American Jurassic Symmetrodonts and Rhaetic "Pantotheres"

Abstract. *The molar morphology of the symmetrodonts* Tinodon *and* Eurylambda *from the late Jurassic of North America is virtually identical to that of so-called "pantotheres" from the Rhaetic of Wales. Therefore a primitive symmetrodont molar pattern was probably present in the phylogeny of pantotherian and tribosphenic molars. Occlusion of* Tinodon *and* Eurylambda *produced complex wear facets unlike the simple trigon-trigonid shear surfaces of* Spalacotherium *and* Peralestes.

Two papers on Mesozoic mammals throw considerable light on the evolution of early mammals. Mills (*1*) has suggested that the tribosphenic molars of eutherians and metatherians could have been derived from paurodont pantotheres such as *Amphitherium* and *Peramus* and that these genera in turn could have been derived from the Rhaetic symmetrodonts from Glamorgan, Wales (*2*). Kermack *et al.* (*3*) supported Mills' phylogeny but concluded that the teeth of the Rhaetic symmetrodonts were actually those of primitive pantotheres. If their diagnosis of the Rhaetic forms as pantotheres and Mills's proposed phylogeny are both correct, it would mean that symmetrodonts (as they are now known) and dryolestid pantotheres were not involved in the ancestry of eutherians and metatherians. This view contrasts to Patterson's (*4*) and claims a very early origin for the pantotheres as a distinct order.

The American Jurassic symmetrodonts, *Tinodon, Amphidon,* and *Eurylambda,* were reexamined with regard to these conclusions. These genera have been described and figured by Simpson (*5–7*). Further preparation of these genera and improved optical equipment have yielded new information on molar morphology, especially wear facets. Our description of the molars is intended as a supplement to Simpson's.

In Fig. 1, A and B, the crown and buccal views of the four molars of *Tinodon bellus* [Y.P.M. (Yale Peabody Museum) 13644] are shown. Contrary to the published figure and statements by Simpson (*5–7*), the molars of *Tinodon* are not symmetrical. This is especially true of $\overline{M}_3$; the main cusp (protoconid) is slightly distal to the center of the crown, and the mesiobuccal surface of the crown is longer than the distobuccal surface. The posterior accessory cusp (metaconid) is more lingual in position than the anterior accessory cusp (paraconid) so that a line connecting the protoconid and metaconid forms an angle 54° with the longitudinal axis of the mandible, whereas a line connecting the protoconid and paraconid forms an angle of approximately 27° (Fig. 1A). The angle of the trigonid is therefore 99°. This falls slightly outside Patterson's definition for acute-angled symmetrodonts which have an angle less than 90° (*8*). The angle of the trigonid decreases progressively; $\overline{M}_1$ = 155°, $\overline{M}_2$ = 115°, $\overline{M}_3$ = 99° ($\overline{M}_4$ is damaged but is probably approximately 115°). In buccal or lingual view the four molars are very similar in outline, and the angle changes of the trigonid are not obvious features unless the teeth are examined in crown view.

On the mesial cingulum of $\overline{M}_2$, $\overline{M}_3$, and $\overline{M}_4$ two small cusps are present. The mesiolingual cingulum cusp has been recognized and described by Simpson (*5, 6*) and is also present in the British symmetrodonts (*7*) and *Spalacotheroides* (*9*). However, the mesiobuccal cingulum cusp has not been de-described previously in Jurassic symmetrodonts. In $\overline{M}_2$ the mesiobuccal cusp is smaller than the mesiolingual and in $\overline{M}_1$ the buccal cusp is represented by a cingulum only. The third premolar has a mesiobuccal cingulum but no mesial cingulum cusps could be recognized. The distal cingulum cusp which is present on all the molars of *Tinodon* fits into the small concavity between the two mesial cingulum cusps of the succeeding molar. A prominent lingual cingulum is present on $\overline{M}_2$, $\overline{M}_3$, and $\overline{M}_4$. A buccal cingulum, such as that present in *Spalacotherium* (*10*) and

