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THE EARLIEST *TEGULORHYNCHIA*
(BRACHIOPODA: RHYNCHONELLIDA) AND ITS
EVOLUTIONARY SIGNIFICANCE

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ABSTRACT—*Tegulorhynchia boongeroodaensis* n. sp. is described from the Early Paleocene–Early Eocene Cardabia Group in the Carnarvon Basin of Western Australia. This is the earliest known occurrence of the genus. Changes in frequency of occurrence of this species correspond with changes in the nature of the sediment: highest frequency of occurrence is in greensands; upward stratigraphic change to calcarenites and ultimately to calcilutites is associated with diminution in frequency of occurrence of the brachiopod and is thought to relate to reduction in suitable sites of attachment. Like descendant species, *T. boongeroodaensis* underwent no morphological change during the course of its time range. Evidence is presented to indicate that evolution of later species of *Tegulorhynchia* and the closely related *Notosaria* proceeded by pedomorphosis. The result of this was attainment of a morphology adapted to regimes of higher hydrodynamic activity.

INTRODUCTION

THE CARDABIA GROUP, which occurs in the northern Carnarvon Basin of Western Australia, outcrops mainly on the flanks of the Giralia Range, south of Exmouth Gulf. This largely carbonate sequence ranges in age (McGowran, 1968, 1978) from the Early Paleocene (planktonic foraminiferal Zone P.2) to the Early Eocene (p.f. Zone P.8) and probably represents the most fossiliferous unit of this age in Australia.

The aim of this paper is to describe the only species of rhyntonellide brachiopod which occurs in the Cardabia Group; to discuss the relationship between its stratigraphic distribution and sediment type; and to reappraise the evolution of the genus *Tegulorhynchia* (within which the species is placed) and the closely related *Notosaria*.

Little work has been carried out on the rich macrofossil fauna of the Cardabia Group which, dominated by echinoids, also commonly contains brachiopods, corals, bryozoans, bivalves and gastropods, as well as occasional crabs. Cockbain (1967) has described the craniid brachiopod *Westralicrania alleni* from borehole material, while Foster and Philip (1978) described two new genera and three new species of holasteroid echinoids and McNamara and Philip (1980) have described the echinoid *Schizaster (Paraster) carinatus*.

All specimens of the newly described species of *Tegulorhynchia* are in the collec-

tions of the Western Australian Museum (WAM). All Grid References (G.R.) refer to the KV section of the Giralia 1:100,000 map sheet.

One new term is introduced: 'paedomorphocline.' This may be defined as a stepped morphological gradient of paedomorphic forms, extending from an ancestral apaeomorph to an 'extreme' paedomorph which possesses adult characteristics found only in the earliest juveniles of the ancestor. The paedomorphocline is an evolutionary gradient which may extend through time and/or space. Examples, apart from that described herein, are the Scottish olenellid trilobite paedomorphocline through space (McNamara, 1978) and the Cretaceous ammonite genus *Protacanthoceras* (Wright and Kennedy, 1980), a paedomorphocline through time.

The counterpart of paedomorphocline will be a 'peramorphocline' (for definition of peramorphosis see Alberch et al., 1979). An example is the morphological gradient through space and time in the lineage of the heart urchin *Schizaster* (McNamara and Philip, 1980). The concepts of the paedomorphocline and the peramorphocline are discussed more fully in McNamara (1982).

STRATIGRAPHY OF THE CARDABIA GROUP

The oldest unit in the Cardabia Group is the Boongerooda Greensand which reaches a maximum thickness of only 3.3 m in its type section in Toothawarra Creek (Condon et al.,

1956). The formation is composed entirely of green glauconitic sand apart from minor phosphatic nodules and reworked phosphatized ammonites derived from the underlying Maastrichtian Miria Marl, which it disconformably overlies. Although Brunnschweiler (1966) favored a Late Cretaceous age for the Boongerooda Greensand, Edgell (1952) and McGowran (1968, 1978) have suggested an Early Paleocene (p.f. Zone P.2) age on the basis of the foraminifers. Brunnschweiler (1966, p. 12) based his conclusion for a Late Cretaceous age, in part, on the occurrence of "brachiopods of the *Cyclothyris* group in great numbers." The youngest known cyclothyrids are Late Cretaceous (Ager, 1965). However, the foraminiferal evidence and the description of the brachiopod herein as a member of the Tertiary to Recent genus *Tegulorhynchia* suggest an early Tertiary age.

The Boongerooda Greensand is conformably overlain by the 25–30 m thick Wadera Calcarenite. The formation consists almost entirely of glauconitic calcarenite (Condon et al., 1956). The overlying Pirie Calcarenite reaches a thickness of 33 m and is composed largely of bryozoal calcarenite with minor intercalations of calcilutite. The uppermost member of the Cardabia Group, the 10 m thick Cashin Calcarenite, differs from the underlying Pirie Calcarenite in the greater proportion of calcilutite and fine-grained calcarenite. Thus, there is a general progressive

upward development of finer-grained carbonate sediments through the Cardabia Group. This change is accompanied by an alteration in the aspect of the fauna.

SYSTEMATIC PALEONTOLOGY

Order RHYNCHONELLIDA Kuhn, 1949

Family HEMITHYRIDIDAE

Rzhonsnitskaya, 1956

Genus TEGULORHYNCHIA Chapman and Crespin, 1923

Type species.—*Rhynchonella squamosa* Hutton, 1873, p. 37.

TEGULORHYNCHIA BOONGEROODAENSIS

n. sp.

Figures 1A–Y

Cyclothyris spp. nov. BRUNNSCHWEILER. In CONDON ET AL., 1956, p. 30.

Holotype.—WAM 80.1523 from the Boongerooda Greensand, 3.6 km NNW of Whitlock Dam, Giralia Station, from head and left bank of gully, Grid Reference Giralia KV115820; collected by G. W. Kendrick 26.8.79. Dimensions of the holotype and paratypes given in Table 1.

