Blood samples (adult: anticubital vein 2.5 ml into EDTA; young children: capillary) were taken from the adult female residents who spent most time in the house and usually from the youngest child. Lead estimations (including blind duplicates) were made by the NHS Supra-Regional Laboratory at Leeds, with sub-samples being analysed at London (Institute of Child Health) and Glasgow (Department of Materia Medica).

The overall water lead and blood lead levels measured are shown in Table 1. Blood lead levels were markedly higher in the lead estate than in the copper estate. This was true for both adults and children, and has been discussed elsewhere[3]. No subject had exposure to lead through occupation. Only one woman has a hobby (in this case, enamelling) which involved the use of lead. However, her blood lead level (1.5 μmol l^{-1}) was below the median level (1.9 μmol l^{-1}) found on the estate on which she lived, suggesting that this hobby did not involve a high exposure to lead.

Detailed analyses (not presented here) of the dependence of blood lead on water lead gave no evidence that any of the water sampling methods—'daytime', 'running' or 'first flush'—was a markedly better predictor of blood lead than the others.

The stability of blood lead within subjects is of interest in this kind of work[6]. We therefore examined this and found that, at least over a period of weeks, blood lead, even when raised, is extremely stable (Table 2).

Table 2 Stability of blood lead (μmol l^{-1}) over time in adult female subjects

Time interval	No. of subjects	Mean of first and second sample	Mean change (s.d.)	c.v. (%)
2 weeks	14	1.6	+0.07 (0.21)	9.7
4 weeks	19	1.8	−0.10 (0.17)	6.6
Over 12 weeks	12	0.8	0.00 (0.15)	13.1

No individual was included in more than one subgroup. Coefficients of variation based on 'within subject' variance. These are very similar to the within laboratory c.v. (see Table 1) which suggests that 'true' blood lead is very stable.

Following the removal of the lead pipes, water lead levels became indistinguishable within a few weeks from those on the copper estate. The fall in blood lead (Table 3) was determined in sub-samples of adult subjects examined up to 9 months after the lead pipes had been removed. The mean decrease after pipe removal was approximately 30% at 3 and 4 months and 50% at 6 and 9 months. The blood lead levels had thus become comparable to those on the copper piped estate in approximately 6 months. Changes in blood lead for a small number of controls on the copper estate were also measured and were negligible. No other changes in lead exposure were apparent during this time and therefore the reduction in water lead may be assumed to have produced the fall in mean blood lead levels observed.

Various empirical models (for example, simple linear, quadratic, square root, cube root) were used for regressing blood lead against water lead in our data. The curvilinear models gave a slightly better fit than the simple linear and Fig. 1 shows the regression line of blood lead on the cube root of first flush water lead. This empirical relationship was suggested by Moore and colleagues[7] from their Scottish data, and the line determined by their regression coefficients is also shown in Fig. 1. The similarity of the curves is interesting as our population sample is quite different from theirs. However, a close similarity between Welsh and Scottish data has also been pointed out previously[8].

The lead piped estate on which this work was based seems to be exceptional in terms of water lead levels. Over 70% of the houses had first flush water lead levels above 0.3 mg l^{-1} compared with less than 1% of the results for Wales in the survey carried out by the Department of Environment[2]. In conjunction with the WWA, we sampled drinking water from over 20 areas in North Wales considered by water boards to have a possible plumbo-solvency problem but no estate was found with lead levels approaching those reported here. It is therefore probable that we are reporting an exceptional case,

Table 3 Mean blood lead levels (μmol l^{-1}) of subgroups of adult females in the lead estate, and the fall in blood lead following removal of the lead pipes

Interval (months)	n*	Initial blood lead (s.d.)	Mean fall after pipe removal (s.d.)	% Mean decrease
3	13	2.2 (0.6)	0.7 (0.3)	32
4	11	1.7 (0.6)	0.6 (0.3)	35
6	10	2.2 (0.5)	1.1 (0.3)	50
9	11	2.3 (0.5)	1.1 (0.3)	48

* No individual included in more than one subgroup.

but water authorities should obviously ensure that no such estates exist within their areas. Where problems exist, removal of lead plumbing is a very effective remedy but other, more economic methods of plumbo-solvency control are being developed[9].