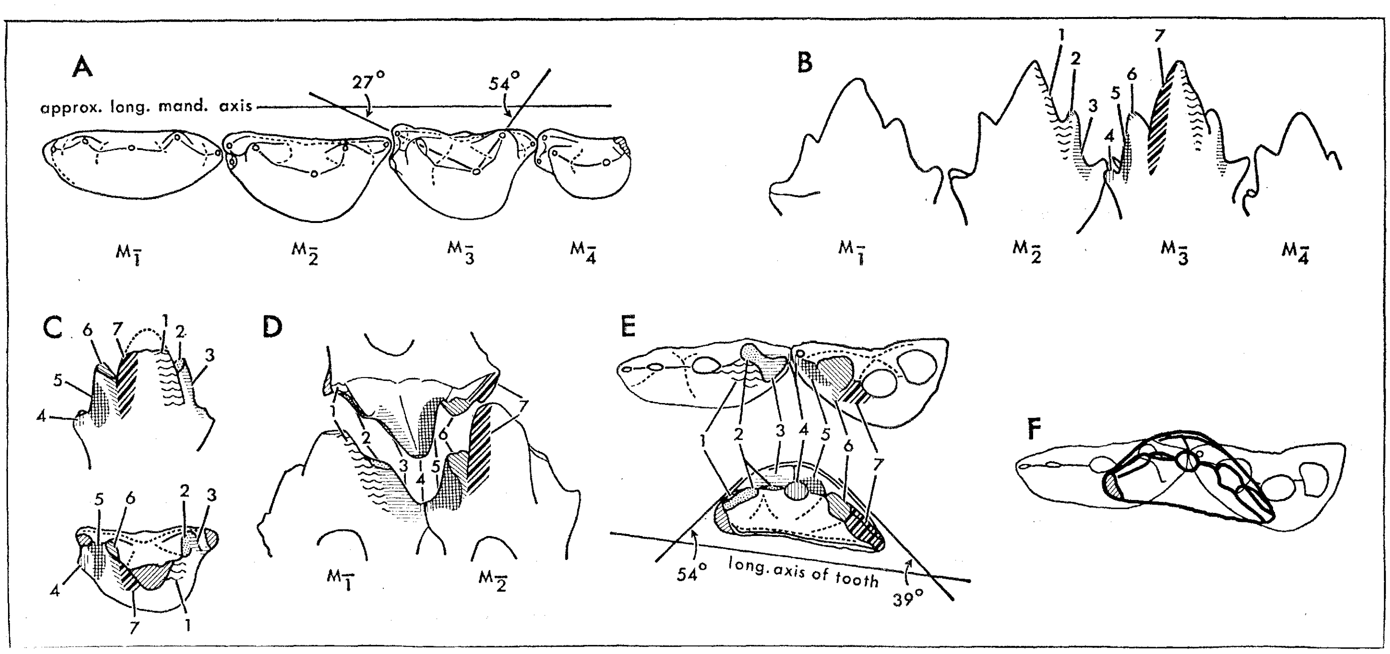

Fig. 1. (A) molars of *Tinodon bellus* (Y.P.M. 13644), occlusal view. (B) The same, buccal view. (C) ?M_3 of *Tinodon* sp. (Y.P.M. 13645), buccal and occlusal views. (D) *Eurylambda aequicrurius* (Y.P.M. 13637), lingual view, and *Tinodon bellus* (Y.P.M. 11843), buccal view. (E) The same, occlusal view. (F) Occlusal reconstruction of *Eurylambda* (heavy lines) and *Tinodon* (light lines).

less completely in *Spalacotheroides* (*9*), is not present in $M_{\overline{2}}$, $M_{\overline{3}}$, or $M_{\overline{4}}$. However, $M_{\overline{1}}$ has a very faint mesiobuccal cingulum as noted above.