Material, localities and horizons.—In addition to the holotype, 158 specimens have been collected from the Cardabia Group. From the Boongerooda Greensand: 44 specimens (including the paratypes WAM 71.161a, b, d, e, 80.1499–80.1502) from the

FIGURE 1—*Tegulorhynchia boongeroodaensis* n. sp. All specimens are from the Early Paleocene Boongerooda Greensand, except for WAM 80.1508 (A, F, G, K) which is from the Late Paleocene Pirie Calcarenite. All magnifications are $\times 2$. A, F, G, K, WAM 80.1508, paratype, from the southern tributary of Toothawarra Creek, about 350 m S of junction with northern tributary, G.R. 070720. Note relatively large foramen, low beak angle, narrow shell, lenticular profile and rectimarginate commissure. B, L, WAM 80.1492, paratype, from the base of Section Hill, G.R. 017543. C, H, WAM 80.146, paratype, from same locality as 80.1492. D, I, WAM 71.148b, paratype, from same locality as 80.1508, but lower in section. Note increasing development of uniplicate commissure through Figures K, L, I. E, WAM 80.1501, paratype, from same locality as 71.148b. Note small foramen. J, WAM 80.1500, paratype, from same locality as 71.148b. M, WAM 71.148c, paratype, from same locality as 71.148b. Development of strong uniplicate commissure initiated at earlier stage of growth than normal in this individual. N, R, WAM 71.161a, paratype, from same locality as 71.178b. Gerontic individual with excess shell growth occurring dorso-ventrally about commissure. P, WAM 71.161e, paratype, from same locality as 71.148b. Individual with narrow profile, but uniplication still very pronounced. Q, WAM 80.1497, paratype, from same locality as 80.1492, showing lemniscate type of pallial sinus pattern in pedicle valve. S, WAM 71.148a, paratype, from Toothawarra Creek, G.R. 070725, showing internal features of brachial valve. T, W, X, Y, WAM 80.1523, holotype, from 3.6 km NNW of Whitlock Dam, Giralia Station, G.R. 115820. U, V, WAM 80.1499, paratype, from same locality as 71.148b.

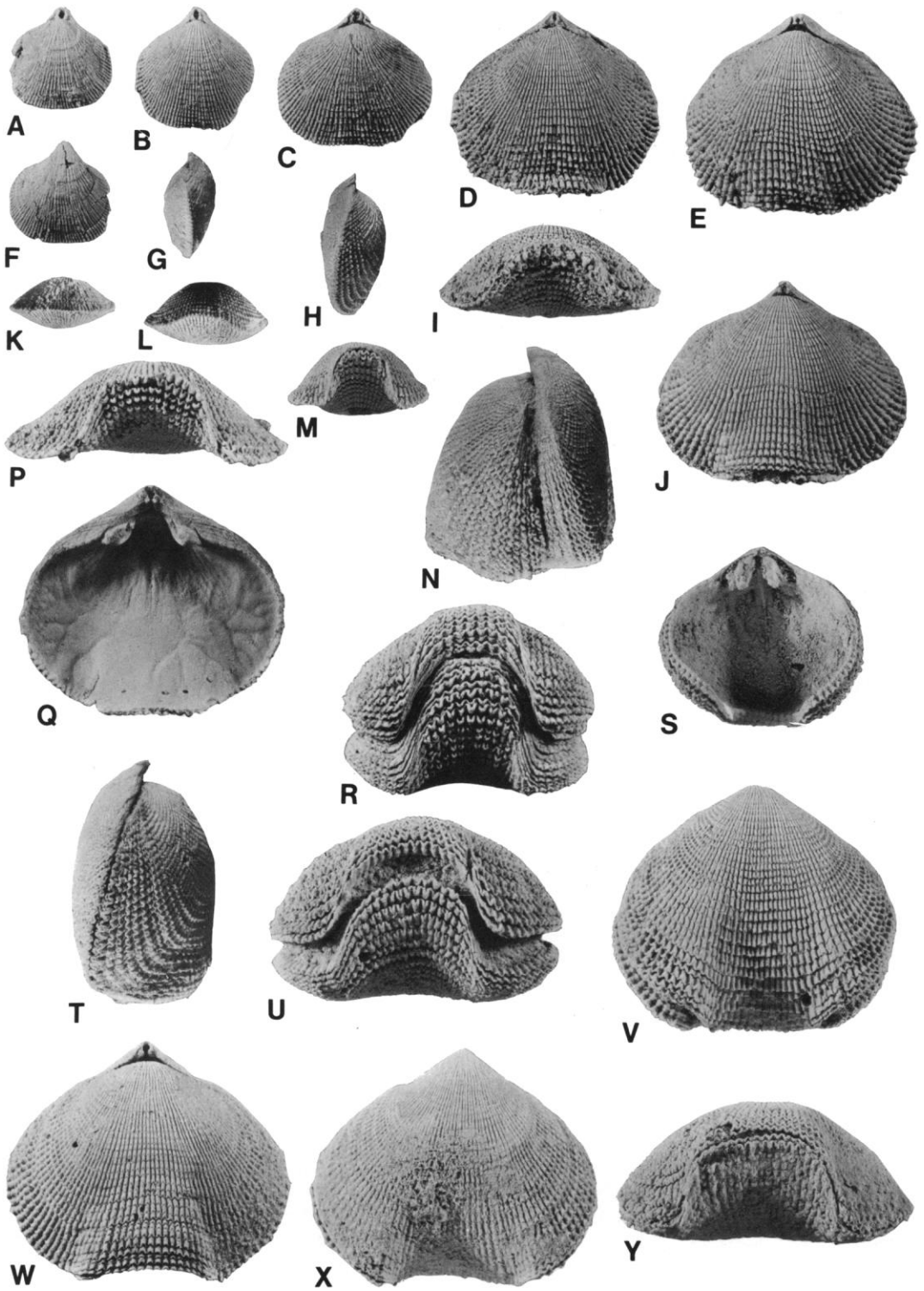


TABLE 1—Selected measurements of holotype and paratypes of *Tegulorhynchia boongeroodaensis* n. sp.

