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Methane production in terrestrial arthropods

(methanogens/symbiosis/anaerobic protists/evolution/atmospheric methane)

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ABSTRACT **We have screened more than 110 representatives of the different taxa of terrestrial arthropods for methane production in order to obtain additional information about the origins of biogenic methane. Methanogenic bacteria occur in the hindguts of nearly all tropical representatives of millipedes (Diplopoda), cockroaches (Blattaria), termites (Isoptera), and scarab beetles (Scarabaeidae), while such methanogens are absent from 66 other arthropod species investigated. Three types of symbiosis were found: in the first type, the arthropod's hindgut is colonized by free methanogenic bacteria; in the second type, methanogens are closely associated with chitinous structures formed by the host's hindgut; the third type is mediated by intestinal anaerobic protists with intracellular methanogens. Such symbiotic associations are likely to be a characteristic property of the particular taxon. Since these taxa represent many families with thousands of species, the world populations of methane-producing arthropods constitute an enormous biomass. We show that arthropod symbionts can contribute substantially to atmospheric methane.**

Biopolymer degradation by anaerobic biota is responsible for most atmospheric methane, but there is still a considerable lack of knowledge about its sources and sinks (1, 2). A long-standing dispute concerns the potential contributions to atmospheric methane by methanogenic bacteria in the hindguts of insects (3–9). We systematically screened representatives of the different arthropod taxa for the presence of symbiotic methanogens to identify sources of atmospheric methane. Intestinal methanogens are easily found by gas chromatograph analyses of arthropod host emissions (5) because a single methanogenic bacterium may release as much as 1 fmol of methane per hr (10). Individual methanogenic bacteria can be detected microscopically by their characteristic blue autofluorescence (11). We expected to find methanogens in all arthropods, irrespective of their taxonomic position, that use cellulose-rich diets. We also anticipated the presence of protists with intracellular methanogenic bacteria in the intestinal tracts of the various arthropods. These findings permit an additional approach to calculate the potential contributions by arthropods to global methane concentrations.

MATERIALS AND METHODS

Animals and Their Diets. The arthropods were collected from their habitats or obtained from laboratory or zoo cultures (Table 1). They were subjected to measurements of gas emissions within 24–48 hr. For this period, the animals were fed their particular diet.

Screening Procedure. The living arthropods were placed into serum vials (50 or 250 ml) and sealed with butyl rubber stoppers. For 2–12 hr the arthropods (0.5–50 g fresh weight, depending on size and availability of specimens) were incubated at room temperature (21°C). The detection limit for methane was in the nmol range, guaranteeing that any significant methane emission could be detected by gas chromatography of gas samples taken at the end of the incubation period. Under these conditions, all methane-emitting species produced >100 nmol of methane during the incubation period. All nonproducers failed to produce methane concentrations higher than the background level (maximum, 10–20 nmol), even if the incubation time was prolonged and higher numbers of arthropods were incubated. Specimens of representative species of nonproducers were subjected to microscopic inspection (cf. Table 1); in all cases, the absence of methanogenic bacteria was confirmed. Small insects mining in wood were incubated *in situ* in heavily populated blocks of wood in 1-liter jars for prolonged periods (up to 1 week, with daily gas measurements).

Quantitative Gas Chromatographic Determinations. Determinations of methane were performed by using ethane as an internal standard (5). Continuous monitoring of the methane emission of the different cockroach species and millipedes with the aid of an experimental photoacoustic CO laser setup confirmed that the intestinal methane was released by breathing and that there was no significant drop of methane production over a period of 12 hr due to starving effects (12).

Microscopy. At least two specimens of each methane-emitting species were dissected in insect Ringer's solution (pH 6.8). The whole intestinal tract was inspected for unique structures and opened. Microbial symbionts were examined by means of phase-contrast and differential interference contrast optics. Aliquots of ingested food and pieces of the intestinal wall were studied with the aid of a fluorescence microscope (5, 11). Photographs were taken on Kodak Ektachrome P800/1600 professional film. No attempts were undertaken to identify protists and bacteria to the species level.