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Reappraisal of energetics of locomotion shows identical cost in bipeds and quadrupeds including ostrich and horse

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Animals use different amounts of energy to move from place to place depending on their size and mode of locomotion[1]. Flyers and swimmers use less energy to move a unit mass a unit distance than do running animals, and small animals use more energy than large ones. For terrestrial animals Taylor *et al.*[2] have defined cost of transport as the slope of the regression line relating weight-specific metabolic power and running speed. Cost of transport, so defined, is a comparative index of the relative energy-cost of locomotion of different animals. Fedak *et al.*[3] had reported that bipeds and quadrupeds have different costs and that, extrapolating from their data, the difference between them would be greatest among large animals. Now, after considering new data from 100-kg ostrich and horse, and reviewing the data collected in the past 5 yr, we find that there are no consistent differences in energy-cost between bipeds and quadrupeds of any size. The apparent differences reported earlier was biased by an unfortunate choice of animals. The new, much more extensive, evidence shows no difference of the scaling of energy requirements for locomotion between bipeds and quadrupeds, but suggests a difference between apparently clumsy and graceful animals.

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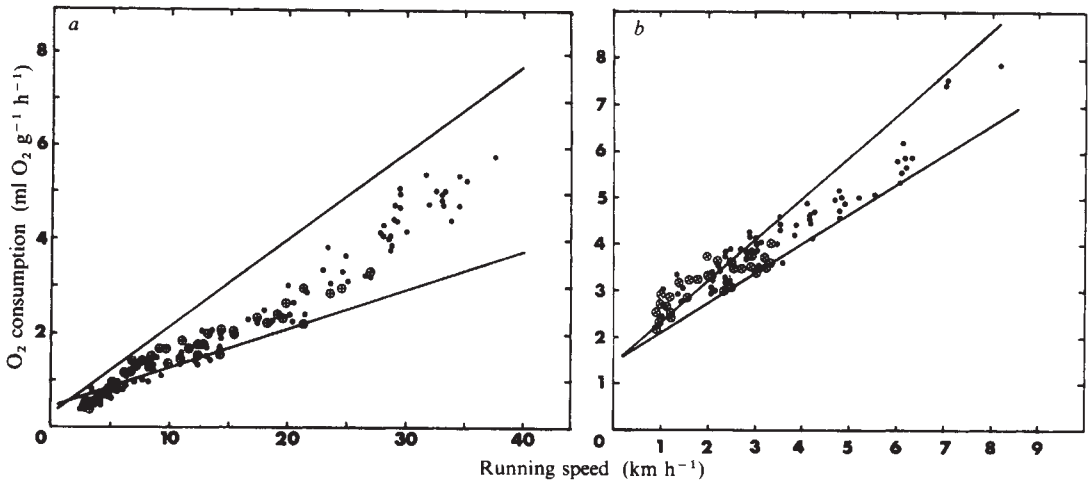

Fig. 1 *a*, The weight-specific oxygen consumption ($\dot{V}_{O2}$ in ml O_2 (g h)$^{-1}$) of the ostrich (⊕, 103 kg) and horse (●, 107 kg) expressed as a function of running speed (km h^{-1}). The upper and lower solid lines are those predicted refs 3 and 2 for 100-kg bipeds and quadrupeds, respectively. Oxygen consumption is a measure of the metabolic power developed by the animal. (To convert ml O_2 (g h)$^{-1}$ to W kg^{-1} multiply by 20.1 W per ml of O_2 consumed). We used an open-flow gas analysis system as described in ref. 3. The large animals ran wearing loose-fitting masks which allowed capture of all expired gas. O_2 and CO_2 concentrations were measured in ambient and post-mask air. Oxygen consumption was calculated by the following formula:

$$\dot{V}_{O_2} = \frac{\dot{V}E(FI_{O_2} - FE_{O_2}) - \dot{V}_{CO_2}}{1 - FI_{O_2}}$$

where $\dot{V}_{O_2}$ is the animal's O_2 consumption; $\dot{V}_{CO_2}$ is CO_2 production; $\dot{V}E$ is flow out of the mask; FI_{O_2} is fractional concentration of O_2 in ambient air; FE_{O_2} is fractional concentration of O_2 in air leaving the mask. The power developed by both animals is nearly identical over the speed range common to both. Regression of $\dot{V}_{O_2}$ on running velocities between 2 and 28 km h^{-1} yields the following equations:

ostrich: $\dot{V}_{O_2} = 0.11x + 0.34$; $r^2 = 93\%$; $syx = 0.20$
horse: $\dot{V}_{O_2} = 0.15x + 0.14$; $r^2 = 96\%$; $syx = 0.34$

where x = running velocity in km h^{-1} and V_{O_2} is in ml O_2 (g h)$^{-1}$.
The slopes of these lines (T_{run}) are used as an index of cost of transport in Fig. 2. The horse data over the entire range of speeds (2–38 km h^{-1}) are better fit by a second degree polynomial:

$$V_{O_2} = 0.0016x^2 + 0.091x + 0.22; \quad r^2 = 97\%; \quad syx = 0.31.$$

b, Data as in *a* for two smaller animals: a bipedal bird (road runner, ⊗, 285 g) and a quadruped (ground squirrel, ●, 205 g). The upper line is that predicted for quadrupeds[2] and the lower is that for bipeds[3], both for animals of 245 g. The regression equations for each are:

road runner: $V_{O_2} = 0.59x + 2.2$; $r^2 = 73\%$; $syx = 0.26$
ground squirrel: $V_{O_2} = 0.64x + 2.0$; $r^2 = 91\%$; $syx = 0.33$.

(On the assumption that 1 ml O_2 consumed yields 20.1 J of energy, then 1 ml O_2 g^{-1}h^{-1} = 5.58 W kg^{-1}.)

Like resting metabolic rate, the energetic cost of locomotion in running animals varies in a regular way with body size. Taylor *et al.*[2] reported that cost of transport in quadrupeds (T_{run}, expressed in units of ml of O_2 (g km)$^{-1}$) decreases as body mass (M) increases, that is, $T_{run} = 8.5\ M^{-0.40}$. Taylor and Roundtree reported no difference in cost between two species of monkeys (3 and 17 kg) trained to run on both two and four legs. However, Fedak *et al.*[3] reported that bipeds in general showed a different allometric relationship with body mass ($T_{run} = 3.1M^{-0.24}$). Because of the relative magnitude of the two constants, the predictions for the metabolic power requirements were nearly identical for animals of 1 kg. However, small bipeds seemed to have a lower cost of transport than small quadrupeds. For example, for a 40-g animal, the predicted cost for a quadruped is 1.5 times that for a biped. Among large animals however, bipeds, not quadrupeds, seemed to face much larger energy costs. For a biped the size of *Aepeornis* (450 kg) the cost would be almost 3 times as high as for a similar-sized quadruped. If this difference in energy cost is extrapolated to animals the size of the largest bipedal dinosaurs (about 5,000 kg for *Tyrannosaurus*) the energy cost for bipeds would be more than 4 times that for quadrupeds. Palaeontologists have suggested, on morphological grounds, that some of the large bipedal dinosaurs were fast-moving cursors[5]. Extrapolations of energy-cost from these previously available data suggested either that the morphological evidence is misleading and these animals had low sustained speeds or that large bipeds had very high metabolic scopes and the means to dissipate heat very rapidly.

The data on which the differences between bipedal and quadrupedal locomotion were based were limited, particularly for larger animals. The largest quadruped for which data were available over a wide range of speed was the dog. Humans were the largest bipeds represented. We decided to make a direct comparison of the largest extant biped (the ostrich, *Struthio camelus*) with a quadruped of equal size (a small horse) to see if the predicted difference in cost of transport indeed existed. The prediction would be that the slope of the metabolic power versus speed curve for the ostrich would be twice that of the horse. This difference would be measured easily. In addition we present new data on a small bipedal bird, the road-runner (*Geococcyx californianus*, 285 g), and a quadrupedal ground squirrel (*Citellus tridecemlineatus*, 205 g).