Specimen no.	Length	Width	Thickness	Ht. plic.	No. ribs	No. ribs sulcus	Foramen diameter	Valve
80.1508 (paratype)	7.5	7.3	3.6	0.1	53	—	0.65	conjoined
80.1492 (paratype)	9.3	9.4	4.5	1.1	64	21	0.55	conjoined
71.148b (paratype)	10.0	10.3	5.0	4.2	55	17	0.45	conjoined
80.1496 (paratype)	10.2	11.7	4.4	1.0	69	21	—	conjoined
80.1502 (paratype)	12.4	13.2	6.3	4.5	62	21	0.60	conjoined
71.148c (paratype)	13.2	15.0	—	—	68	22	0.45	conjoined
71.148a (paratype)	14.0	16.0	6.7	4.1	69	24	—	brachial
80.1501 (paratype)	14.5	17.3	8.2	4.4	67	20	0.40	conjoined
71.161b (paratype)	14.6	16.5	9.0	4.5	73	24	0.55	conjoined
71.161d (paratype)	15.0	17.0	9.1	5.2	62	21	—	conjoined
80.1504 (paratype)	15.0	17.0	8.2	4.6	66	19	0.40	conjoined
80.1500 (paratype)	15.2	18.7	8.2	4.6	72	22	0.60	conjoined
80.1493 (paratype)	15.2	17.7	—	—	73	23	0.50	pedicle
71.161e (paratype)	15.5	20.2	6.5*	7.4	73	21	0.60	conjoined
71.161a (paratype)	16.7	17.7	13.8	6.5	64	21	0.60	conjoined
80.1497 (paratype)	16.7	20.0	—	—	80	24	0.70	pedicle
80.1523 (holotype)	17.4	21.0	10.4	6.2	77	23	0.60	conjoined
80.1499 (paratype)	18.2	20.7	12.9	6.8	75	23	—	conjoined

* Specimen crushed.

southern tributary of Toothawarra Creek, about 300 m S of the type section of the Boongerooda Greensand, GR 070720; 38 specimens (including the paratypes WAM 71.148a, b, c) from Toothawarra Creek, overlying the type section of the Miria Marl, GR 070725; 6 specimens (including the paratype WAM 80.1504) from a creek in the Giralia Range 6.5 km E of No. 10 Bore, GR 026617; 33 specimens (including the paratypes 80.1492, 80.1493, 80.1496, 80.1497) from the base of Section Hill, GR 017543; 7 specimens from 3.6 km NNW of Whitlock Dam, GR 115820; 1 specimen from 300 m W of Section Hill, GR 014543; 3 specimens from the southern tributary of CY Creek, 4–500 m E of fence, 1 km S of dry bore, GR 044665.

From the basal Wadera Calcarenite: 10 specimens from the southern tributary of CY Creek, 4–500 m E of fence, 1 km S of dry bore, GR 044665; from higher in the Wadera Calcarenite 1 specimen 500 m upstream from creek crossing Giralia-Bullara road, 10.7 km W of Giralia Homestead, GR 184912.

From the Pirie Calcarenite: 13 specimens from the southern tributary of Toothawarra Creek, about 350 m S of junction with northern tributary, GR 070720; 1 specimen from 10 km NW of No. 10 Bore, between fence and creek, GR 040675.

From the Cashin Calcarenite 1 specimen 500 m W of Section Hill, GR 012543.

Diagnosis.—Shell thick and appreciably wider than long; bears up to 80 fine costellae;

most branching of costellae occurs in small shell. Beak short, rounded with small round foramen and conjunct deltidial plates. Commissure with strong anterior uniplicate fold.

Description (external).—Shell impunctate; outline of small shells subtriangular, becoming subpentagonal in large shells. Length/width ratio >1 for shells less than 3 mm length (pedicle valve), <1 for larger shells. In large shells, which reach a maximum known shell length of 18.4 mm, length/width ratio 1:1.1–1.25. Profile of small shells lenticular, becoming subglobose with growth. Shell thickness increases with increasing shell size, from 33% shell length in juveniles 7.5 mm in length, to a maximum of 75% shell length in largest individuals. Small pedicle and brachial valves thicknesses similar (Figure 1G); large brachial valve almost twice depth of pedicle valve. Anterior commissure rectimarginate in small individuals less than 5 mm shell length; becomes progressively strongly uniplicate with growth, uniplication reaching as much as 70% of shell thickness in large individuals (Figures 1P, R, U). With cessation of increase in length at about 18 mm shell growth may continue by thickening of shell about the anterior commissure (Figure 1R). Anterior commissure of pedicle valve may develop a medial projecting lip in large individuals. Shell surface ornamented by numerous, fine costellae. Large shells possess up to 80 costellae; 17 type specimens, ranging in size from 9.3 mm to 18.2 mm (Table 1)

have an average of 68 costellae. Shells with length as little as 8.4 mm may have up to 67 costellae. Increase in number of costellae occurs by bifurcation at intersection of costellae with growth lines. Most bifurcation had occurred before shell length of 6 mm was attained. A rapid increase in number of costellae occurs at smaller shell sizes. At a shell length of 2 mm there are only about 25 costellae. This number doubles with a doubling of shell length. Thereafter branching of costellae occurs at a much reduced rate. Well preserved costellae possess short, spinose, distal extensions up to 1 mm in length; they are most strongly developed toward the margin of the shell. Beak long and prominent in small individuals becoming relatively shorter and more rounded in large specimens. Beak angle about 70° in 7.5 mm long shell and 120° in 18.4 mm long shell. Hypothyridid foramen large and oval in small individuals which have disjunct deltidial plates. During shell growth deltidial plates became conjunct then extended adapically so that foramen remained about same size throughout shell growth. Foramen round and situated close to apex of beak (Figure 2). The principal ontogenetic changes are summarized in Table 2.