RESULTS

Methane Production as a Taxonomic Character. Table 1 shows that methane emission was restricted to Diplopoda, Blattaria, Isoptera, and Cetonidae. The representatives of the other arthropod taxa proved to be negative. Characteristically, nearly all tropical species belonging to a positive taxon emitted methane—regardless of the origin of the different specimens and the duration of culturing in captivity. However, several millipedes, cockroaches, and beetles, mainly from European temperate environments, failed to produce methane. Instead, they emitted hydrogen or neither of the two gases (Table 1). Furthermore, the competence for hosting of methanogens could be demonstrated in the pill millipede *Glomeris* sp., collected in a temperate deciduous forest (Table 1). While devoid of methanogens in its natural habitat, it emitted methane after cocultivation with African diplopods under laboratory conditions. By contrast, crickets and saw-

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Table 1. Screen for methane emission

Species	H_2	CH_4	Met	Hgut	Source
Araneae (spiders)					
*Araneus diadematus** (A)	+	−	ND	ND	Gr
Acari (mites and ticks)					
Boophilus microplus (A)	−	−	ND	ND	By
Isopoda (sowbugs)					
*Oniscus asellus** (A)	−	−	ND	ND	Ar, Gr, Re
Porcellio scaber (A)	−	−	ND	ND	By
Chilopoda (centipedes)					
Lithobius forficatus (A)	−	−	ND	ND	Gr
Diplopoda (millipedes)					
Chicobolus sp. (J)	+	+	M	No	Dü
Mestosoma hylaeicum (A)	−	−	No	No	Ma
Orthoporus sp. (J)	+	+	F+C	No	Ma
Pycnotropis acuticollis (A)	+	+	ND	ND	Ma
Rhapidostreptus virgator (A)	+	+	F+C	No	Gi
Unident. A (J)	+	+	F	No	Am
Unident. B (J)	+	+	F	No	Dü
Unident. D (J)	+	+	F+C	No	Dü
Unident. K (J)	+	+	F+(C)	No	Co
Glomeris sp.* (A)	+	−	No	Pou	Re
Julus sp.* (A)	−	−	No	No	Re
Polydesmus sp.* (A)	−	−	No	No	Re
*Tachypodojulus niger** (A)	−	−	ND	ND	St
Thysanura (bristletails)					
Lepisma saccharina (A)	−	−	ND	ND	By
Collembola (springtails)					
Folsomia candida (J, A)	−	−	No	No	By
Acrididae (short-horned grasshoppers)					
Locusta migratoria (A)	−	−	No	No	Ny, Dü
Schistocerca gregaria (A)	−	−	No	No	Dü
Unident.* (A)	−	−	No	No	Wy
Gryllidae (crickets)					
Acheata domesticus (A)	−	−	No	Brush	Ny, Dü
Decticus sp.* (A)	−	−	ND	ND	Re
Gryllus bimaculatus (A)	−	−	No	Brush	Ny, Dü
Ventralla quadrata (A)	−	−	ND	ND	Am
Phasmidae (stick and leaf insects)					
Eurycantha calcarata (A)	−	−	ND	ND	Dü
Pharnacia acanthopus (A)	−	−	ND	ND	Dü
Sipyloidea sipylus (A)	−	−	ND	ND	Dü
Mantidae (mantids)					
Hierodula membranacea (A)	−	−	ND	ND	Dü
Blattidae (cockroaches)					
Blaberus craniifer (A)	+	+	F+C	Brist	Ha, Co
Blaberus fuscus (L, A)	−	+	F+C	Brist	Dü, By, Bo
Blaberus giganteus (L)	+	+	F+C	Brist	Am
Blatta orientalis (A)	+	+	F	Brist	By
Blattella germanica (A)	+	+	F	Brist	Co, Fr
Blattella germanica (A)	+	−	No	Brist	Dü, Mg
Ectobius sp.* (A)	−	−	No	—	Gb
Gromphodorrhina portentosa (L, A)	+	+	F+C	Brist	Am, By, Co, Dü
Leucophaea sp. (A)	+	+	F	Brist	By, Dü
Panchlora nivea (A)	−	−	No	—	Am
Periplaneta americana (L, A)	−	+	F+C	Brist	Am, By, Dü, Ny
Periplaneta australasia (L, A)	+	+	F+(C)	Brist	Ar, Dü, Ha
Pycnoscelus surinamensis (L, A)	+	+	F+C	Brist	Ar, Dü
Supella supellectilium (L, A)	−	+	F+M	Brist	By
Isoptera (termites)					
Cryptotermes brevis (A)	−	+	ND	ND	Kr