A 103-kg female ostrich and two Shetland ponies (mean body mass, 107 kg) were trained to run on a motorised treadmill while we measured oxygen consumption using an open-circuit gas analysis system. The measurement system and calculations have been described previously (Fig. 1, ref. 3). Both animals ran on the same treadmill and their oxygen consumption was measured using the same system and identical methods during the same 2-month period. All data are for runs of 5 min or longer. The data for oxygen consumption are values below the animal's maximum oxygen consumption and represent the entire metabolic power developed by each of the animals for the ranges of speed for which data are included. The ostrich would run steadily for 5 min or longer at speeds of 3–28 km h^{-1}. The bird could run much faster for brief bursts but would not sustain

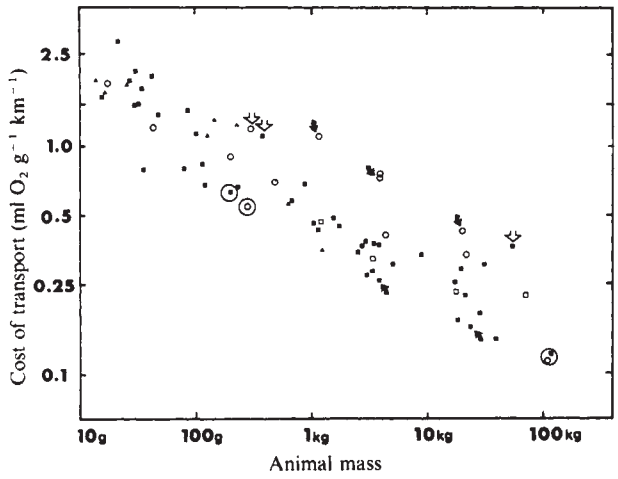

Fig. 2 T_{run}, an index of energy cost of running, plotted as a function of body size for 69 kinds of lizards (▲), birds (○) and mammals (□, ■). Bipeds are represented by open symbols and quadrupeds by solid symbols. The symbols for the road runner, ground squirrel, ostrich and horse are surrounded by circles. Solid arrows point to T_{run} data for penguins and geese at the top of the distribution and for dogs at the bottom of the distribution. Open arrows indicate the data for the white rat, tinamou and lion in order of increasing size. The most awkward-looking runners such as geese and penguins show the highest T_{run} for their size while fleet animals such as ground squirrels, dogs and horses, and the ostrich, show a low T_{run}. The slopes of the least square regression lines for bipeds and quadrupeds are not significantly different ($T = 0.2$ for $69-2$ degrees of freedom). The equation and regression statistics for the pooled data follow: $T_{run} = 3.89M^{-0.28}$. For the log-transformed data: $r^2 = 84\%$ (adjusted for 67 d.f.); $syx = 0.14$; s.d. of intercept = 0.05; s.d. of slope = 0.015. The data in this figure come from the following sources.

Animal	Weight (kg)	Ref.
Mammals (7)	2–18	2
Birds (7)	0.04–4	3
Capuchin	3.3	4
Chimpanzee	17.5	4
Lizards (8)	0.014–1.2	5
Mammals (5)	0.2–100	6
Marsupial	0.030	7
Rodent	0.027	7
Marsupials	0.015–1.1	8
Wallaby	3	9
Quakka	3	9
Lion	30	10
Lion	55	10
'Primitive' mammals (5)	0.12–5	11
Hopping mouse	0.037	12
Echidnas (2)	1.5–3.5	13
Human	70	14
Primates (3)	1–4	15
Penguins (3)	1–21	16
Mouse	0.030	17
Chimpanzee	17	17
Rhea	20	18
Mammals (3)	28–44	19
Dog	3	20
African hunting dog	9	20
Squirrel	0.086	21
Squirrel	0.079	22
Capuchin*	4	—
Plovers†	0.018	—

* Personal communication from S. A. Mahoney.
† Personal communication from P. Nicolyasen.

higher speeds long enough to get reliable metabolism measurements. The horse would run steadily at sustained speeds of 38 km h^{-1} without exceeding its maximum oxygen consumption as indicated by steady low blood-lactate concentrations.

Oxygen consumption accounts for all the metabolic power developed by an animal if there is no steady increase in whole-animal lactate even if individual muscles are producing lactate. We used blood lactate concentration as an index of whole-animal lactate content. Blood lactate in the ostrich never increased above 5 mM at the highest speeds we observed on the treadmill. Higher blood lactate levels (15 mM) could be measured if we caused the animal to run in its pasture towing the authors by a harness. The horse did not show continuously increasing blood lactate until it reached speeds of 38 km h^{-1}. At speeds above this, blood lactate increased continuously to levels of greater than 30 mM and oxygen consumption no longer increased. Details of horse blood lactate and maximum oxygen consumption can be found in ref. 6.