The wear pattern of symmetrodonts is best understood by examining a series of specimens representing successive stages of wear. Specimens of *Tinodon bellus* (Y.P.M. 13644) and *Tinodon lepidus* [U.S.M.N. (United States National Museum) 2131] display well-preserved and only lightly worn dentitions, but wear may be determined as follows. Distinct but faint facets are present upon the distobuccal surfaces of the protoconid and the metaconid (Fig. 1B, facets 1 and 3). Faint wear facets are also present on the mesiobuccal surfaces of the protoconid and the paraconid, numbered 7 and 5, respectively. A small but distinct facet is present on the apex of the paraconid (facet 6) and on the tip of the mesiobuccal cingulum cusp (facet 4).

A single tooth of *Tinodon* sp. (Y. P.M. 13645) (Fig. 1C) represents a stage of intermediate wear. Although slightly damaged (apices of main, mesiolingual cingulum and posterior cingulum cusps are missing) its outline matches extremely closely that of $M_{\overline{3}}$ of Y.P.M. 13644 and U.S.N.M. 2131. In this tooth the wear facets described above are more deeply incised but there is still clear separation between facets 1 and 3 and between facets 7 and 5. The facet on the paraconid (facet 6) is heavily worn, and it extends ventrally onto the buccal surface of the paraconid, becoming confluent with the base of wear facet 7. Wear facet 4 is enlarged but still quite distinct from facet 5. In this tooth the tip of the metaconid (facet 2) is also worn.

In the type of *Tinodon bellus* (Y. P.M. 11843), the facets are deeply incised (see Fig. 1 D and E for buccal and occlusal views of $M_{\overline{1}}$ and $M_{\overline{2}}$), and the specimen represents a stage of advanced wear. In both teeth, facets 4 and 5 are enlarged and confluent. All traces of a mesiobuccal cingulum cusp have been obliterated and wear facet 4 extends onto the talonid so that facets 3, 4, and 5 are confluent. Wear on the talonid in *Tinodon* molars was only possible after the mesiobuccalcusp of the preceeding tooth had been effaced by wear. Wear facet 6 is greatly enlarged so that the apex of the paraconid is worn down to its base where it separates from the protoconid. The apical surface of wear facet 6 is directed dorsally and slightly buccally, and on the buccal surface of the crown it is confluent with facet 7. Despite the overlap due to increased wear of the teeth, facets 6 and 7 are nevertheless recognizable because they are oriented in slightly different directions. The metaconid has been almost completely effaced by wear, and facet 2 is extremely large. Facets 1 and 3 are still distinct from one another and face in slightly different directions.

The single known upper molar of a Morrison symmetrodont, *Eurylambda aequicrurius* (Fig. 1, D and E), is extremely worn. Along the lingual base of the paracone there is a faint cingulum which disappears mesially above the stylocone and distally above the metacone. In crown view the tooth is distinctly asymmetrical, although the asymmetry is reflected more in the outline of the crown than in the position of the cusps. The mesiolingual surface (Fig. 1E) of the base of the crown forms an angle of 54° with the longitudinal axis of the tooth, whereas the distolingual surface of the base of the crown forms an angle of 39° with the longitudinal axis of the tooth. It is not possible to measure accurately the angle of the trigon because the tooth is badly worn, but it appears to be about 160° rather than "approximately 135°," the figure given by Patterson (*11*) for the "wide-angled" symmetrodonts.

