Comp. Biochem. Physiol. Vol. 75A, No. 3, pp. 313–324, 1983
Printed in Great Britain

0300-9629/83 $3.00 + 0.00

MINIREVIEW

CELLULOSE DIGESTION IN INSECTS

MICHAEL M. MARTIN
Division of Biological Sciences, University of Michigan, Ann Arbor, MI 48109, USA

(*Received* 20 *September* 1982)

Abstract—1. Cellulose digestion has been demonstrated in the Thysanura (Lepismatidae), Orthoptera (Cryptocercidae, Blattidae), Isoptera (Mastotermitidae, Kalotermitidae, Hodotermitidae, Rhinotermitdae, Termitidae), Coleoptera (Buprestidae, Anobiidae, Scarabaeidae, Cerambycidae), and Hymenoptera (Siricidae).

2. In all but the scarab beetles, cellulose digestion is brought about by a complex of three types of enzymes (C_1-cellulases, C_x-cellulases, and cellobiases), as in fungi.

3. Many insects are able to synthesize their own C_x-cellulases and cellobiases, but few (if any) can synthesize C_1-cellulases.

4. Insects compensate for their inability to synthesize C_1-cellulases by exploiting the cellulolytic potential of protozoa, bacteria, or fungi.

5. The maintenance of permanent populations of hindgut protozoa, the maintenance of permanent populations of hindgut bacteria, and the ingestion of fungal cellulases are described as three distinct mechanisms by which insects have been shown to use the cellulolytic potential of microorganisms.

6. A process in which ingested cellulolytic bacteria proliferate in one region of the gut at the expense of ingested cellulose, only to be digested and assimilated in a more posterior section, is a fourth possible mechanism by which insects might accomplish the digestion of cellulose with the help of microorganisms.

INSECTS THAT DIGEST CELLULOSE

The ability of many insects to thrive on wood, foliage and detritus has naturally stimulated investigations of the extent to which such species are able to digest the structural polysaccharides in their food. Species that have been shown to possess a capacity to digest cellulose are listed in Table 1. Based upon the values of the approximate digestibilities or assimilation efficiencies that have been determined for a few species, it appears that termites are more efficient cellulose digesters than the wood-boring beetles and siricid wood wasps. The silverfish, *Ctenolepisma lineata*, and the American cockroach, *Periplaneta americana*, are omnivorous species that readily include both cellulosic and non-cellulosic items in their diets. The rest of the species listed in Table 1 are wood-feeders. Foliage and detritus-feeders are conspicuously absent. No evidence for significant digestion of cellulose by foliage-feeding Orthoptera, Coleoptera or Lepidoptera or by detritus-feeding Plecoptera, Coleoptera, Diptera or Trichoptera has been reported, although low levels of hydrolytic activity toward cellulose powder have been detected in the gut fluids of a few species of locusts (Evans & Payne, 1964; Morgan, 1975a, 1976). The grasshopper, *Melanoplus bivittatus*, is able to degrade hypocotl cell walls of bean seedlings, but there is no evidence to indicate that cellulose is among the cell wall constituents digested (Talmadge & Albersheim, 1969). The absence of any enzymatic activity toward cellulose powder in the digestive fluids of a number of Lepidopteran larvae has been noted (Shinoda, 1930; Babers & Woke, 1937; Mathur, 1966; Chattoraj & Mall, 1969; Khan & Kasting, 1969; Burton *et al.*, 1977; Dixit & Mall, 1978; Mall *et al.*, 1978). McGinnis & Kasting (1969) conclusively demonstrated the inability of the pale western cutworm, *Agrotis orthogonia*, to digest cellulose by observing that less than 0.5% of the carbon-14 from ingested labelled cellulose was respired in the form of $^{14}CO_2$. Although wood-feeders dominate the list of cellulose digesters, there are many species of insects which feed upon bark, phloem tissue, and wood that are unable to digest the cellulose they consume. Beetles from the families Bostrychidae, Curculionidae, Lyctidae and Scolytidae exemplify such species (Parkin, 1940; Chararas, 1979).

THE CELLULOLYTIC ENZYMES OF INSECT GUT FLUIDS

Cellulose digestion in insects is generally accomplished by a collection of enzymes believed to be similar to the ones responsible for cellulolytic ability in fungi (Table 2). The "cellulase complex" includes three major classes of hydrolytic enzymes: endoglucanases (C_x-cellulases), cellobiohydrolases (C_1-cellulases), and β-glucosidases (cellobiases) (Reese & Mandels, 1971; Wood & McCrae, 1979; Ghose *et al.*, 1981). The digestion of native cellulose is believed to be initiated when endoglucanases attack isolated amorphous regions of the predominantly crystalline cellulose matrix, creating nick sites in the linear cellulose chains. The cellobiohydrolases attack at the nick sites liberating cellobiose, exposing additional potential sites for attack by the endoglucanase, and generally disrupting the highly ordered structure of the cellulose aggregates. The continued combined action of the C_1- and C_x-cellulases results in the eventual complete degradation of the original cellulose and the production of cellobiose and a mixture of soluble linear oligosaccharides of varying chain lengths. The cellobiose, which is a potential inhibitor of the C_1- and C_x-cellulases, is hydrolyzed to glucose by cellobiase, and the various oligosaccharides are further degraded, ultimately to glucose, by the action of both the C_x-cellulases and the cellobiases. Thus, the utilization of cellulose is dependent upon the concerted and synergistic action of three types of enzymes. If any one of the three is missing, cellulose digestion cannot occur.

The presence of a complete cellulase complex in an insect's digestive juices is indicated by the capacity of the gut fluid or a cell-free extract of gut contents to liberate reducing sugars from, or to solubilize such forms of crystalline cellulose as, Avicell®, filter paper or cotton. The presence of the entire cellulase complex is generally taken as evidence for the presence of enzymes comparable to the C_1-cellulases of fungi, that is enzymes specific for crystalline cellulose. It is now common practice to refer to such enzyme from insect gut fluids as C_1-cellulases, although to date none has actually been shown to be a cellobiohydrolase. Digestive C_x-cellulases are conveniently detected in insects by assaying gut fluids for the capacity to degrade carboxymethylcellulose (CMC) or some form of swollen, amorphous, or reprecipitated cellulose. Cellobiase activity is readily assayed by measuring the capacity of gut fluid to hydrolyze cellobiose to glucose.

When subjected to the appropriate assay procedures, gut fluids from a number of cellulose digesting insects have been found to exhibit activity attributable to C_x-cellulases, C_1-cellulases, and cellobiases. One notable exception is the scarab beetle, *Oryctes nasicornis*, in which no soluble cellulases of any kind have been detected. In this insect, cellulose digestion is thought to be brought about by hindgut bacteria (Bayon & Mathelin, 1980). The cellulase complex of bacteria consists of only two principal components, endoglucanases or C_x-cellulases and β-glucosidases or cellobiases. Cellobiohydrolases or C_1-cellulases have been demonstrated in only a few species of bacteria (Ghose *et al.*, 1981). Furthermore, bacteria produce cell-bound as well as extracellular enzymes. The failure to detect any cellulases in the gut fluids of *O. nasicornis* could be explained if cellulose digestion is accomplished by the cell-bound enzymes of bacteria that are attached to the fragments of plant tissue present in the insect's hindgut, and not by soluble enzymes presented in the gut fluids. This species provides an emphatic reminder that the failure to detect cellulolytic activity in an insect's digestive fluids is not compelling evidence against the digestion of dietary cellulose, especially in species with abundant populations of bacteria housed in enlarged segments of the gut.