Heterotermes indicola (A)	−	+	F+M	Pou	Kr
Mastotermes darwiniensis (A)	−	+	F+M	Pou	Kr
Reticulotermes santonensis (A)	−	+	F+M	Pou	Kr
Dermaptera (earwigs)					
*Forficula auricularia** (A)	−	−	ND	ND	Gr
Heteroptera (bugs)					
Dysdercus intermedius (L, A)	+	−	No	Pou	Co
Oncopeltus fasciatus (L, A)	−	−	ND	ND	Dü
Platymerus biguttata (A)	−	−	ND	ND	Am
Pyrrhocoris apterus (L, A)	−	−	ND	ND	Co
Cicadoidea (cicadas)					
Nephotettix cincticeps (A)	−	−	ND	ND	By
Aphididae (aphids)					
Aphis fabae (L, A)	−	−	ND	ND	By
Apidae (bees)					
Apis mellifera (A)	−	−	No	No	Gr
Carabidae (ground beetles)					
Carabus sp.* (A)	−	−	ND	ND	Re
*Pterostichus niger** (A)	−	−	ND	ND	Gr
Silphidae (carrion beetles)					
*Necrophorus vespillo** (A)	−	−	ND	ND	Gr
Dermestidae (Dermestid beetles)					
Dermestes frischi (A)	−	−	ND	ND	Ma
Tenebrionidae (darkling beetles)					
Oryzaephilus sp. (L, A)	−	−	ND	ND	Kr
Scarus tristis (L)	−	−	ND	ND	Dü
Tenebrio sp. (L)	−	−	ND	ND	Ny
Tribolium confusum (L, A)	−	−	ND	ND	By, Ny
Zophobas morio (L, A)	−	−	No	No	Ma
Cryptophagidae (silken fungus beetles)					
Alphitobius diapecurius (L, A)	−	−	ND	ND	By
Bostrychidae (branch and twig borers)					
Acanthocelides panaceae (L, A)	−	−	ND	ND	By
Rhizopertha dominica (L, A)	−	−	ND	ND	By
Sitophilus graminarius (L, A)	−	−	ND	ND	By
Anobiidea (death-watch beetles)					
Anobium punctatum (L)	−	−	ND	ND	Kr
Oligomerus ptilinoides (L)	−	−	ND	ND	Kr
Ptilinus pectinicorni (L)	−	−	ND	ND	Kr
Stegobium panaceum (A)	−	−	ND	ND	By
Xestobium rufovillosum (L)	−	−	ND	ND	Kr
Lyctidae (powder-post beetles)					
Lyctus africanus (L)	−	−	ND	ND	Kr
Lyctus brunneus (L)	−	−	ND	ND	Kr
Minthea rugicollis (L)	−	−	ND	ND	Kr
Dynastinae (rhinocers beetles)					
Dynastes hercules (L)	+	+	F+M	Brush	Dü
Cetoniidae (rose chafers)					
Cetonia aurata (L)	+	+	F+M	Brush	Am
Dicronorrhina micans (L)	+	+	F+M	Brush	Am
Eudicella gralli (L, A)	+	+	F+M	Brush	Ha
Eudicella smittii (L)	+	+	F+M	Brush	Am
Pachnoda bhutana (L, A)	+	+	F+M	Brush	Co, Ha
Pachnoda ephippuata (L)	+	+	F+M	Brush	Am
Pachnoda marginata (L)	−	+	F+M	Brush	Dü
Pachnoda nachtigalli (L, A)	−	+	F+M	Brush	Dü
Pachndoa savignyi (L, A)	−	+	F+M	Brush	Dü
Potassia cuprea (L, A)	+	+	F+M	Brush	Ha
*Phyllopertha horticola** (A)	−	−	No	Pou	Gr
Geotrupinae (dung beetles)					
Geotrupes sp.* (A)	+	−	ND	ND	Re
Geotrupes sp.* (A)	−	−	ND	ND	Gr
Cerambycidae (longhorn beetles)					
Hylotrupes bajulus (L)	−	−	No	No	Kr
Chrysomelidae (leaf beetles)					
*Crioceris asparag** (A)	−	−	ND	ND	Gr
Diabrotica baltea (A)	−	−	ND	ND	By
Leptinotarsa decemlineata (A)	+	−	ND	ND	Gr
Phaedon cochleariae (L, A)	+	−	ND	ND	By
Curculionidae (weevils)					
Otiorrhynchus sulcatus (A)	+	−	ND	ND	By
Lepidoptera (butterflies and moths)					
*Aphomia sociella** (L)	+	−	No	No	Un
Bombyx mori (L)	−	−	ND	ND	Ny
Caligo memnon (L)	−	−	ND	ND	Dü
Danaus plexippus (L)	+	−	ND	ND	Co
Ephestia kühniella (L)	−	−	ND	ND	Co
*Galleria mellonella** (L, A)	−	−	No	No	Gr
Heliotis virescens (L)	−	−	ND	ND	By
*Pieris brassicae** (L)	−	−	ND	ND	Gr
Plutella xylostella (L)	−	−	ND	ND	By
Spodoptera frugiperda (L)	−	−	ND	ND	By
Trabala vishnou (L)	−	−	ND	ND	Dü
Diptera (flies)					
Hylemyia antiqua (L)	−	−	No	No	By
Musca domestica (P, A)	−	−	No	No	By
Tipula sp.* (L)	+	−	No	Pou	Gr
Siphonaptera (fleas)					
Ctenocephalides felis (L)	−	−	ND	ND	By