Description (internal).—Pedicle valve (Figure 1Q) possesses prominent, strong hinge teeth which are buttressed by dental plates. Diductor scars large, ovate, occupying 40% shell length; surround cordate adductor scars. Adjustor scars large. Pallial sinuses on pedicle valve (Figure 1Q) of lemniscate type comprising short vascular media which branch at mid valve, one branch extending toward the anterior commissure and bifurcating near margin into two pairs which extend almost to the commissure, and a second branch extending laterally and branching three times before almost reaching the lateral margin.

Brachial valve (Figure 1S) with very small cardinal process, extending into short, low median septum which runs to almost half shell length; flanked by small adductor muscle scars. Hinge sockets very deep and coarsely striated. Crura short, radulifer type.

Discussion.—The type species of *Tegulorhynchia*, *T. squamosa* (Hutton, 1873), occurs on South Island and Chatham Island, New Zealand where it ranges from the Early Eocene to the Early Miocene (Lee, 1980). Within this

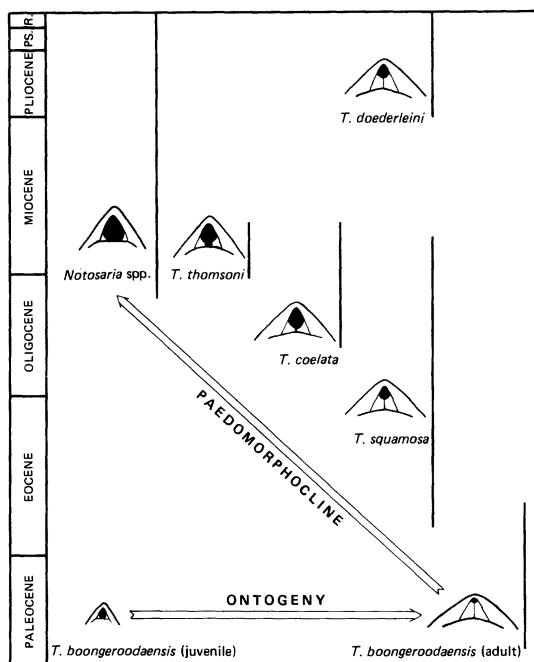


FIGURE 2—Ranges of apaedomorphic *T. boongeroodaensis* and Australian and New Zealand neotenic species of *Tegulorhynchia* and *Notosaria* with reconstructions of umbonal region. *T. boongeroodaensis-squamosa* (*doederleini-coelata-thomsoni-Notosaria* spp. form a paedomorphocline, illustrated by the retention in the adult phase of progressively more juvenile characters through time, shown here by the nature of the foramen, deltidial plates and beak angle. Morphological changes along the paedomorphocline follow the opposite pathway to ontogenetic change in the apaedomorph, *T. boongeroodaensis*. Reconstruction of juvenile umbonal region of *T. boongeroodaensis* drawn at twice the size of other reconstructions.

species Lee (1980) has synonymized *Hemithyris depressa* Thomson and *Tegulorhynchia masoni* Allan. *T. boongeroodaensis* can be distinguished from the type species by its finer, more numerous costellae, of which there are only up to 60 in *T. squamosa*; its smaller adult size, *T. squamosa* reaching up to 24.6 mm shell length; stronger uniplication of the commissure; its relatively greater shell width; its smaller adult foramen and shorter, more rounded beak. The other New Zealand species, *T. sublaevis* (Thomson, 1918) from the Early Oligocene of Kakanui has an adult form like early juveniles of *T. boongeroodaensis* (see below), that is with subtriangular

TABLE 2—Summary of the principal morphological changes occurring during the ontogeny of *T. boongeroodaensis* n. sp., contrasted with the changes which occurred through phylogeny resulting in the paedomorphic attainment of progressively more juvenile characters along the *Tegulorhynchia*-*Notosaria* paedomorphocline.

Character	Ontogeny of <i>Tegulorhynchia boongeroodaensis</i> (E. Paleocene–E. Eocene)	Phylogeny of <i>Tegulorhynchia</i> and <i>Notosaria</i> (E. Paleocene–Recent)
Plication of commissure	Increases in height	Decreases in height
Number of costellae	Increases to 80	Decreases from 80 to 25
Shell width	Relatively increases	Decreases
Shell thickness	Relatively increases	Decreases
Foramen size	Relatively decreases	Increases
Deltidial plates	Become conjunct	Become disjunct
Beak angle	Increases to 120°	Decreases from 120° to 75°

shell; far fewer costellae than adult *T. boongeroodaensis*; large foramen; pointed beak; deltidial plates only just in contact; and weakly developed plication (Lee, 1980, p. 233, fig. 4).

The two other Australian species of *Tegulorhynchia*, the Mid Oligocene–Mid Miocene *T. coelata* (Tenison Woods, 1878) from South Australia, Victoria and Tasmania, and *T. thomsoni* Chapman and Crespin, 1923 from the Early Miocene of Tasmania, both possess coarser and less numerous costellae than *T. boongeroodaensis*; weaker plication of the commissure; narrower shell; and larger foramen with disjunct deltidial plates (Chapman and Crespin, 1923, p. 183, Pl. 11, figs. 3–6). The rare living species *T. doederleini* (Davidson, 1886), which has been collected from between Japan and Borneo, and off St. Paul Island (Lee, 1980, fig. 10), is similar to *T. squamosa* and is retained at present as a separate species by Lee (1980, p. 235) on account of the large stratigraphic and geographic discontinuities.

T. boongeroodaensis, which ranges from the Early Paleocene to Early Eocene, is consequently the earliest known species of *Tegulorhynchia*.