THE SECRETION OF THE ENZYMES OF THE CELLULASE COMPLEX BY INSECTS

Table 3 is a comprehensive tabulation of insect species in which C_x-cellulase activity has been demonstrated in the gut fluids by assays using CMC or a

Table 1. Cellulose digesting insects

Order Family Species	Evidence for capacity to digest cellulose	References
THYSANURA		
Lepismatidae		
Ctenolepisma lineata	AD (72–87), ^{14}C, EN, NU	Lasker & Giese (1956)
ORTHOPTERA		
Cryptocercidae		
Cryptocercus punctulatus	EN, NU	Cleveland *et al.* (1934)
Blattidae		
Periplaneta americana	^{14}C	Bignell (1977)
ISOPTERA		
Mastotermitidae		
Mastotermes darwiniensis	EN	Veivers *et al.* (1981)
Kalotermitidae		
Kalotermes flavicollis	AD (74–91)	Seifert & Becker (1965)
Neotermes bosei	EN	Mishra (1979)
Hodotermitidae		
Zootermopsis angusticollis	AD (82), EN	Trager (1932); Hungate (1938)
Rhinotermitidae		
Coptotermes formosanus	^{14}C	Mauldin *et al.* (1972)
Heterotermes indicola	AD (78–89)	Seifert & Becker (1965)
Reticulitermes flavipes	AD (91), ^{14}C, EN, NU	Trager (1932); Esenther & Kirk (1974); Mauldin (1977)
R. lucifugus	AD (96–99), EN, NU	Seifert & Becker (1965); Orlova (1974)
R. speratus	EN, NU	Orlova (1974); Yamaoka & Nagatani (1975)
Termitidae		
Macrotermes natalensis	EN	Martin & Martin (1978, 1979)
M. subhyalinus	EN	Abo-Khatwa (1978)
Nasutitermes ephratae	AD (91–97)	Seifert & Becker (1965)
Trinervitermes trinervoides	EN	Potts & Hewitt (1973, 1974a,b)

Table 1—*continued*

Order Family Species	Evidence for capacity to digest cellulose	References
COLEOPTERA		
Buprestidae		
Capnodis sp.	EN	Rivnay (1945)
Chalcophora mariana	EN	Schlottke (1945)
Anobiidae		
Anobium punctatum	AD (33), EN	Parkin (1940); Spiller (1951)
A. striatum	AD (31)	Müller (1934)
Ernobius mollis	EN	Parkin (1940)
Ptilinus pectinicornis	EN	Parkin (1940)
Xestobium rufovillosum	AD (49), EN	Norman (1936); Parkin (1940)
Scarabaeidae		
Oryctes nasicornis	AD (68), ^{14}C	Rössler (1961); Bayon & Mathelin (1980)
Sericesthis geminata	EN	Soo Hoo & Dudzinski (1967)
Cerambycidae		
Acanthocinus aedilis	EN	Schlottke (1945)
Aegosoma scabricornae	EN	Ivanovic & Barbic (1966)
Cerambyx cerdo	EN	Ripper (1930); Müller (1934)
Ergates faber	EN	Schlottke (1945); Chararas & Libois (1976)
Gracilia minuta	AD (33)	Müller (1934)
Hylotrupes bajulus	AD (12–21)	Falck (1930); Becker (1942)
Leptura rubra	AD (33)	Müller (1934)
Macrotoma palmata	AD (14–47)	Mansour & Mansour-Bek (1934a)
Morimus funerus	EN	Ivanovic & Barbic (1966)
Oxymirus cursor	AD (49), EN	Müller (1934)
Phymatodes testaceus	EN	Parkin (1940)
Plagionotus detritus	EN	Schlottke (1945); Ivanovic & Barbic (1966)
Rhagium bifasciatum	EN	Ripper (1930); Müller (1934)
R. inquisitor	EN	Deschamps (1944); Schlottke (1945)
R. mordax	EN	Parkin (1940); Schlottke (1945)
Saperda populinae	EN	Schlottke (1945)
Smodicum cucujiforme	EN	Parkin (1940)
Stromatium barbatum	AD (30–57), EN	Mishra & Singh (1978)
S. fulvum	EN	Mansour & Mansour-Bek (1937)
Xylotrechus rusticus	EN	Parkin (1940)
HYMENOPTERA		
Siricidae		
Sirex cyaneus	EN	Kukor & Martin (1983)
S. gigas	AD (22)	Müller (1934)
S. phantoma	AD (31)	Müller (1934)

Abbreviations: AD, cellulose digestion demonstrated by comparing the cellulose contents of food and frass; the number in the parenthesis is the approximate digestibility of cellulose; ^{14}C, cellulose digestion demonstrated by noting the production of $^{14}CO_2$ or the incorporation of ^{14}C into tissues following ingestion of U-^{14}C-cellulose; EN, gut fluid demonstrated to possess the enzymatic capacity to degrade filter paper, cotton, Avicell® or some other form of crystalline cellulose; NU, ability to digest cellulose inferred from capacity to survive on a diet of pure cellulose.

suitable form of amorphous cellulose as the test substrate. It is a long list that includes not only familiar cellulose-digesting species, such as termites, wood roaches and cerambycid beetles, but also many species from groups which are not thought to be capable of assimilating cellulose. In a number of the investigations summarized in Table 3, C_x-cellulase activity was found to be present in extracts of salivary glands and midgut tissues, indicating that the enzymes were produced by the insects and not by microbial symbionts residing in the gut. C_x-cellulases of insect origin have been demonstrated in 17 species of roaches, 8 termites, and 31 aphids. To be sure, in many of the species listed, C_x-cellulase activity is low may be due to enzymes which normally exert their catalytic action on non-cellulosic poly- or oligosaccharides. Nonetheless, it seems clear that the presence of enzymes with C_x-cellulase activity is not unusual in insect gut fluids, and that the rather restricted occurrence of the ability to digest cellulose in insects is not due to the restricted distribution of this class of enzymes.

Cellobiase activity has also been detected in the gut fluids of a diverse array of insect species, both digesters and non-digesters of cellulose, and has been demonstrated in extracts of salivary glands or midgut tissues from 2 species of locusts, 6 termites, one pyrrhocorid bug, the larvae of one sciarid fly, and even from silkworms (Table 4). β-Glucosidase activity has been detected in the gut fluids, gut tissues, and salivary glands of many additional species, and it is very probable that cellobiose would be hydrolyzed by the digestive fluids of many of these species as well. Thus, the presence of enzymes able to hydrolyze cellobiose are of common occurrence in insects, and the inability of most insects to digest cellulose cannot be attributed to the narrow distribution of the requisite cellobiases.

Table 2. Enzymes of cellulose digestion in fungi and probably also in insects

Enzyme (Alternate designations)	Mode of action and products	Substrates
The cellulase complex	A combination of the three categories of enzymes designated below, which brings about the complete digestion of native cellulose to glucose.	Microcrystalline cellulose powder, Avicell®, cotton, and filter paper.
1,4-β-D-Glucan 4-glucanohydrolase (EC 3.2.1.4) (Endo-β-1,4-Glucanase) (Endoglucanase) (Carboxymethylcellulase) (CMCase) (C_x-Cellulase)	Random attack on β-1,4-glucosidic bonds, generating transient cellodextrins, cellobiose, and glucose.	CMC and other soluble derivatives of cellulose, phosphoric acid swollen cellulose, and cellodextrins (increasing activity with increasing chain length). No activity toward crystalline cellulose. Hardly any activity toward cellobiose.
1,4-β-D-Glucan cellobiohydrolase (EC 3.2.1.91) (Cellobiohydrolase) (C_1-cellulase)	Removal of cellobiose units from the non-reducing end of a linear chain by attack on penultimate β-1,4-glucosidic bonds.	Microcrystalline cellulose powder, Avicell®, cotton, swollen cellulose, and cellodextrins (increasing activity with increasing chain length). Limited activity toward CMC.
1,4-β-D-Glucoside 4-glucohydrolase (EC 3.2.1.21) (β-D-Glucosidase) (Cellobiase)	Hydrolysis of the β-1,4-glucosidic bond of cellobiose to generate glucose.	Cellobiose, other β-linked disaccharides of glucose, and cellodextrins. No activity toward cellulose.