Similar methods were used to measure the oxygen consumption of the smaller animals (three ground squirrels and two road runners) except that the animals were run in ventilated chambers rather than wearing masks.

Figure 1*a* is a plot of the oxygen consumption of both the ostrich and the horses as a function of running speed. Dotted lines indicate values predicted by the equations currently presented in the literature for bipeds and quadrupeds of this size[2,3]. The relationship between metabolic power and speed was the same for both animals over the range of speeds they both would run. From 3 to 28 km h^{-1} the increase in power input with increasing speed is approximately linear. Data from both animals show an inflection in the function when they change from a walk to a run or trot. There is no obvious inflection in the power versus speed relationship when the horse changes from a trot to a gallop (at 17 km h^{-1}).

When the horses ran faster than 28 km h^{-1}, an increase in the rate of change of oxygen consumption with speed became apparent. Most animals, including the ostrich, cannot easily be trained to sustain the high oxygen consumption necessary to establish whether or not this is a general phenomenon. The value of T_{run} we used in Fig. 2 was always the slope of a straight line fitted to the metabolism data. In the case of a horse we only used the data up to 28 km h^{-1}. In all other animals the regression line was fitted to data from the entire range of speeds.

Regression lines relating predicted and observed metabolic power and running speed for two species of small bipeds and quadrupeds (road runner and ground squirrel) are presented in Fig. 1*b*. Metabolic power increases much more rapidly with speed in these small animals but again there is no difference between the slopes of the regression lines for the quadruped and the biped.

Comparison of all the energy cost of locomotion data now available for a wide variety of animals representing 66 species shows no consistent differences between cost for bipeds and quadrupeds of any size (Fig. 2). This figure includes cost data from reptiles, mammals and birds for various styles of terrestrial locomotion (sources of data in ref. 7). We include all animals for which we could find data over a speed range wide enough to determine a slope. For any given size animal, energy-cost may vary by a factor of nearly two. It is tempting to conclude that animals we tend to think of as cursorial, fast or graceful seem to fall near the lower end of the distribution for their size (that is horses and dogs) while animals we think of as awkward tend to fall high in the distribution (that is, geese and penguins) but this is only a subjective *a posteriori* impression. There are numerous animals represented which show similar costs with quite different styles of locomotion and vice versa (for example, compare the points for the white rat, tinamou and lion indicated by open arrows in Fig. 2). Note that the variation in cost for a given size is small compared to the over 15-fold variation seen between large and small animals. The decrease in energy cost of locomotion with increasing size first reported by Taylor *et al.*[2] is generally true for all types of terrestrial animal studied regardless of locomotory mode or taxonomic group and is thus of very general predictive value.

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Gut-associated microflora of *Limnoria tripunctata* in marine creosote-treated wood pilings

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The marine isopod *Limnoria tripunctata* is unique among wood borers in its ability to inhabit and severely damage creosote-treated wooden structures, yet little is known of the nature of this apparent resistance to creosote. When the animal is reared on untreated wood, its digestive tract appears to be free of microorganisms[2–6]. In contrast, we report here that microorganisms are readily observed in the digestive tract of *L. tripunctata* inhabiting creosote-preserved wooden pilings. Furthermore, isopods from such preserved wood apparently possess a resident gut microflora, which is in close association with the lining of the intestinal tract and is separated by a peritrophic membrane from other microorganisms ingested during wood boring.

Samples of *L. tripunctata* were collected at the US Naval Base at Roosevelt Roads, Puerto Rico in December 1976 and October 1977, from creosote-treated wooden pilings severely damaged by these wood borers. Specimens were preserved immediately and examined later by light and electron microscopy (Fig. 1).

The digestive system of *L. tripunctata* consists of an alimentary tract (mouth, gastric mill, tubular intestine and anus), and two bilobed diverticula which join the alimentary tract just behind the gastric mill[7]. Ingested wood and associated microorganisms were found in the alimentary tracts of *L. tripunctata* specimens examined; however, no ingested material or microorganisms were observed in the digestive diverticula. Gut contents were present in 12 of the 13 specimens examined, and consisted of minute pieces of wood and various prokaryotic microorganisms concluded to be bacteria (Fig. 1*a*). These bacteria attached by capsular material (that is, polysaccharides stained by ruthenium red) are presumed to represent the microflora growing on the surfaces of the creosote-treated wood of the pilings and isopod tunnels. Occasionally bacterial cell debris was observed; however, most of the gut microorganisms were intact and some cells were located in pits in the ingested wood (Fig. 1*a*, arrow). In contrast to wood fragments, ingested bacteria were not uniformly present throughout the gut, suggesting that their presence depended on whether the isopod had been feeding on superficial layers of wood that had been colonised by microorganisms or on the underlying layers of wood not subjected to microbial attack.