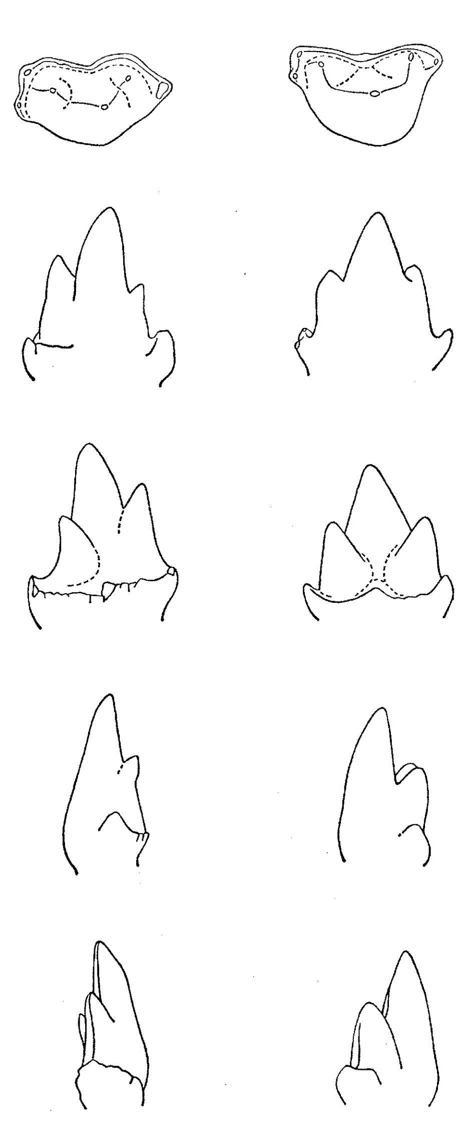

Fig. 2. Comparison of a typical lower molar of a Welsh "pantothere" [after Kermack *et al.* (*3*)] and *Tinodon*. From top to bottom, occlusal, buccal, lingual, distal, and mesial views.

The crown and buccal views of $M_{\overline{1}}$ and $M_{\overline{2}}$ of *Tinodon* and the molar of *Eurylambda* are compared in Fig. 1, D and E. Unfortunately the mesial cingulum area has been damaged and lost in *Eurylambda*. In order to compare occluding surfaces, the lingual wear facets of the upper are illustrated in Fig. 1D. This is as they would appear if one could see through the buccal side of the tooth to the occluding surface. An outstanding feature of the upper molar is the large wear facet $\underline{6}$ on the apex of the metacone. This facet is directed slightly lingually and would match the wear facet on the dorsal surface of the paraconid ($\bar{6}$). Lying distally to wear facet $\underline{6}$ of the upper molar is an elongated wear facet $\underline{7}$ terminating at the distal extremity of the crown. This facet is directed more lingually than the more mesially placed facet $\underline{6}$ and would match the wear facet on the mesiobuccal surface of the protoconid ($\bar{7}$). A distinct wear facet ($\underline{4}$) is present on the apex of the paracone and could be accounted for by occlusion with the mesiolabial cingulum cusp of the lower molar ($\bar{4}$). Facets $\underline{3}$ and $\underline{5}$ on the mesiolingual and distolingual surfaces of the paracone would match wear facets $\bar{3}$ and $\bar{5}$ of the two adjacent lower molars. All that remains of the stylocone is a prominent mesially directed wear facet $\underline{2}$ which is apparently the result of extensive wear against the apex of a metaconid on a preceding tooth ($\bar{2}$); some doubt remains, however, about the occlusal relationships of the stylocone and metaconid because the orientation of occlusal surfaces are slightly different. On the mesiolingual face of the stylocone is a near vertical facet ($\underline{1}$) which is probably the result of wear against the distobuccal surface of the protoconid (1). Unfortunately the critical area for a complete determination of this facet in *Eurylambda* is missing. The molar outlines and correspondence of wear facets make it extremley probable that the genus *Eurylambda* represents the upper dentition of *Tinodon*. The preservation of the maxilla of *Eurylambda* is such that it is not possible to determine the numerical position of the single molar preserved. It is clear, however, from the occlusion diagram shown in Fig. 1F that the upper of *Eurylambda* would fit best between $M_{\overline{1}}$ and $M_{\overline{2}}$, and by this reasoning the *Eurylambda* molar could well be an M_1. It has been shown in *Tinodon* that the angle of the trigonid decreases progressively in the $M_{\overline{1}}$ to $M_{\overline{3}}$ series from 155° to 99°, and thus the wide-angled trigon of the *Eurylambda* molar may indicate that it is a mesial molar. The wear facets of *Amphidon* lower molars have been studied but do not match those of *Eurylambda*.