Table 3. Insects with digestive C_x-cellulases

Insect Order Family Species	Capacity to digest cellulose	Identified sources of C_x-cellulases in digestive fluids	References
ORTHOPTERA			
Cryptocercidae			
Cryptocercus punctulatus	High	SG, HGP	Trager (1932); Wharton & Wharton (1965)
Blattidae			
Blatta orientalis	Unknown	SG	Wharton & Wharton (1965)
Periplaneta americana	Moderate	SG, GB	Wharton & Wharton (1965); Cruden & Markovetz (1979)
P. australasiae	Unknown	SG	Wharton & Wharton (1965)
P. fuliginosa	Unknown	SG	Wharton & Wharton (1965)
Blaberidae			
Blaberus craniifer	Unknown	SG	Wharton & Wharton (1965)
B. discoidalis	Unknown	SG	Wharton & Wharton (1965)
B. giganticus	Unknown	SG	Wharton & Wharton (1965)
Byrostria fumigata	Unknown	SG	Wharton & Wharton (1965)
Capucina patula	Unknown	SG	Wharton & Wharton (1965)
Diploptera punctata	Unknown	SG	Wharton & Wharton (1965)
Eublaberus posticus	Unknown	SG, GB	Wharton & Wharton (1965); Cruden & Markovetz (1979)
Gromphadorhina brunneri	Unknown	SG	Wharton & Wharton (1965)
Leucophaea maderae	Unknown	SG	Wharton & Wharton (1965)
Nauphoeta cinera	Unknown	SG	Wharton & Wharton (1965)
Phortioeca phoraspoides	Unknown	SG	Wharton & Wharton (1965)
Pycnoscelus surinamensis	Unknown	SG	Wharton & Wharton (1965)
Acrididae			
Locusta migratoria	Limited or none	Unknown (WA)	Morgan (1976)
Melanoplus bivittatus	Limited or none	Unknown (WA)	Talmadge & Albersheim (1969)
Schistocerca gregaria	Limited or none	Unknown (WA)	Evans & Payne (1964)
ISOPTERA			
Mastotermitidae			
Mastotermes darwiniensis	Presumably high	SG, MGT, HGP	Veivers *et al.* (1981)
Kalotermitidae			
Neotermes bosei	High	SG, MGT	Mishra (1980)

Table 3—*continued*

Insect Order Family Species	Capacity to digest cellulose	Identified sources of C_x-cellulases in digestive fluids	References
Hodotermitidae			
Hodotermes mossambicus	High	MGT	Botha & Hewitt (1979)
Rhinotermitidae			
Coptotermes lacteus	Presumably high	MGT, HGP	O'Brien *et al.* (1979)
Reticulitermes speratus	High	SG, HGP	Yokoe (1964); Yamaoka & Nagatani (1975)
R. hesperus	Presumably high	HGB	Thayer (1978)
Zootermopsis sp.	High	HGP	Yamin & Trager (1979)
Termitidae			
Macrotermes natalensis	Presumably high	SG, MGT, IFT	Martin & Martin (1978, 1979)
M. subhyalinus	Presumably high	MGT, IFT	Abo-Khatwa (1978)
Microcerotermes edentatus	Presumably high	Unknown	Kovoor (1970)
Nasutitermes exitiosus	High	MGT	O'Brien *et al.* (1979)
Termes obesus	Presumably high	Unknown	Misra & Ranganathan (1954)
Trinervitermes trinervoides	Presumably high	MGT	Potts & Hewitt (1973, 1974a,b)
PLECOPTERA			
Pteronarcyidae			
Allonarcys proteus	Limited or none	Unknown (WA)	Sinsabaugh *et al.* (1981)
Pteronarcys californica	Limited or none	Unknown (WA)	Martin *et al.* (1981b)
P. pictetei	Limited or none	Unknown (WA)	Martin *et al.* (1981b)
PSOCOPTERA			
Pseudocaeciliidae			
Pseudocaecilius elutus	Unknown	Unknown	Sinha & Srivastava (1970)
HEMIPTERA			
Pentatomidae			
Palomena angulosa	Unknown	Unknown	Hori (1975)
Eurydema rugosum	Unknown	Unknown	Hori (1975)
Coreidae			
Coreus marginatus	Unknown	Unknown	Hori (1975)
HOMOPTERA			
Aphididae			
Acyrthosiphon caragenae	Unknown	SG	Adams & Drew (1965)
A. pisum	Unknown	SG	Adams & Drew (1965)
Aphis fabae	Unknown	SG	Adams & Drew (1965)
A. helianthi	Unknown	SG	Adams & Drew (1965)
A. pomi	Unknown	SG	Adams & Drew (1965)
Aulacorthum solani	Unknown	SG	Adams & Drew (1965)
Betulaphis quadrituberculata	Unknown	SG	Adams & Drew (1965)
Calaphis (?) *betulaecolens*	Unknown	SG	Adams & Drew (1965)
Dactynotus cirsii	Unknown	SG	Adams & Drew (1965)
D. russellae	Unknown	SG	Adams & Drew (1965)
D. taraxaci	Unknown	SG	Adams & Drew (1965)
D. sp.	Unknown	SG	Adams & Drew (1965)
Eriosoma lanigerum	Unknown	SG	Adams & Drew (1965)
Hydaphis foeniculi	Unknown	SG	Adams & Drew (1965)
Macrosiphon californicum	Unknown	SG	Adams & Drew (1965)
M. euphorbia	Unknown	SG	Adams & Drew (1965)
M. ptericoleus	Unknown	SG	Adams & Drew (1965)
Metopolophium dirhodum	Unknown	SG	Adams & Drew (1965)
Myzocallis walshii	Unknown	SG	Adams & Drew (1965)
Myzus cerasi	Unknown	SG	Adams & Drew (1965)
M. persicae	Unknown	SG	Adams & Drew (1965)
Nearctaphis bakeri	Unknown	SG	Adams & Drew (1965)
Neomyzus circumflexus	Unknown	SG	Adams & Drew (1965)
Pentatrichopus thomasi	Unknown	SG	Adams & Drew (1965)
Periphylus lyropictus	Unknown	SG	Adams & Drew (1965)
P. negundinus	Unknown	SG	Adams & Drew (1965)
Prociphilus leselata	Unknown	SG	Adams & Drew (1965)
Pterocomma bicolor	Unknown	SG	Adams & Drew (1965)
Rhopalosiphum sp.	Unknown	SG	Adams & Drew (1965)
R. padi	Unknown	SG	Adams & Drew (1965)
R. cerasifoliae	Unknown	SG	Adams & Drew (1965)
COLEOPTERA			
Scarabaeidae			
Sericesthis geminata	Unknown	Unknown	Soo Hoo & Dudzinski (1967)
Cerambycidae			
Ergates faber	Presumably moderate	Unknown	Chararas (1979)