STRATIGRAPHICAL AND SEDIMENTOLOGICAL DISTRIBUTION OF *T. BOONGEROODAENSIS*

Of the 158 specimens of *T. boongeroodaensis* collected from outcrops of the Cardabia Group on the flanks of the Giralialia Range, 83% are from the Boongerooda Greensand, where they comprise about 99% of the brachiopod fauna and are the dominant constituent of the macroinvertebrate fauna. A few fragments of indeterminate terebratuloid are the only other brachiopod remains known from this horizon.

With the sedimentological change from greensand to calcarenite in the overlying Wadera Calcarenite, there is a sharp reduction in numbers of *T. boongeroodaensis* and an incoming of species of the terebratuloid *Gryphus*. Greatest concentration of *T. boongeroodaensis* occurs in the lower part of the formation, where it may comprise up to 70% of the brachiopod fauna at any one locality. Higher in the formation terebratuloids dominate, and may make up 100% of the brachiopod fauna locally.

Tegulorhynchia boongeroodaensis forms a similar proportion of the brachiopod fauna, an average of about 20%, in the overlying Pirie Calcarenite. In the Wadera and Pirie Calcarenites more than 70% of the specimens are conjoined valves; in the Boongerooda Greensand only 54% are conjoined. Isolated pedicle and brachial valves occur in similar proportions. The higher incidence of isolated valves in the Boongerooda Greensand is presumably as a result of more post-mortem, pre-depositional reworking. The youngest member of the Cardabia Group, the Cashin Calcarenite, has yielded only one specimen of *T. boongeroodaensis*.

Thus decreasing numbers of specimens of *T. boongeroodaensis* and a decrease in their proportion of the brachiopod fauna correspond with change from greensand to calcarenite, and an upward fining of the sediments to finer calcarenites and calcilutites. This may reflect not so much a reduction in hydrodynamic activity as a reduction in number of suitable substrates for attachment of the shells. The Boongerooda Greensand, which contains reworked phosphate nodules from the underlying Miria Marl, probably formed during a period of low sediment deposition when numerous hardgrounds pro-

vided many suitable substrates for attachment. Increase in sedimentation rates during formation of the overlying calcarenites and calcilutites probably resulted in reduction in number of suitable sites. It is interesting to note that *T. boongeroodaensis* does not occur in the Paleocene Kings Park Formation in the Perth Basin in Western Australia. This marine formation is composed of shale and siltstone and would have offered few suitable sites for attachment. Other species of *Tegulorhynchia* inhabit a variety of sediments (Lee, 1980, p. 243–245), but occur most frequently in greensands, limestones and tuffs.

Although a suitable sedimentary environment existed in New Zealand during the Paleocene *Tegulorhynchia* did not appear until the Early Eocene. The earlier appearance of *Tegulorhynchia* in Western Australia than in either eastern Australia or New Zealand accords well with observations on the easterly migration of faunal elements into New Zealand during the Eocene (Fleming, 1962). Foster and Philip (1978) note a trans-Tasman migration of echinoids from west to east throughout the Tertiary, perhaps related to the anticlockwise current in the Indian Ocean, both before and after opening of the seaway between Antarctica and Australia. This current would have facilitated an easterly spread of marine invertebrate larvae, including those of brachiopods.

EVOLUTION OF *TEGULORHYNCHIA* AND *NOTOSARIA*

General.—The Early Eocene to Recent species of *Tegulorhynchia* exhibit a number of adult morphological characteristics which occur at earlier stages of shell development in the oldest species, the Early Paleocene to Early Eocene *T. boongeroodaensis*, indicating that evolution within the genus has proceeded by paedomorphosis. Chapman and Crespin (1923) noted the variation in number of costellae between species of *Tegulorhynchia* and observed a general reduction in number from “*T.*” *patagonica* (von Ihering, 1903), with 12–15 costellae in the sulcus to as few as 4 in the New Zealand species *Terebratula nigricans* Sowerby, 1846, which Chapman and Crespin placed in *Tegulorhynchia*. Although these two end members have been subsequently placed in different genera (*Patagorhynchia* Allan, 1938 and *Notosaria*

Cooper, 1959 respectively) the trend in reduction of costellae is still apparent in *Tegulorhynchia*. *Notosaria nigricans* can be considered to represent the ‘extreme’ paedomorph of the *T. boongeroodaensis* morphotype, whilst the other species of *Tegulorhynchia*, *T. squamosa*, *T. coelata*, *T. thomsoni* and *T. doederleini*, represent intermediate members of a paedomorphocline between the two morphological end-members (Figure 2).

The adult *T. boongeroodaensis* is differentiated from later species on shell outline and profile, plication of commissure, number of costellae and the nature of the beak, foramen and deltidial plates. All of these features vary substantially during the ontogeny of the species, and to a much greater degree than in later species. In these later species there is a relative retardation in morphological development. Such retardation can be produced in two ways, i.e., there are two different processes which can produce paedomorphosis. One process is a general retardation in the rate of morphological development (neoteny); the other is precocious sexual maturation (progenesis) (Gould, 1977). Both of these processes result in the retention of ancestral juvenile characters in the descendant adult. They appear to have been important modes of speciation in *Tegulorhynchia*, with neoteny leading to the evolution of *Notosaria*.