A, adult; J, juvenile; L, larva; P, pupa; Met, methanogens; F, free methanogenic bacteria in the hindgut; C, ciliates with intracellular methanogens; M, mastigotes, with or without intracellular methanogens; ( ), small numbers of protists; Hgut, hindgut differentiations; Pou, pouch, dilated hindgut; bristles (Brist) and brushes (Brush) include the presence of a pouch (cf. Fig. 1); ND, not determined; No, absent; +, gas emission; −, no gas emission. Am, Artis, Amsterdam, The Netherlands; Ar, Burgers Zoo, Arnhem, The Netherlands; Bo, Zoology Dept., Bochum, Germany; By, Bayer AG, Monhein, Germany; Co, Zoology Dept. or Zoo, Cologne, Germany; DS, Dar-es-Salaam, Tanzania, kept at Nijmegen, The Netherlands; Dü, Löbbecke Museum, Düsseldorf, Germany; Fr, France, kept at By; Gb, Griether Busch, Zoology Inst., Griether Busch, Germany; Gi, Zoology Dept., Giessen, Germany; Gr, Groesbeek, The Netherlands; Ha, Hortus, Haren, The Netherlands; Kr, Desowag AG, Krefeld, Germany; Ma, Zoology Dept., Marburg, Germany; Mg, Mönchengladbach, Germany; Ny, Zoology Dept., Nijmegen, The Netherlands; Re, Reichswald, Germany; St, Zoology Dept., Stuttgart, Germany; Un, Unna, Germany; Wy, Wyler, Germany.
*Endemic European species from the field.

bugs could not be "infected" with methanogens by either cocultivation or feeding with methane-emitting cockroaches.

Localization of the Methanogenic Bacteria. The methanogens were found exclusively in the hindgut of their arthropod hosts, posterior to the junction of the Malpighian tubes. In nearly all cases, the hindguts of the methane-positive species revealed distinctive differentiations—i.e., the gut was dilated to form a kind of pouch (Table 1). The Julidae (Diplopoda) seemed to be the only exception. In most cockroach species, the inner surface of the hindgut was covered with chitinous bristles that projected into the lumen of the paunch (Table 1; Fig. 1). These bristles were covered with a mucous layer containing complex bacterial biota. Complex, lampbrush-shaped support structures for numerous methanogenic bacteria were seen in the hindguts of all rose chafers (Cetoniidae) (Table 1; Fig. 1). Counts of the number of brushes per hindgut and the biometrical analysis of individual brushes suggest that these hollow, cuticular structures increase the surface of the hindgut by an order of magnitude.

Methane Production and Protist Symbionts. Whereas all methane-emitting species harbored methanogenic bacteria, the presence of protists with methanogenic endosymbionts was limited (Table 1). Many cockroach species and some millipedes harbored ciliates of the *Nyctotherus* type (Fig. 1). These carried >4000 methanogens per ciliate cell. Methanogens were also found in their cysts. The cockroach *Supella supellectilium* harbored small mastigotes containing intracellular methanogens, while most mastigotes of the termites *Mastotermes darwiniensis*, *Reticulotermes santonensis*, and *Heterotermes indicola* and most of the rose chafers (Cetoniidae) were devoid of intracellular methanogens (Table 1).

