

seterica fossa developed on the dentary).

The difficulty of attempting to assign *Chronoperates* to a grouping of 'mammal-like reptiles' is that this latter is not a monophyletic group with a unique history. Instead, the 'mammal-like reptiles' are a paraphyletic assemblage. There is no character by which membership can be recognized. Mammal-like reptiles are mammals without the specializations of modern mammals.

The fact that *Chronoperates* lacks double-rooted cheek teeth, a cingulum or prismatic enamel tells us nothing since these are all primitive features, to be expected in a wide variety of early mammals as well as other amniotes. Fox *et al.*¹ further argue for the presence of postdentary bones based on the presence of a trough on the dentary. These, they say, would exclude *Chronoperates* from the mammals (the modern members of which have a single bone — the dentary — in the lower jaw) and justify its placement as a mammal-like reptile. There are two issues involved: the interpretation of the fossil specimen and the significance of the reconstruction. Fox *et al.*¹ believe that the fossil is incomplete and that the trough is evidence of other bones articulating at this point. But Sues³ argues that the fossil is intact, that the trough received soft tissue and that postdentary bones were not present. Absence in fossils is always difficult to explain because it can be either real or preservational. But even if Fox *et al.* were correct, this would not deny the mammalian affinities of *Chronoperates* because the existence of postdentary bones is the primitive mammalian condition.

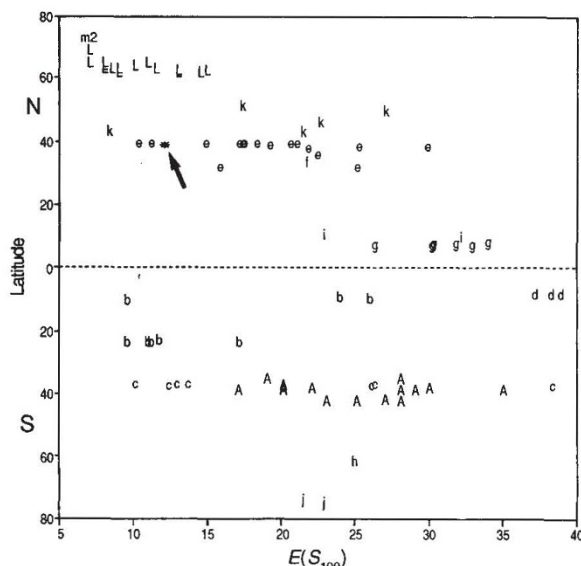
To argue that *Chronoperates* is a mammal-like reptile is a futile exercise as the claim can never be justified by observable characters, although it may be possible to show that it belongs to a monophyletic subgroup. Fox *et al.* are right to claim that *Chronoperates* belongs to the mammalian (their cynodont) clade, but exactly where it belongs depends on the recognition of synapomorphies with one or other of the included taxa.

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Marine species richness

SIR — Estimates for the number of species in the deep sea¹ have been discussed in News and Views². Grassle and Maciolek¹ reported on 14 samples taken within 176 km from the slope (depth range 1,500–2,500 m) of the north-western Atlantic where they found 798 species of invertebrates among 90,677 individuals in 21 m² of box-core samples. Using rarefaction methods and estimates of species change along spatial gradients



Expected number of species in 100 individuals ($E(S_{100})$) versus latitude. A, Southeastern Australia⁵; b, Angola Basin; c, Argentine Basin; d, Brazil Basin; e, Gay Head-Bermuda transect; f, Mediterranean Sea; g, Guiana Basin; h, Scotia Basin; i, Sierra Leone Basin; j, Weddell Sea; k, West European Basin⁴; L, Norwegian Basin; m, Greenland Basin³; asterisk, off New Jersey and Delaware (arrow, United States¹).

they calculated a global species deep-sea biodiversity of 10^7 invertebrate species. May² questioned these assumptions, specifically, that species replacement along global gradients is linear. He proposed that, because about half the species discovered were already known, the number is unlikely to exceed half a million.

We have independently collected data on isopods from the same depth range on continental slopes in several places in the Pacific and Atlantic oceans, and have information from the Arctic³ (see figure). These figures show that Grassle and Maciolek's data are far from typical and their species estimates are, in fact, at the lower end of those available from the oceans generally. Their estimate of the number of species of isopods expected to be represented in 100 individuals, $E(S_{100})$, is 12 whereas our data range from 7 in the Norwegian sea to 39 in the Argentine Basin. These data are variable

but show that the Norwegian and Greenland seas are relatively impoverished (as expected), that there are more species in mid-latitudes in both hemispheres, and that tropical slopes may be richer in species than temperate ones. The median $E(S_{100})$ of all data in the figure, Arctic species excluded, is 22 species.

These new data bring into question the appropriateness of using data from one site in the North Atlantic for global estimates. New calculations of isopod richness from samples taken during the Gay Head-Bermuda transect⁴ are consistently higher than Grassle and Maciolek's figure from the same region

but are on average lower than those for a similar latitudinal range off south-eastern Australia (manuscript submitted). The oceans of the Southern Hemisphere are much larger than those of the Northern Hemisphere and the North Atlantic is relatively young compared to the Pacific. Therefore, extrapolations to the global species number should include data from the South Pacific. We suspect new estimates could be much higher than so far admitted.