Neoteny.—The Early Eocene to Early Miocene *T. squamosa* reaches a maximum length of 24.6 mm. At a shell length greater than 15 mm the width exceeds the length (Lee, 1980, p. 240). This change occurs in *T. boongeroodaensis* at a shell length of only 3 mm. *Tegulorhynchia boongeroodaensis* attained a thicker shell earlier than *T. squamosa*. According to Lee (1980, p. 240) shell thickness does not exceed half shell length until the shell length is 15 mm. This thickness was attained earlier in *T. boongeroodaensis* at a shell length of about 11 mm (Table 1). Bifurcation of costellae occurs mainly in the posterior 5 mm of the shell in *T. boongeroodaensis* producing a rapid increase in number of costellae at a small size. Bifurcation proceeded at a much reduced rate through adult growth. Rate of bifurcation was reduced in *T. squamosa* relative to *T. boongeroodaensis* resulting in an adult shell with fewer, coarser

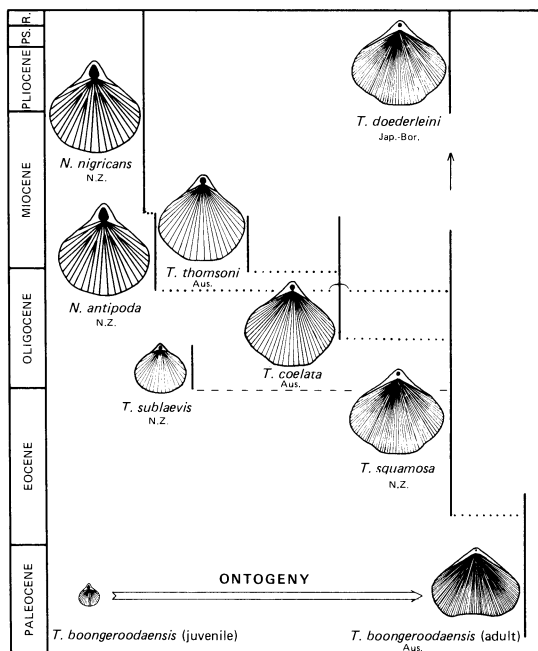


FIGURE 3—Ranges of Australian and New Zealand living and fossil species of *Tegulorhynchia* and *Notosaria*. Dotted lines represent suggested neontenic relationships. Dashed line represents suggested progenetic pathway. All adult reconstructions $\times 1$; juvenile reconstruction $\times 2$. Reconstructions based on following sources: *T. boongeroodaensis*—type material; *T. squamosa*, *T. doederleini*, *T. sublaevis*—Lee (1980); *T. coelata*, *T. thomsoni*—type material; *Notosaria* spp.—Lee and Wilson (1979).

costellae. Juveniles of *T. boongeroodaensis* have no plication of the commissure. Development of a sulcus was initiated at a shell length of about 5 mm and increased to become very pronounced in adults about 18 mm in length. Even though *T. squamosa* attained a greater size than *T. boongeroodaensis*, plication is less well developed. Similarly the narrow, long, pointed beak of juveniles of *T. boongeroodaensis* changed to a lower, more rounded beak with growth, while the large oval foramen became smaller and circular in the adult as the deltidial plates became conjunct, then grew adapically to partially close the foramen. The beak of the adult *T. squamosa* retains more the shape of the juvenile *T. boongeroodaensis*, being more pointed and having a larger foramen, as conjunction of the deltidial plates is delayed until later in the shell's ontogeny. The larger size attained

by *T. squamosa* suggests that, as is often the case when neoteny is operative, onset of sexual maturity was also delayed, resulting in a longer period being spent in the more rapid period of juvenile growth, resulting in a larger final adult size.

T. coelata and *T. thomsoni* attain almost as large a size as *T. boongeroodaensis*. Like *T. squamosa* their paedomorphic character relative to *T. boongeroodaensis* is shown by the development of fewer costellae in the adult, larger foramen, disjunct deltidial plates, and less strongly developed plication. The adult characters of these species are more juvenile in aspect than those of *T. squamosa* in possessing fewer costellae, a narrower shell, disjunct deltidial plates, larger foramen and more pointed beak. Stratigraphically *T. coelata* and *T. thomsoni* are younger than both *T. boongeroodaensis* and *T. squamosa*, suggesting a paedomorphocline with increasing degrees of paedomorphosis from the *T. boongeroodaensis* morphotype through *T. squamosa*, thence to *T. coelata* and *T. thomsoni* (Figure 3). *T. thomsoni*, with fewer costellae than *T. coelata* (28 as opposed to 36–40 (Chapman and Crespin, 1923)), more prominent beak, valves of similar depth and larger foramen, continues the trend as it is both relatively more retarded in morphological development than *T. coelata* and is younger, appearing as it does in the Early Miocene. *T. coelata* first appeared in the Mid Oligocene.

The appearance of *T. squamosa* in New Zealand during the Eocene corresponds with the spread of a number of Australian marine invertebrates (Fleming, 1962) at this time. While this morphotype has persisted in New Zealand, later paedomorphs *T. coelata* and *T. thomsoni* occur only in eastern Australia, indicating either spread of these forms from New Zealand, or evolution from a local *T. squamosa* morphotype which has not been preserved.

Although *Notosaria nigricans* and *N. antipoda* (Thomson, 1918) were placed in *Tegulorhynchia* by Chapman and Crespin (1923), Cooper (1959) preferred to consider them as belonging in a separate genus on account of their few, coarse costellae, large oval foramen, disjunct deltidial plates throughout ontogeny, and weak plication of the com-

missure. The internal morphology of *Notosaria* differs little from that of *Tegulorhynchia* indicating a close relationship between the two genera. The only difference lies in the presence of large adjustor muscles in *Tegulorhynchia*; in *Notosaria* they are weakly developed or absent (Richardson, 1979). Rudwick (1962) noted the similarity in lophophore structure between *N. nigricans* and *T. doederleini*. The close relationship between these two genera is also illustrated by comparison of the adult morphology of *N. nigricans* with the *Tegulorhynchia* pedomorphocline, as the trends apparent from *T. boongeroodaensis* through to *T. thomsoni* are continued into *N. antipoda* and *N. nigricans*. *Notosaria nigricans* first appeared in the Mid Miocene and has persisted to the present day in New Zealand, to where it is restricted. Consequently, it is possible to consider *T. boongeroodaensis* and *N. nigricans* as the end members of the pedomorphocline. *Notosaria nigricans*, although larger than *T. boongeroodaensis* (shell length up to 24 mm (Lee, 1978b)), possesses morphological characters found in the very early juveniles of *T. boongeroodaensis*: few (up to 25 (Lee and Wilson, 1979)), coarse costellae, showing no spinose development; weak plication of the commissure, which wasn't initiated until a shell length of 6–10 mm (Lee and Wilson, 1979); long, pointed beak, with a very large, oval foramen and widely disjunct deltidial plates; and valves of similar depth. The Late Oligocene to Early Miocene *N. antipoda* differs from *N. nigricans* only in its possession of spinose costellae (Lee and Wilson, 1979).