Quantitative Aspects of Methane Production. Quantitative determinations of methane production revealed a considerable variation between the individuals, the sexes, the different developmental stages, and the different populations. The large standard deviations of the methane measurements of several cockroach species shown in Table 2 indicate the extent of these variations; they have biological and no experimental reasons. Cockroach species with substantial numbers of intestinal protists consistently produced methane at significantly higher rates (Table 2). Measurements of several species of diplopods (with and without intestinal protists) gave comparable results (data not shown).

DISCUSSION

Numerous symbiotic associations between bacteria and arthropods have been described emphasizing their role in the host's nutrition (13). However, no simple relationship between the presence of methanogenic symbionts and the preferential diet of their hosts seems to exist (Table 1). Our study shows that symbiotic associations between methanogens and arthropods are rare and that they are not randomly distributed over the different taxa of arthropods; methane

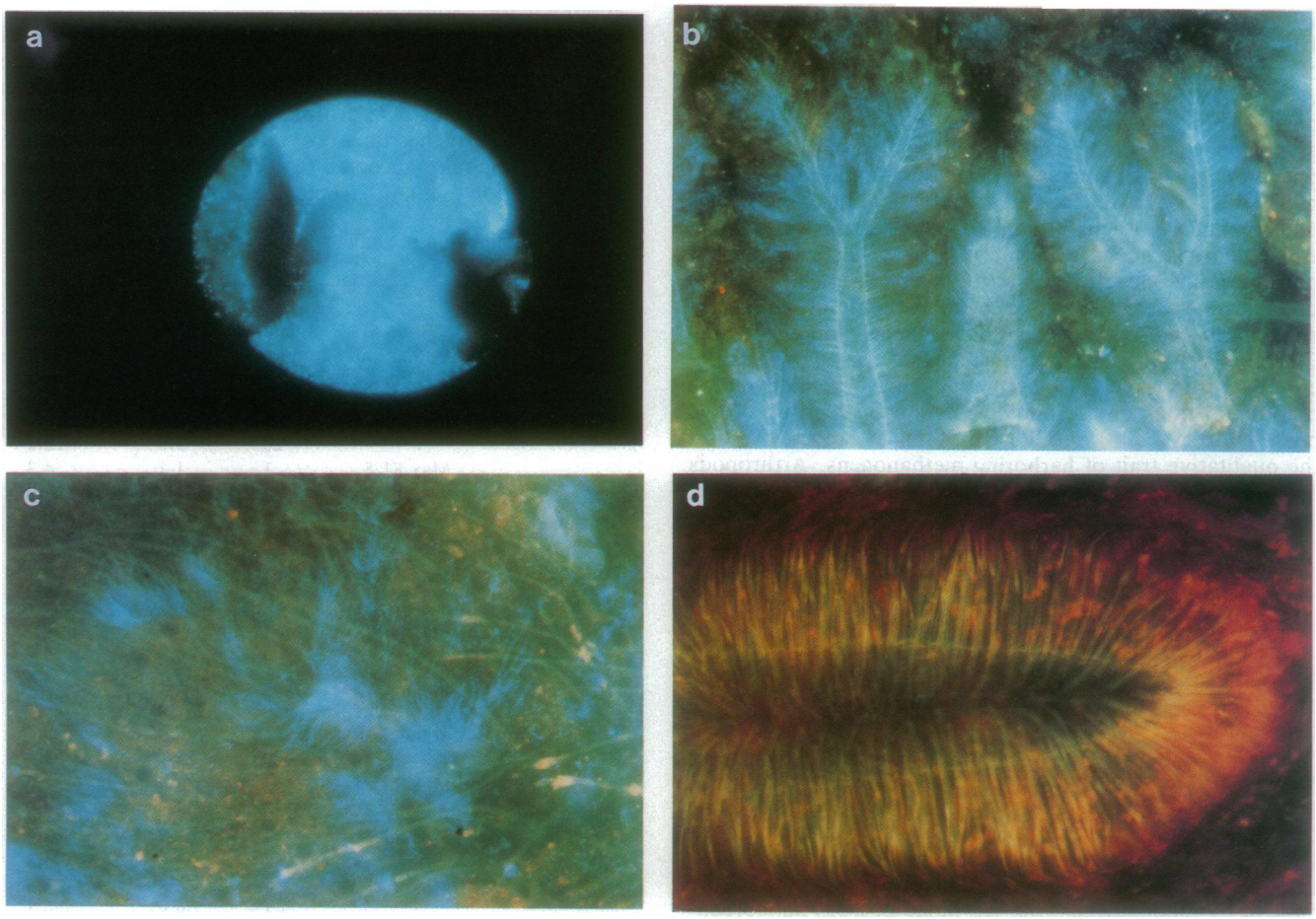

FIG. 1. Different types of symbiosis between methanogens and arthropods, as seen with the epifluorescence microscope. (*a*) Ciliate of the *Nyctotherus* type from the hindgut of a big, African diplopod (unident. D in Table 1). It carries >4000 endosymbiotic methanogens, which exhibit a strong blue autofluorescence. (*b*) Lampbrush-like brushes (light fluorescence of chitinous structures) from the paunch of *Pachnoda marginata* carry numerous methanogenic bacteria (blue fluorescence). (*c*) Free methanogens are also found in the hindguts of cockroaches, frequently loosely associated with the chitinous bristles covering the inner surface of the hindgut. (*d*) Gryllidae also possess brush-like supports for bacteria in their hindguts. In contrast to the Cetoniidae, they never harbor methanogens as documented by the absence of any blue fluorescence and the lack of methane emissions.

Table 2. Methane production by different cockroach species

	Mean	SD	Max	*n*	S	Protists
Blaberus sp.*	49	27	109	9	6	Ciliates
Blatta orientalis	22	9	36	5	1	No
Blattella germanica (Co)†	31	—	—	1	1	No
Gromphodorrhina portentosa	49	27	107	8	4	Ciliates
Leucophea sp.	18	9	28	2	1	No
Periplaneta americana	85	67	255	11	5	Ciliates
Periplaneta australasia	31	18	49	6	3	(Ciliates)/ no‡
Pycnoscelus surinamensis	80	71	268	13	2	Ciliates
Supella supellectilium	49	31	80	2	1	Mastigotes

Mean, mean of methane production rates (nmol per g fresh weight per hr); SD, standard deviation; Max, maximum value of methane production measured in the course of our experiments; *n*, number of independent measurements; S, number of different strains (see Table 1); Protists, predominant protists with intracellular methanogens.
