last from half a second to 2 seconds per call. Behavioral biologist H. Carl Gerhardt from the University of Missouri, Columbia, found that females head for long calls heard through a loudspeaker, even if the short calls are closer and louder. "They avoid the very short calls," he says.

C. GERHARDT

Frog Don Juan. For gray tree frogs, it's the good genes, not just the long song, that win over the females.

To explore whether the longer call signaled good genes, Welch, a graduate student, manipulated frog reproduction. For 2 years she removed the eggs from about 10 female tree frogs, then fertilized half the eggs with sperm from a short-calling male and half with sperm from a long caller. Next, working with Missouri ecologist Raymond Semlitsch, she compared how the offspring fared as tadpoles and after they metamorphosed into frogs, measuring their growth rates under regimes of scarce and plentiful food. Descendants of long callers won out. "Every single significant effect was in favor of the long callers," says Gerhardt.



Stalk envy. Although seemingly useless, long stalks in male stalk-eyed flies appeal to potential mates.

P. SAVOIE

Other researchers praise the study because it neatly circumvents problems plaguing other "good genes" experiments, such as biased provisioning of eggs by the mother, which alters the offspring's chances. And unlike many studies, Welch's work can rule out the possibility that flamboyant males offer some benefit to their offspring other than good genes, such as food or rich territories, says population geneticist Mark Kirkpatrick of the University of Texas, Austin. Male tree frogs have no contact with their offspring except for fertilization, so their only contribution is genetic. "It's one of the most convincing documentations [of the "good genes" theory] that I've seen," says Brian Charlesworth, a population geneticist at the University of Edinburgh in Scotland.

Kirkpatrick adds that Welch's large sample sizes will help the researchers quantify the extra fitness that long callers confer on their offspring: The study "gives us some numbers that will give us an estimate of how strong the 'good gene' influence is [in these organisms]." But Welch's team says it may be a while before they can answer the biggest question of all—what makes the long callers and their descendants more fit.

Another recent experiment, however, may have identified an actual genetic advantage that accompanies the females' seemingly arbitrary tastes. Gerald Wilkinson, a behavioral ecologist at the University of Maryland, College Park, and his colleagues studied species of stalk-eyed flies in which females generally outnumber males. The team determined that the biased sex ratio was caused by certain "selfish" genes on the X chromosome, which somehow attack Y-bearing sperm. As a result, during mating, the male contributes many X-bearing sperm but few Y's, and the next generation has more females than males. (In flies, as in humans, males have one X and one Y chromosome, while females have two X's.) These selfish genes are overly represented in each successive generation.

But some males have a gene on their Y chromosome that protects against the "selfish" X. And in the 15 January issue of *Nature*, the team showed in selective breeding experiments that this protective gene is linked to longer eyestalks. Populations descended from long-stalked males had an even sex ratio, and sometimes more males than females, showing that they had overcome the effects of the selfish X chromosome.

The researchers surmise—although they did not prove—that female flies prefer long stalks because they are genetically linked to a gene that blocks the selfish X chromosome, allowing the birth of males. That helps propagate the female's genes because their sons, as scarce males among females, will likely have many offspring. The work "provides a powerful but unusual example of how the 'good genes' mechanism can operate," says Kirkpatrick, who was once something of a "good genes" skeptic. The Welch experiment, in contrast, shows the expected and perhaps more general outcome of good genes—enhanced fitness in the offspring.

For frogs, longer calls are costly to sustain, suggesting that the same genes—perhaps for stamina or more efficient metabolism—may underlie both calling and the enhanced survival of the young. But in the flies, the only link between long stalks and the restored sex ratio may be that the genes for both traits lie near each other on the Y chromosome. In either case, the female's choice is far from capricious, says Gerhardt. Instead, "they are making [life] better for their offspring"—and that's what good genes are all about.

–Elizabeth Pennisi

DEVELOPMENTAL BIOLOGY

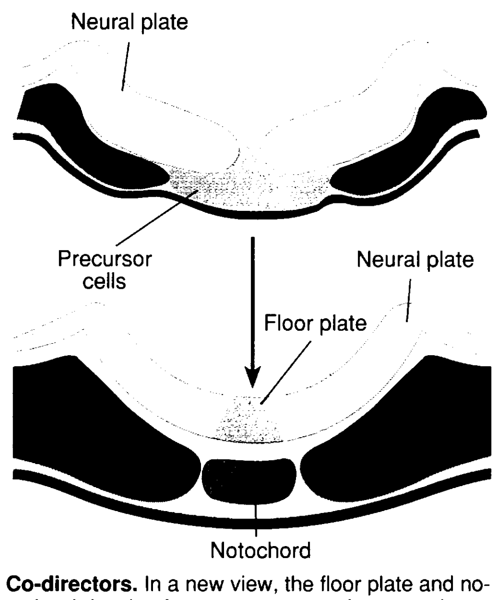
Embryo's Organizational Chart Redrawn

Organizing the developing nervous system requires a formidable bureaucracy. In the classic organizational chart, the notochord, a rodlike group of cells running from the embryonic head to the tail, is the CEO of neural cell fate. Early in development, it sends out a command to tissue destined to be part of the spinal cord, ordering it to differentiate into a specialized sheet of cells called the floor plate. In turn, the floor plate—the middle manager in this hierarchy—sends out signals that trigger the formation of motor neurons, which transmit signals between the spinal cord and muscles.

But now both developmental and genetic evidence suggests that this textbook version of the organizational chart is wrong. Work presented last month at a meeting of developmental scientists* by Nicole Le Douarin of the College de France in Nogent-sur-Marne and her colleagues suggests that the floor plate is not ordered into existence by the notochord. Rather, it is another member of the executive committee, forming at the same time and from the same group of precursor cells as the notochord itself.

This and genetic studies in the zebrafish are forcing embryologists to reconsider some of their basic assumptions. "It really does change the view of how the patterning of the nervous system happens," says developmental biologist Igor Dawid of the National Institute of Child Health and Human Development.

The view that the floor plate is created in response to orders from the notochord grew out of a set of elegant experiments begun in the 1980s. Biologists had already shown that early in development, a sheet of cells called



SOURCE: N. LE DOUARIN

Co-directors. In a new view, the floor plate and notochord develop from precursors at the same time.

the neural plate curls into a tube that eventually develops into the spinal cord. In the middle of the ventral side of the tube is a layer of cells called the floor plate. If the floor plate fails to form correctly, an embryo's ner-

* Molecular Genetics of Development, 6–9 May, Airlie, Virginia. Sponsored by the National Institute of Child Health and Human Development.