Table 3—*continued*

Insect Order / Family / Species	Capacity to digest cellulose	Identified sources of C_x-cellulases in digestive fluids	References
Phoracantha semipunctata	Presumably moderate	Unknown	Chararas (1979)
Rhagium inquisitor	Presumably moderate	Unknown	Chararas (1979)
Stromatium barbatum	Moderate	Unknown	Mishra & Singh (1978)
Curculionidae			
Cryptorrhynchus lapathi	Limited or none	Unknown	Chararas (1979)
Hylobius abietes	Limited or none	Unknown	Chararas (1979)
Pissodes barcyniae	Limited or none	Unknown	Chararas (1979)
P. notatus	Limited or none	Unknown	Chararas (1979)
Scolytidae			
Carphoborus minimus	Limited or none	Unknown	Chararas (1979)
Ips amitinus	Limited or none	Unknown	Chararas (1979)
I. sexdentatus	Limited or none	Unknown	Chararas (1979)
I. typographus	Limited or none	Unknown	Chararas (1979)
Phloeosinus cedri	Limited or none	Unknown	Chararas (1979)
Scolytus intricatus	Limited or none	Unknown	Chararas (1979)
S. multistriatus	Limited or none	Unknown	Chararas (1979)
S. numidicus	Limited or none	Unknown	Chararas (1979)
S. scolytus	Limited or none	Unknown	Chararas (1979)
MEGALOPTERA			
Sialidae			
Sialis lutaria	Limited or none	Unknown	Monk (1976)
TRICHOPTERA			
Limnephilidae			
Ecclipsopteryx guttulata	Limited or none	Unknown (WA)	Bjarnov (1972)
Halesus sp.	Limited or none	Unknown	Monk (1976)
Potomophylax sp.	Limited or none	Unknown	Monk (1976)
Silo nigricornis	Limited or none	Unknown (WA)	Bjarnov (1972)
Rhyacophilidae			
Rhyacophila septentrionis	Limited or none	Unknown (WA)	Bjarnov (1972)
Brachycentridae			
Oligoplectrum maculatum	Limited or none	Unknown (WA)	Bjarnov (1972)
Polycentropodidae			
Neureclipsis angustipennis	Limited or none	Unknown	Bjarnov (1972)
Plectrocnemia geniculata	Limited or none	Unknown	Monk (1976)
Polycentropus flavomaculatus	Limited or none	Unknown	Monk (1976)
Hydropsychidae			
Hydropsyche angustipennis	Limited or none	Unknown	Bjarnov (1972)
Phryganeidae			
Agrypnia vestita	Limited or none	Unknown	Martin *et al.* (1981a)
Phryganea sp.	Limited or none	Unknown	Martin *et al.* (1981a)
DIPTERA			
Tipulidae			
Tipula abdominalis	Limited or none	Unknown (WA)	Sinsabaugh *et al.* (1981)
Chironomidae			
Chironomus anthracinus	Limited or none	Unknown	Bjarnov (1972)
Sciaridae			
Rhyncosciara americana	Limited or none	Unknown	Terra *et al.* (1979)
HYMENOPTERA			
Siricidae			
Sirex cyaneus	Moderate	IFT	Kukor & Martin (1983)
Eurytomidae			
Eurytoma amygdali	Unknown	Unknown	Ishaaya & Plant (1974)

Abbreviations: WA, weak activity; GB, gut bacteria; HGB, hindgut bacteria; HGP, hindgut protozoa; IFT, ingested fungal tissue; MGT, midgut tissue; SG, salivary glands.

As indicated in Table 1, the gut fluids of a number of insects, including the silverfish, the wood roach, several termites, and quite a few beetles, are able to effect the degradation of microcrystalline cellulose. Therefore, C_1-cellulases or comparable enzymes must be present. In contrast to the numerous reports of C_x-cellulase and cellobiose production by insects, data suggesting that insects are able to secrete their own C_1-cellulases exist for only three species, and even in these the evidence is not completely unam-

Table 4. Insects with digestive cellobiases

Insect Order Family	Capacity to digest cellulose	Identified sources of cellobiases in digestive fluids	References
THYSANURA			
Lepismatidae			
Ctenolepisma lineata	Moderate	Unknown	Lasker & Giese (1956)
ORTHOPTERA			
Blaberidae			
Byrostria fumigata	Unknown	Unknown	Fisk & Rao (1964)
Acrididae			
Locusta migratoria	Limited or none	MGT	Morgan (1975b)
Schistocerca gregaria	Limited or none	SG, NGT	Evans & Payne (1964)
ISOPTERA			
Mastotermitidae			
Mastotermes darwiniensis	Presumably high	SG	Veivers *et al.* (1981)
Kalotermitidae			
Neotermes bosei	High	MGT	Mishra (1980)
Rhinotermitidae			
Coptotermes lacteus	Presumably high	HGP	McEwen *et al.* (1980)
Termitidae			
Macrotermes subhyalinus	Presumably high	MGT	Abo-Khatwa (1978)
Microcerotermes edentatus	Presumably high	Unknown	Kovoor (1970)
Nasutitermes exitiosus	High	Probably MGT	McEwen *et al.* (1980)
N. walkeri	Presumably high	Probably MGT	McEwen *et al.* (1980)
Trinervitermes trinervoides	Presumably high	MGT	Potts & Hewitt (1973)
PSOCOPTERA			
Pseudocaeciliidae			
Pseudocaecilius elutus	Unknown	Unknown	Sinha & Srivastava (1970)
HEMIPTERA			
Miridae			
Stenotus binotatus	Unknown	Unknown	Takanona & Hori (1974)
Pyrrhocoridae			
Dysdercus fasciatus	Unknown	SG	Khan & Ford (1967)
COLEOPTERA			
Carabidae			
Brosus cephalotes	Unknown	Unknown	Nielsen (1962)
Pterostichus oblongopunctatus	Unknown	Unknown	Nielsen (1962)
Staphylinidae			
Philonthus decorus	Unknown	Unknown	Nielsen (1962)
Scarabaeidae			
Sericesthis geminata	Unknown	Unknown	Soo Hoo & Dudzinski (1967)
TRICHOPTERA			
Sericostomidae			
Crunoecia irrorata	Limited or none	Unknown	Bjarnov (1972)
Sericostoma pedemontanum	Limited or none	Unknown	Bjarnov (1972)
Limnephilidae			
Ecclipsopteryx guttaluta	Limited or none	Unknown	Bjarnov (1972)
Chaetopteryx villosa	Limited or none	Unknown	Bjarnov (1972)
Potamophylax nigricornis	Limited or none	Unknown	Bjarbov (1972)
Silo nigricornis	Limited or none	Unknown	Bjarnov (1972)
Rhyacophilidae			
Rhyacophila septentrionis	Limited or none	Unknown	Bjarnov (1972)
Brachycentridae			
Oligoplectum maculatum	Limited or none	Unknown	Bjarnov (1972)
Polycentripodidae			
Neureclepsis bimaculata	Limited or none	Unknown	Bjarnov (1972)
Hydropsychidae			
Hydropsyche angustipennis	Limited or none	Unknown	Bjarnov (1972)
LEPIDOPTERA			
Bombycidae			
Bombyx mori	Limited or none	SG	Mukaiyama (1961)
DIPTERA			
Chironomidae			
Chironomus anthracinius	Limited or none	Unknown	Bjarnov (1972)
C. plumosus	Limited or none	Unknown	Bjarnov (1972)
Sciaridae			
Rhyncosciara americana	Limited or none	MGT	Ferreira & Terra (1980)
HYMENOPTERA			
Tenthredinidae			
Diprium pini	Unknown	Unknown	Schulze & Ehrhardt (1963)

Abbreviations: HGP, hindgut protozoa; MGT, midgut tissue; SG, salivary glands.

biguous and compelling. The silverfish, *Ctenolepisma lineata*, is the best candidate for a genuine C_1-cellulase producer. Silverfish have simple guts with no enlarged segments or blind sacs which might function as fermentation chambers. Lasker & Giese (1956) were unable to culture any cellulolytic bacteria from these insects, and were also able to demonstrate efficient cellulose digestion in nymphs which were presumed to be symbiont free, having been reared from surface sterilized eggs on a diet of sterile, dried rolled oats. Lasker and Giese were unable to culture any bacteria from the guts of their presumed symbiont-free nymphs, but they did not perform total direct counts of bacteria in the gut. Thus the possibility is not absolutely ruled out that the presumed symbiont-free specimens still contained cellulolytic microbes of a type which could not be isolated as viable colonies using the culturing methods employed. Also, the diet of sterile, rolled oats was assumed to be free of cellulolytic microbes and enzymes, although that assumption appears not to have been tested experimentally. Thus, while the case for C_1-cellulase secretion by the midgut of *Ctenolepisma lineata* is quite convincing, it falls just short of being absolutely air-tight.