Reports of cellulase activity in the digestive diverticula of *L. tripunctata*[8,9], coupled with the absence of microorganisms in the digestive tract of isopods reared on unpreserved wood[2–6], indicate that *L. tripunctata* can derive nutrition from ingested wood without the aid of microorganisms. Wood is a nitrogen-poor food source and several investigators have suggested that ingested microorganisms supplement the diet of this isopod by providing an additional nitrogen source, essential amino acids and possibly other micronutrients[2,10]. However, there have been conflicting reports as to the ability of *Limnoria* to attack sterilised wood[11–14]. Our finding that numerous microorganisms are ingested by *L. tripunctata* during wood boring offers some support for a microbial role in the nutrition of this isopod.

The gut contents, including bacteria, were encased in a peritrophic membrane isolating the ingested material from the intestinal lining (Fig. 1*a*). The peritrophic membrane of arthropods, which is composed of chitin and protein, is thought to act as a barrier to mechanical abrasion, as well as microbial infection, of the gut epithelium[15–17]. This same membrane covers egested faecal pellets and may delay microbial attack of

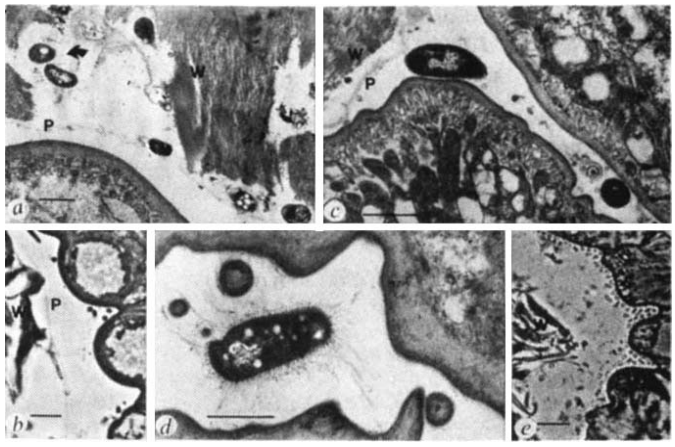

Fig. 1 Sections through the intestinal tract of *L. tripunctata* from creosote-treated wooden pilings at Roosevelt Roads, Puerto Rico. After fixation at the time of collection in a 1% gluteraldehyde solution in sterile seawater with 500 p.p.m. ruthenium red for 2–4 d at 4 °C, whole specimens or dissected digestive tracts were fixed for a further 3 h at 25 °C in 1% osmium tetroxide (0.1 M sodium cacodylate, *p*H 7.4), then dehydrated (acetone series) and embedded in a known orientation in Epon 812 epoxy plastic. Sections (1–5 μm) were collected, stained with 0.25% safranin (1 min, 60 °C) and examined by phase contrast light microscopy (*b*, *e*). In areas of interest thin sections (50–70 nm) were collected, stained with uranyl acetate and lead citrate and examined by electron microscopy (*a*, *c* and *d*). *a*, Ingested wood fragments (W) and associated bacteria separated from intestinal epithelium by the peritrophic membrane (P). Arrow denotes pit apparently formed by microbial wood digestion (scale bar, 1 μm). *b*, Gut-associated bacteria, in invaginations of the intestinal tract. Peritrophic membrane indicates border of gut contents (scale bar, 10 μm). *c*, Gut-associated bacteria in an invagination of the intestinal lining (scale bar, 1 μm). *d*, Gut-associated bacterium with electron transparent cytoplasmic inclusions and capsular fibrils; longer capsular fibrils connect to an intestinal microvillus in the gut invagination (scale bar, 1 μm). *e*, Abundant gut-associated bacteria lining intestinal wall and attached to periphery of gut contents in specimen in which peritrophic membrane was not completely intact (scale bar, 10 μm).

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