An important finding that emerges from this study of wear facets of *Tinodon* and *Eurylambda* teeth is that the mesiobuccal and distobuccal surfaces of the trigonid and the mesiolingual and distolingual surfaces of the trigon do not form continuous shearing surfaces. In *Tinodon* and *Eurylambda* the metacone and stylocone in the upper and the metaconid and paraconid in the lowers are out of line, and their apices are subjected to the most wear. This is in contrast to British symmetrodonts in which the shearing surfaces on the mesial and distal surfaces of the main cusps (protoconid; paracone) are continuous with those of the mesial and distal surfaces of the accessory cusps (metaconid, paraconid: metacone, stylocone) (*12*).

In Fig. 2 the lower molar of a Welsh "pantothere" figured by Kermack *et al.* (*3*) is compared with that of the third molar of *Tinodon*. Except for minor differences, the teeth of the two genera are almost identical. Both are asymmetrical and have an incipient talonid supporting a small cuspule (hypoconulid?). In both, the teeth have two mesial cuspules; between these the distal surface of the talonid of the preceding tooth fits. Finally, both molar types have a well-developed lingual cingulum and a prominent wear facet on the apex of the paraconid. The Welsh form has a short cingulum which is not present in either the second or third molar of *Tinodon*; however, a small bucco-

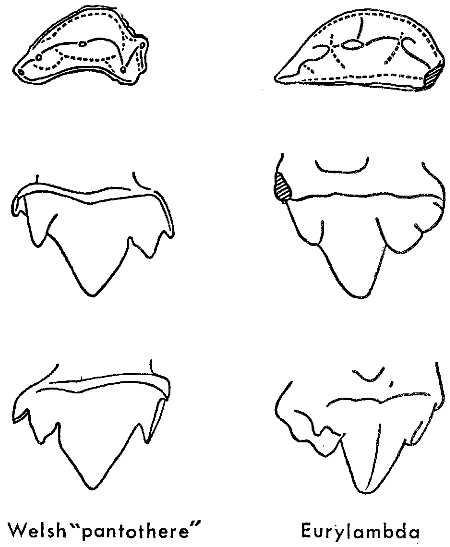

Fig. 3. Comparison of a typical upper molar of a Welsh "pantothere" [after Kermack *et al.* (*3*)] and *Eurylambda*. From top to bottom, occlusal, buccal, and lingual views.

mesial cingulum is present in the first molar and third premolar of *Tinodon*.

In Fig. 3 the upper molar of a Welsh "pantothere" figured by Kermack *et al.* (*3*) is compared with the single known molar of *Eurylambda*. Both are asymmetrical in crown view. In both, the posterior portion of the crown which supports the metacone and posterior cingulum cusp is slender, and the paracone, metacone, and posterior cingulum cusp are roughly in line. The upper molar of the Welsh "pantothere" has a well-developed lingual and buccal cingulum. The buccal cingulum of *Eurylambda* is well developed but the lingual cingulum is faint and only clearly formed in the region above the paracone. The stylocone in *Eurylambda* does not appear to be as well developed as it is in the Welsh form, but questions of relative size are difficult to settle conclusively in view of the extensive wear on the *Eurylambda* molar. An unequivocal difference between the teeth is the more buccal location of the stylocone in the Welsh form, but this and other minor differences are probably due to the fact that a comparison is being made between molars from different positions in the molar series.