Potts & Hewitt (1973, 1974a,b) have suggested that the midgut of the higher termite, *Trinervitermes trinervoides*, secretes a single enzyme with both C_x- and C_1-cellulase activity. This proposal rests upon the claim that the C_1- and C_x-cellulolytic activity present in a chromatographic fraction obtained during the purification of a homogenate of worker abdomens was due to a single enzyme, the same C_x-enzyme that had previously been detected in an extract of midgut tissue.

Veivers *et al.* (1981) detected low levels of C_1-cellulase activity in an extract of the salivary glands of the primitive termite, *Mastotermes darwiniensis*. Only 10% of the total C_1-activity assayed in this termite was present in the salivary extract, however. Most of the activity (73%) was in the hindgut, which houses an abundant protozoan population. The proposal that the C_1-cellulase activity in the salivary extract is due to enzymes secreted by the termites rests upon the assumption that no contamination of the salivary gland preparations occurred during dissection.

It is often stated that the wood-boring anobiid and cerambycid beetles secrete all of their own cellulases. While there is no evidence to preclude this possibility, neither is there any to support it. The assumption is based entirely upon the lack of any correlation between a capacity to digest cellulose and the presence of intracellular symbionts (Mansour & Mansour-Bek, 1934b; Parkin, 1940). The origins of the C_1-cellulases of these insects remain completely unknown at the present time.

In summary then, while additional research may confirm the ability of a few insects to produce C_1-cellulases, this ability is certainly not widespread, and should be regarded as the exception rather than the rule. Thus it seems evident that it is the inability to synthesize and secrete C_1-cellulases that explains the inability of most insects to digest cellulose. With the possible exception of the silverfish, insects which are able to assimilate cellulose do so by exploiting the cellulolytic potential of protozoa and fungi which produce soluble C_1-cellulases or of bacteria which digest cellulose without the necessary secretion of such enzymes.

CONTRIBUTIONS OF PROTOZOA, BACTERIA AND FUNGI TO CELLULOSE DIGESTION IN INSECTS

Three distinctly different types of insect-microbial interactions have been shown to serve as mechanisms by which insects digest cellulose using the cellulolytic potential of microorganisms. Termites and wood roaches maintain permanent populations of cellulolytic protozoa in their hindguts. Scarab beetles and the American cockroach house permanent populations of bacteria in their hindguts, presumably including cellulolytic strains. The fungus-growing termites and the siricid wood wasps culture cellulolytic fungi and ingest cellulolytic enzymes when they consume their symbiont along with their food. A fourth mechanism which has not yet been demonstrated in insects, but which may prove to be important in certain species, is the rapid proliferation in the gut of cellulolytic bacteria ingested along with a cellulosic substrate, followed by the digestion of the bacteria in a more posterior section of the alimentary tract. Endosymbiotic bacteria or yeasts, housed in specialized cells (mycetocytes) or organs (mycetomes), represents a fifth type in insect-microbial interaction which is quite widespread. It was once thought that such symbionts might also be involved in cellulose digestion, but no evidence in support of that idea has ever been presented. The significance of such intracellular symbionts lies instead in their provision of B-vitamins, sterols, and essential amino acids.

The obligatory dependence of the lower termites and of the wood roach upon hindgut protozoa for cellulose digestion has been widely recognized since the classic investigations of Cleveland (1924), Cleveland *et al.* (1934), Trager (1932) and Hungate (1938, 1943), and has been thoroughly reviewed (Honigberg, 1970; O'Brien & Slaytor 1982; Breznak, 1982). The protozoan symbionts are anaerobic species from unique genera of oxymonad, trichomonad and hypermastigote flagellates restricted to the four families of lower termites and to the wood roach family. Trager (1932) demonstrated that cellulolytic enzymes, including C_1-cellulases, were produced by intestinal flagellates present in the roach, *C. punctulatus*, and in two species of termites, *R. flavipes* and *T. angusticollis*. For many years it was not certain whether the enzymes were actually produced by the protozoa or by bacteria invariably present in the protoplasm of the protozoa. That uncertainty has recently been resolved by the successful cultivation of bacteria-free protozoa (Yamin & Trager, 1979), and the clear demonstration that cellylolytic enzymes, including C_1-cellulases, are produced by the protozoa themselves and not by intracellular bacterial symbionts. Considering the impressive efficiency with which the exploitation of protozoan C_1-cellulases has allowed the lower termites to digest and assimilate cellulose, it seems surprising that this mechanism for acquiring cellulolytic capacity is not more widespread among wood-feeders. Perhaps a better understanding of the biochemical requirements of these unique protozoa, which should be possible to attain now that successful culturing methods have been developed, will explain the narrow phylogenetic distribution of this type of insect-microbial symbiosis.

It has often been presumed that cellulose digestion by the higher termites is accomplished by hindgut bacteria, since the Termitidae lack the xylophagous protozoa typical of the lower termites. However, evidence in support of this presumption is meager. Bacterial isolates with cellulolytic activity have been obtained from a few termite species, but there are no data to suggest that such bacteria are of any quantitative importance to cellulose digestion *in vivo* (Lee & Wood, 1971; Breznak, 1975, 1982; O'Brien & Slaytor, 1982). Cellulolysis by resident hindgut bacteria has been proposed in the rhinocerus beetle, *O. nasicornis* (Bayon, 1980; Bayon & Mathelin, 1980), and may occur in other scarabs as well (Wiedmann, 1930; Couturier, 1961), although cellulolytic bacteria have not actually been isolated from the intestinal tracts of these species. Gut bacteria, both from the midgut and hindgut, have been implicated in cellulose digestion in two species of roaches, *P. americana* (Bignell, 1977; Cruden & Markovetz, 1979) and *E. posticus* (Cruden & Markovetz, 1979). Many insects harbour abundant gut floras, and it is quite possible that further research will identify other species which exploit the cellulolytic capacities of their gut bacteria. However, it should be borne in mind that hindgut bacteria have also been shown to ferment sugars, fix nitrogen, degrade uric acid, synthesize amino acids, and participate in a host of biochemical processes besides cellulose digestion. Thus, the mere presence of an abundant gut flora from which cellulolytic strains of bacteria can be isolated does not constitute sufficient evidence to conclude that an insect derives any benefit from the cellulolytic potential of the bacteria it harbors within its alimentary tract.

Recently it has been demonstrated that the fungus-growing termites *Macrotermes natalensis* (Martin & Martin, 1978, 1979) and *M. subhyalinus* (Aba-Khatwa, 1978), and the larvae of the siricid wood wasp, *Sirex cyaneus* (Kukor & Martin, 1983) acquire a capacity for cellulose digestion by ingesting fungal enzymes. The termites are able to produce some of their own cellobiases and C_x-cellulases, but the C_1-cellulases and some of the C_x-cellulases in their midgut fluids are derived from the conidiophores of a symbiotic fungus, *Termitomyces sp.*, which the termites culture in their nests and consume in small quantities along with the wood and other cellulosic substrates which make up the bulk of their food. In like manner, wood wasps are associated with a symbiotic fungus which is the source of digestive C_1- and C_x-cellulases, as well as hemicellulases and probably also pectinases, which allow the larvae to digest plant cell wall polysaccharides (Kukor & Martin, 1983). The fungal symbiont of *S. cyaneus* is *Amylostereum chailletii*. It is introduced into timber along with the wood wasp's egg during oviposition, and grows on the surfaces of the galleries produced by the feeding larvae. The larvae consume a mixture of wood and fungal mycelium. It is not known at present whether the ingestion of fungal cellulases is a common mechanism by which insects acquire a capacity to digest cellulose, or whether it is a process restricted to species involved in complex, highly coevolved symbiotic associations with fungi. It may prove to be very common (Martin, in press). Indeed, it is possible that many of the cerambycid beetles, which have been assumed to produce the entire complex of cellulases present in their digestive juices, acquire the C_1-cellulases in their midgut fluids by ingesting fungal associates. Cellulases of fungal origin have been reported in the amphipod, *Gammarus fossorum*, an aquatic detritus-feeder (Bärlocher, 1982).