*_Blaberus_ sp. indicates pooled data from _Blaberus cranifer_ and _Blaberus fuscus_ (likely to be the same species) and from _Blaberus giganteus_ that is very similar to the other species.
†Strain Cologne.
‡Two strains harbored only small numbers of ciliates; one did not host any.

emission is restricted to Diplopoda, Blattidae, Isoptera, and Scarabaeidae. Because of the enormous number of arthropod species, we cannot exclude additional taxa as methane producers, especially tropical species, after an extended search. However, the absence of methanogens from a large number of species with diets similar to those of methane producers clearly demonstrates the importance of the host's taxonomic position and suggests evolution of the symbiosis between arthropods and methanogens. An inspection of fossil arthropods in Dominican amber supports this interpretation: only millipedes, cockroaches, and termites exhibit gas bubbles that are closely attached to the abdomens or spiracles of the embedded specimens. (Larvae of scarab beetles were not present in the collection.) The studies of Brauman *et al.* (6) on 24 termite species show that, with 2 exceptions, all species studied emitted methane regardless of the type of feeding. Quantitative differences between the various methane-emitting insect species (6) and influences of the diets on the production rates or the number of intestinal protists have been reported (5, 14), but these differences are irrelevant to the qualitative trait of harboring methanogens. Arthropods not belonging to a "positive" taxon failed to emit methane, and fluorescence microscopy revealed no methanogenic bacteria in locusts and crickets, springtails, bugs, bees, beetles, butterflies, and flies (Table 1). Some species (and populations) of diplopods, cockroaches, and termites do not emit methane (Table 1; cf. ref. 6), probably due to a secondary loss of the methanogens. The absence of methanogens in millipedes and cockroaches in temperate European climates may reflect the sensitivity of intestinal methanogens for low temperatures.

The absence of methane emissions does not imply an equivalent release of hydrogen (Table 1). Rather, the hydrogen generated by intestinal fermentation is used by other bacteria. Consequently, the availability of an anaerobic environment and even the presence of a highly differentiated intestine do not suffice to guarantee colonization of the hindgut by methanogens; the Gryllidae possess lampbrush-like supports similar to those of the Cetoniidae (Fig. 1), but all species tested by us were devoid of methanogens (Table 1).