Allan (1940) discounted a phyletic relationship between Australian and New Zealand species of *Tegulorhynchia* as no two species are common to the two areas. However, a general progressive pedomorphosis is apparent in the species of *Tegulorhynchia* and *Notosaria* in the two countries. The derivation of many New Zealand faunal elements from Australia (Fleming, 1962) and the very widespread distribution of living species of *Tegulorhynchia* make it probable that the Australian and New Zealand species form part of a single evolving plexus. The morphotype attained by *T. squamosa* in the Early Eocene persists to the present day in

the form of the Pliocene to Recent *T. doederleini*, illustrating how the evolution of a new pedomorphic morphotype, such as *Notosaria* from *T. squamosa*, need not necessarily result in the extinction of the ancestral species, as the morphology of the descendant may be sufficiently distinctive to achieve ecological separation, so avoiding interspecific competition for substrate or food resources. In this model geographic separation of species is to be expected (McNamara, 1982), explaining the wide geographic distribution of the fossil and living species of these brachiopods.

Progenesis.—The small species *T. sublaevis* (Thomson, 1918) has size and other morphological characteristics which suggest it evolved by progenesis: that is, the juvenile aspect of the adult shell was attained as a result of earlier onset of sexual maturity than in the ancestral species. If morphological development through the juvenile phase of the two forms was similar, this would have resulted not only in retention of juvenile characters, but also restriction of growth to a smaller size than its progenitor. *T. sublaevis* was contemporaneous with *T. squamosa* in New Zealand during the Early Oligocene. At the shell's maximum length of 13 mm (Lee, 1980, p. 233) it has a larger, more oval foramen and longer beak than *T. squamosa*, weaker plication of the commissure, valves of similar depth and only 25 costellae. Like juveniles of morphologically more advanced species of *Tegulorhynchia*, spinose projections of the costellae did not develop. Specimens placed in this species are not merely juveniles of *T. squamosa*, as its morphological characteristics would have occurred in juveniles of *T. squamosa* of a smaller size.

Discussion.—The attainment of a similar morphology in *T. sublaevis* and *N. nigricans* shows how the two processes, progenesis in *T. sublaevis* and neoteny in *N. nigricans*, can result in evolution of homeomorphic species. Their origin by different processes is reflected in their differing size, one being smaller than the ancestor, the other generally larger; and in differences in rates of juvenile development, the progenetic form developing at the same rate as the ancestral juvenile. The similarity between these two species led Cooper (1959) to place *T. sublaevis* in *Notosaria*, but

in a recent study Lee (1980) has returned it to *Tegulorhynchia*, illustrating, perhaps, the artificiality of the generic separation of species placed in *Notosaria* from those in *Tegulorhynchia*.

Williams and Wright (1961) have noted how in a number of living brachiopods sexual maturity may occur when the shell is one-quarter to one-third the mature adult size, and consider that terebratuloids evolved by paedomorphosis in the Late Silurian by precocious maturation of juvenile spiriferoids. This illustrates how a relatively minor modification, in the form of earlier onset of maturity, can result in large-scale morphological changes in the descendant form.

Rudwick (1970) has attributed much of the success of terebratuloids to the evolution of resorptive growth, which allows enlargement of the foramen and the pedicle during growth. This facility does not occur in rhynchonellides, the foramen being infilled to different degrees by growth of the deltidial plates through ontogeny. However, some species of *Tegulorhynchia* and species of *Notosaria* have attained a large foramen and pedicle phylogenetically; not by resorption, but by paedomorphosis which enabled the adult to retain the relatively larger juvenile foramen and pedicle. The nature of the pedicle of *Notosaria* has been described by Richardson (1979). It consists of a stout, muscular pedicle which attaches very firmly to the substrate, the attachment surface covering an area far in excess of the pedicle shaft itself.

Owen (1980) has recently described a new rhynchonellide from the Lower Campanian of James Ross Island, Antarctica, which he placed in a new genus, *Protegulorhynchia*. Owen placed the genus in the Hemithyrididae and considers it to be closely related to *Tegulorhynchia*. All other hemithyridids are restricted to the Tertiary with *T. boongeroodaensis* being the oldest. In fact no rhynchonellide family ranges from the Cretaceous into the Tertiary. Ager's (1965) record of a Late Cretaceous to Miocene age for *Aetheia* is incorrect (Lee, 1978a, p. 95), its true range being Mid Eocene to Early Miocene. Nothing is known of the internal morphology of *Protegulorhynchia* and, as Cooper (1959, p. 2) has stressed, higher taxonomic relationships in rhynchonellides ought not to be made without due consideration of the internal

morphology. In terms of its stratigraphic occurrence it would seem more likely that *Protegulorhynchia* is a cyclothyrid, but without details of its internal morphology, assignment to any particular family would be undesirable. Whether or not *Protegulorhynchia* is a suitable candidate as an ancestor for *T. boongeroodaensis* cannot be demonstrated.