The proliferation in the gut of ingested bacteria has been demonstrated in the rhinocerus beetle, *Oryctes nasicornis* (Bayon & Mathelin, 1980), and in several soil-feeding invertebrates, including the termite, *Procubitermes aburiensis* (Bignell *et al*., 1980), the millipede, *Glomeris marginata* (Anderson & Bignell, 1980), and the isopod *Tracheoniscus rathkei* (Reyes & Tiedje, 1976a). This proliferation of bacteria is accompanied by the degradation of hemicellulose and the assimilation of microbial cells in *Tracheoniscus* (Reyes & Tiedje, 1976b). Thus, the indigestible constituents of the ingested detritus are transformed into microbial biomass which is digestible by the isopod. Although to date there has been no demonstration that the proliferation of ingested bacteria occurs at the expense of ingested cellulose, that possibility clearly exists, and needs to be considered as an additional mechanism by which insects might accomplish the digestion of cellulose by exploiting the metabolic capabilities of microorganisms. It is even possible that this process is responsible for the digestion of a portion of the ingested cellulose in the midgut of the rhinocerus beetle.

CONCLUSION

The investigation of insect–microbial interactions, pioneered with such elegance and insight by Buchner and Cleveland over a half a century ago, is experiencing something of a renaissance at the present time. Recent studies continue to uncover an ever growing number of ways by which insects exploit the biochemical characteristics of microorganisms, including their capacity to digest cellulose. These studies not only contribute to a greater understanding of the nutritional ecology of insects, but also promise to provide basic insights into the biochemical processes which mediate interactions between insects and microorganisms, and perhaps to help identify some of the factors which determine whether an interspecific interaction evolves into one of mutualism, commensalism or parasitism.

REFERENCES

Abo-Khatwa N. (1978) Cellulase of fungus growing termites: a new hypothesis on its origin. *Experientia* **34**, 559–560.

Adams J. B. & Drew M. E. (1965) A cellulose-hydrolyzing factor in aphid saliva. *Can. J. Zool.* **43**, 489–496.

Anderson J. M. & Bignell D. E. (1980) Bacteria in the food, gut contents and faeces of the litter-feeding millipede *Glomeris marginata* (Villers). *Soil Biol. Biochem.* **12**, 251–254.

Babers F. H. & Woke P. A. (1937) Digestive enzymes in the southern armyworm. *J. agric. Res.* **54**, 547–550.

BÄRLOCHER F. (1982) The contribution of fungal enzymes to the digestion of leaves by *Gammarus fossarum* Koch. *Oecologia* **52**, 1–4.

BAYON C. (1980) Volatile fatty acids and methane production in relation to anaerobic carbohydrate fermentation in *Oryctes nasicornis* larvae (Coleoptera: Scarabaeidae). *J. Insect Physiol.* **26**, 819–828.

BAYON C. & MATHELIN J. (1980) Carbohydrate fermentation and by-product absorption studied with labelled cellulose in *Oryctes nasicornis* larvae (Coleoptera: Scarabaeidae). *J. Insect. Physiol.* **26**, 833–840.

BECKER G. (1942) Untersuchungen über die Ernahrungsphysiologie der Häusbockkafer. *Z. vergl. Physiol.* **29**, 315–388.

BIGNELL D. E. (1977) An experimental study of cellulose and hemicellulose degradation in the alimentary canal of the American cockroach. *Can. J. Zool.* **55**, 579–589.

BIGNELL D. E., OSKARSSON H. & ANDERSON J. M. (1980) Distribution and abundance of bacteria in the gut of a soil-feeding termite *Procubitermes aburiensis* (Termitidae, Termitinae). *J. gen. Microbiol.* **117**, 393–403.

BJARNOV N. (1972) Carbohydrases in *Chironomus*, *Gammarus* and some Trichopteran larvae. *Oikos* **23**, 261–263.

BOTHA T. C. & HEWITT P. H. (1979) Study of the gut morphology and some physiological observations on the influence of a diet of green *Themeda triandra* on the harvester termite, *Hodotermes mossambicus* (Hagen). *Phytophylactica* **11**, 57–60.

BREZNAK J. A. (1975) Symbiotic relationships between termites and their intestinal microbiota. *Symp. Soc. exp. Biol.* **29**, 559–580.

BREZNAK J. A. (1982) Intestinal microbiota of termites and other xylophagous insects. *A. Rev. Microbiol.* **36**, 323–343.

BURTON R. L., STARKS K. J. & SAUER J. R. (1977) Carbohydrate digestion by the larval midgut of *Heliothis zea*. *Ann. ent. Soc. Am.* **70**, 477–480.

CHARARAS C. (1979) *Ecophysiologie des Insectes Parasites des Forêts*. Published by the author, Paris.

CHARARAS C. & LIBOIS G. (1976) Studies on enzymes hydrolyzing glycosides in the larvae of *Ergates faber* (Coleoptera: Cerambycidae). *C. R. hebd. Séanc. Acad. Sci., Paris* **283**, 1523–1525.

CHATTORAJ A. N. & MALL S. B. (1969) Hydrogen ion concentration and digestive enzymes in the mature larvae of *Marasmia trapezalis* Guen (Pyralidae). *Indian J. Ent.* **31**, 121–126.

CLEVELAND L. R. (1924) The physiological and symbiotic relationship between the intestinal protozoa of termites and their hosts, with special reference to *Reticulitermes flavipes* Kollar. *Biol. Bull. mar. biol. Lab., Woods Hole* **46**, 117–227.

CLEVELAND L. R., HALL S. R., SANDERS E. P. & COLLIER J. (1934) The wood feeding roach *Cryptocerus*, its protozoa, and the symbiosis between protozoa and roach. *Mem. Am. Acad. Arts Sci.* **17**, 185–342.

COUTURIER S. (1961) Recherche anatomique et histologique sur l'iléon des Melolonthinae (Coleoptères Scarabaeides). *Ann. Epiphyties* **12**, 317–346.

CRUDEN D. L. & MARKOVETZ A. J. (1979) Carboxymethylcellulose decomposition by intestinal bacteria of cockroaches. *Appl. env. Microbiol.* **38**, 369–372.

DIXIT A. & MALL S. B. (1978) Digestive enzymes of mature larvae of *Chilena similis* Walker (Lepidoptera: Lasciocampidae). *Indian J. Ent.* **39**, 319–323.

DESCHAMPS P. (1944) Sur la digestion du bois par les larves des cérambycides. *Bull. Soc. ent. Fr.* **49**, 104–110.

ESENTHER G. R. & KIRK T. K. (1974) Catabolism of aspen sapwood in *Reticulitermes flavipes* (Isoptera: Rhinotermitinae). Ann. ent. Soc. Am. **67**, 989–990.

EVANS W. A. L. & PAYNE D. W. (1964) Carbohydrases of the alimentary tract of the desert locust, *Schistocerca gregaria*. *J. Insect Physiol.* **10**, 657–674.

FALCK R. (1930) Die Scheindestruktion des Koniferenholzes durch die Larven des Hausbockes (*Hylotrupes bajulus* L.). *Cellulose Chem.* **11**, 89–91.

FERREIRA C. & TERRA W. R. (1980) Intracellular distribution of hydrolases in midgut caecae cells from an insect with emphasis on plasma membrane-bound enzymes. *Comp. Biochem. Physiol.* **66B**, 467–473.