The significance of enteric protists for insect phylogeny has been discussed (15), since most termites and the woodroach *Cryptocercus* harbor large polymastigotes (16, 17), while many cockroaches and diplopods harbor ciliates of the *Nyctotherus* type (Table 1; cf. refs. 5, 18, 32, and 33). The nonrandom distribution of intestinal protists among the different taxa suggests a high specificity in the symbioses. The presence of intestinal protists is nonobligatory, but acquisition of protists carrying intracellular methanogens improves the methane release in millipedes and cockroaches (refs. 5 and 19; Table 2). Among the termites, complex biota consisting of free methanogens and dense populations of distinguishable protists, with and without intracellular methanogens, comparably impact the methane production rates. The presence of elaborated hindgut differentiations of the Cetoniidae apparently allows an increase in methane production (Table 3).

Table 3. Mean methane production by higher taxa

	Mean	SD	Max	*n*	S
Diplopoda	58	121	415	11	6
Blattidae	46	32	268	57	9
Isoptera	380	317	808	3	3
Cetoniidae	255	214	741	19	7

Mean, mean of methane production rates (nmol per g fresh weight per hr); SD, standard deviation; Max, maximum value of methane production measured in the course of our experiments; *n*, number of independent measurements; S, number of different species (see Table 1).

The fact that most tropical arthropod species belonging to the four positive taxa emit methane offers an additional approach for estimation of the global fluxes of methane. Laboratory measurements of methane production allow the calculation of an average value for a whole taxon that bears fewer uncertainties for the global estimation than other approaches (Tables 2–4; cf. ref. 1). The biomass and abundance data for higher taxa provided by the ecological literature are generally accepted (21–30), and the restriction of our calculation to humid, tropical, and subtropical areas (20)

Table 4. Estimation of global annual methane production by arthropods

	Annual production, $ml \cdot g^{-1} \cdot year^{-1}$	Biomass, $g \cdot m^{-2}$	Tropical forests,* Tg/year	Humid tropics/subtropics Tg/year†
Diplopoda	Mean 11.4	1	0.15	0.61
		20	3.0	12.1
	Max 81.5	1	1.1	4.3
		20	21.4	86.9
Blattidae	Mean 9.6	1	0.12	0.51
		10	1.3	5.1
	Max 52.6	1	0.7	2.8
		10	6.9	28.0
Isoptera	Mean 74.5	1	0.98	5.6
		6	5.9	23
	Max 158.6	1	2.1	8.5
		6	12.3	50.7
Scarabaeidae	Mean 49.9	1	0.66	2.7
		20	13.1	53.1
	Max 145.4	1	1.9	7.7
		20	38.2	154.9
Sum	Mean	1	1.9	9.4
		>1	23.3	93.3
	Max	1	5.8	23.3
		>1	78.8	320.4

Annual production is based on laboratory measurements shown in Table 3. Mean is based on average production rates; Max is based on maximum production rates measured in the laboratory; these values are lower than most of the values given in the literature. For biomass, low and high data were used; they were derived from refs. 21–30.
*Tropical forests occupy an area of 18.5×10^{12} m^2 (20).
†Humid tropics and humid subtropics occupy 75×10^{12} m^2 (20).

leaves the possibility for additional biogenic sources in the arid and temperate areas. Earlier global estimations considered only the potential contributions by termites estimated between 25 and 150 Tg/year (1). Our calculations for termites fit well into this range, but our studies reveal three more taxa of methane producers that contribute additional, significant quantities (Table 4). In preliminary experiments, no significant oxidation of methane by the surface litter layer of a deciduous forest was found, making it unlikely that significant amounts of arthropod methane are oxidized shortly after release. Furthermore, our data might suggest that the increase of atmospheric methane during the past 2 centuries (1, 2) might be caused in part by anthropogenic ecological changes that favored the expansion of methane-producing arthropods (7, 29). Since important sinks for methane, like forest soils and wetlands, are also affected by anthropogenic activities, we speculate that the recent slowing of the global methane increase witnesses the ecological consequences of the rapid global deforestation rather than a putative increase of methane degradation by anthropogenic OH radicals (31).

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