May's estimate from Grassle and Maciolek's data on the basis of fraction of known species may be unreliable. In Grassle and Maciolek's samples 31% of peracarid crustaceans were identified to species, a figure which might apply to isopods in the northwestern Atlantic but which is known to be

six times higher than in the Central Pacific. In southeastern Australia the equivalent figure is 10%. But isopods have received more recent taxonomic attention in Australia than most other invertebrate taxa and half of the known species have been described in the past 7 years by only three principal authors (G. C. B. P., N. L. Bruce and J. Just). The known fraction of other invertebrate species in this region is also consistently low, for example in aplousobranch molluscs⁵. May used a factor of 2 to extrapolate from known to total fauna; a factor exceeding 20 might be more reasonable for the oceans as a whole.

The discussion so far has been limited to data on the benthos of mid-slope communities, which are only a small part of the ocean floor. Equivalent data from the oceanic basins are scarce but do suggest that species richness measured in

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the way outlined here may be higher than on the slope. For example, $E(S_{100})$ values of up to 48.9 isopod species have been recorded from the central Pacific Ocean⁶.

Grassle and Maciolek also suggested that shallow marine environments outside of the tropics have relatively few benthic species compared to the deep sea. They cite 200 species as the number expected for large collections from the Georges Bank. In southeastern Australia the fauna is far richer: more than 700 infaunal benthic species in Port Phillip Bay⁷; more than 800 species in 10 m² of benthos in Bass Strait (unpublished data). This is further evidence that the North Atlantic is not typical of oceanic biodiversity and that further exploration in the little-studied Southern Hemisphere will significantly add to estimates of marine species richness.

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MAY REPLIES — Poore and Wilson make an important contribution to discussions of benthic macrofaunal diversity. They emphasize that benthic fauna can vary greatly from place to place, so that estimates of total species numbers based on patterns found in any one location can easily be confounded by different patterns in other locations. Poore and Wilson suggest an overall factor of 20 might be appropriate in extrapolating from known to total benthic faunas,

leading to an estimate of around 5 million species. This is ten times my rather conservative guess², but still well below that in Grassle and Maciolek's important and provocative paper¹ (they estimated a few hundreds of millions, but scaled it back to 10 million or so to express their view that species numbers are likely to be lower on the floors of ocean basins than on continental shelves or mid-slopes; note that Poore and Wilson believe, to the contrary, that species richness may be higher in ocean basins).

Poore and Wilson use $E(S_{100})$, the average number of different species found in a sample of 100 individuals, as a guide to species numbers, inferring that more species are present when $E(S_{100})$ is higher. But $E(S_{100})$ measures evenness, not species richness. Very often a larger value of this index will indicate more species are present. But it is perfectly possible for two communities to have very different values of $E(S_{100})$, even though both have the same total of species (just as two countries with similar total populations and total wealth can have the wealth distributed in very different ways, from egalitarian to feudal extremes).

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result would imply that it is highly unlikely that the global mean temperature depends on this cycle length.

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Purity of nature?

SIR — The description by G. H. Gonnet and S. A. Benner (*Nature* **361**, 121; 1993) of their search of the one-letter coded sequences of proteins for long English words stirred memories of 32 years ago when I was writing a review on peptides and proteins for the Annual Reports of the Chemical Society. The one-letter code had recently been introduced by the late Professor F. Šorm of the Czech Academy of Sciences. Not many protein sequences were then known but they were clearly going to appear at an ever-increasing rate.

I enquired of the editor if I might use Šorm's code to save space; permission was withheld on the grounds that obscene sequences might be forthcoming. I wrote to Professor Šorm telling him of the decision and my frustration. He replied that he had written out all the sequences known at that time and had not found any sequence that could be construed as obscene. With tongue in cheek, he attributed this to the purity of nature.

In fact, with a characteristic versatility, he displayed a good working knowledge of the English vernacular and avoided the use of letters such as u, o and b, which might have given rise to obscene sequences. There are, however, some indelicate words that can be constructed from the partial alphabet used by Šorm.

With the immense databank of protein sequences now available, it would be interesting to know if Šorm's attribution of verbal purity to nature is really true. Whatever the answer, it appears from the two recondite examples cited by Gonnet and Benner that nature indulges in sesquipedalianism. Perhaps this is a reflection of the tendency of naturally occurring macromolecules to contain redundant sequences.

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Solar output and global warming

SIR — The debate as to whether solar variability is a significant cause of the rise in global mean surface air temperature^{1–4} has been based on data analysis. Although theoretical mechanisms have been postulated, they are difficult to test because of the lack of historical data on the variability of the solar output.

However, there is a terrestrial parameter which is highly sensitive to variations in the solar ultraviolet radiation — the atmospheric semi-diurnal tide⁵. Unlike the ocean tides, the atmospheric tides are predominantly forced by solar heating⁶. In particular, the semi-diurnal (12-hour) tide is driven by absorption of ultraviolet radiation in the stratosphere and thus is sensitive to wavelengths where solar output varies significantly⁷.

Historical data on the amplitude of the atmospheric semi-diurnal tide could therefore provide an indication of the magnitude of solar variability with sunspot cycle length.

Such a dataset is available as the semi-diurnal tide dominates the variations in atmospheric pressure in the tropics⁶. Hourly pressure data (required to calculate the tide) over many decades are available for various tropical meteorological stations.

I would like to suggest that someone who can access these data calculates the variation in the annual mean semi-diurnal tide in the tropics over the past 100 years. According to the above theory, this should show whether or not the solar ultraviolet output varies with the sunspot cycle length. A negative