One of the reasons why Kermack *et al.* (*3*) classified the Welsh forms as "pantotheres" is that there occurs a mesial beveling of the apex of the paraconid which is caused, in their opinion, by contact with the distolingual cingulum of the upper molars. They believed this distolingual cingulum to be the precursor of the protocone. The paraconid of *Tinodon* is worn in the same way as that of the Welsh forms, that is, with a mesial bevel. We have shown that in *Tinodon* the paraconid wear facet, shearing against the metacone, enlarges with increasing wear and that it could not have resulted from occlusion with the lingual cingulum. Admittedly the upper molar lingual cingulum in the Welsh form is larger than in *Eurylambda*, but despite this we doubt, in view of the great similarity of the molar structure of the two groups, that the beveling of the paraconid in the Welsh forms could have been caused by the occlusion of the paraconid and upper lingual cingulum.

On the basis of tooth morphology, we would hesitate to place the molars of *Tinodon, Eurylambda,* and the Welsh "pantotheres" in two different orders of Mesozoic mammals, especially as the molars of *Tinodon* and *Eurylambda* are more similar in appearance to those of the Welsh "pantotheres" than the latter are to the primitive pantotheres *Amphitherium* and *Peramus*. We believe that the Welsh Rhaetic forms should continue to be classified as symmetrodonts, as was originally suggested, rather than pantotheres. The molars of *Tinodon* and *Eurylambda* appear to be conservative within the symmetrodonts, having retained the primitive form of Rhaetic symmetrodonts. The more advanced *Spalacotherium, Peralestes*, and *Spalacotheroides* can also be derived from the Rhaetic forms. These three genera developed symmetrical molars in which the three main cusps formed an acute-angled isosceles triangle; they possessed a simple shearing-type occlusion, lost the mesiobuccal cingulum cusp of the lower molars, and reduced the talonid (*13*).

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References and Notes

1. J. R. E. Mills, *Proc. Linnean Soc. London* **175**, 117 (1964).
2. H. Kühne, *Nature* **166**, 695 (1950).
3. K. A. Kermack, P. M. Lees, F. Mussett, *Proc. Roy. Soc. Ser. B.* **162**, 535 (1965).
4. B. Patterson, *Fieldiana Geol.* **13**, 1 (1956). Patterson concluded that the evolution of the tribosphenic molar could be traced structurally from a symmetrodont through a pantothere molar type. On the basis of this conclusion, Patterson has homologized most of the molar cusps in symmetrodont, pantothere, and tribosphenic teeth. In view of the limited number of Jurassic mammals and lack of clarity concerning their interrelations, Simpson [*Kongr. Vl. Acad. Wetensch. Sch. Kunsten*