FISK F. W. & RAO B. R. (1964) Digestive carbohydrases in the Cuban burrowing cockroach. *Ann. ent. Soc. Am.* **57**, 40–44.

GHOSE T., MONTENECOURT B. S. & EVELEIGH D. E. (1981) *Measure of Cellulase Activity*. International Union of Pure and Applied Chemistry, Commission of Biotechnology.

HONIGBERG B. M. (1970) Protozoa associated with termites and their role in digestion. In *Biology of Termites* (Edited by KRISHNA K. K. & WEESNER F. M.), Vol. 2, pp. 1–36. Academic Press, New York.

HORI K. (1975) Digestive carbohydrases in the salivary gland and midgut of several phytophagous bugs. *Comp. Biochem. Physiol.* **50B**, 145–151.

HUNGATE R. E. (1938) Studies on the nutrition of *Zootermopsis*. II. The relative importance of the termite and the protozoa in wood digestion. *Ecology* **19**, 1–25.

HUNGATE R. E. (1943) Quantitative analyses on the cellulose fermentation by termite protozoa. *Ann. ent. Soc. Am.* **36**, 730–739.

ISHAAYA I. & PLANT H. N. (1974) Digestive enzymes in *Eurytoma amygdali* and their relation to food digestion and to the boring process of the emergence holes in almond fruits. *Comp. Biochem. Physiol.* **48A**, 37–44.

IVANOVIC J. & BARBIC F. (1966) Comparative studies of amylase and cellulase activity in insect larvae living in bark and wood. *Arh. biol. Nauka* **18**, 1–2. *Chem. Abstr.* **67**, 1147y (1967).

KHAN M. R. & FORD J. B. (1967) The distribution and localization of digestive enzymes in the alimentary canal and salivary glands of the cotton stainer, *Dysdercus fasciatus*. *J. Insect Physiol.* **13**, 1619–1628.

KHAN M. R. & KASTING R. (1969) Digestive enzymes of sixth-instar larvae of the pale western cutworm, *Agrotis orthogonia*. *Can. Ent.* **101**, 494–499.

KOVOOR J. (1970) Presence d'enzymes cellulolytique dans l'intestin d'un termite supérieur *Microcerotermes edentatus* (Was.). *Annls. Sci. Nat. (Zoologie)* **12**, 65–71.

KUKOR J. J. & MARTIN M. M. (1983) Siricid wood wasps acquire digestive enzymes from their fungal symbiont. *Science, N.Y.* (in press).

LASKER R. & GIESE A. C. (1956) Cellulose digestion by the silverfish *Ctenolepisma lineata*. *J. exp. Biol.* **33**, 542–553.

LEE K. E. & WOODS T. G. (1971) *Termites and Soils*. Academic Press, New York.

MALL S. B., SINGH A. R. & DIXIT A. (1978) Digestive enzymes of mature larvae of *Atteva fabriciella* (Lepidoptera: Yponomentidae) *J. Anim. Morph. Physiol.* **25**, 86–92.

MANSOUR K. & MANSOUR-BEK J. J. (1934a) On the digestion of wood by insects. *J. exp. Biol.* **11**, 243–256.

MANSOUR K. & MANSOUR-BEK J. J. (1934b) The digestion of wood by insects and the supposed role of microorganisms. *Biol. Rev.* **9**, 363–382.

MANSOUR K. & MANSOUR-BEK J. J. (1937) On the cellulase and other enzymes of *Stromatium fulvum* Villers (Cerambycidae). *Enzymologia* **4**, 1–6.

MARTIN M. M. (1984) The role of acquired enzymes in digestive processes in insects. In *Animal-Microbial Interations* (Edited by ANDERSON J. M., RAYNER A. D. M. & WALTON D.), in press. Cambridge University Press, Cambridge.

MARTIN M. M. & MARTIN J. S. (1978) Cellulose digestion in the midgut of the fungus-growing termite *Macrotermes natalensis*: the role of acquired digestive enzymes. *Science, N.Y.* **199**, 1453–1455.

MARTIN M. M. & MARTIN J. S. (1979) The distribution and origins of the cellulolytic enzymes of the higher termite *Macrotermes natalensis*. *Physiol. Zool.* **52**, 1–11.

MARTIN M. M., KUKOR J. J., MARTIN J. S., LAWSON D. L. & MERRITT R. W. (1981a) Digestive enzymes of larvae of three species of caddisflies (Trichoptera). *Insect Biochem.* **5**, 501–505.

MARTIN M. M., MARTIN J. S., KUKOR J. J. & MERRITT R. W. (1981b) The digestive enzymes of detritus-feeding stonefly nymphs (Plecoptera: Pteronarcyidae). *Can. J. Zool.* **59**, 1947–1951.

MATHUR L. M. L. (1966) Studies on the digestive enzymes of noctuid caterpillars feeding on cauliflower. *Indian J. Ent.* **28**, 215–223.

MAULDIN J. K. (1977) Cellulose catabolism and lipid synthesis in normally and abnormally faunated termites, *Reticulitermes flavipes*. *Insect Biochem.* **7**, 27–31.

MAULDIN J. K., SMYTHE R. V. & BAXTER C. C. (1972) Cellulose catabolism and lipid synthesis by the subterranean termite, *Coptotermes formosanus*. *Insect Biochem.* **2**, 209–217.

MCEWEN S. E., SLAYTOR M. & O'BRIEN R. W. (1980) Cellobiase activity in three species of Australian termites. *Insect. Biochem.* **10**, 563–567.

MCGINNIS A. J. & KASTING R. (1969) Digestibility studies with cellulose-U-C^{14} on larvae of the pale western cutworm, *Agrotis orthogonia*. *J. Insect Physiol.* **15**, 5–10.

MISHRA S. C. (1979) Studies on deterioration of wood by insects: 4. Digestibility and digestion of major wood components by the termite *Neotermes bosei* (Isoptera: Kalotermitide). *Mater. Org.* **14**, 269–278.

MISHRA S. C. (1980) Carbohydrases in *Neotermes bosei* Snyder (Isoptera: Kalotermitidae). *Mater. Org.* **15**, 253–261.

MISHRA S. C. & SINGH P. (1978) Polysaccharide digestive enzymes in the larvae of *Stromatium barbatum* (Fabr.), a dry wood borer (Coleoptera: Cerambycidae). *Mater. Org.* **13**, 115–122.

MISRA J. N. & RANGANATHAN V. (1954) Digestion of cellulose by the mound building termite, *Termes (Cyclotermes) obesus* (Rambur). *Proc. Indian Acad. Sci.* **39B**, 100–113.

MONK D. C. (1976) The distribution of cellulase in freshwater invertebrates of different feeding habits. *Freshwater Biol.* **6**, 471–475.

MORGAN M. R. J. (1975a) A qualitative survey of the carbohydrases of the alimentary tract of the migratory locust, *Locusta migratoria migratorioides*. *J. Insect. Physiol.* **21**, 1045–1053.

MORGAN M. R. J. (1975b) Relationship between gut cellobiase, lactase, aryl β-glucosidase and ayrl β-galactosidase activities of *Locusta migratoria*. *Insect. Biochem.* **5**, 609–619.

MORGAN M. R. J. (1976) Gut carbohydrases in locusts and grasshoppers. *Acrida* **5**, 45–58.

MUKAIYAMA F. (1961) Occurrence of several digestive enzymes in the salivary gland of the larva of the silkworm, *Bombyx mori*. *Nippon Sanshigaku Zashi* **30**, 1–8. *Chem. Abstr.* **59**, 11940d (1963).

MÜLLER W. (1934) Untersuchungen über die Symbiose von Tieren mit Pilzen und Bakterien. *Archs. Mikrobiol.* **5**, 84–147.