There is no evidence to suggest any gradual morphological change in *T. boongeroodaensis* during the 10 million years of its range from the Early Paleocene to the Early Eocene, even though there is a change in the character of the sediments in which the species occurs. Lee (1980) has similarly shown that the morphotype *T. squamosa-doederleini*, although exhibiting a certain degree of phenotypic variation, underwent no directional morphological change for over 40 million years, from the Late Eocene to the present day. These species, therefore, remained essentially morphologically static throughout their entire time ranges. Lee and Wilson (1979) have similarly established that temporal morphological stability has resulted in less variation from the Miocene to the Recent than between present-day populations of *N. nigricans*.

FUNCTIONAL SIGNIFICANCE OF PAEDOMORPHOSIS

Observations on the occurrence of living species of *Tegulorhynchia* and *Notosaria* throw some light on the functional advantage gained by retaining juvenile characters of early species of *Tegulorhynchia* into the adult period of highly paedomorphic species of *Tegulorhynchia* and *Notosaria*. The living species, *T. doederleini*, which is only slightly paedomorphic, has not been collected from water shallower than 100 m (Lee, 1980) and has been obtained from as deep as 635 m (Dall, 1920). Lee (1980) believes that *Tegulorhynchia* (that is, early paedomorphs) "lived on open, uncrowded substrates such as rocks, tuffaceous pebbles, corals, bryozoans or molluscs in deep or relatively quiet water."

The highly paedomorphic *Notosaria*, on the other hand, commonly occurs in the intertidal zone (Allan, 1960; Percival, 1960; Rudwick, 1962), and, although extending to depths as great as 790 m, is most commonly found in water less than 200 m deep (Lee, 1978b). Lee and Wilson (1979, p. 447) con-

sider *N. antipoda* to also have inhabited a shallow water, high hydrodynamic environment.

Thus the living *Tegulorhynchia* occupies regimes of lower hydrodynamic activity than the shallow water living species of *Notosaria*. As would be expected from a species which inhabits a shallow water environment, the size of the foramen, and consequently the pedicle, is relatively larger in *Notosaria* than in *Tegulorhynchia*, which in its quiet water environment is able to attach securely to its preferred substrate with a smaller, tethering pedicle. Lee (1980, figs. 5.7, 5.8) has illustrated specimens of *T. doederleini* attached to coral and to rock fragments. The juvenile *Tegulorhynchia*, with its relatively larger foramen, presumably possesses a relatively thicker pedicle as it is important for a small shell to attach itself securely to the substrate owing to its greater susceptibility to dislodgement by current activity than the larger adults (Richardson, 1981). The growth of larger adjustor muscles in adult *Tegulorhynchia* than in *Notosaria* may indicate a greater degree of mobility, perhaps enabling the shell to be oriented to an optimum position with respect to direction of current. Retention of a large foramen and pedicle in adults of *Notosaria* and some species of *Tegulorhynchia* by paedomorphosis would have enabled colonization of shallower water, higher hydrodynamic environments by mature adults, a habitat not capable of being colonized by the small-pedicle bearing species of *Tegulorhynchia*. Larvae of apaedomorphic species of *Tegulorhynchia* settling in shallower water environments would have been less well adapted to maintaining a secure attachment into the adult period than forms which retained the juvenile aspect of large foramen and pedicle into the adult period.

The retention of few, coarse costellae in adult *Notosaria* would provide better adaptation to higher hydrodynamic conditions than possession of much finer sculpture by most species of *Tegulorhynchia*. Development of the plication of the anterior commissure is related to the development of the spiral lophophore, the spirolophe, from the schizolophe (Rudwick, 1970, p. 135). The relatively greater shell thickness attained by some species of *Tegulorhynchia* corresponds with development of the prominent unipli-

cation. Thus in addition to the development of a greater area of commissure without increase in shell length, increased shell thickness would have enabled attainment of a deeper spirolophe. Juveniles of *Tegulorhynchia* would only require a relatively shallow spirolophe with a small shell, even though they inhabited a low hydrodynamic environment. Increase in shell size necessitated development of a deeper spirolophe in the adult to act more efficiently in a low hydrodynamic environment. Neotenic retention by adult *Notosaria* of the shallower spirolophe, as deduced from the narrower shell profile, was possible, as it could operate quite efficiently in a higher hydrodynamic near-shore environment. Hurst and Watkins (1978) have similarly related development of a sulcus, and deduced deeper spirolophous lophophore, in species of the Silurian orthide *Isorthis* to occupation of a quiet water environment.

Intermediate species along the paedomorphocline between *Notosaria* and *T. boongeroodaensis* may be considered as being adapted to intermediate environmental conditions between the predominantly near-shore, high hydrodynamic environment of *Notosaria* and the deeper water, low hydrodynamic environment of the *T. boongeroodaensis* morphotype.

Theoretically there is the potential for any number of morphotypes to develop along the neotenic paedomorphocline. However, only a small number of morphotypes become established as viable species. Obviously the restriction in development of the number of distinct species is dependant on there being sufficient morphological separation to avoid inhibitive competition between morphotypes. This will result in ecological, geographical and, consequently, genetic separation (McNamara, 1982).

CONCLUSION

It is considered that progressive paedomorphosis in species of *Tegulorhynchia*, giving rise along a paedomorphocline to *Notosaria*, led to the attainment of an adult morphology which was capable of colonizing a shallower water, higher hydrodynamic environment. The morphological changes which occurred along the paedomorphocline follow the opposite trend to morphological changes which occurred during the ontogeny

of the earliest species of *Tegulorhynchia*, the paedomorph *T. boongeroodaensis* (Table 2). Evolution by any of the paedomorphic processes allows the efficient and rapid attainment of new, quite distinct adult morphologies with the minimum of genetic change. Pronounced morphological discontinuities exist between the species along the paedomorphocline, and evidence also suggests that the species remained morphologically reasonably static within their individual time ranges. Evolution of a number of morphotypes, successively better adapted to a shallower water, higher energy hydrodynamic environment, along the neotenic paedomorphocline from an older, deep water, low energy hydrodynamic environment inhabiting morphotype, provides an explanation for the temporally directional morphological aspect of the paedomorphocline.

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