België **1**, 57 (1961)] expressed doubts about homologies proposed by Patterson, but Mills's (*1*) functional studies essentially support the cusp homologies proposed by Patterson. In our paper we have adopted Patterson's cusp nomenclature.
5. G. G. Simpson, *Am. J. Sci.* **10**, 451 (1925).
6. ———, *Mem. Yale Peabody Mus.* **3**, (1929).
7. ———, *A Catalogue of the Mesozoic Mammalia in the Geological Department of the British Museum* (W. Clowes, London, 1928). Simpson placed *Tinodon* (on the basis of lower teeth and jaws only) in the Spalacotheriidae together with the British genera *Spalacotherium* and *Peralestes*. He considered *Eurylambda* (on the basis of a crushed right maxilla with a single molar) to be a symmetrodont *incertae sedis*. He discussed the possibilities that *Eurylambda* may represent either an upper of *Amphidon* or of *Tinodon*, but he concluded that, in view of the doubtful character of the evidence, it was best to place it in a separate genus. Simpson figured the crown view of *Tinodon* (*6*) as having the three main molar cusps arranged in a symmetrical triangle; furthermore, he stated in *The Catalogue of the Mesozoic Mammalia* that *Tinodon* had molars more symmetrical than the British *Spalacotherium*. On the basis of the comparable asymmetry of the crowns of *Spalacotherium* and *Peralestes*, he concluded that they were probably upper and lower teeth of the same animal.
8. Patterson (*4*) divided the symmetrodonts into two distinct groups. One group, the "acute-angled" symmetrodonts, includes *Spalacotheroides, Spalacotherium* and *Peralestes*. In these genera the three cusps of the trigon and trigonid form an angle of less than 90°. The second group includes forms with more open triangles, that is, *Eurylambda, Tinodon*, and *Manchurodon*. He considers the second group as more specialized than the acute-angled symmetrodonts and that members of this group tend toward the development of mesiodistal shear (for example, the triconodonts).
9. B. Patterson, *Fieldiana Zool.* **37**, 689 (1955).
10. W. A. Clemens, *Palaeontology* **6**, 55 (1963).
11. B. Bohlin, *Bull. Geol. Inst. Univ. Upsala* **31**, 363 (1945), [as quoted by Patterson (*4*) in this regard].
12. G. G. Simpson, *Palaeobiologica* **5**, 127 (1933), stated that jaw movements in symmetrodonts were strictly orthal, but Patterson (*4, 9*) cited oblique, parallel wear striations in *Spalacotheroides* as evidence of ectental movement during jaw closure. We have observed similar features in *Tinodon lepidus* (U.S.N.M. 2131) and agree with Patterson's interpretation.
13. Supported by an NSF grant.

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Equilibration Temperatures of Iron and Magnesium in Chondritic Meteorites

Abstract. *The distribution coefficients for Fe^{++} and Mg^{++} were calculated from new microprobe analyses of coexisting olivine, orthopyroxene, and calcic pyroxene in chondritic meteorites. Interpretation of the data shows that (i) the equilibration temperatures were of the order of 850°C, and (ii) the olivine-orthopyroxene partition does not reflect ideal behavior. This equilibration temperature is much lower than previous estimates.*

One of the major problems in meteoritics is determination of the temperatures represented by the partition of Fe^{++} and Mg^{++} among coexisting olivine, orthopyroxene, and calcic pyroxene in chondritic meteorites that have uniform silicate compositions. Previous studies of this problem (*1, 2*), which dealt only with the data on the partition of Fe^{++} and Mg^{++} between coexisting olivine and orthopyroxene, have arrived at temperatures of >900°C (*1*) and ~1250°C (*2*). On the basis of these temperatures some authors (*3*) have concluded that the Fe^{++}–Mg^{++} partition results from equilibrium crystallization of olivine and orthopyroxene at or near the liquidus, and have discounted the influence of metamorphism on the compositions of the silicates in chondrites. On the basis of evidence discussed below, one may now argue that the temperatures previously deduced are too high by as much as 400°C.

The use of the compositions of coexisting olivine and orthopyroxene for geothermometry depends upon the partitioning of Fe^{++} and Mg^{++} between these phases according to the reaction

$$\underset{\text{olivine}}{\tfrac{1}{2}Mg_2SiO_4} + \underset{o\text{-pyroxene}}{FeSiO_3} = \underset{\text{olivine}}{\tfrac{1}{2}Fe_2SiO_4} + \underset{o\text{-pyroxene}}{MgSiO_3}$$

The equilibrium constant for this reaction may be written

$$K_1 = [(\gamma_{Fe}^{OL} \cdot \gamma_{Mg}^{OPX})/(\gamma_{Mg}^{OL} \cdot \gamma_{Fe}^{OPX})] \times [(X_{Fe}^{OL} \cdot X_{Mg}^{OPX})/(X_{Mg}^{OL} \cdot X_{Fe}^{OPX}) \quad (1a)$$

where X_A^a denotes the mole fraction of element A in mineral a, and γ_A^a denotes the activity coefficient of element A in mineral a; K_1 is dependent on P and T, and γ_A^a is dependent on P, T, and the composition of the mineral phase. In the special case where both mineral species are ideal solid solutions (γ_A^a = 1),

$$K_1 = Kd_1 = (X_{Fe}^{OL} \cdot X_{Mg}^{OPX})/(X_{Mg}^{OL} \cdot X_{Fe}^{OPX}) \quad (1b)$$

where Kd_1 is the distribution coefficient determined from the compositions of the coexisting phases and assumed ideality.