NIELSEN C. O. (1962) Carbohydrases in soil and litter invertebrates. *Oikos* **13**, 200–215.

NORMAN A. G. (1936) The destruction of oak by the death watch beetle. *Biochem. J.* **30**, 1135–1137.

O'BRIEN R. W. & SLAYTOR M. (1982) Role of microorganisms in the metabolism of termites. *Aust. J. biol. Sci.* **35**, 239–262.

O'BRIEN G. W., VEIVERS P. C., MCEWEN S. E., SLAYTOR M. & O'BRIEN R. W. (1979) The origin and distribution of cellulase in the termites, *Nasutitermes exitiosus* and *Coptotermes lacteus*. *Insect. Biochem.* **9**, 619–625.

ORLOVA E. A. (1974) Influence of the intestinal symbiont complex on the intensity of food consumption and the longevity of the termites *Reticulitermes*. In *Termites (Collected Articles)*, (Edited by ZOLOTAREV E. K.), *Transactions of the Entomological Division* No. 5, pp. 165–180. University Publishing House, Moscow.

PARKIN E. A. (1940) The digestive enzymes of some woodboring beetle larvae. *J. exp. Biol.* **17**, 364–377.

POTTS R. C. & HEWITT P. H. (1973) The distribution of intestinal bacteria and cellulase activity in the harvester termite *Trinervitermes trinervoides* (Nasutitermitinae). *Insectes soc.* **20**, 215–220.

POTTS R. C. & HEWITT P. H. (1974a) The partial purification and some properties of the cellulase from the termite *Trinervitermes trinervoides* (Nasutitermitiae). *Comp. Biochem. Physiol.* **47B**, 317–326.

POTTS R. C. & HEWITT P. H. (1974b) Some properties and reaction characteristics of the partially purified cellulase from the termite *Trinervitermes trinervoides* (Nasutitermitinae). *Comp. Biochem. Physiol.* **47B**, 327–337.

REESE E. T. & MANDELS M. (1971) Degradation of cellulose and its derivatives; enzymic degradation. In *High Polymers* (Edited by BIKALES N. M. & SEGAL L.) 2nd edn, Vol. 5, pp. 1079–1094. Wiley-Interscience, New York.

REYES V. G. & TIEDJE J. M. (1976a) Ecology of the gut microbiota of *Tracheoniscus rathkei* (Crustacea, Isopoda). *Pedobiologia* **16**, 67–74.

REYES V. G. & TIEDJE J. M. (1976b) Metabolism of ^{14}C-labelled plant materials by woodlice (*Tracheoniscus rathkei* Brandt) and soil microorganisms. *Soil Biol. Biochem.* **8**, 103–108.

RIPPER W. (1930) Zur Frage des Celluloseabbaus der Holzverdauung xylophager Insektenlarven. *Z. vergl. Physiol.* **13**, 314–333.

RIVNAY M. S. (1945) Physiological and ecological studies of the species of *Capnodis* in Palestine (Col., Buprestidae). II—studies on the larvae. *Bull. ent. Res.* **36**, 103–119.

RÖSSLER M. E. (1961) Ernahrungsphysiologische Untersuchungen an Scarabaeidlarven (*Oryctes nasicornis* L., *Melolontha melolontha* L.). *J. Insect. Physiol.* **6**, 62–80.

SCHLOTTKE E. (1945) Uber die Verdauungsfermente im Holzfressender Käferlarven, *Zool. Jb., Allgemeine Zoologie und Physiologie der Tiere* **61**, 88–140.

SCHULZE E. F. & ERHARDT P. (1963) Nachweis Kohlenhydratspaltender Fermente im Darmtrakt verschiedener Entwicklungsstadian von *Diprion pini* L. (Hym., Tenthredinidae). *Ent. exp. appl.* **6**, 114–122.

SEIFERT K. & BECKER G. (1965) Der chemische Abbau von Laub- und Nadelholzarten durch verschiedenden Termiten. *Holzforschung* **19**, 105–111.

SHINODA O. (1930) Contributions to the knowledge of intestinal secretion in insects—III. On the digestive enzymes of the silkworm. *J. Biochem., Tokyo* **11**, 345–367.

SINHA T. B. & SRIVASTAVA D. C. (1970) Cellulose digestion in *Pseudocaecilius elutus* (Psocoptera). *Enzymologia* **39**, 84–86.

SINSABAUGH R. L., BENFIELD E. F. & LINKINS A. E. (1981) Cellulose digestion and assimilation by a stream shredder. *Abstract, 29th Annual Meeting of the North American Benthological Society*, Provo, Utah, April 27–30, 1981.

SOO HOO C. F. & DUDZINSKI A. (1967) Digestion by the larvae of the pruinose scarab. *Ent. exp. Appl.* **10**, 7–15.

SPILLER D. (1951) Digestion of alpha-cellulose by larvae of *Anobium punctatum* DeGeer. *Nature, Lond.* **168**, 209–210.

TAKANONA T. & HORI K. (1974) Digestive enzymes in the salivary gland and midgut of the bug *Stenotus binotatus*. *Comp. Biochem. Physiol.* **47A**, 521–528.

TALMADGE K. W. & ALBERSHEIM P. (1969) Plant cell wall polysaccharide degrading enzymes of *Melanoplus bivittatus*. *J. Insect Physiol.* **15**, 2273–2283.

TERRA W. R., FERREIRA C. & DEBIANCHI A. G. (1979) Distribution of digestive enzymes among the endo- and ectoperitrophic spaces and midgut cells of *Rhynchosciara* and its physiological significance. *J. Insect Physiol.* **25,** 487–494.

THAYER D. W. (1978) Carboxymethylcellulase produced by facultative bacteria from the hindgut of the termite *Reticulitermes hesperus. J. gen. Microbiol.* **106,** 13–18.

TRAGER W. (1932) A cellulase from the symbiotic intestinal flagellates of termites and of the roach, *Cryptocercus punctulatus. Biochem. J.* **26,** 1762–1771.

VEIVERS P. C., MUSCA A. M., O'BRIEN R. W. & SLAYTOR M. (1981) Digestive enzymes of the salivary glands and gut of *Mastotermes darwiniensis. Insect Biochem.* **12,** 35–40.

WHARTON D. R. A. & WHARTON M. L. (1965) The cellulase content of various species of cockroaches. *J. Insect Physiol.* **11,** 1401–1405.

WIEDMANN J. F. (1930) Die Celluloseverdauung bei Lamellicornierlarven. *Z. Morph. Okol. Tiere* **19,** 228–258.

WOOD T. M. & MCCRAE S. I. (1979) Synergism between enzymes involved in the solubilization of native cellulose. In *Hydrolysis of Cellulose: Mechanisms of Enzymatic and Acid Hydrolysis* (Edited by BROWN R. D. & JURASEK L.), Advances in Chemistry Series, No. 181, pp. 179–209. American Chemical Society, Washington.

YAMAOKA I. & NAGATANI Y. (1975) Cellulose digestion system in the termite *Reticulitermes speratus* (Kolbe). I. Producing sites and physiological significance of two kinds of cellulase in the worker. *Zool. Mag., Tokyo* **84,** 23–29.

YAMIN M. A. (1981) Cellulose metabolism by the flagellate *Trichonympha* from a termite is independent of endosymbiotic bacteria. *Science, N.Y.* **211,** 58–89.

YAMIN M. A. & TRAGER W. (1979) Cellulolytic activity of an axenically-cultivated termite flagellate, *Trichomitopsis termopsidis. J. gen. Microbiol.* **13,** 417–420.

YOKOE Y. (1964) Cellulase activity in the termite *Leucotermes speratus* with new evidence in support of a cellulase produced by the termite itself. *Scientific Papers of the College of General Education, University of Tokyo* **14,** 115–120.