A similar set of equations can be written for the mineral pair orthopyroxene–calcic pyroxene:

$$\underset{c\text{-pyroxene}}{MgCaSi_2O_6} + \underset{o\text{-pyroxene}}{FeSiO_3} = \underset{c\text{-pyroxene}}{FeCaSi_2O_6} + \underset{o\text{-pyroxene}}{MgSiO_3} \quad (2)$$

$$K_2 = [(\gamma_{Fe}^{Ca-PX} \cdot \gamma_{Mg}^{OPX})/(\gamma_{Mg}^{Ca-PX} \cdot \gamma_{Fe}^{OPX})] \times [(X_{Fe}^{Ca-PX} \cdot X_{Mg}^{OPX})/(X_{Mg}^{Ca-PX} \cdot X_{Fe}^{OPX})] \quad (2a)$$

and, on the assumption of ideality,

$$K_2 = Kd_2 = (X_{Fe}^{Ca-PX} \cdot X_{Mg}^{OPX})/(X_{Mg}^{Ca-PX} \cdot X_{Fe}^{OPX}) \quad (2b)$$

The temperature dependence of K, at constant pressure, may be given by

$$\ln K = -\Delta G^{\circ}/RT \quad (3)$$

where ΔG° is the change in standard free energy for the reaction involved.

Both exchange reactions have been discussed in terms of terrestrial mineral assemblages by several authors, with the following results. (i) Attempts (*4, 5*) to demonstrate a simple relation between the compositions of coexisting olivine and orthopyroxene and rock type (for example, igneous versus metamorphic) have largely failed. Little, if any, evidence indicates that Eq. 1 represents partition between ideal solid solutions; rather, the evidence suggests that the partition relations for Eq. 1 are complex. (ii) Several authors (*5–7*) have shown that Eq. 2 *does* behave as though both mineral species were ideal solid solutions; furthermore, that one can separate high-temperature (igneous) rocks from moderate-temperature (metamorphic) rocks on the basis of their Fe^{++}–Mg^{++} partition as defined by Eq. 2b. The data from one such author (*7*) are presented in Fig. 1. The 45° lines show the curves obtained from Eq. 2b for Kd = 0.54 and 0.73.

Little usable data from experimental petrology exists for geothermometry by the above systems. Older data (*8*) have been used (*1, 2*) to obtain information for the olivine-orthopyroxene pair, but the data are much too imprecise to

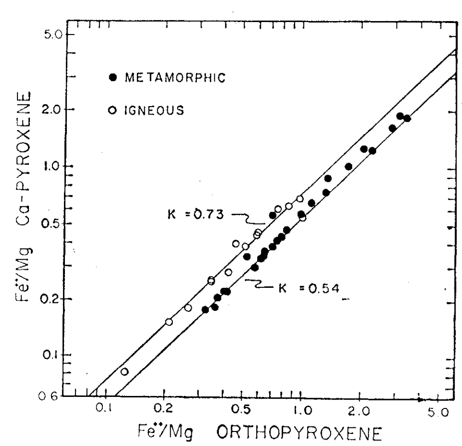

Fig. 1. Composition of coexisting orthopyroxene and calcic pyroxene from terrestrial rocks (*7*). The lines for $K = 0.54$ and 0.73 are for solutions of Eq. 2b: ideal solid-solution partition. The near-ideal behavior of this mineral pair in nature is illustrated by the nearly colinear plot of data points.